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ADAPTATIONS BY THE LOCOMOTOR SYSTEMS OF TERRESTRIAL AND AMPHIBIOUS CRABS WALKING FREELY ON LAND AND UNDERWATER

A Thesis

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Master of Science in The Department of Biological Sciences

by

Jennifer Nuss Schreiner
B.S., Louisiana State University, 2001
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ABSTRACT

What are the mechanisms underlying adaptation to load by locomotor systems? Amphibious shore crabs (*Carcinus maenas*) must routinely accommodate large load changes as they move in and out of water, where buoyancy supports a large percentage of their weight. Terrestrial fiddler crabs (*Uca pugilator*), aquatic red claw crabs (*Sessarma mederi*) and aquatic spider crabs (*Libinia emarginata*) are not routinely exposed to such large load changes. By comparing these species walking underwater and on land, it is possible to gain insight into general principles underlying load accommodation during locomotion. Crabs were videotaped walking freely in a behavioral arena, and a 3-D motion analysis system was used to reconstruct limb kinematics. When walking laterally, all four crab species predominately used an alternating tetrapod gait. In spider crabs walking forwards, a 4-3-2-1 metachronal gait was exclusively used in all load conditions. A significant decrease in the duration of swing occurred when fiddler, red claw and shore crabs walked in loaded conditions. Analyses of the meropodite-carpopodite (MC) joints in shore crabs showed trailing excursions significantly greater than leading excursions on land, while the angular velocities of the return strokes were significantly greater on land than underwater. Fiddler crabs showed trailing excursions underwater significantly smaller than those on land, yet there was no difference in angular velocity between load conditions. Both leading and trailing limbs appear to contribute equally to locomotion on land in fiddler crabs and underwater in shore crabs. In contrast, trailing legs contribute more on land in shore crabs and underwater in fiddler crabs. Spider crabs showed no significant differences in MC joint excursions and angular velocities between load conditions. The propodite-dactyl (PD) joints in shore crabs acted as struts, supporting the
weight of the crab during locomotion. In trailing legs on land, however, PD joints acted as thrust generators. Several common themes emerged from these experiments: all crabs decreased the duration of swing as load increased and changed joint usage depending on both lifestyle and load condition. Potential mechanisms for dealing with load also included the recruitment of struts into motors and changes in the timing of stepping patterns.
INTRODUCTION

For more than a century, numerous studies have been conducted on locomotion in its various forms. In 1899, Eadweard Muybridge studied the movements of assorted animals when walking and running at various speeds. Since then, many scientists observed and published data concerning terrestrial locomotion in humans (Fenn 1930, Inman et al. 1981), quadrupeds (Manter 1938, Pandy et al. 1988), and various arthropods (Cruse 1976, Herried and Fourtner 1981, Blickhan and Full 1987, Ting et al. 1994). By studying locomotion in arthropods, it is possible to examine interlimb coordination (Jamon and Clarac 1997), kinematics and muscle activity during walking or running (Clarac et al. 1987, Watson and Ritzmann 1998a, b), and reflexes associated with locomotion (Cannone and Bush 1982, Belanger et al. 2000). Intertidal crustaceans confront unique challenges because their locomotor systems must adapt to walking on land as well as underwater, where drag and lift forces are greatly increased and a large portion of their weight is supported by buoyancy (Martinez et al. 1998). By studying locomotion in crabs that routinely adapt to load changes as they move in and out of the water, several questions can be addressed. What adaptations are made during locomotion to accommodate these environmental load changes? How do the kinematics of walking underwater compare to those of walking on land? It is hypothesized that crabs may modify gait parameters, stepping velocities, muscle activity, or a combination of these things to cope with changes in load.

Because of their ability to walk in many different directions (forwards, backwards, and laterally), decapod crustaceans are excellent models for research on locomotion. Many previous studies dealt with the kinematics and kinetics of locomotion in crabs,
crayfish, and lobsters, including comparative examinations of loaded and unloaded conditions (on land and underwater). When underwater as compared to when on land, crabs, crayfish and lobsters adapt to these different load conditions in several ways, including increasing the duration of the swing phase (i.e. decreasing duty factor; Hui 1992, Martinez et al. 1998), increasing step length (Hui 1992, Martinez et al. 1998, Pond 1975, Grote 1981, Jamon and Clarac 1995), increasing stepping frequency (Hui 1992, Pond 1975, Grote 1981), and adopting a wider stance (Martinez et al. 1998, Grote 1981). However, these adaptations are not universal for all decapod crustaceans; contradicting results, including the adoption of a wider stance on land (Hui 1992) and no change in stepping frequencies on land and underwater have been reported (Martinez et al. 1998).

The present study examines differences between walking underwater and on land in four species of crabs chosen for their diverse lifestyles: fiddler crabs (Uca pugilator), red claw crabs (Sessarma mederi), shore crabs (Carcinus maenas), and spider crabs (Libinia emarginata). The taxonomic relationships between these four species and selected other decapods are seen in Figure 1. Fiddler crabs are mostly terrestrial, spending most of their time in burrows on sandy shores; yet, they submerge themselves in water every so often to keep their gills wet (Gosner 1978). Red claw crabs, on the other hand, are mostly aquatic, but they do come ashore occasionally to forage for food or to escape predators (Depaus 2002). Shore crabs are amphibious, splitting their time equally between land and water habitats (Clarac et al. 1987). However, spider crabs are exclusively aquatic, and are found near the shoreline in bays or in subtidal areas to depths of more than 160 feet (Gosner 1978). The diversity of lifestyles represented by these four species of crab allows one to consider the effects of lifestyle on adaptation to load. For
**Figure 1:** Taxonomic relationships between selected decapods. Of the four crabs examined in this study, three predominately walk in the lateral direction (shore crabs - *Carcinus maenas*, fiddler crabs - *Uca pugilator*, and red claw crabs - *Sessarma mederi*), while spider crabs (*Libinia emarginata*) most often walk forwards (relationships based on Martin and Davis 2001).
example, how do the adaptations of terrestrial and aquatic crabs compare when walking in an environment to which they are not accustomed? It is hypothesized that crabs of all four species will change some aspects of their locomotion in order to accommodate environmental and imposed load changes.
REVIEW OF LITERATURE

Analysis of Legged Locomotion

Since life forms began inhabiting the earth, animals have been dependent upon their surroundings and their physiological make-up to determine their unique methods of travel. The movement of animals from one place to another comes easily by nature, but is far more intricate when analyzed thoroughly. Animal locomotion involves the complex coordination of the entire animal, including the central nervous system, sense organs, muscles, and the skeleton (Manter 1938). Several different types of animal locomotion occur, but all are dependent upon the differing environments in which the specific animal lives. In aquatic environments, fish move through the water using fins. Birds, bats, and flying insects fly through the air with wings, and many land dwelling creatures depend upon some number of legs to traverse the earth.

Legged locomotion is the primary mode of movement for most terrestrial animals. Both kinematic and kinetic analyses have been performed on animal models in various gaits (Cruse 1976, Blaszczyk and Dobrzecka 1989, Blickhan and Full 1987, Full and Tu 1991), and the neuronal control mechanisms underlying these motions are currently being investigated (Orlovsky et al. 1999, Pearson 1993, Kiehn et al. 1998).

Terminology

Animals move from one place to another by using a variety of styles of traveling on limbs. Birds and humans adopted a bipedal gait when navigating the earth, while most mammals like dogs and horses are quadrupeds. Arthropods, including insects and many crustaceans, generally have either a six or eight legged gait. The most common methods of legged locomotion in terrestrial animals are walking and running, with some
animals opting to leap or crawl. Each of these different gaits has distinct step patterns, ground reaction forces, and energetics (Alexander 1977).

Before beginning analyses of these different gaits, one must first distinguish between the basics: a step versus a stride, stance phase versus swing phase, and the concept of the center of gravity of an object. Muybridge (1899), a pioneer in the field of animal locomotion, defined a step as when one leg of an animal is "lifted from the ground, thrust in the direction of the movement, [and] placed again on the ground…” He further defined a stride as requiring each of the supporting legs of the animal to be lifted from the ground, propelled in the direction of motion, and replaced in the same relative position to the body and the other legs as at the beginning of the action. In simpler terms, it is measured as an event on one leg to the same event on the same leg (for example, right heel contact to right heel contact in humans). In summary, while one complete stride of a biped consists of two steps, one complete stride of a quadruped consists of four steps. The rate at which the animal steps, as well as the stepping pattern, determines whether the animal is walking, trotting, running, or jumping.

Each step is further broken down into two phases: the stance phase and the swing phase. The stance phase, or power stroke, of an animal's gait occurs when the leg is in contact with the substrate. While generating thrust in the direction of locomotion, the leg supports a portion or all of the animal’s body weight (Bowerman 1977). During forward walking, the stance phase begins when the leg is in the anterior extreme position (AEP). At the end of the stance phase, the swing phase, or return stroke, begins. This is marked by the posterior extreme position (PEP) in forward walking, and occurs when the leg is not in contact with the substrate. No support or propulsion is generated in this phase; the
leg is returning to the AEP in order to begin another power stroke in the stance phase (Duysens et al. 2000).

