"I salute the echinoderms as a noble group especially designed to puzzle the zoologist."

Libbie H. Hyman (1955), The Invertebrates, Vol. 4. Echinodermata

University of Alberta

The size dependence of sea star locomotion: Does bigger mean faster?

by

Emaline M. Montgomery

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Masters of Science
in
Systematics and Evolution

Department of Biological Sciences

Fall 2013
Edmonton, Alberta

Abstract

As a general rule, larger-bodied animals within a species move at faster absolute speeds independently of locomotive mode. The relationship between body size and speed in sea stars is decidedly less clear. One species of sea star follows the general trend, three species show no correlation between body size and speed, and one species exhibits the opposite relation. To address these puzzling observations, I quantified body size, body shape, and crawling speed in four previously unstudied species of Northeast Pacific sea stars: the multi-armed stars *Pycnopodia helianthoides* and *Solaster stimpsoni,* and the fixed-arm number *Dermasterias imbricata* and *Leptasterias hexactis*. Only *L. hexactis* exhibited statistically significant allometries in arm width, arm length, and oral disk. When correlating measures body size with crawling speeds, larger individuals within the multi-armed species were faster - but larger individuals of fixed-arm species crawled slower. Crawling speed differences between plastic and fine sand differed among species.

Acknowledgements

I would like to thank my supervisor Dr. A. Richard Palmer for all of his support and guidance in my research and growth as a scientist. My lab mates N. W., S. A., M. B., and T. M. have also been wonderful for their continued support and all the boating adventures. And to my parents and Diva - I couldn’t have done it without you!

Table of Contents

List of Tables

Chapter 2

List of Figures

Chapter 2

Chapter 3

Chapter 1

Why does size matter in biology?

Body size and shape are fundamental to understanding animal design (Schmidt-Nielsen, 1975; Vogel, 2003). How size and shape vary within species can reveal physiological and physical constraints to basic vertebrate and invertebrates systems such as energy use, feeding, and locomotion (Biewener, 2005; Vogel, 2008).

Mass ($\propto$length^3) is commonly used as the main size metric because it can be universally measured and understood (Schmidt-Nielsen, 1975). Metabolic-rate and oxygen consumption are tightly coupled with body mass and larger-bodied animals are generally more efficient at using energy than smaller individuals (Vogel, 2003; Hughes *et al*., 2011). This increased energy efficiency relative to body mass is partially responsible for why heavier animals are generally able to move with faster absolute speeds independent of mode of locomotion (Schmidt-Nielsen, 1975). Larger-bodied mammals, for example, consume less oxygen per gram of tissue and generally move faster than smaller individuals of the same species (Schmidt-Nielsen, 1975).

The need to maximize surface area ($\propto$length^2) for feeding and respiration while minimizing volume ($\propto$length^3, $\propto$mass) is also crucial to animal design (Vogel, 2003; Vogel, 2008; McKinney and Sumrall, 2011). For example, coral colony surface area, crown area in anemones, and food groove area in fossil crinoids all scale positively allometrically with body mass (Vollmer and Edmunds, 2000; Brower, 2006; McKinney and Sumrall, 2011). The relationship between body area and mass can influence locomotion as well. An allometric increase in body mass without a corresponding proportional increase in the area of locomotive structures can increase the cost to locomotion (Vogel, 2008; Montgomery and Palmer, 2012). This can clearly be seen in the reduced crawling speeds of hermit crabs with shells compared to those without (Herreid and Full, 1986). The legs of these hermit crabs do not scale allometrically with body size to compensate for the increased mass contributed by carrying a shell, which therefore yields lower locomotive efficiency (Herreid and Fall, 1986). Hermit crabs with shells also do not alter their behavior to mitigate the effect of the extra mass (Herreid and Fall, 1986).

Linear measures of size (length^1) are often used to quantify the biomechanical costs to locomotion in animals (Schmidt-Nielsen, 1975; Pontzer, 2007). Critical lengths vary among species but are defined as the fundamental length on which locomotion mechanics depends (Schmidt-Nielsen, 1975; Pontzer, 2007). For example, limb length and hip height are critical for explaining among-species variation in locomotion for running mammals, reptiles, and arthropods (Schmidt-Nielsen, 1975; Pontzer, 2007). In general, longer limbs enable animals to travel farther (increased stride length) and take fewer “steps” (reduced stride frequency) (Pontzer, 2007). Arm length (limb length) has also been suggested as a critical length for locomotion in sea stars despite their unique mode of locomotion: crawling with hydraulically powered tube feet that row back and forth analogous to running in terrestrial animals (Montgomery and Palmer, 2012).

Sea stars (Class Asteroidea; Phylum Echinodermata) are a fascinating group to examine body size and shape variation both within and among species due to their immense diversity of forms (Lambert, 2000). This clade can be characterized by a relatively solid aboral ("dorsal") surface, and an oral ("ventral") surface composed of ambulacral grooves from which the tube feet extend (Lawrence, 1987; Lambert, 2000). Despite these unifying features, diversity can be found in: a) arm number, which ranges from 4 to 24 among species, b) oral disk size, and c) aspect ratio (ratio of arm length to arm width) (Lambert, 2000; Lamb and Hanby, 2005). Surprisingly, virtually no studies have asked basic questions about scaling of body shape in sea stars (but see Montgomery and Palmer, 2012) and few others have examined how body size affects biological activities such as locomotion, feeding, and energy usage, despite the great ecological significance of many sea stars (Hughes *et al.*, 2011; Mueller *et al.*, 2011; Montgomery and Palmer, 2012).

Body size has a large impact on locomotion. Larger-bodied animals of the same species generally move faster across a diversity of taxa ranging from jellyfish to terrestrial mammals (Schmidt-Nielsen, 1975). In contrast, the association between body size and locomotion speed in sea stars is rather unclear. Larger individuals of *Arcaster typicus* crawl faster than smaller ones, but three other Indo-Pacific species show no relationship between body size and crawling speed (Mueller *et al*., 2011). And larger-bodied *Patiria miniata* actually crawl slower than their smaller relatives (Montgomery and Palmer, 2012). This diversity of size-dependent patterns suggests that unique biomechanical or physiological constraints may exist in the Asteroidea that are not found in other taxa. Clearly, some fundamental questions regarding locomotion in sea stars remain to be answered. For example: why do larger-bodied individuals crawl faster in some species but slower in others?

The primary goals of this thesis were to quantify a) how body shape changes with body size and b) how crawling speed varies with body size, in five species of Northeast Pacific sea star with different adult body sizes, arm shape and arm number. The sun star *Pycnopodia helianthoides* and the striped sun star *Solaster stimpsoni* have size-dependent arm numbers: they predictably add arms as they grow larger (Lambert, 2000). They are also both active predators of other echinoderms (Lambert, 2000; Lamb and Hanby, 2005). In comparison, the five-armed stars *Dermasterias imbricata* and *Patiria miniata*, and the six-armed star *Leptasterias hexactis* have fixed arm numbers: they do not add arms as they grow (Lambert, 2000; Lamb and Hanby, 2005). These fixed-arm species are also predators but tend to favor slower moving prey such as mussels and snails (Menge, 1972; Lambert, 2000). These differences in arm number and ecological role make these five sea star species ideal for studies of body size and locomotion. I also tested the effects of natural versus artificial substrate on crawling performance as previous studies have yielded contradictory results (Ferlin, 1973; Schiebling, 1981; Mueller *et al*., 2011).

1.1 References

Biewener, A. A. (2005). Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665-1676.

Brower, J. C. (2006). Ontogeny of the food-gathering system in Ordovician crinoids. *J. Paleo*. **80**, 430-446.

Ferlin, V. (1973). The mode of dislocation of *Astropecten aranciacus*. *Helgol. Mar. Res.* 24, 151-156.

Herreid II, C. F. and Full, R. J. (1986). Energetics of hermit crabs during locomotion: The cost of carrying a shell. *J. Exp. Biol.* **120**, 297-308.

Hughes, S. J. M., Ruhl, H. A., Hawkins, L. E., Hauton, C., Boorman, B., and Billet, D. S. M. (2011). Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea, and Ophiuroidea. *J. Exp. Biol.* **214**, 2512-2521.

Lamb, A., and Hanby, B. P. (2005). *Marine Life of the Pacific Northwest*. Harbour Publishing: Madeira Park, British Columbia.

Lambert, P. (2000). *Sea Stars of British Columbia, Southeast Alaska, and Puget Sound*. UBC Press: Vancouver, British Columbia.

McKinney, M. L., and Sumrall, C. D. (2011). Ambulacral growth allometry in edrioasteroids: functional surface-volume change in ontogeny and phylogeny. *Lethaia* **44**, 102-108.

Menge, B. A. (1972). Competition for food between two intertidal starfish species and its effects on body size and feeding. *Ecology* **53**, 635- 644.

Montgomery, E. M., and Palmer, A. R. (2012). Effects of body size and shape on locomotion in the bat star (*Patiria miniata*). *Biol. Bull.* **222**, 222-232.

Mueller, B., A. Bos, R. Graf, G., and Gumanao, G. S. (2011). Size-specific locomotion rate and movement pattern of four common Indo-Pacific sea stars (Echinodermata; Asteroidea). *Aquat. Biol.* **12,** 157-164.

Pontzer, H. (2007). Effective limb length and scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* **210**, 1752-1761.

Scheibling, R. E. (1981). Optimal foraging movements of *Oreaster reticulatus* (Echinodermata: Asteroidea). *J. Exp. Mar. Biol. Ecol.* **81,** 173-185.

Schmidt-Nielsen, K. (1975). Scaling in biology: The consequences of size. *J. Exp. Biol.* **194**, 287-308.

Vogel, S. (2003). *Comparative Biomechanics: Life's Physical World*. Princeton University Press, New Jersey, USA.

Vogel, S. (2008). Modes and scaling in aquatic locomotion. *Int. Comp. Biol.* **48**, 702-712.

Vollmer, S. V. and Edmunds, P. J. (2000). Allometric scaling in small colonies of the scleractinian coral *Siderastrea siderea*. *Biol. Bull.* **199**, 21-28.

Chapter 2

Size-dependence of body shape in Northeast Pacific sea stars

2.1 Introduction

Closely related species can share a similar body plan but still can differ greatly in growth pattern and body shape (Schmidt-Nielsen, 1975). How body shape varies with size can provide clues about physiological and biomechanical constraints experienced by animals or about the functional significance of particular structures (Biewener, 2005; Vogel, 2008). Body mass is typically considered a useful metric of body ‘size’ because it avoids potential pitfalls associated with linear measures of body size (Schmidt-Nielsen, 1975; West *et al.*, 1997). Nonetheless, linear measurements are quite valuable for describing, and helping to interpret, shape variation both within and among species (Schmidt-Nielsen, 1975; Pontzer, 2007). For example, the length of forelimb long bones and hip height are considered fundamental lengths in running mammals (Schmidt-Nielsen, 1975; Biewener, 2005; Pontzer, 2007). The identities of such fundamental trait metrics may vary greatly among species and enable predictions to be made regarding the benefits or costs of particular traits or shapes (Schmidt-Nielsen, 1975; Sebens, 1987).

The relationship between body mass and linear size parameters also has direct consequences for the locomotive and energetic abilities of organisms (Schmidt-Nielsen, 1975; Vogel, 2003). While features such as forelimb length and hip height are crucial to understanding running speeds in terrestrial mammals, the diameter of their bones (and therefore cross-sectional area) provides structural support that prevents the animals from collapsing under the force of gravity (Schmidt-Nielsen, 1975; Vogel, 2003). Because mass increases more rapidly than cross-sectional area with increasing body size, the cross sectional area of mammalian bones scales positively allometrically with body mass (Schmidt-Nielsen, 1975). However, larger species also exhibit modified limb posture and movement behaviour, as bone strength remains the same across a great size range of mammals (Biewener, 1982). Allometry is also common in food gathering structures such the food grooves (ambulacral grooves) of two classes of fossil echinoderms (Brower, 2006; McKinney and Sumrall, 2011). Larger-bodied crinoids and edrioasteroids both show positive allometry in the width and area of their ambulacral grooves relative to increased body mass/ volume (Brower, 2006; McKinney and Sumrall, 2011), similar to the increase in feeding crown area seen in larger-bodied extant anemones (McKinney and Sumrall, 2011).

The class Asteroidea (sea stars) is a fascinating group of living echinoderms to examine body size and shape variation both within and among species because of their great diversity of form. Sea stars all share some basic body features, such as secondary radial symmetry, an aboral surface on the “dorsal” side that lacks locomotory appendages, and a “ventral” side with many hydraulically-powered podia in rows that radiate down the length of each arm (Lawrence, 1987; Lambert, 2000). Despite these shared features, sea stars occupy a diverse array of habitats and ecological roles and exhibit considerable variation in arm number (deviating from the typical five-armed form) and body shape (Lambert, 2000). Remarkably, few studies have examined how body shape changes with size in sea stars and what impact this might have on even such basic phenomena as locomotion and energetics (but see Hughes *et al.*, 2011; Montgomery and Palmer, 2012). Given the immense variation in body form among sea stars, two fundamental questions arise: what effects do a) arm number and b) overall body shape have on scaling relationships?

I studied the relationship between body size and shape in five common sea stars found in the Pacific Northwest: the sun star *Pycnopodia helianthoides*, the striped sun star *Solaster dawsoni*, the six-armed star *Leptasterias hexactis*, the leather star *Dermasterias imbricata*, and the bat star *Patiria miniata*. These species were selected because of their ecological significance (Mayo and Mackie, 1976; Van Veldhuizen and Oakes, 1981) and the diversity of body forms they represent: the sun stars *P. helianthoides* and *S. stimpsoni* have many arms and arm number increases with increasing body size, whereas *D. imbricata, P. miniata,* and *L. hexactis* all have fewer arms (typically five or six) and do not add arms as they grow (Lambert, 2000). Although *D. imbricata,* and *P. miniata* typically have five arms, arm number may range from four to nine. However, this variation is thought to result from developmental errors or injury and not from programmed addition like the sun stars *P. helianthoides* and *S. stimpsoni*

(Hotchkiss, 2000; Montgomery and Palmer, 2012). Scaling data for *P. miniata* were obtained and re-analyzed from Montgomery and Palmer (2012).

2.2 Methods

2.2.1 Specimen and data collection

Pycnopodia helianthoides (Stimpson, 1862; Order Forcipulatida, Lambert, 2000), and *Dermasterias imbricata* (Sladen, 1889; Order Valvatida, Lambert, 2000) were hand-collected from Grappler Inlet, near Bamfield, British Columbia (48°49’51”N, 125°06’57”W). *Solaster stimpsoni* (Stimpson, 1850; Order Velatida, Lambert, 2000) were collected by SCUBA from Bamfield Inlet and Trevor Channel, British Columbia. I avoided collecting very young juveniles of each species as they may have different scaling relations. Juveniles often have different colours, habitats, and arm numbers than adults (Birkeland *et al.*, 1971; Hotchkiss, 2000). For instance: young *S. dawsoni* and *P. helianthoides* have only 6 arms, have oral disk diameters around 2 mm, and often can be found on/in tube-worm tubes (Birkeland *et al.*, 1971; Hotchkiss, 2000). *P. helianthoides*, *D. imbricata*, and *S. stimpsoni* were held during testing in flow-through seawater tables at the Bamfield Marine Sciences Center, Bamfield, British Columbia. Animals were left undisturbed for three days prior to testing to acclimatize to laboratory conditions.