The center of mass of an object is the point about which the mass of the object is evenly distributed. It can also be thought of as the mass of the object concentrated at a single point (Alexander 1983). This point is not always located within the object, and in segmented bodies, it often changes location. For example, in animals that have large heads and forequarters that are heavily muscled, the center of mass is closer to the head of the animal. This is seen in such animals as the bison, and allows for greater stability in the horizontal quadrupedal position. On the other hand, some animals have large tails and greatly developed hindquarters, thus allowing a center of mass closer to the tail of the animal. This body style occurs in running dinosaurs and in jumping kangaroos. These animals have greater stability in the bipedal position (Morton 1952).

The center of gravity describes the vertical line that passes through the center of mass (Gray 1968). In walking or standing quadrupeds, for example, the center of gravity usually runs through the interior of the triangle or quadrilateral made by the three or four legs that are in contact with the ground (Alexander 1977). This triangle (or quadrilateral) of support provides stability for the animal at low speeds. If, for any reason, the center of gravity falls outside the perimeter of the triangle or quadrilateral, the animal is unstable and may fall (Ting et al. 1994). The center of mass rises and falls during the step cycle, and the vertical path taken differs in walking and running.

**Types of Gaits**

Animals move along the surface of the earth using many different gaits. These gaits are analyzed by the sequence of both leg movements and the successive stages in
the cycle (Gambaryan 1974). In order to study legged locomotion in depth, Muybridge (1899) adopted symbols to designate the actual footfall pattern of quadrupedal animals, which can be applied to animals with varying numbers of legs (Fig. 2a). In these diagrams, the arrow heads indicate the direction of movement, while the triangles and circles represent the fore feet and hind feet of the animal, respectively. The darkened symbols represent the right side of the animal, while the light symbols represent the left side of the animal. This convention was not used in the present study because of the complexity of the drawings in comparison to other standards of gait analysis. More recently, there have been studies which represent the stepping patterns of animals using hash marks and open spaces to indicate swing and stance phases, respectively (Fig. 2b, Blaszczyk and Dobrzecka 1989).

Gaits may be symmetrical or asymmetrical (Gambaryan 1974). Symmetrical gaits in quadrupeds are characterized by two things. First, the movement of a forelimb is followed by the movement of either of the two hind limbs, and this cycle repeats. Secondly, the two halves of the cycle are symmetrical. This means that the right side of the step cycle is the mirror image of the left side, and vice versa (Gambaryan 1974). Symmetrical gaits include the walk, the amble (or accelerated walk), the trot, and the canter. Asymmetrical gaits, on the other hand, are different from symmetrical gaits in the sequence of limb movement. There is no left-right symmetry in the cycle, as both fore limbs move and then both hind limbs move (Gambaryan 1974). Asymmetrical gaits include very slow walks, the gallop, and the ricocheting saltation (the jump used by rabbits, kangaroos, and other small rodents).
Figure 2: Symbols used in gait analysis. A) Arrowheads indicate the direction of movement, while triangles and circles represent the fore legs and hind legs of the animal, respectively. The darkened circle and triangle represent the right side of the animal while the light circle and triangle represent the left side of the animal (adapted from Muybridge 1899; this convention was not used in the present study). B) The stepping pattern of animals has also been illustrated by using hash marks and open spaces indicating swing and stance phases, respectively. Depicted here is a trot, in which the diagonal limbs descend simultaneously. LH: left hind, LF: left fore, RH: right hind, RF: right fore.
Arthropod Locomotion

Hexapedalism

Arthropods represent an extremely diverse group of animals which differ in methods of locomotion. Insects have six legs, arachnids possess eight legs, and some crustaceans are decapods. As hexapods, insects have a unique stepping pattern, paired with vertical and horizontal ground reaction forces similar to those of bipeds (Hughes 1952, Ting et al. 1994, Jindrich and Full 1999). The most common hexapodal gait is described as an alternating tripod, in which the right front, left middle, and right hind legs act as one leg of a bipedal animal. One stepping pattern of the American cockroach demonstrates this alternating tripod gait, in which each tripod moves out of phase with the second tripod of the pair (Full and Tu 1991). In Figure 3a, the darkened circles in the symbol indicate which of the six legs is in retraction (stance phase) during the step cycle, while the white circles indicate which legs are in protraction (swing phase).

The vertical and lateral ground reaction forces of the American cockroach have also been recorded (Full and Tu 1990) and are shown in Figure 3b. The lateral forces acting on the cockroach are generated from the side of the animal with two legs of the tripod on the ground. The vertical ground reaction forces clearly demonstrate the two "legs" of the alternating tripod as each generates propulsive forces.

Octopedalism

Although arachnids comprise the second of the three large arthropod groups, they are not used as often as the insects and crustaceans in studies of legged locomotion. Therefore, there is little information on the walking mechanisms of spiders and scorpions. The stepping patterns of scorpions walking forwards and backwards reveal a
Figure 3: Hexapedal gaits and ground reaction forces. The symbolic interpretation of the alternating tripod gait is shown above for the cockroach. The darkened circles indicate which of the six legs is in retraction (stance phase) during the step cycle, while the white circles indicate which legs are in protraction (swing phase). The lateral forces acting on the cockroach are generated from the side of the animal with two legs of the tripod on the ground. By looking at the vertical ground reaction forces, one can see the two "legs" of the alternating tripod as they generate propulsive forces. The cockroach's body weight is 0.025 N, shown by the solid horizontal line in the vertical ground reaction force trace (adapted from Full and Tu 1990).
metachronal stepping pattern, in which the legs on either side of the animal move in a wave-like pattern (Bowerman 1981). Wilson (1967) observed stepping patterns in tarantula spiders, which used both metachronal and alternating tetrapod gaits. Ground reaction forces for the scorpions and tarantulas were not measured.

Decapedalism

The last of the three groups, crustaceans, are considered by some to be slow walkers (Clarac 1981). Although decapod crustaceans possess ten legs, only eight are usually used in locomotion. The chelae (which are legs 1 on both sides when numbered anterior to posterior) are not normally used in locomotion in decapod crustaceans (Barnes 1975, Jamon and Clarac 1995). While crayfish and lobsters most frequently exhibit either a forwards or backwards gait, most crabs normally move laterally. Depending on the direction of motion, the right and left legs are described as leading or trailing.

The kinetic and potential energies recorded from walking crabs were also described by Blickhan and Full (1987). The horizontal kinetic energy is completely out of phase with the potential energy of the crab. As the crab is vaulted over a stiff leg, the height of the center of mass increases, thus potential energy increases. As this happens, horizontal velocity decreases, thus decreasing horizontal kinetic energy. However, during running in crabs, the potential and kinetic energies are in phase with each other, which is indicative of a bouncing gait (Blickhan and Full 1987). As kinetic energy increases, potential energy increases also, and vice versa.

Similar to what is seen in the cockroach with the alternating tripod gait, crabs may move with what is described as an alternating tetrapod gait (Barnes 1975). This gait is based on the same principle of the alternating tripod; that is, each group of four legs
acts as one leg of a biped. One group consists of the leading legs 2 and 4 and trailing legs 3 and 5. When these legs are in the swing phase, the other legs (leading legs 3 and 5 and trailing legs 2 and 4) are in the stance phase. Crabs, crayfish, and lobsters are also known to use a metachronal gait, in which ipsilateral legs move in synchronous waves on either side of the body (Wilson 1966).

One other distinguishing characteristic of many crustaceans is their ability to locomote on land and under water. Several studies were performed on this one feature of decapod crustacean locomotion (Grote 1981, Hui 1992, Clarac et al. 1987, Libersat et al. 1987, Duysens et al. 2000), which is one of the central themes of this thesis. The distal segments of the walking legs of crabs are operated by seven muscles (Clarac et al. 1987) and fifteen motoneurons (Wiens et al. 1988). Vertebrates, however, have several more muscles which are innervated by hundreds, or even thousands, of motoneurons. Because of this simpler system in crabs, it is much easier to begin to understand how the neuromuscular system adjusts to changes in load during locomotion. Nevertheless, the basic biomechanics of crab locomotion must be studied initially in order to elucidate the similarities and differences in walking sequences on land and underwater.
MATERIALS AND METHODS

Four species of crabs obtained from the Marine Biological Laboratories (Woods Hole, Massachusetts) or from local suppliers were used in these studies: fiddler crabs (*Uca pugilator*), red claw crabs (*Sesarma mederi*), shore crabs (*Carcinus maenas*) and spider crabs (*Libinia emarginata*). Fiddler, shore and spider crabs were maintained in 24” x 18” x 9½” plastic holding tanks half-filled with saltwater with specific gravity in the range of 1.020 to 1.023 (marine salt in solution from 27 to 31 ppt), while red claw crabs were cared for in smaller plastic holding tanks (12” x 6½” x 5”). Fiddler and red claw crab tanks were lined with sand along the bottom and built up on one side to create an amphibious environment. All crabs were separated by species with up to 20 crabs per tank. Animals were fed weekly with pellet food or squid pieces. Three-quarters of the saltwater in each holding tank was siphoned off each week and replaced with fresh saltwater to eliminate buildup of food and waste products. All crabs investigated possessed eight walking legs; if a leg was injured or pulled off during marking, taping, or socializing with other crabs, the crab was not used in the final gait analysis.

Marking the Crabs

In order to digitize and track the crabs, the crabs were marked on their carapace and walking legs with small, contrasting points. The crabs were anesthetized on ice for roughly 15 minutes (depending on the size of the crab) before marking. Once anesthetized, the crabs were anchored to a dissecting tray with pins (which were criss-crossed over the legs in order to not damage the exoskeleton in any way) for better access to the walking legs and to prevent them from spoiling the points already made. Marks were made via many different methods depending on the crab size and species. These
marks include light colored nail polish, white out, glow in the dark paints, and small pieces of painted paper super glued to the exoskeleton of the crab. Types of points, as well as their positions, also depended upon the crab species. Red claw crabs were marked on their carapace only. No joint data was taken from the red claw crabs; therefore, the walking legs needed no markings. Fiddler crabs and spider crabs were marked both on their carapace and third walking legs. Marks were painted at the midpoint (1) and distal end (2) of the meropodite and the distal end (3) of the propodite of each of the third walking legs (Fig. 4). These three marks on the walking legs served to outline the meropodite-carpopodite joint (MC joint). The position of the markings on the walking legs was unique to shore crabs in that a mark at the distal end (4) of the dactyl was added, outlining the propodite-dactyl joint (PD joint). These four marks were glued onto the second, third and fourth walking legs in shore crabs.

**Spider Crabs**

Because spider crabs did not lift their carapaces off the ground in land conditions (see Results), special experiments were designed to test the effects of load on locomotion in these animals. Each spider crab’s mass was measured and small “backpacks” were made to account for both ¼ and ⅛ of the crab’s body mass. These backpacks were made out of various sizes of lead round split shot tied together with a small thread. The backpacks were then tied to the middle of the crab’s carapace, carefully avoiding the markings already there, and the crabs were allowed to run in underwater conditions.

It was also observed that spider crabs preferred not to walk in the lateral direction as do the three other species studied. Spider crabs walk in the forward direction more often than not, so experiments were also designed to accommodate this habit.
Figure 4: Markings on the walking legs of fiddler crabs, shore crabs, and spider crabs. All four points on each leg were digitized in three camera views for each trial. Only the third walking legs of fiddler and spider crabs were marked and digitized, while walking legs two, three, and four were marked and digitized in shore crabs.
Consequently, spider crabs were examined underwater on two main levels: forward walking and lateral walking, both with no load, ¼ load backpacks, and ⅛ load backpacks.

**Filming the Crabs**

Once marked, the crabs were ready to be filmed walking underwater or on land. Various sized aquaria were prepared as behavioral arenas in which the crabs performed, with the size of the tank proportional to the size of the crab species. All of the tanks were lined with pre-rinsed sand at the bottom to provide traction for the crab, as well as a natural surface on which to walk. Fiddler crabs and red claw crabs were filmed on white sand while shore crabs and spider crabs were filmed on black sand. The different sand colors allowed for better observation of footfall patterns depending on the color of the exoskeleton of the crab. Water tanks were filled with 20 cm of saltwater prepared in the same fashion as that in the holding tanks, while the sand in land tanks was thoroughly dried before taping to prevent sand from sticking to the crabs and distorting the view of the footfall pattern. Three video cameras were set up at different angles along one long side of a rectangular aquarium, focused in on a three dimensional calibration frame made from square metal rods, again held together by superglue. Four different sized calibration frames were made for the various sizes of crabs and aquariums, ranging in size from 51cm x 21.5cm x 16.5cm to 8cm x 8cm x 7.5cm. The calibration frame occupied roughly 90% of the filming volume. Trials were videotaped using Canon GL1 digital video cameras recording at 60 fields/s, with a minimum spatial resolution of 0.71mm. The three digital video cameras were synchronized by an audio pulse and by a small blinking LED light, which were manually triggered during a walking sequence. Lighting was adjusted for the best possible view of the points on the crab. Crabs were occasionally
stimulated to move from one end of the tank to the other by prodding them with a small stick. Trials were used only when the crabs moved steadily from one end of the field of view to the other. Starting and stopping sequences were not used in the analysis.

**Gait and Joint Analysis**

After filming, the video from the three cameras was imported into the Peak Motus motion analysis program (Peak Performance Technologies, Inc., version 7.0). The software tracked the movement of each of the marked points in the video and used the direct linear transform (DLT, Abdel-Aziz and Karara 1971) to convert these into the three-dimensional motion of the points in space. Raw data were filtered using a Butterworth digital filter with a cutoff frequency of 6 Hz. These data were then used to calculate the linear velocity of the crab, joint angular velocity of both the MC and PD joints, and amplitudes of the MC and PD joints.

For each leg, one step consists of two phases: swing (when the leg is not in contact with the substrate) and stance (when the leg is in contact with the substrate). A step cycle was defined as the time from which the first (anterior to posterior) leading leg lifted off the substrate in the swing phase to the time when that same leg lifted off the substrate in swing again (Fig. 5). In order to facilitate comparisons between animals and species, the durations of swing and stance for all of the other walking legs were normalized to the cycle period of the first leading leg. Likewise, the onset time for each of the other walking legs was calculated as the time from which the first leading leg lifts off the substrate to the time when each of the other legs lifts off the substrate. There was no difference in overall gait analysis when the walking legs were normalized to the first left leg as crabs walked from left to right, making it possible to use the first leading leg in
Figure 5: Gait parameters used in evaluating footfall patterns. The start of a step cycle is defined as the time when the first walking leg on the leading side lifted off the substrate. The black and red boxes represent the average swing phase of the step cycle for leading legs 1 and 2, with error bars for both onset time and duration of swing before and after it, respectively. Colors are used to further illustrate stepping patterns in all subsequent gait summaries. To facilitate comparisons between animals, the durations of swing (leg off the substrate) and stance (leg in contact with substrate) were normalized to the cycle period of this first leading leg. These parameters were used in evaluating the gait summaries of all four species of crabs walking in both loaded and unloaded conditions, and in both the lateral and forward directions.
final analyses. For spider crabs walking in the forward direction, all legs were normalized to the cycle period of the first left leg.

Of the 23 crabs that were studied, 6 were fiddler crabs, 5 were red claw crabs, 7 were shore crabs, and the remaining 5 were spider crabs. As much as possible, comparisons between loaded and unloaded conditions were made on the same crab, except in instances of injury or death. Between five and ten steps were analyzed from each crab in each condition.

**Statistical Analysis**

Statistical analyses were performed using SigmaStat (Access Softek Inc., version 2.03 for Windows), while descriptive statistics and graphs were generated using StatMost (Dataxiom Software Inc., version 3.5 for Windows). Comparisons between gaits of individuals walking on land versus walking underwater were made using a one way analysis of variance. MC joint excursions and angular velocities in all species, both on land and underwater, were analyzed using one-way repeated measures analyses of variance. Analyses of the relationships between the percentage of time in the swing phase and the duration of the step cycle as well as the relationship between MC joint angular velocity and walking speed were performed via linear regression. The resulting \( r^2 \) values were interpreted as follows: 0.0 – 0.3: weak relationship between variables, 0.4 – 0.6: moderate relationship, 0.7 – 1.0: strong relationship (Martin and Bateson 1993). Differences were considered significant at \( P < 0.05 \).
RESULTS

Introduction to Gaits

The four species of crabs used three definite stepping patterns while locomoting in loaded or unloaded conditions. Most often, an alternating tetrapod gait was used, in which four of the eight walking legs were in contact with the substrate at any given time: legs 1 and 3 on the leading side of motion and legs 2 and 4 on the trailing side of motion are all in the swing phase of the step cycle at the same time (Fig. 6a). As these legs touch down in stance, leading legs 2 and 4 and trailing legs 1 and 3 lift off the substrate in swing. This pattern alternates in a well-ordered regimen as the crab walks, creating an alternating tetrapod gait. This gait can also be described as a very strict, regimented metachronal gait.

A metachronal gait is one in which consecutive legs enter the swing phase of the step cycle in a wave-like fashion. For example, waves begin as the first leg on both leading and trailing sides lifts off the substrate in swing. The second, third and fourth legs swing successively, creating synchronized waves on both the leading and trailing sides of the crab. Figure 6b illustrates a 1-2-3-4 metachronal gait. Leading legs 1 and 3 enter swing phase at roughly the same time as trailing legs 1 and 3, each beginning and continuing the synchronized metachronal waves from the first legs to the fourth legs.

A second metachronal gait, a 4-3-2-1 metachronal gait, was observed exclusively in forward walking spider crabs (Fig. 6c). This gait is similar to a 1-2-3-4 metachronal gait, but there are some distinct differences. The legs still move in a wave-like fashion, yet the wave starts with the fourth legs and moves to the first legs. Furthermore, the waves are not synchronized. When right leg 4 begins a new step cycle in swing, left leg
Figure 6: Examples of individual footfall patterns depicting the three organized gaits observed in this study. Red and black bars represent the swing phase of the step cycle; colors are used to indicate legs acting together. A) An alternating tetrapod gait consists of four legs in contact with the substrate simultaneously. Leading legs 1 and 3 are in swing at the same time as trailing legs 2 and 4 (red lines). As these legs touch down in stance, leading legs 2 and 4 as well as trailing legs 1 and 3 begin the swing phase (black lines). B) A 1-2-3-4 metachronal gait. Leading legs 1 and 3 (red lines) enter the swing phase of the step cycle at roughly the same time as trailing legs 1 and 3 (black lines), each beginning and continuing the synchronized metachronal waves from the first legs to the fourth legs. C) The 4-3-2-1 metachronal gait is slightly different than the 1-2-3-4 metachronal gait. When right leg 4 (red line) begins a new step cycle in swing, left leg 4 is in stance. Alternatively, when left leg 4 (black line) begins a new step cycle in swing, right leg 4 touches down in stance, this time evidenced by the absence of a red line. This pattern is continued as the wave moves asynchronously from the fourth legs to the first legs.
4 is in stance. Alternately, as left leg 4 begins a new step cycle in swing, right leg 4 touches down in stance. This pattern is continued as the wave moves asynchronously from the fourth legs to the first legs.