Leptasterias hexactis (Fisher, 1930; Order Forcipulatida, Lambert, 2000) were hand-collected from the foreshore region of Friday Harbor Laboratories, Friday

Harbor, Washington (48°32’44”N, 123°00’47”W). Similar to the above species, only adults were collected. *L. hexactis* reach maturity with the growth of their sixth arm at approximately 2g wet mass (Menge, 1975). *L. hexactis* were held in flow-through seawater tables at the Friday Harbor Laboratories. As above, animals were acclimated to laboratory conditions for three days before testing. Given the tendency of *L. hexactis* to seek out dark places, opaque containers were provided in the seawater tables to prevent undue stress before testing (Menge, B, OSU, pers. comm., 2012).

Data for *Patiria miniata* (Sladen, 1889; Order Valvatida, Lambert, 2000) were obtained from a previous study: Montgomery and Palmer (2012). This prior work was also done at the Bamfield Marine Sciences Center under similar conditions experienced by *P. helianthoides*, *D. imbricata*, and *S. stimpsoni* in the current study.

2.2.2 Measures of size and shape

The immense variation in body form both among and within sea star species makes comparable measurements of body ‘size’ difficult. Here I used similar measures to Montgomery and Palmer (2012) but with modifications to allow for natural sea star behaviours (i.e., arm curling and partial rotation). Certain species also have the ability to increase their arm length by up to 30% after a crawling event (e.g., *Patiria miniata,* pers. obs., 2011). Because of this increase, I took digital images during crawling and used these to measure size instead of 5 min after completion as done previously (Montgomery and Palmer, 2012). *ImageJ* software was used for this image analysis (Rasband, W. S., U. S. National Institutes of Health, Bethesda, MD, http://rsb.info.nih.gov/ij/, 1997–2010).

To describe basic sea star shape I measured three linear dimensions: arm length, arm width, and oral disk radius (Fig. 2.1). I measured arm length from the tip of each arm to the center of the base between the arm pits (Fig. 2.1). Average arm length was then taken to be the average of only straight arms, as curved arms could not be measured accurately. Arm width was measured across the base of each arm and averaged for each individual (Fig. 2.1). Oral disk radius was calculated from the oral disk areas measured in *ImageJ* approximating the oral disk as a circle. A single repeat measurement was performed on the same image for arm length, arm width, and oral disk area to test the accuracy of landmark placement (10 individuals per species). The percent error for all measurements was below 6% (mean = 4.4%; Table 2.1). Wet mass was obtained by removing individuals from seawater, dabbing them on a stack of paper towels and immediately placing them on a tared balance (as per Montgomery and Palmer, 2012). Any excess water left on the weighing tray was subtracted from the total but this was usually less than 5g.

2.2.3 Scaling analysis

Prior to scaling analysis, all data were log10 transformed. Simple linear regressions were computed for each pair of scaling variables using *R* (64-bit client for Macintosh, R Development Core Team, 2008). Least squares (LS) slopes were converted to reduced major axis (RMA) slopes by dividing the LS slope by the correlation coefficient to correct scaling coefficients for the bias in LS slopes that arises when uncontrolled (error) variation is present in both x and y variables (Smith, 2009; Montgomery and Palmer, 2012). Expected values for scaling coefficients were the expected exponent of the power function relating un-transformed values of y to x for each pair of measurements.

2.2.4 Statistical methods

All statistical tests were conducted using *R* (64-bit client for Macintosh, R Development Core Team, 2008) and GraphPad Online (GraphPad Statistical Software Inc., 2013). To test the statistical significance of allometric coefficients, calculated scaling coefficients were compared to expected values using a Student's one-sample T-test. All statistical tests for significance of allometry were two-tailed. Sequential Bonferroni corrections for multiple tests were used per species (4 tests) to reduce the likelihood of false positives resulting from multiple Student's T-tests (Holm, 1979).

2.3 Results

No evidence of allometry was observed in *Pycnopodia helianthoides*. Arm width (Fig. 2.2A, Table 2.2, $p = 0.245$) and disk radius (Fig. 2.2B, Table 2.2, $p = 0.839$) both increased isometrically with increasing arm length. Relative to wet mass, oral disk radius and arm length also increased isometrically (Fig. 2.2C-D, Table 2.2, p = 0.882, p = 0.811 respectively).

No evidence of allometry was observed in *Solaster stimpsoni* either. Both arm width (Fig. 2.3A, Table 2.3, p = 0.219) and disk radius (Fig. 2.3B, Table 2.3, p = 0.276) increased isometrically relative to arm length. Oral disk radius and arm length also varied isometrically relative to wet mass (Fig. 2.3C-D, Table 2.3, p = 0.056, p = 0.386 respectively).

Dermasterias imbricata exhibited weak allometry in all traits examined. Both arm width (Fig. 2.4A, Table 2.3, p = 0.088) and disk radius (Fig. 2.4B, Table 2.3, p = 0.018) exhibited positive allometry relative to arm length. *D. imbricata* also had wider oral disk radii relative to wet mass (Fig. 2.4C, Table 2.4, p = 0.056), and arm length was proportionally shorter for heavier *D. imbricata* (Fig. 2.4D, Table 2.4, p = 0.086). However, none of these relations remained significant statistically after a Sequential Bonferroni correction for multiple tests was applied (4 tests; Holm 1979).

Patiria miniata also showed no evidence of allometric variation. Oral disk radius and arm width increased isometrically relative to arm length (Fig. 2.5A-B, Table 2.5, p = 0.770, p = 0.983 respectively), as did oral disk radius and arm length relative to wet mass (Fig. 2.5C-D, Table 2.5, p = 0.224, p = 0.380 respectively).

Several strong allometries were observed in *Leptasterias hexactis.* Arm width and oral disk radius exhibited strong negatively allometry with respect to arm length (Fig. 2.6A-B, Table 2.6, p = 0.001, p = 0.003 respectively). Although oral disk radius varied isometrically with wet mass (Fig. 2.6C, Table 2.6, p = 0.798), heavier individuals had proportionally longer arms than predicted from isometry (Fig. 2.6D, Table 2.6, p = 0.002). All of these relations remained significant after Sequential Bonferroni correction for multiple tests (4 tests; Holm 1979).

2.4 Discussion

The Asteroidea is a diverse group that exhibits a variety of body shapes while sharing common elements of arm form and structure. Surprisingly, only one species, the six-armed star *Leptasterias hexactis* showed statistically significant allometries. This was particularly puzzling given the diversity of arm numbers and body shapes (arm aspect ratios [arm length / arm width]) sampled in this study and many previous observations that isometric growth is rare in biology (Schmidt-Nielsen, 1975; Vogel, 2003). These results also contrast with an earlier study where 50% of the tests for allometry on five and six-armed *Patiria miniata* revealed significant differences in shape at larger body sizes (Montgomery and Palmer, 2012). However, this is likely because different measures of size (e.g., total oral surface area and ambulacral groove area) were included in the analysis (Montgomery and Palmer, 2012).

The sun sea stars *Pycnopodia helianthoides* and *Solaster stimpsoni* add arms as they grow (Hotchkiss, 2000; Lambert, 2000). *P. helianthoides* typically have 10-15 arms when small and can have up to 24 when they are full sized (Lambert, 2000; pers. obs.). *S. stimpsoni* range from 6-8 arms to a maximum of 12 as adults (Lambert, 2000; pers. obs.). Despite these anatomical differences, oral disk radius increased isometrically with respect to arm length in both species (Table 2.7). This seems unusual at first given the large number of arms added by *P. helianthoides.* However marked differences in arm positioning and the angles among arm tips can be seen between small and large *P. helianthoides* and between *P. helianthoides* and *S. stimpsoni* (Table 2.7). A greater proportion of arms touch at the base in larger *P. helianthoides* relative to smaller individuals of this species (Table 2.7). In comparison, arms are much slenderer in *S. stimpsoni* and do not converge as much at the base (Table 2.7). These observations are likely the result of geometry similar to that of spokes on a bicycle wheel - increasing the number of spokes decreases the angle between them at the tip and makes the basal regions closer together. In the intertidal, counting the arms of a large *P. helianthoides* can be quite challenging as they often overlap and can be found pressed together from the base to the arm tip (pers. obs., 2012). The ratio between oral disk radius and arm length is visibly different in these two sun-star species (Table 2.7, Fig. 2.7). Since *P. helianthoides* has more oral disk radius (relative to arm length) to begin with, there may already be enough space to double in arm number as an adult. Given the fast crawling speeds reported for *P. helianthoides,* the potential constraints to locomotion associated with arms crowding each other may be overcome by the addition of so many more tube feet with the addition of arms (Montgomery and Palmer, 2012).

Scaling of arm shape (arm length and arm width) also did not vary between the species with variable arm numbers. Both *Pycnopodia helianthoides* and *Solaster stimpsoni* exhibited isometric relationships between wet mass and arm length (Table 2.7). Arm width also varied isometrically with arm length in these two species. These isometries in arm shape may have consequences for locomotion. Arm width controls the width of the ambulacral groove area in sea stars - the region through which the hydraulic tube feet extend (Lawrence, 1987). Despite their importance to daily activities such as feeding and locomotion, little is known about scaling in the size or number of tube feet as sea stars grow larger (Montgomery and Palmer, 2012). Even if arm width grows isometrically with arm length, the rowing motion of the podia during crawling could still be impacted if tube feet do not also scale isometrically (Lawrence, 1987; Montgomery and Palmer, 2012). *Patiria miniata,* a species with a very narrow ambulacral groove, exhibits slower crawling speeds at larger body sizes (Montgomery and Palmer, 2012). However this is not true for *P. helianthoides* - the fastest predatory sea star in the northeastern Pacific (Kjerschow-Agersborg, 1922). In *P. helianthoides*, the addition of arms during growth, and therefore a corresponding increase in the numbers of podia, may be enough to offset any potential locomotory constraints imposed by isometric growth in arm width. The ambulacral groove area (region where tube feet reside) is also relatively much larger in *P. helianthoides* than *S. stimpsoni* (Fig. 2.7A). Although crawling speeds of *S. stimpsoni* are unknown, *P. helianthoides* may be more effective at crawling since the total number of tube feet is proportionally greater at larger body sizes, because of greater total ambulacral area and larger arm numbers (Fig. 2.7B).

The five-armed stars *Dermasterias imbricata* and *Patiria miniata* exhibited similar growth patterns to each other and to the species with size-dependent arm number (Table. 2.7). Any difference between *D. imbricata* and *P. miniata*, though, was unexpected given the similar body shape of these two species (relatively short, blunt arms with “webbing” between them, Table. 2.7) and the shared presence of relatively narrow ambulacral grooves (Fig. 2.7C-D). *D. imbricata* had a slightly wider oral disk radius relative to arm length at larger body sizes (Table 2.7). However, longer-armed individuals of this five-armed species had isometrically wider arms than their shorter-armed counterparts - similar to the two size-dependent arm-number species (Table 2.7). Any increase in oral disk radius (and likely body volume) may come at a locomotive / motility cost to *D. imbricata* due to the increased body mass per unit area of tube feet. A larger oral disk radius might also provide some benefits to *D. imbricata* such as increased internal body volume for gonads or increased aboral surface for respiration (Lambert, 2000; Levitan, 1995; McKinney and Sumrall, 2011). But given the low statistical significance, more data will be needed to further explore the benefits and/or costs associated with size relations in *D. imbricata.*

In contrast to *Dermasterias imbricata*, oral disk radius and arm width varied isometrically with arm length in *Patiria miniata* (Table 2.7). Arm length and oral disk radius also varied isometrically with wet mass (Table 2.7). This was curious given that all relations in *Pycnopodia helianthoides* and *Solaster stimpsoni* were isometric as well. There are no overall similarities in shape or ecological role between the species with size-dependent arm number and *P. miniata* (Table 2.7; Van Veldhuizen and Oakes, 1981). Isometric growth in the oral disk radius and arm width (relative to arm length) may increase the total body mass per unit area of tube feet in *P. miniata* due to the narrow ambulacral grooves and the negative allometry in oral surface area relative to arm length reported previously in this species (Fig. 2.7C, Lawrence, 1987; Montgomery and Palmer, 2012). There was also no proportional increase in arm length (relative to body mass) in *P. miniata* to potentially offset this biomechanical challenge and by adding proportionally more podia at larger body masses (Table 2.7).

Unlike the sea stars with size-dependent arm number, *Dermasterias imbricata* and *Patiria miniata* maintain the same fundamental arm number throughout their entire post-metamorphic lives. Regeneration errors may increase arm number in these species but such mistakes likely do not affect survival or locomotion of *P. miniata*: five and six-armed individuals crawled at the same velocity relative to body size (Hotchkiss, 2000; Montgomery and Palmer, 2012). Although many five-armed sea stars are active predators, they often preferentially feed on sessile prey such as barnacles, mussels, and anemones (Lambert, 2000; Lamb and

Hanby, 2005). As a result, selection for fast crawling speed may be less important than in *Pycnopodia helianthoides* or *Solaster stimpsoni* (Kjerschow-Agersborg, 1922). In *P. miniata*, for example, larger individuals actually crawl more slowly than smaller ones (Montgomery and Palmer, 2012). Despite their differences in body size scaling, I would still expect a similar decrease in crawling speed with increasing size in *D. imbricata* due to their similar ecological role, relatively narrow ambulacral groove areas, and overall body shape (Lambert, 2000) (see Chapter 3).

In contrast to size-dependent or five-armed sea-star species, the six-armed star *Leptasterias hexactis* exhibited strikingly different scaling relations. Most notably, longer-armed *L. hexactis* had relatively narrower arm widths and smaller oral disk radii than smaller individuals, which can clearly be seen when images of large and small individuals are scaled to the same size (Table 2.7). In contrast, *L. hexactis* had proportionally longer arms at larger body masses (Table 2.7). Reduced arm widths (relative to arm length) in *L. hexactis* may result in a similar decrease in locomotive performance seen at larger body sizes in *P. miniata* but the effect could be reduced in this species since the relative ambulacral area of *L. hexactis* is greater than both five- and six-armed *P. miniata* (Fig. 2.7). In comparison, the proportional increase in arm length in *L. hexactis* (and presumably proportional increase in the number of tube feet) relative to body mass is a unique feature not seen in the other four species studied here. It is not clear if and how greatly this may affect locomotion in this species given the proportional reduction in arm width at longer arm lengths (Table 2.7) (but see Chapter 3).