To summarize, there were three different organized gaits seen in crabs walking in both loaded and unloaded conditions: an alternating tetrapod gait, a 1-2-3-4 metachronal gait, and a 4-3-2-1 metachronal gait.

**Gait Usage**

Among these three organized gaits observed, how often was each gait used? Do crabs use a different gait when walking on land versus when walking underwater? When walking laterally, in both loaded and unloaded conditions, crabs of all four species used predominantly an alternating tetrapod gait (Fig. 7). Fiddler crabs and shore crabs used an alternating tetrapod gait significantly more often than all other gaits combined both on land and underwater. Although red claw crabs and laterally walking spider crabs used predominately an alternating tetrapod gait, they did not use this gait significantly more often than other gaits.

Spider crabs demonstrated a dramatic difference in gait walking in the forward versus lateral directions. Instead of using an alternating tetrapod gait or a 1-2-3-4 metachronal gait, forward walking spider crabs used a 4-3-2-1 metachronal gait exclusively in both loaded and unloaded conditions. This is the only circumstance in which a 4-3-2-1 metachronal gait was observed.

For all species walking laterally or forward, there was no significant difference in gait usage in loaded conditions versus unloaded conditions. Now that it is known which gaits are used and how often they are used, the question now begging to be answered is
Figure 7: Gait usage by the four crab species studied. All four species used mainly an alternating tetrapod gait (purple bars) when walking laterally. A 1-2-3-4 metachronal gait (yellow bars) was also seen in all species and conditions except fiddler crabs walking on land and spider crabs walking with a 1/4 load backpack. Other unorganized gaits (grey bars) were seen as well. Spider crabs walking in the forwards direction used a 4-3-2-1 metachronal gait 100% of the time in all load conditions.
this: How do these gaits change with load?

**Gait Summaries**

While using an alternating tetrapod gait, crabs of all four species decreased the amount of time their legs are in the swing phase of the step cycle when moving from unloaded conditions to loaded conditions (Fig. 8). Aquatic spider crabs showed the largest change in gait, mainly due to the fact that they did not stand on land. Instead of using regimented stepping patterns on land, the spider crabs moved in a crawling manner, burying themselves in sand as they inched across the tank. In contrast, the fiddler, red claw, and shore crabs simply decreased the duration of swing on land. In amphibious shore crabs, the duration of swing was significantly decreased from $55.9 \pm 8.9\%$ of the step cycle underwater to $35.6 \pm 5.8\%$ of the step cycle on land ($P < 0.001$). The terrestrial fiddler crabs also significantly decreased the duration of swing on land from $58.4 \pm 7.8\%$ of the step cycle underwater to $36.5 \pm 3.5\%$ on land ($P = 0.002$), and aquatic red claw crabs showed the smallest reduction of swing duration ($53.0 \pm 11.0\%$ underwater to $44.1 \pm 12.7\%$ on land).

In addition to this reduction of swing duration, variability of onset time decreased in all crabs as well (Figs. 8 and 9). Lessening of swing phase variability, however, was not evident in laterally walking spider crabs when moving from $\frac{1}{8}$ load backpacks to $\frac{1}{4}$ load backpacks. Swing phase variability was decreased in all other crab species and load conditions.

Forward walking spider crabs, using a 4-3-2-1 metachronal gait, were like laterally walking spider crabs in that there was no significant difference in gait between load conditions (Fig. 9). Crabs of all four species walking in the lateral direction used
Figure 8: Alternating tetrapod gait summaries comparing lateral walking sequences from fiddler crabs, red claw crabs, and shore crabs both on land and underwater. When walking on land, the three crab species decreased the duration of swing, as well as the variability of both onset time and duration of swing, compared to walking underwater.
Figure 9: Lateral versus forward gait summaries for spider crabs walking in both loaded and unloaded conditions. When walking in the lateral direction, an alternating tetrapod gait was used most often. When walking in the forward direction, however, the spider crabs adopted a completely different gait, a 4-3-2-1 metachronal gait. There was no significant difference in duration of swing and onset variability as load increased.
both an alternating tetrapod gait and a 1-2-3-4 metachronal gait. As seen in Figure 7, the crabs did not use this gait very often; fiddler crabs walking on land and spider crabs with ¼ load backpacks did not use this gait at all. Of those shore crabs and red claw crabs that did use a 1-2-3-4 metachronal gait (Fig. 10), the duration of swing was not significantly reduced when comparing walking sequences from water and land. Onset variability in shore crabs, however, increased slightly as load increased.

To reiterate, crabs that were able to walk both on land and underwater showed a difference in the timing of gait between conditions, whereas spider crabs showed no significant differences in gait timing.

**Double Steps**

Walking sequences were occasionally observed that contained an extra, or double, step within one step cycle. These double steps were seen in all eight walking legs of all four species of crab at one time or another, in both loaded and unloaded conditions (Fig. 11). It was hypothesized that crabs would take more double steps when walking in loaded conditions than when walking in unloaded conditions. Gravity plays a much larger role on land because buoyancy is no longer supporting a large portion of the weight of the animal, therefore increasing the probability of overbalancing or stumbling. However, there were no significant differences in the occurrence of double steps in loaded versus unloaded conditions for any species.

Since one reason for double steps could be legs cycling at different frequencies, the individual periods of each leg were compared. In every case, there were no significant differences between the step cycle periods of each leg and that of the first leading leg, indicating that all legs were cycling at roughly the same frequency as the first
Figure 10: 1-2-3-4 metachronal gait summaries comparing lateral walking sequences from fiddler crabs, red claw crabs, shore crabs and spider crabs in loaded and unloaded conditions. On land, or in loaded conditions, fiddler crabs and spider crabs did not use a 1-2-3-4 metachronal gait. Furthermore, only one spider crab used this gait when walking laterally in unloaded conditions.
Figure 11: Number of "double steps" taken by each species of crab in both loaded and unloaded conditions. Double steps (grey bars) are extra steps within a regular step cycle that crabs took in order to balance themselves or for extra support. Double steps were seen in all eight walking legs of all crab species studied at one time or another.
leading leg (Figs. 12 and 13). Thus, the occurrence of double steps was not due to legs
cycling at different frequencies.

**Walking Speeds**

A difference in timing of gait was observed between load conditions. Is this
change reflected in other behavioral aspects of locomotion as well? Crabs showed no
significant difference in walking speed when moving from loaded to unloaded
conditions. The ranges of walking speeds were comparable in loaded versus unloaded
conditions for each species of crab (Fig. 14). Shore crabs walked with speeds
significantly faster than those of red claw crabs in both loaded and unloaded conditions
(land: 10.0 ± 3.4 cm/s vs. 2.9 ± 1.0 cm/s, \( P < 0.001 \); water: 10.7 ± 4.5 cm/s vs. 5.3 ± 2.9
cm/s, \( P = 0.007 \)). Fiddler crabs walked with speeds from 2 cm/s to 11 cm/s in both load
conditions. Spider crabs walking in both directions showed no significant difference in
walking speed between load conditions.

**Relationship: Percentage of Time in the Swing Phase
and Duration of the Step Cycle**

As an exploratory experiment, the relationship between the percentage of time in
the swing phase and the duration of the step cycle was studied in the first leading and
trailing legs of all crabs walking in loaded and unloaded conditions. It was hypothesized
that the duration of swing (in seconds) remains constant as the duration of the step cycle
increases, resulting in a decrease in the percentage of time in swing as the duration of the
step cycle increases. In leading leg 1 of shore crabs and fiddler crabs, there was evidence
in support of this hypothesis, though moderately weak, both on land and underwater (Fig.
15, \( r^2 \) values ranging from 0.122 to 0.407, \( P < 0.01 \)). Red claw crabs on land, however,
showed an increase in the percentage of time in swing as the duration of the step cycle
Figure 12: Box-whisker plots showing the ranges of step cycle durations for red claw crabs, fiddler crabs, and shore crabs in loaded and unloaded conditions. The step cycle for each leg was normalized to that of the first leading leg, shown by the small triangle at leading leg 1 (L1). The step cycle periods for leading leg 2 (L2) through trailing leg 4 (T4) were then divided by the step cycle period for L1.
Figure 13: Box-whisker plots showing the ranges of step cycle durations for spider crabs walking laterally and in the forward direction in loaded and unloaded conditions. See Figure 12 for explanation.
Figure 14: Box-whisker plots depicting the ranges of walking speeds used by each species of crab when walking in loaded and unloaded conditions. Each division of the box-whisker plot signifies (from top to bottom) maximum, 90th, 75th, 50th (median), 25th, 10th and minimum percentiles. A) Fiddler, red claw, and shore crabs walking in both loaded and unloaded conditions showed a slight decrease in walking speed while in loaded conditions. Overall, the smaller fiddler crabs and red claw crabs had similar ranges of walking speeds, while the larger shore crabs walked much faster in both loaded and unloaded conditions (significantly faster than red claw crabs on land P < 0.001 and underwater P = 0.007). B) Spider crabs walking both laterally and in the forward direction showed no significant difference in walking speed across load conditions.
**Figure 15:** Linear regressions depicting the relationship between the duration of the step cycle and the percentage of time in swing for leading and trailing legs 1 (both normalized to the cycle period of L1), and trailing leg 1 normalized to the cycle period of T1 in fiddler crabs, red claw crabs, and shore crabs. There was a weak to moderate relationship between the duration of swing and the duration of the step cycle across species and conditions.
increased. For shore, fiddler, and red claw crabs, there was only a weak to moderate relationship between the duration of swing and the duration of the step cycle across species and conditions (Fig. 15). Interestingly, the relationship strengthened for fiddler crabs underwater, but for shore crabs and red claw crabs on land. There were no significant relationships for trailing leg 1 when normalized to the step cycle of leading leg 1. Spider crabs also showed mostly weak to moderate relationships between the duration of swing and the duration of the step cycle walking forwards and laterally. What’s also noteworthy is that forward, but not laterally, walking spider crabs showed a significant correlation between duration of swing and duration of the step cycle, but only in the moderately loaded condition (Fig. 16).

**Meropodite-Carpopodite Joint (MC Joint)**

As noted previously, there are changes in the timing of gaits, but not in the overall walking speed between load conditions. So what is responsible for this change in timing? Since movement of joints in the walking legs is what makes the animal move, the degree and rate of extension and flexion in the MC joint (see Fig. 4) were measured in fiddler crabs, shore crabs, and spider crabs, walking in both lateral and forward directions, for all load conditions. In both fiddler crabs and spider crabs, only the third leading and trailing legs (or left and right legs) were analyzed, while leading and trailing legs 2, 3, and 4 were analyzed in shore crabs.

Fiddler crabs, shore crabs and laterally walking spider crabs in all load conditions displayed a pattern of MC joint extension and flexion specific to either an alternating tetrapod gait or a metachronal gait (Fig. 17). When using an alternating tetrapod gait, extension and flexion of legs on opposite sides of the body were in phase (Fig. 17a).
Figure 16: Linear regressions depicting the relationship between the duration of the step cycle and the percentage of time in swing in spider crabs walking laterally (top row) and in the forward direction (bottom row). Spider crabs also displayed a weak to moderate relationship between the duration of swing and the duration of the step cycle walking forwards and laterally.
Figure 17: Crabs walking in all load conditions displayed a pattern of meropodite-carpopodite (MC) joint extension and flexion specific to the particular gait used. To the left are individual stepping patterns, while the graphs to the right display the MC joint movements for those particular stepping patterns. A) When using an alternating tetrapod gait, extension and flexion of legs on opposite sides of the body were in phase with each other. B) Leading and trailing extension and flexion are out of phase when crabs used a 1-2-3-4 metachronal gait. C) Forward walking spider crabs show an out of phase pattern of MC joint movements similar to that of a 1-2-3-4 metachronal gait when using a 4-3-2-1 metachronal gait. Joint movements of leading and trailing legs 3 are depicted here.
A) Alternating Tetrapod Gait

Lead 1
Lead 2
Lead 3
Lead 4
Trail 1
Trail 2
Trail 3
Trail 4

Time in Seconds

B) 1-2-3-4 Metachronal Gait

Lead 1
Lead 2
Lead 3
Lead 4
Trail 1
Trail 2
Trail 3
Trail 4

Time in Seconds

C) 4-3-2-1 Metachronal Gait

Left 1
Left 2
Left 3
Left 4
Right 1
Right 2
Right 3
Right 4

Time in Seconds
While the leading leg is extending in swing, the trailing leg is extending in stance, generating force and completing a step cycle. Likewise, as the leading leg begins flexion in stance, the trailing leg flexes in swing. In using a 1-2-3-4 metachronal gait, however, leading and trailing extension and flexion are completely out-of-phase with each other (Fig. 17b). Because the leading and trailing legs begin and end each step cycle simultaneously, the leading leg flexes as the trailing leg extends in stance. In swing, the leading leg extends as the trailing leg flexes. Forward walking spider crabs showed a similar pattern of MC joint movements when using a 4-3-2-1 metachronal gait. As the left leg flexes in swing, the right leg extends in stance and vice versa, creating a relationship between extension and flexion that is out of phase (Fig 17c).

**MC Joint Excursions**

Extension and flexion of the MC joint is what probably generates most of the thrust necessary to propel the crabs laterally during locomotion. In comparing the range of motion of this joint in leading and trailing legs, it is possible to ascertain if and how the legs are used differently in loaded and unloaded conditions. When walking on land, fiddler crabs showed no significant differences between both extension and flexion in the third trailing leg as compared to the third leading leg (Fig. 18a). Underwater, however, there was an obvious difference between leading and trailing legs. Trailing flexion excursions on land were significantly greater than those underwater ($P = 0.023$).

Shore crabs, when walking both on land and underwater, showed trends in MC joint excursions opposite to those of fiddler crabs (Figs. 18b and 18c). When walking on land, shore crabs exhibited a very distinct difference between the leading and trailing legs. Trailing extension and flexion amplitudes for all three legs studied were much
Figure 18: Box-whisker plots displaying the ranges of MC joint excursions in fiddler crabs (leading and trailing legs 3) and shore crabs (leading and trailing legs 2, 3, and 4) on land and underwater. A) When walking on land, fiddler crabs showed no significant difference between leading and trailing legs. Underwater, however, leading extension and flexion amplitudes are much higher than trailing extension and flexion amplitudes. Trailing flexion on land is significantly greater than that underwater ($P = 0.023$). B) On land, shore crabs showed much higher MC joint excursions in trailing legs 2, 3, and 4 compared to those of the leading legs, though only significantly so in leg 3 (ext: $P = 0.026$, flex: $P = 0.021$). C) Underwater, shore crabs displayed MC joint excursions opposite to those seen in fiddler crabs walking underwater. In leading and trailing legs, extension and flexion excursions are similar. Leading leg 4 excursions are significantly lower than the excursions of leading legs 2 and 3 ($P \leq 0.014$).
greater than leading extension and flexion, though only significantly so in leg 3 (ext: $P = 0.026$, flex: $P = 0.021$). Leading excursions stayed in the range of roughly 40° to 70°, while trailing excursions varied from 60° to 90°. Underwater, the extension and flexion amplitudes of the MC joint in the second and third leading and trailing legs were similar. However, in the fourth legs, leading extension and flexion amplitudes were significantly lower than leading extension and flexion amplitudes for legs 2 and 3 (ext: leg 2 $P < 0.001$, leg 3 $P = 0.014$; flex: leg 2 $P < 0.001$, leg 3 $P = 0.005$).

When comparing land and water MC joint excursions in shore crabs, trailing leg 2 extension and flexion excursions were significantly greater when walking on land than underwater (ext: $P = 0.009$, flex: $P = 0.005$). However, leading excursions for legs 2 and 3 were equivalent on land and underwater; trailing flexion in leg 4 was significantly greater ($P = 0.030$) on land.

There were no significant differences in excursion of the MC joint under any of the conditions in spider crabs (Fig. 19). Spider crabs walking forward did show significantly smaller MC joint excursions than crabs walking sideways ($P \leq 0.022$).

From these data, it is clear that crabs also changed the use of the MC joint in loaded and unloaded conditions. Fiddler crabs used trailing legs less when walking underwater than on land, while shore crabs used trailing legs more than the leading legs on land. Possibly, the load difference in spider crabs was not enough to elicit a significant difference in MC joint usage in either walking direction.

**MC Joint Angular Velocities**

In addition to changing the range of motion of the MC joint, crabs could also change the rate of opening and closing of the joint, or the MC joint angular velocity. The
Figure 19: Box-whisker plots displaying the ranges of MC joint excursions in the leading and trailing legs 3 of spider crabs walking laterally (A) and forwards (B) in loaded and unloaded conditions. There were no significant differences across load conditions in either direction. Spider crabs walking forwards had significantly lower MC joint excursions than spider crabs walking laterally ($P \leq 0.022$).
difference in timing of gaits between load conditions could be due to these possible changes in rate. Fiddler crabs displayed no significant difference in MC joint angular velocities in leading and trailing legs 3 both on land and underwater (Fig. 20a). Nonetheless, the distributions of angular velocities on land and underwater are basically equivalent at around 150°/s to 500°/s.

MC joint excursions for fiddler crabs and shore crabs were dissimilar, as were the MC joint angular velocities. On land, the angular velocities of the return strokes (leading extension and trailing flexion) of shore crabs were significantly greater than those of the power strokes (leading flexion and trailing extension, Fig. 20b and 20c; \( P < 0.001 \) for all legs except leading leg 4 and trailing leg 3). The rates of leading return strokes fall within 150°/s to 450°/s, while the rates of trailing return strokes are slightly higher at 250°/s to 550°/s. Underwater, however, shore crabs exhibited no significant differences between the angular velocities of power and return strokes.

Spider crabs walking laterally displayed no obvious difference in MC joint angular velocity between power strokes and return strokes (Fig. 21a). Spider crabs walking in the forward direction displayed MC joint angular velocities that were generally much lower than the rates of change in laterally walking spider crabs (forward: 10°/s to 120°/s vs. lateral: 30°/s to 220°/s), but were also not different for power and return strokes (Fig. 21b).