Like *Dermasterias imbricata* and *Patiria miniata*, *Leptasterias hexactis* has the same number of arms following metamorphosis (six in this case) and does not add more as it grows. *L. hexactis* also feeds primarily on sessile or slow-moving prey such as barnacles or snails (Menge, 1972). This suggests that adult body form may also be less influenced by a need for speed since their prey are slower moving – a similar ecological role to the five-armed species (Lambert, 2000). However unlike the five-armed *D. imbricata* and *P. miniata*, *L. hexactis* broods embryos instead of broadcast spawning into the plankton (Strathmann and Strathmann, 1982). A proportionally smaller oral disk radius at larger body size might seem disadvantageous to a parent sea star where a larger oral-disk area might permit them to hold more offspring (Strathmann and Strathmann, 1982). But the proportional increase in arm length (relative to mass) may help overcome this constraint from both a biomechanical and geometric perspective. *L. hexactis* commonly occur in exposed intertidal locations with strong wave forces up to 15 m/s (Menge, 1972; Vogel, 2003). More podia per unit projected area (area in the direction of flow) may reduce risk of dislodgement under such conditions. Since tube feet can only be added longitudinally in a sea star with fixed arm number, increasing arm length is the only way to compensate (Lawrence, 1987). This is certainly true in the five-armed star *Pisaster ochraceus* that have relatively longer arms in exposed conditions to aid in attachment (Hayne and Palmer, in press). Longer arms may also provide *L. hexactis* an extended brooding space around the base of the arms with no relative loss of attachment strength (Strathmann and Strathmann, 1982).

Caution must be applied when interpreting the significance of measured allometries in scaling analysis such as these. First, four tests were done for each of five species, so the probability of false positives goes up. Second, sample sizes were small and size ranges were limited for some species (e.g., 80-170g mass range in *Dermasterias imbricata*, and 32-55mm arm length range in *Patiria miniata*). Nonetheless, the fact that allometries were significant (or nearly significant) for traits even with relatively small sample size, suggests that these would be more significant if based on larger samples sizes and size ranges. The four size parameters I used here were chosen to describe the components of sea star shape previously reported to be fundamental to biological activities such as: locomotion, reproduction, and feeding (Lawrence, 1987; Levitan, 1995; Mueller *et al*., 2011; Montgomery and Palmer, 2012). As a result, any allometries among these critical features should be considered to have potential implications for sea star ecology.

Taken together, these data reveal sea stars to be a diverse group of animals often with distinct, species-specific growth patterns despite similarities in overall body form (e.g., arm number, general shape) and ecological role. Within each species, scaling relationships provide valuable insight and predictions as to the potential biomechanical and physiological constraints experienced during everyday actions such as locomotion. A general relationship exists between body size / shape and speed of locomotion in many taxa (Schmidt-Nielsen, 1975; Heglund and Taylor, 1988). As a general trend, larger individuals within species tend to move faster independent of mode of locomotion (Schmidt-Nielsen, 1975; Heglund and Taylor, 1988). But given the complexity and diversity of size in sea stars presented here one fundamental question remains: do larger sea stars move faster?

2.5 References

Biewener, A. A. (1982). Bone strength in small mammals and bipedal birds - do safety factors change with body size. *J. Exp. Biol.* **98**, 289-301.

Biewener, A. A. (2005). Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665-1676.

Birkeland, C., Fu-Shiang, C., and Strathmann, R. R. (1971). Development, substratum selection, delay of metamorphosis and growth in the seastar, *Mediaster aequalis* Stimpson. *Biol. Bull.* **141**, 99-108.

Brower, J. C. (2006). Ontogeny of the food-gathering system in Ordovician crinoids. *J. Paleo*. **80**, 430-446.

Heglund, N. C., and Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: How do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Statist.* **6**, 65-70.

Hotchkiss, F. H. C. (2000). On the number of rays in starfish. *Amer. Zool*. **40**, 340-354.

Hughes, S. J. M., Ruhl, H. A., Hawkins, L. E., Hauton, C., Boorman, B., and Billet, D. S. M. (2011). Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea, and Ophiuroidea. *J. Exp. Biol.* **214**, 2512-2521.

Kjerschow-Agersborg, H. P. (1922). The relation of the madreporite to the physiological anterior end in the twenty-rayed starfish, *Pycnopodia helianthoides* (Stimpson). *Biol. Bull.* **42**, 202-215.

Lamb, A., and Hanby, B. P. (2005). *Marine Life of the Pacific Northwest*. Harbour Publishing: Madeira Park, British Columbia.

Lambert, P. (2000). *Sea Stars of British Columbia, Southeast Alaska, and Puget Sound*. UBC Press: Vancouver, British Columbia.

Lawrence, J. M. (1987). *A Functional Biology of Echinoderms*. Croom Helm, London.

Mayo, P and Mackie, A. M. (1976). Studies of avoidance reactions in several species of predatory British seastars (Echinodermata: Asteroidea). *Mar. Biol.* **38**, 41-49.

McKinney, M. L., and Sumrall, C. D. (2011). Ambulacral growth allometry in edrioasteroids: functional surface-volume change in ontogeny and phylogeny. *Lethaia* **44**, 102-108.

Menge, B. A. (1972). Competition for food between two intertidal starfish species and its effects on body size and feeding. *Ecology* **53**, 635- 644.

Menge, B. A. (1975). Brook or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.* **31**, 87-100.

Montgomery, E. M., and Palmer, A. R. (2012). Effects of body size and shape on locomotion in the bat star (*Patiria miniata*). *Biol. Bull.* **222**, 222-232.

Pontzer, H. (2007). Effective limb length and scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* **210**, 1752-1761.

Schmidt-Nielsen, K. (1975). Scaling in biology: The consequences of size. *J. Exp. Biol.* **194**, 287-308.

Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Ann. Rev. Ecol. Syst.* **18**, 371-407.

Smith, R. J. (2009). Use and misuse of the reduce major axis for line-fitting. *Amer. J. Phys. Anthro*. **170**, 476-486.

Strathmann, R. R., and Strathmann, M. F. (1982). The relationship between adult size and brooding in marine invertebrates. *Amer. Nat.* **199**, 91-101.

Van Veldhuizen, H. D., and Oakes, V. J. (1981). Behavioural responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni*. *Oecologia* **48**, 214-220.

Vogel, S. (2003). *Comparative Biomechanics: Life's Physical World*. Princeton University Press, New Jersey, USA.

Vogel, S. (2008). Models and scaling in aquatic locomotion. *Int. Comp. Biol.* **48**, 702-712.

West, B. G, Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122-126.

2.6 Figures and Tables

Table 2.1. Average percent error (%) of sea star linear dimensions

Species	*P. helianthoides*	*S. stimpsoni*	*D. imbricata*	*P. miniata*	*L. hexactis*
Arm length (mm)	4.2	5.1	3.7	4.7	3.5
Arm width (mm)	3.9	4.6	3.5	4.2	4.7
Oral disk radius (mm)	5.0	5.8	3.7	4.9	4.6

Table 2.2. Scaling relations in *Pycnopodia helianthoides*

Tested parameters[a] (y vs. x)	Linear regression model (± SE)[b]	Correlation coefficient (R)	Corrected scaling coefficient[c]	Expected scaling coefficient	Significance of scaling
AW vs. AL (Fig. 2.2A)	**y** = 0.81(± 0.100)**x** – 0.25, $p < 0.001$	0.919	0.88	1.00	$p = 0.245$
DR vs. AL (Fig. 2.2B)	**y** = 0.94(± 0.115)**x** – 0.08, $p < 0.001$	0.921	1.02	1.00	$p = 0.839$
DR vs. M (Fig. 2.2C)	**y** = 0.32(± 0.017)**x** + 0.81, $p < 0.001$	0.984	0.33	0.33	$p = 0.882$
AL vs. M (Fig. 2.2D)	**y** = 0.29(± 0.042)**x** + 1.04, $p < 0.001$	0.893	0.32	0.33	$p = 0.811$

[a] Parameter abbreviations: AW (arm width [mm]), AL (arm length [mm]), DR (oral disk radius [mm]), M (wet body mass [g])

[b] N= 14 for all models; analyses conducted on $\log_{10}$ transformed data

[c] Reduced major axis (RMA) slopes

Table 2.3. Scaling relations in *Solaster stimpsoni*

Tested parameters[a] (y vs. x)	Linear regression model (± SE)[b]	Correlation coefficient (R)	Corrected scaling coefficient[c]	Expected scaling coefficient	Significance of scaling
AW vs. AL **(**Fig. 2.3A)	$\mathbf{y} = 1.00(\pm 0.194)\mathbf{x} - 0.69$, $p < 0.001$	0.798	1.25	1.00	$p = 0.219$
DR vs. AL **(**Fig. 2.3B)	$\mathbf{y} = 0.64(\pm 0.141)\mathbf{x} + 0.31$, $p < 0.001$	0.760	0.84	1.00	$p = 0.276$
DR vs. M **(**Fig. 2.3C)	$\mathbf{y} = 0.19(\pm 0.041)\mathbf{x} + 1.21$, $p < 0.001$	0.757	0.24	0.33	$p = 0.056$
AL vs. M **(**Fig. 2.3D)	$\mathbf{y} = 0.24(\pm 0.043)\mathbf{x} + 1.54$, $p < 0.001$	0.817	0.29	0.33	$p = 0.386$

[a] Parameter abbreviations as defined in Table 2.2 legend

[b] N= 17 for all models; analyses conducted on $\log_{10}$ transformed data

[c] Reduced major axis (RMA) slopes

Table 2.4. Scaling relations in *Dermasterias imbricata*

Tested parameters[a] (y vs. x)	Linear regression model (± SE)[b]	Correlation coefficient (R)	Corrected scaling coefficient[c]	Expected scaling coefficient	Significance of scaling
AW vs. AL (Fig. 2.4A)	$\mathbf{y} = 1.20(\pm 0.214)\mathbf{x} - 0.55$, $p < 0.001$	0.862	1.40	1.00	$p = 0.088$
DR vs. AL (Fig. 2.4B)	$\mathbf{y} = 1.45(\pm 0.236)\mathbf{x} - 1.02$, $p < 0.001$	0.881	1.65	1.00	$p = 0.018$
DR vs. M (Fig. 2.4C)	$\mathbf{y} = 0.40(\pm 0.049)\mathbf{x} + 0.63$, $p < 0.001$	0.928	0.43	0.33	$p = 0.056$
AL vs. M (Fig. 2.4D)	$\mathbf{y} = 0.23(\pm 0.036)\mathbf{x} + 1.23$, $p < 0.001$	0.891	0.26	0.33	$p = 0.086$

[a] Parameter abbreviations as defined in Table 2.2 legend

[b] N= 13 for all models; analyses conducted on $\log_{10}$ transformed data

[c] Reduced major axis (RMA) slopes

Table 2.5. Scaling relations in *Patiria miniata*

Tested parameters[a] (y vs. x)	Linear regression model (± SE)[b]	Correlation coefficient (R)	Corrected scaling coefficient[c]	Expected scaling coefficient	Significance of scaling
AW vs. AL (Fig. 2.5A)	$\mathbf{y} = 0.89(\pm 0.119)\mathbf{x} + 0.20$, $p < 0.001$	0.920	0.96	1.00	$p = 0.770$
DR vs. AL (Fig. 2.5B)	$\mathbf{y} = 0.89(\pm 0.140)\mathbf{x} + 0.14$, $p < 0.001$	0.896	1.00	1.00	$p = 0.983$
DR vs. M (Fig. 2.5C)	$\mathbf{y} = 0.36(\pm 0.057)\mathbf{x} + 0.83$, $p < 0.001$	0.894	0.40	0.33	$p = 0.224$
AL vs. M (Fig. 2.5D)	$\mathbf{y} = 0.31(\pm 0.082)\mathbf{x} + 0.96$, $p < 0.01$	0.770	0.40	0.33	$p = 0.380$

[a] Parameter abbreviations as defined in Table 2.2 legend

[b] N= 12 for all models; analyses conducted on $\log_{10}$ transformed data

[c] Reduced major axis (RMA) slopes

Table 2.6. Scaling relations in *Leptasterias hexactis*

Tested parameters[a] (y vs. x)	**Linear regression model (± SE)[b]**	**Correlation coefficient (R)**	**Corrected scaling coefficient[c]**	**Expected scaling coefficient**	**Significance of scaling**
AW vs. AL (Fig. 2.6A)	**y** = 0.44(± 0.102)**x** + 0.35, $p < 0.001$	0.712	0.62	1.00	$p = 0.001$
DR vs. AL (Fig. 2.6B)	**y** = 0.44(± 0.108)**x** + 0.37, $p < 0.001$	0.697	0.64	1.00	$p = 0.003$
DR vs. M (Fig. 2.6C)	**y** = 0.30(± 0.036)**x** + 0.72, $p < 0.001$	0.893	0.34	0.33	$p = 0.798$
AL vs. M (Fig. 2.6D)	**y** = 0.47(± 0.057)**x** + 0.92, $p < 0.001$	0.891	0.53	0.33	$p = 0.002$

[a] Parameter abbreviations as defined in Table 2.2 legend

[b] N= 20 for all models; analyses conducted on $\log_{10}$ transformed data

[c] Reduced major axis (RMA) slopes

Table 2.7. Summary of scaling relations in Northeast Pacific sea stars

Species	*P. helianthoides*	*S. stimpsoni*	*D. imbricata*	*P miniata*	*L. hexactis*
AW vs. AL[a]	○	○	○	○	🔴🔴🔴*
DR vs. AL	○	○	🟢	○	🔴🔴*
DR vs. M	○	○	○	○	○
AL vs. M	○	○	○	○	🟢🟢*
Average aspect ratio[b]	3.6	5.1	1.6	1.0	2.1
Arm number	16-24	8-12	5†	5†	6
Small individual[c]					
Large individual					

[a] Parameter abbreviations: AW (arm width [mm]), AL (arm length [mm]), DR (oral disk radius [mm]), M (wet body mass [g])
[b] Aspect ratio = arm length / arm width
[c] All sea star images adjusted to the same arm tip diameter to permit easier visualization of shape differences between small and large stars. Actual sizes of individuals in these images were [small/large]: *P. helianthoides* [211g/1.7kg], *S. stimpsoni* [480g/736g], *D. imbricata* [55g/150g], *P. miniata* [104g/302g], and *L. hexactis* [1.0g/8.9g].

Colours indicate scaling relationships – refer to Tables 2.2-2.6 for details. Red = Negative Allometry, Green = Positive Allometry, Open = Isometry
• = $p \leq 0.05$, •• = $p \leq 0.01$, ••• = $p \leq 0.001$, ° = no statistical significance
† = arm number in natural populations ranges from 4 -9 free of body size
* allometry still significant after sequential Bonferroni correction for multiple tests (4 tests per species).