In addition to the change in timing of gaits and the change in the use of the MC joint, shore crabs also changed how fast they moved the MC joint in loaded and unloaded conditions. The rates of return strokes on land were significantly increased, while those in fiddler and spider crabs were not.
**Figure 20:** Box-whisker plots displaying the ranges of MC joint angular velocities in fiddler crabs (leading and trailing legs 3) and shore crabs (leading and trailing legs 2, 3, and 4) on land and underwater.  

**A)** Fiddler crabs showed no significant difference in MC joint angular velocities in leading and trailing legs 3 both on land and underwater.  

**B)** On land, the angular velocities of the return strokes are significantly higher than those of the power strokes in shore crabs ($P < 0.001$).  

**C)** Underwater, shore crabs show no significant differences between the angular velocities of power and return strokes in leading and trailing legs 2, 3, and 4.
Figure 21: Box-whisker plots displaying the ranges of MC joint angular velocities in the leading and trailing legs 3 of spider crabs walking laterally and forwards in loaded and unloaded conditions. A) Spider crabs walking laterally displayed no obvious difference in MC joint angular velocities between power strokes (leading flexion and trailing extension) and return strokes (leading extension and trailing flexion). B) When walking in the forward direction, spider crabs display MC joint angular velocities lower than those when walking laterally.
**Relationship: MC Joint Angular Velocity and Walking Speed**

In laterally walking animals, propulsion can come from both the MC and PD joints (see Fig. 4). If the MC joint is the major thrust generating joint during lateral locomotion in crabs, strong correlations with walking speed should be seen. Therefore, the relationship between MC joint angular velocity and walking speed was examined. The analyses were done on all load conditions via linear regressions, and r² values (also known as the coefficient of determination) were used to describe the strength of the relationship (Sokal and Rohlf 1995).

As seen in Figure 22, fiddler crabs walking on land displayed strong correlations between rate of change of the MC joint and walking speed during both extension and flexion in leading legs. Ninety-three percent of the variability in the rate of extension was accounted for by the speed at which the crab was walking on land, while 83.3% of the variability in the rate of flexion was explained by walking speed. Trailing leg 3 displayed a strong relationship (r² = 0.712) between the rate of flexion of the MC joint and walking speed. Underwater, however, there was no significant correlation between MC joint angular velocity and walking speed in leading legs. The rate of trailing extension had a strong, significant correlation with the walking speed of crabs.

The rates of MC joint angle change during the power stroke of shore crabs walking on land all had strong correlations with walking speed (r²: 0.718 – 0.866, Fig. 23). The relationships between return strokes and walking speed were generally much weaker (r²: 0.394 – 0.826). Underwater, the correlations between MC joint angular velocity and walking speed were also weaker (r²: 0.267 – 0.841), but generally significant (Fig. 24).
Figure 22: Linear regressions depicting the relationship between MC joint angular velocity and walking speed in the third leading and trailing legs of fiddler crabs both on land and underwater. Leading leg 3 (left column) shows an exceptionally strong correlation between walking speed and the rates of extension and flexion on land; while underwater, the strength of this relationship is much weaker. In trailing leg 3 (right column), however, it was observed that the rate of trailing extension had a strong, significant correlation with walking speed underwater.
Figure 23: Linear regressions depicting the relationship between MC joint angular velocity and walking speed in the second, third and fourth leading and trailing legs of shore crabs walking on land. The rates of MC joint angle change during the power stroke all have strong correlations with walking speed. The relationships between return strokes and walking speed were generally much weaker.
Figure 24: Linear regressions depicting the relationship between MC joint angular velocity and walking speed in the second, third and fourth leading and trailing legs of shore crabs walking underwater. The correlations between MC joint angular velocity and walking speed were weaker than those on land, but generally significant.
A similar trend was seen in laterally walking spider crabs (Fig. 25). Strong correlations ($r^2$: 0.910 – 0.962) were found between MC joint angular velocity and walking speed in animals carrying ¼ load backpacks, but these were weaker ($r^2$: 0.462 – 0.684) in the no load condition. There was no systematic correlation between MC joint velocity and load in spider crabs walking forwards (Fig 26).

The relationship between MC joint angular velocity and walking speed was examined in order to further confirm that the MC joint is the major thrust generating joint in the legs of laterally walking crabs. The strong, significant correlations observed between these two variables supported the hypothesis that a causal relationship exists between the rate of MC joint change and the walking speed of the crabs.

**Propodite-Dactyl Joint (PD Joint)**

The MC joint is not the only joint that can contribute to locomotion in the walking legs. The propodite-dactyl joint, or the PD joint, acts mostly as a strut, supporting the weight of the crab as it walks. PD joint excursions were measured in legs 2, 3, and 4 in shore crabs. On land, both leading and trailing legs displayed PD joint excursions between 80° and 140° (Fig. 27). Underwater, however, leading legs displayed PD joint amplitudes in the range of 85° to 130°, while those of trailing legs fell in a slightly higher range of 90° to 145° (Fig. 28).

There was a definite difference in PD joint movements between leading and trailing legs as the crab traveled from one side of the tank to the other both on land and underwater. In trailing legs, the crab opened the PD joint at the end of each swing phase, although not nearly as much as at the end of the stance phase. Leading legs, however, did not show this additional increase in PD joint amplitude as the swing phase ends.
Figure 25: Linear regressions depicting the relationship between MC joint angular velocity and walking speed in the third leading and trailing legs of spider crabs walking laterally in both loaded and unloaded conditions. Strong correlations were found between MC joint angular velocity and walking speed in animals carrying 1/4 load backpacks, but these were weaker in the no load condition.
Figure 26: Linear regressions depicting the relationship between MC joint angular velocity and walking speed in the third left and right legs of spider crabs walking in the forward direction in both loaded and unloaded conditions. There was no systematic correlation between MC joint velocity and load conditions in spider crabs walking forwards.
**Figure 27:** Meropodite-carpopodite (MC) and propodite-dactyl (PD) joint movements of the third leading (A) and trailing (B) legs of a shore crab when walking on land. The upper panel in each case depicts a stick figure representation of the meropodite, carpopodite, and dactyl, plotted every 17.5ms as the animal takes several steps. The lower panel shows the joint angles as a function of time, with the shaded regions indicating stance. The lines join equivalent time points between the two panels.
**Figure 28:** MC and PD joint movements of the third leading (A) and trailing (B) legs of a shore crab when walking underwater. See Fig. 27 for details.
Leading PD joint excursions remained relatively unchanged during the step cycle. This general trend was observed in legs 2, 3, and 4, though Figures 27 and 28 are examples of leading and trailing legs 3 on land and underwater, respectively.
DISCUSSION

This study used three-dimensional motion analysis to examine the adaptations made by the locomotor systems of four species of crabs under different load conditions. By comparing these terrestrial, amphibious and aquatic species walking on land and underwater, it is possible to gain insight into general principles underlying load accommodation during locomotion.

**Footfall Patterns and Walking Speed: Land vs. Water**

There were several consistent changes in the footfall patterns of the four species of crabs in walking sequences under loaded conditions (on land) or unloaded conditions (underwater). Primarily, when walking in loaded conditions in both forward and lateral directions, the duration of the swing phase (return stroke) was much shorter in all four species than when walking in unloaded conditions. The gravitational pull of the earth when crabs are walking on land is in no way counterbalanced by buoyancy as it is when walking underwater. The crabs compensate by keeping their legs in contact with the substrate for a longer period of time in order to support their weight. To maintain the similar step cycle periods seen on land and underwater (Figs. 13 and 14), the crabs must decrease the amount of time the leg is in swing to make up for this increase in stance period. Although not to the same degree as the other three species of crabs, the spider crabs also shortened the return stroke duration when walking with a load backpack. Other decapod crustaceans show similar changes. The duty factor (stance duration expressed as a proportion of step cycle period) on land is much higher than that underwater in the shore crabs *Carcinus maenas* (Clarac et al. 1987) and *Pachygrapsus crassipes* (Hui 1992) and the intertidal rock crab *Grapsus tenuicrustatus* (Martinez et al.
The crayfish *Procambarus clarkii* demonstrated an increase in the power stroke burst duration as seen in electromyograms of the remotor muscles; the duration of promotor burst activity (return stroke) did not change (Grote 1981). However, the actual durations of the power stroke and return stroke were not measured.

In addition to the decrease in the duration of swing phase, there was also a decrease in the swing phase variability and onset variability in fiddler crabs, red claw crabs, and shore crabs walking on land. Martinez *et al.* (1998) provided ample evidence in support of their hypothesis that underwater gaits in the intertidal rock crab *Grapsus tenuicrastatus* are less constrained than those on land, showing greater variability in leg kinematics as well as footfall patterns. The stepping patterns of the crabs in the present study seemed to become more regular when walking in loaded conditions. This suggests that the motor programs controlling locomotion become more specific, therefore the footfall patterns become more ordered. Macmillan (1975) studied the effects of load on walking in the lobster, *Homarus americanus*. By looking at myograms recorded from the walking legs in unloaded conditions, he determined that the patterns of antagonistic muscle activity overlapped; therefore the footfall patterns were less constrained. For example, the extensor burst would end after the flexor burst began, and so on. In loaded conditions, however, these patterns did not overlap nearly as much; the extensor burst was completed before the flexor burst began, suggesting that the footfall patterns generated were more strictly controlled.