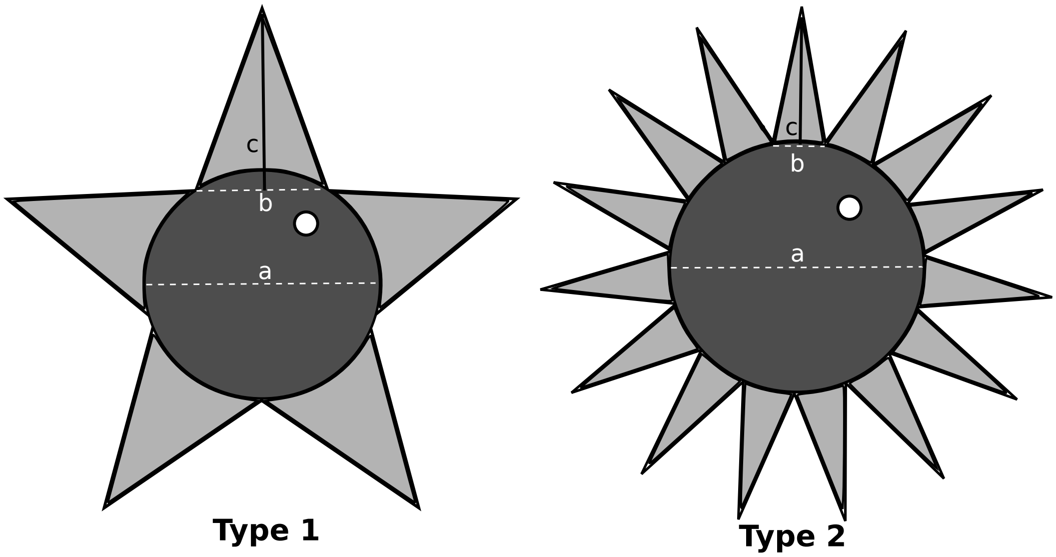

Fig. 2.1. Linear measurements used to describe shape in sea star species with fixed adult arm number (type 1) and species with size-specific arm number (type 2). Oral disk radius (defined as 0.5 the length of a) was derived from the oral disk area (dark grey shading). Arm width (b) was measured between two arm bases. Arm length (c) was measured from the center of the base of each arm to the tip. ◦ = madreporite

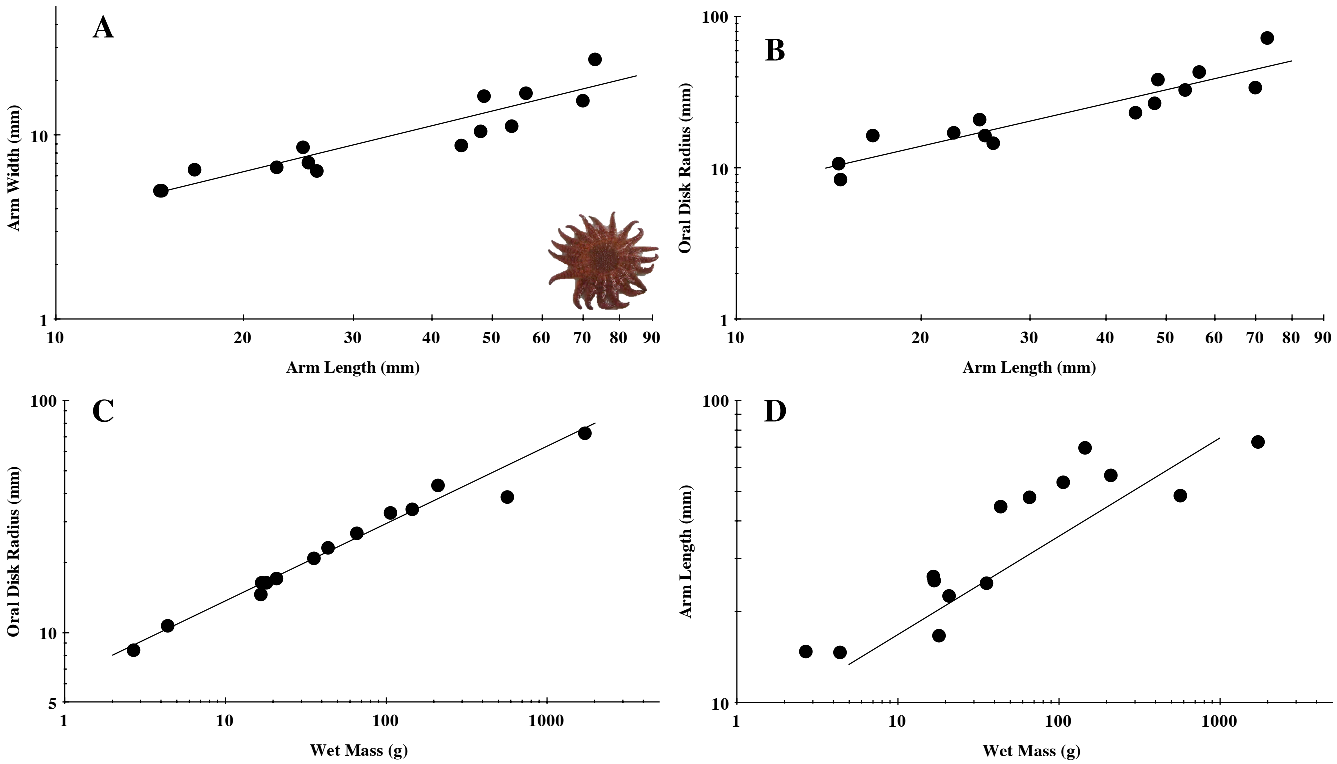

Figure 2.2A-D. Scaling relations in the sun star *Pycnopodia helianthoides*. Linear regressions were performed on $\log_{10}$-$\log_{10}$ transformed size data for scaling analysis. See Table 2.2 for scaling statistics and tests.

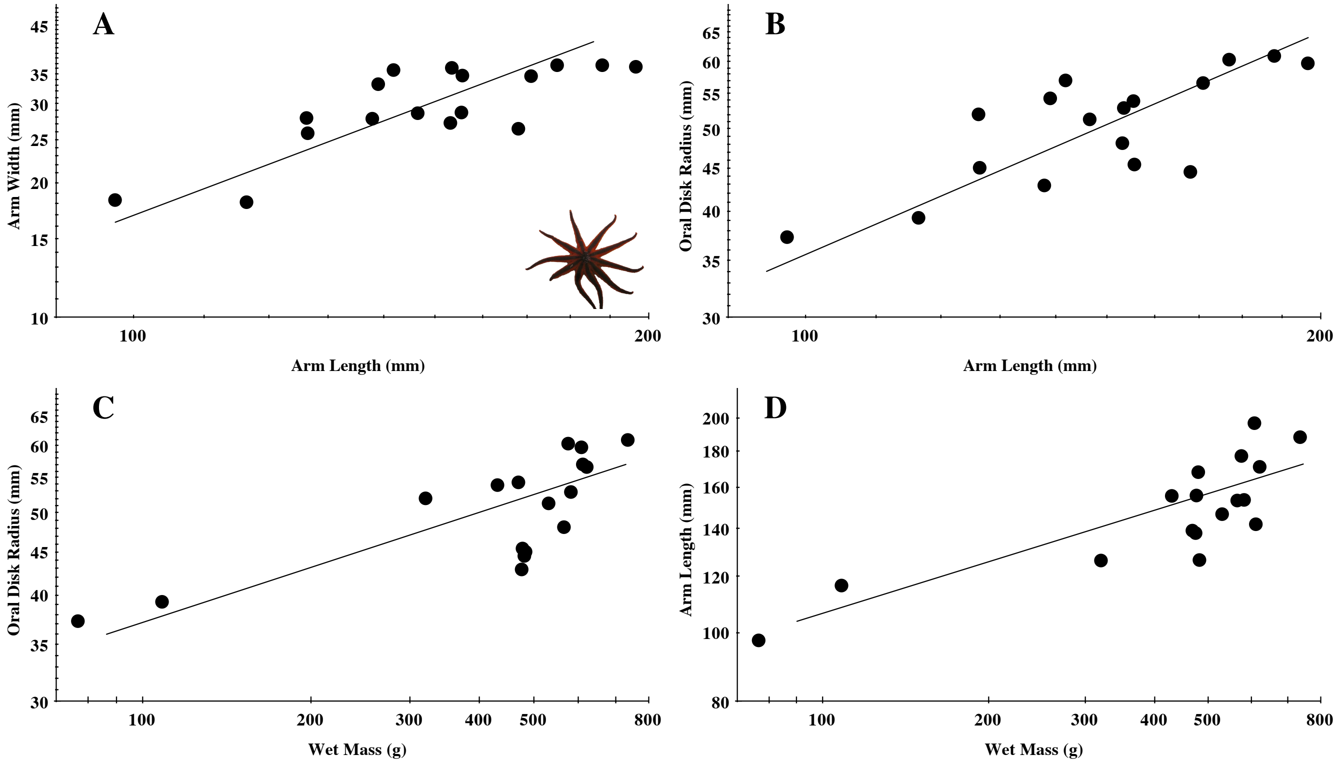

Figure 2.3A-D. Scaling relations in the sun star *Solaster stimpsoni*. Linear regressions were performed on $\log_{10}$-$\log_{10}$ transformed size data for scaling analysis. See Table 2.3 for scaling statistics and tests.