Increased hydrodynamic drag forces in unloaded conditions might be expected to reduce walking speeds. Several other decapod crustaceans were shown to walk faster or with a higher stepping frequency in unloaded conditions, such as the shore crab (Hui
1992), the intertidal rock crab (Martinez et al. 1998), and the crayfish (Pond 1975; Grote 1981). The present study did not examine either stepping frequency (steps/s) or stride length, therefore walking speed was defined as the distance covered in a specified amount of time. Walking speeds for all four species of crabs walking laterally and in the forward direction were, however, similar in loaded and unloaded conditions, suggesting that these crabs are better adapted to load than those in previous studies. Fiddler crabs, red claw crabs and shore crabs have oblong carapaces and flattened legs which are able to cut through the water with little difficulty, ensuring smooth locomotion. Thus, the body structure of these crabs minimizes hydrodynamic drag in unloaded conditions, therefore allowing for faster walking speeds (Martinez 2001).

**Spider Crabs: Morphology and Gait**

If given a choice, spider crabs would usually walk in the forward direction with a 4-3-2-1 metachronal gait rather than laterally with an alternating tetrapod gait. What is it that gives spider crabs such a different gait? Unlike the other species, spider crabs are completely aquatic. This may explain why spider crabs did not stand on land, as well as the much more dramatic modification of stepping patterns on land. The body structure of the spider crab also provides a possible explanation as to this behavioral phenomenon. Sleinis and Silvey (1980) described the morphology of the forward walking soldier crab, *Mictyris platycheles*, which is very much like that of the spider crab in the present study. In both species, the carapace is longer than it is wide, giving a more egg-shaped appearance to the crab. The morphology of the laterally walking ocypodid crab *Heloecius cordiformis*, which is like that of the fiddler, red claw, and shore crabs in the present study, was also detailed by Sleinis and Silvey (1980). Fiddler, red claw and shore
crabs are different than the spider and soldier crabs in that their carapace is characteristically wider than it is long. Furthermore, the legs of the forward walking crabs radiate to points all around the carapace, creating wide spaces between legs necessary for protraction and retraction during forward walking. In contrast, the legs of laterally walking crabs project laterally with very little space between legs. Also, the range of motion of joints responsible for forward walking are larger in the soldier and spider crabs, while those responsible for lateral walking are smaller than those in laterally walking crabs (Sleinis and Silvey 1980). Locomotive studies based on forward walking spider crabs are unavailable; thus the difference in gait between the spider crabs and the fiddler, red claw and shore crabs is most readily explained by morphology.

**Step Cycle Periods and Stroke Durations**

The present study examined the relationship between the percentage of time in the swing phase (based on return stroke duration) and the step cycle period of the first leading and trailing (lateral) or left and right (forward) legs. Step cycle period is the sum of both the power stroke (stance) duration and the return stroke (swing) duration. As step cycle period decreases, the stepping frequency, or walking speed, increases. Therefore, it follows that in order to decrease the step cycle period, either one or both stroke durations must be shortened. In an alternating tetrapod gait, both the power stroke and return stroke durations are reduced equally with increased stepping frequency (provided that stepping frequency is reciprocally related to step cycle period; Clarac 1981). For this to occur, the percentage of time in swing should remain the same as the step cycle period is increased. As step cycle period increases (and stepping frequency decreases), there was an overall decrease in the percentage of time in swing in both the leading and trailing (or
right and left) first legs. This suggests that the return stroke duration remains relatively constant as the step cycle period increases. The obvious exception to this trend is the leading leg 1 of loaded red claw crabs, where there was a marked increase in the percentage of time in swing as the step cycle period increased. This suggests that the duration of the return stroke actually decreases with a decrease in step cycle period. When step cycle duration was small, the duration of the power stroke was longer, suggesting that there was more thrust generation in leading leg 1. In forward walking of the soldier crab *Mictyris platycheles* in unloaded conditions, there was a significant correlation between both the power stroke and the return stroke durations and the step cycle period (Sleinis and Silvey 1980). As stepping frequency increased (and step cycle period decreased), both stroke durations decreased in a linear fashion. In unloaded animals, both the power stroke duration and the return stroke duration can be altered in order to regulate the step cycle period or stepping frequency (Clarac 1981). However, in loaded animals, the return stroke duration is adjusted to change the step cycle period and coordinate with other legs since the weight of the animal is not supported during the return stroke; changing the duration of the power stroke is therefore responsible for changing the speed of the animal (Clarac 1981). There is something different taking place within the loaded system of red claw crabs as compared to those of the other species that portends possible changes in motor control mechanisms dealing with locomotion. With no previous studies done on locomotion in red claw crabs, it is difficult to pinpoint exactly what is different in this system.
Phase Relationships Based on MC Joint Activity during Locomotion

Movement of the meropodite – carpopodite joints (MC joints) of contralateral legs during locomotion was indicative of the gait used by the crabs in the present study (Fig. 18). When MC joint extension in leading leg 3 is in phase with MC joint extension in trailing leg 3, typically an alternating tetrapod gait is being used. Leading legs are in swing when extending, executing a return stroke at the same time as trailing legs are in stance when extending, executing a power stroke. This pattern then alternates with alternating functional groups, with the leading legs in stance when flexing (power stroke) and the trailing legs in swing when flexing (return stroke). The MC joints of the contralateral leg pairs move in tandem with each other; however, the legs themselves move out of phase with their contralateral counterparts. Leading legs are in swing while trailing legs are in stance, and vice versa. In previous studies (Barnes 1975, Hui 1992, Macmillan 1975), it was common for contralateral legs to have a phase value of around 0.5 when compared to each other. Phase value represents the fraction of the step cycle completed by the leading leg of the pair when the trailing leg of the pair begins its step cycle, and vice versa. With a phase value at or near 0.5, the leading leg of the pair has completed 50% of its step cycle when the trailing leg begins its step (Bowerman 1977). Other decapod crustaceans walking laterally with contralateral leg pairs out-of-phase include the fiddler crab *Uca pugnax* (Barnes 1975) and the shore crab *Pachygrapsus crassipes* walking on land and underwater (Hui 1992).

When MC joint extension and flexion of equivalent leading and trailing legs (respectively) are out-of-phase with each other, either of the metachronal gaits is being used. In the lateral 1-2-3-4 metachronal gait, as a leading leg extends in swing, its
trailing counterpart flexes in swing. Both legs in the contralateral pair execute their power and return strokes at the same time. Shultz (1987) studied the fishing spider *Dolomedes triton* and found that on land, the spider walked with contralateral leg pairs out-of-phase. However, when the spider walked on the surface of water, contralateral leg pairs moved in phase with one another. Also, the crayfish *Procambarus clarkii* was found to walk with contralateral legs moving in phase with one another (Jamon and Clarac 1995, 1997).

On the other hand, a 4-3-2-1 metachronal gait seen in the forward walking spider crabs is slightly different than a 1-2-3-4 metachronal gait in that the left and right legs of the contralateral leg pair do not perform return strokes or power strokes in chorus. While left and right MC joint extension and flexion are still out-of-phase with one another, the contralateral leg pair 3 moves out-of-phase with one another. In other words, left leg 3 extends during stance (power stroke) while right leg 3 flexes during swing (return stroke). This relationship is also seen in the following forward walking decapod crustaceans: the lobster *Homarus americanus* (Macmillan 1975), the soldier crab *Mictyris platycheles* (Sleinis and Silvey 1980), and the crayfish *Procambarus clarkii* (Jamon and Clarac 1995). Shultz (1987) also reported contralateral legs out-of-phase with one another in the wolf spider *Lycosa rabida* walking both on land and on the surface of the water.

Furthermore, extension and flexion about the MC joint is not the primary source of thrust in forward walking spider crabs; protraction (return stroke) and retraction (power stroke) about the thoraco-coxopodite joint (TC joint) provide the crabs with forward propulsion. Movement about the TC joint was not measured in the present study. When either leg
was in retraction (the power stroke), the MC joint was in extension, possibly adding thrust in the direction of motion at the end of the stance phase.

The patterns of MC joint movements during locomotion provide an additional approach in the identification and characterization of a particular gait. Each gait elicits unique leg movements; therefore the motion of the joints in each leg is specific to that particular stepping pattern.

**MC Joint Excursions and Angular Velocities: Fiddler Crabs**

The patterns of MC joint excursions for the third leading and trailing legs of fiddler crabs walking on land and underwater displayed large differences. While it was suggested that leading legs may often have a sensory role in locomotion, collecting information concerning the landscape over which the crab walks (Full 1997), there are indications that both trailing and leading legs generate force at slower speeds in loaded conditions (Blickhan and Full 1987). On land, leading and trailing excursions were similar in fiddler crabs, hovering around a mean angle of 70° (Figure 19a). It is likely that both the leading and trailing legs generate the force needed for locomotion by pulling and pushing, respectively. The intertidal rock crab *Grapsus tenuicrustatus* also exhibited no difference between kinematic variables in leading and trailing legs on land, suggesting that both leading and trailing legs played a role in generating locomotive force (Martinez et al. 1998). The duration of the power stroke in fiddler crabs on land was longer than that underwater, allowing more time for the legs to pull or push the crab in the direction of motion and thereby flex and extend further about the MC joint.

Furthermore, the MC joint angular velocities of fiddler crabs walking on land were similar for return strokes (leading extension and trailing flexion) and power strokes...
(leading flexion and trailing extension). The return strokes do not generate force by pushing or pulling against the substrate, nor do they support the animal’s weight; the crab’s leg encounters negligible resistance while moving through the air. Based on these observations, return stroke MC joint angular velocities of fiddler crabs might be expected to be significantly greater than those of the power strokes, yet they were not. Return stroke MC joint angular velocities also played a major role in walking speed (Fig. 23). As walking speed increased, the MC joint angular velocity also increased in both the power strokes and return strokes. The return strokes of both leading and trailing legs were better correlated with the animal’s walking speed than the power strokes, suggesting that as walking speed increased, the duration of the return strokes decreased more than that of the power strokes. The strength of these correlations between MC joint angular velocities and walking speed in both the power and return strokes suggests that both leading and trailing legs generate the forces needed for locomotion on land.

In the present study, MC joint excursions in fiddler crabs walking on land were greater than those underwater, significantly so for trailing flexion (Fig. 19a). Previous studies showed that trailing legs provided more propulsion for locomotion by pushing or extending against the substrate during the power stroke (Clarac et al. 1987). In light of these previous studies, it is assumed in the present study that the trailing legs of fiddler crabs generate more locomotive force than the leading legs, which act as tactile sensors. Since the duration of stance (power stroke) is shorter underwater than on land, the fiddler crabs may be generating more trailing propulsive force in a shorter amount of time while walking underwater. Furthermore, the correlation between walking speed and trailing extension in fiddler crabs underwater is particularly strong, lending more support to this
hypothesis. However, the kinematic data alone for the crabs in the present study is insufficient to support this hypothesis; EMG recordings and ground reaction forces must also be examined in order to better understand the patterns of MC joint excursions in fiddler crabs.

**MC Joint Excursions and Angular Velocities: Shore Crabs**

Shore crabs walking both on land and underwater exhibited patterns of MC joint excursions in leading and trailing legs 2, 3, and 4 that were unlike those found in fiddler crabs under the same conditions. Fiddler crabs walking on land had similar leading and trailing MC joint excursions, while shore crabs in the same condition had trailing excursions that were significantly greater than leading excursions (Fig. 19b). Underwater, trailing legs of fiddler crabs had MC joint excursions that were smaller than leading excursions, although not significantly. Shore crabs walking underwater, on the other hand, displayed similar MC joint excursions in both leading and trailing legs. Fiddler crabs and shore crabs use their walking legs differently in each load condition, yet they adopt similar alternating tetrapod gaits. It is unknown why amphibious shore crabs and terrestrial fiddler crabs have such differing joint movements during the same gait; however, these differences in MC joint excursions may be due to how well adapted each species is to the environment in which they are walking.

Previous studies showed that trailing legs often generate more thrust than leading legs during locomotion on land, or in loaded conditions. Ground reaction force recordings in the ghost crab *Ocypode quadrata* demonstrated both pulling and pushing forces in the leading and trailing legs during slow walking on land, though pushing in the trailing legs dominated (Blickhan and Full 1987). Clarac *et al.* (1987) reported evidence
for greater propulsive forces in trailing legs rather than leading legs via EMG recordings in the shore crab *Carcinus maenas* during walking both on land and underwater. Compared to leading legs in the present study, the greater trailing MC joint excursions in shore crabs walking on land are therefore suggestive of greater trailing propulsive forces on land. Angular velocities of trailing legs show that the legs move about the MC joint much faster during the return stroke, covering the same range in a shorter amount of time compared to the trailing power stroke. The rates of change of the MC joint in leading leg strokes are similar to their respective trailing strokes (i.e. return strokes are greater than power strokes), although the excursions in the leading legs remain smaller than those of the trailing legs. These smaller leading excursions are suggestive of the leading legs acting in a sensory manner, scanning the environment to come (Blickhan and Full 1987; Cruse 1976), which suggests that the leading legs do not generate the major part of the locomotive force. Nonetheless, the relationship between walking speed and the rate of MC joint change of the power strokes is strong for both leading and trailing legs (Fig. 24). Based on these findings, it is evident that shore crabs, when walking on land, push more with trailing legs rather than pull with leading legs.

Underwater, leading and trailing legs 2 and 3 have similar ranges of MC joint excursions (Fig. 19c). The pattern of MC joint excursions in leg 4, however, resembles that seen in all three legs on land, i.e. trailing excursions are somewhat greater than leading excursions. Leading leg 4 may act in a sensory manner, indicated by the small MC joint excursions, or act only as needed for additional support. Other species of crabs (like the blue crab *Callinectes*) have fourth legs that are adapted into paddles for use during swimming, and are rarely used as walking legs during aquatic locomotion (Hessler
Nonetheless, no differences were observed in the MC joint angular velocities for both the leading and trailing power and return strokes, further suggesting that both leading and trailing legs generate both pulling and pushing forces. Furthermore, in legs 2 and 3, the correlation between walking speed and the MC joint angular velocities is strongest in leading power strokes and trailing return strokes. These findings concerning shore crabs walking underwater are indicative of both the leading and trailing legs pulling and pushing the crabs in the direction of locomotion, rather than the trailing legs generating the majority of the locomotive force.

**MC Joint Excursions and Angular Velocities: Spider Crabs**

Analysis of the third leading and trailing legs of spider crabs walking laterally in both loaded and unloaded conditions revealed the following points of interest: 1) MC joint excursions in trailing leg 3 were greater than in leading leg 3 in all load conditions, while the rates of MC joint change were similar in both leading and trailing legs in all load conditions, and 2) The relationship between walking speeds and MC joint angular velocities became stronger in both power strokes and return strokes as load increased. Taking into consideration that spider crabs do not normally prefer to walk laterally, it is suggested that both leading and trailing legs are generating the forces necessary for lateral locomotion.

Forward walking spider crabs, however, must use the TC joint and not the MC joint as the primary joint generating propulsive force during locomotion. Thus, excursions and angular velocities of the MC joint in these crabs are significantly less than those of crabs walking laterally. During a step cycle, the return stroke (protraction of the TC joint) was coupled with flexion about the MC joint, and the power stroke (retraction
of the TC joint) was coupled with extension. The relationship between walking speed and MC joint angular velocity is much stronger in left and right extensions than in flexions, supporting the hypothesis that the extra extension during the power stroke generates force at some point during locomotion. The same pattern of coupling was observed in large crayfish of the species *Procambarus clarkii*, where extension of the MC joint during retraction provided extra stretch in the direction of locomotion (Jamon and Clarac 1997). The MC joint is also active to some extent during forward walking in small crayfish of the species *Procambarus clarkii* (Jamon and Clarac 1997), and in the lobster *Homarus americanus* (Ayers and Davis 1977); however, the MC joint instead extended during protraction and flexed during retraction.

**PD Joint Movements in Shore Crabs**

The movement of the propodite-dactyl (PD) joint was also analyzed in the leading and trailing legs of shore crabs walking on land and underwater. Of the various parameters analyzed, the only difference was a slight decrease in the range of motion of the PD joint underwater when compared to land. At times, it was observed that the dorsal edge of the dactyl in leading and trailing legs was used as a surface on which to bear increased weight, thereby moving the PD joint slightly during the step cycle. This was also observed in the same species by Jamon and Clarac (1987) and Libersat *et al.* (1987). The leading legs displayed PD joint movements unlike those of the trailing legs, where the PD joint was found to move biphasically with the MC joint (Figs. 27 and 28). For instance, when the crab’s trailing leg begins the return stroke, the PD joint has just finished opening in order to push the crab along and further the efforts of the MC joint. Once the dactyl is lifted off of the substrate, the PD joint then closes in tandem with MC
joint flexion. However, immediately before the dactyl touches down in stance, the PD joint opens slightly in order for this touchdown to occur, creating the biphasic movement during the return stroke. When contact is made, the PD joint then closes slightly as the weight of the crab descends upon it, and then opens again in order to push the crab along again in another power stroke. This pattern of PD joint movements was not seen in leading legs, suggesting the crabs used the leading dactyls more like struts during walking.

**Conclusions**

The four species of crabs studied showed distinct similarities and differences when walking on land and underwater. When walking laterally, an alternating tetrapod gait was used most often, while forward walking spider crabs changed gaits entirely and used a 4-3-2-1 metachronal gait exclusively in both loaded and unloaded conditions. The crabs deal with load similarly with a change in the timing of gaits; they decreased duration of swing as load increased. Across species, there is a difference in the ability to deal with increased load based on natural environments. In other words, fiddler crabs, red claw crabs, and shore crabs were all able to deal with large load changes, whereas spider crabs apparently could not. Each species of crab also used their legs differently during locomotion. Based on MC joint excursions, angular velocities and the relationship between angular velocities and walking speed, fiddler crabs generated more propulsive thrust with trailing legs underwater, while shore crabs generated more propulsive force with trailing legs on land. Now that there is a basic understanding of the biomechanics behind locomotion on land and underwater, it is possible to begin exploring how the nervous systems produce these changes.
REFERENCES


VITA

Jennifer Nuss Schreiner was born in Metairie, Louisiana, on February 5, 1979, receiving her high school diploma from Mount Carmel Academy in 1997. She then went on to receive a Bachelor of Science degree in zoology from Louisiana State University in December of 2001. In January of 2002, she was accepted into the graduate program at Louisiana State University, where she studied load adaptations of the locomotor systems of crabs walking freely on land and underwater in the lab of Dr. Jim Belanger. During her graduate career, she served one semester each as a teaching assistant for the Introductory Biology Laboratory and the Vertebrate Physiology Laboratory, and was also appointed with a research assistantship. In August of 2004, she will begin medical training at Louisiana State University School of Medicine in New Orleans.