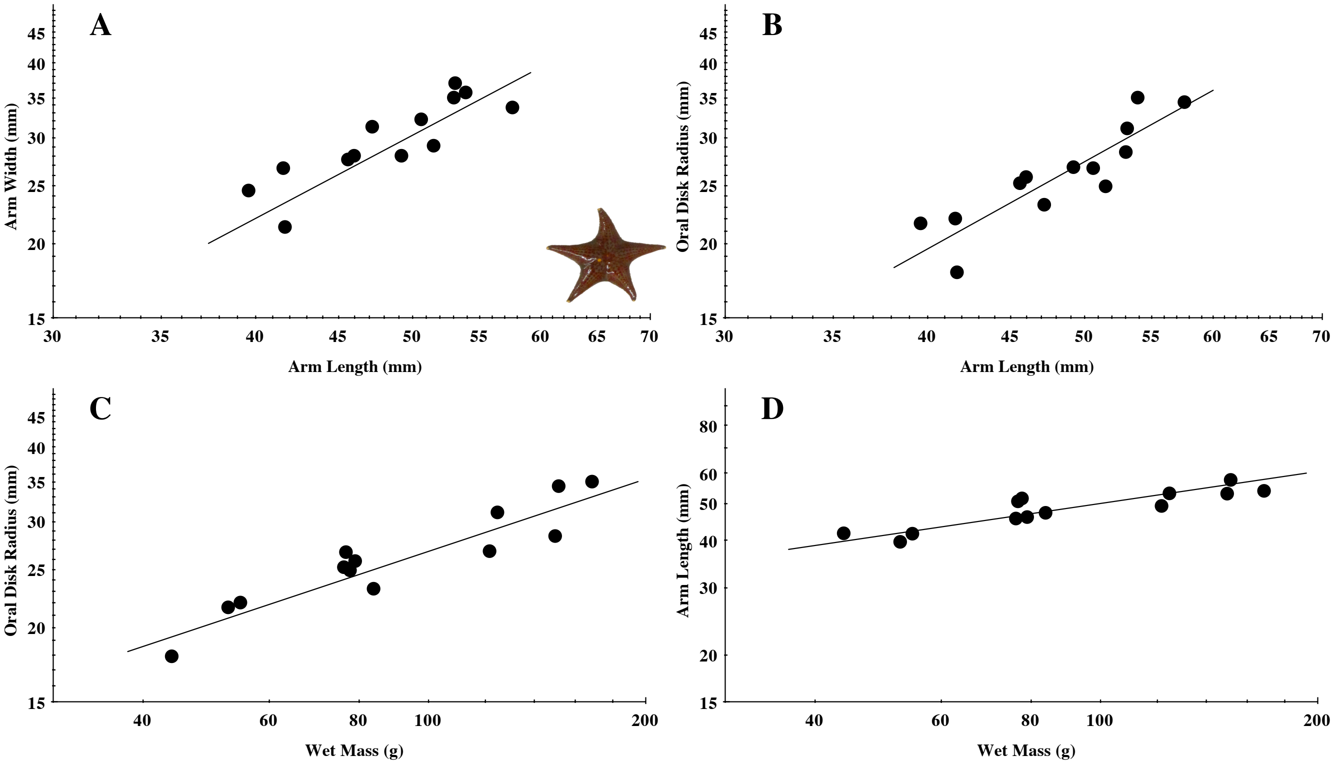

Figure 2.4A-D. Scaling relations in the five-armed sea star *Dermasterias imbricata*. Linear regressions were performed on $\log_{10}$-$\log_{10}$ transformed size data for scaling analysis. See Table 2.4 for scaling statistics and tests.

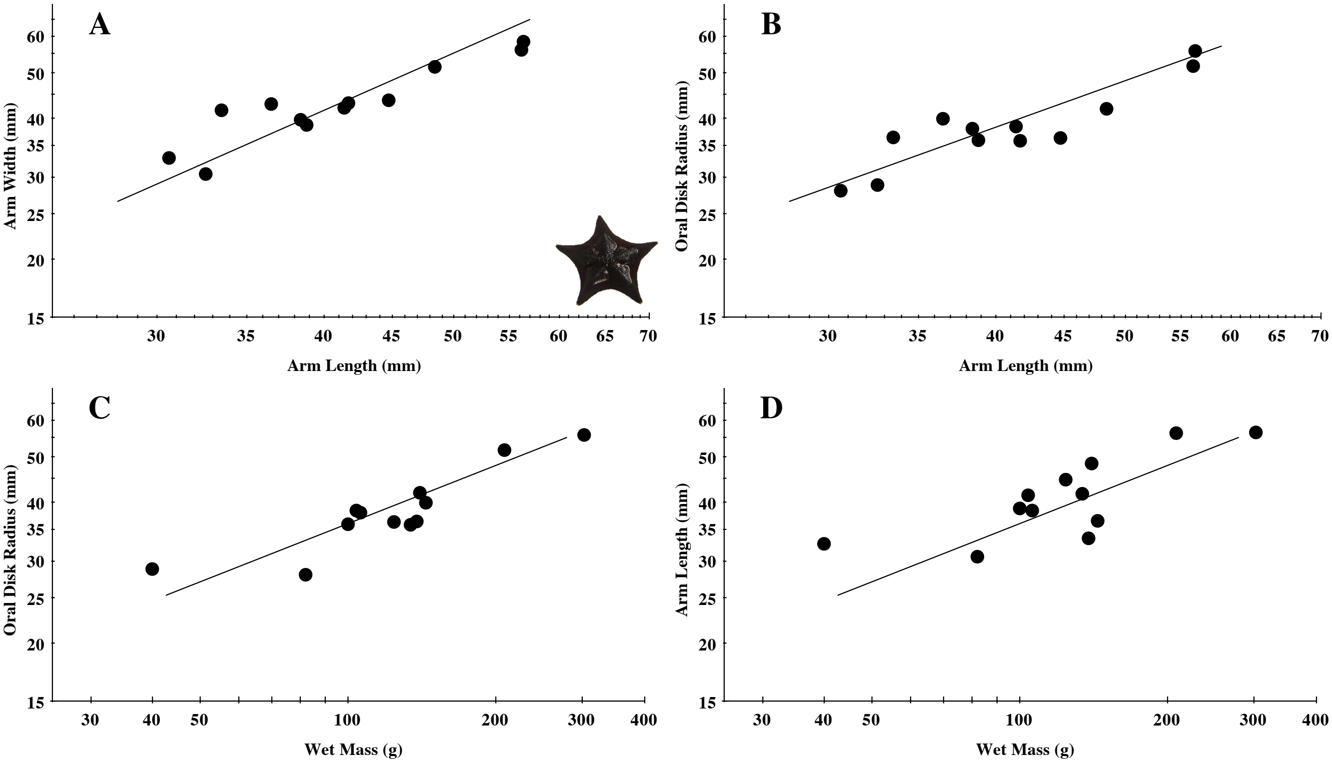

Figure 2.5A-D. Scaling relations in the five-armed sea star *Patiria miniata*. Linear regressions were performed on $\log_{10}$-$\log_{10}$ transformed size data for scaling analysis. See Table 2.5 for scaling statistics and tests.

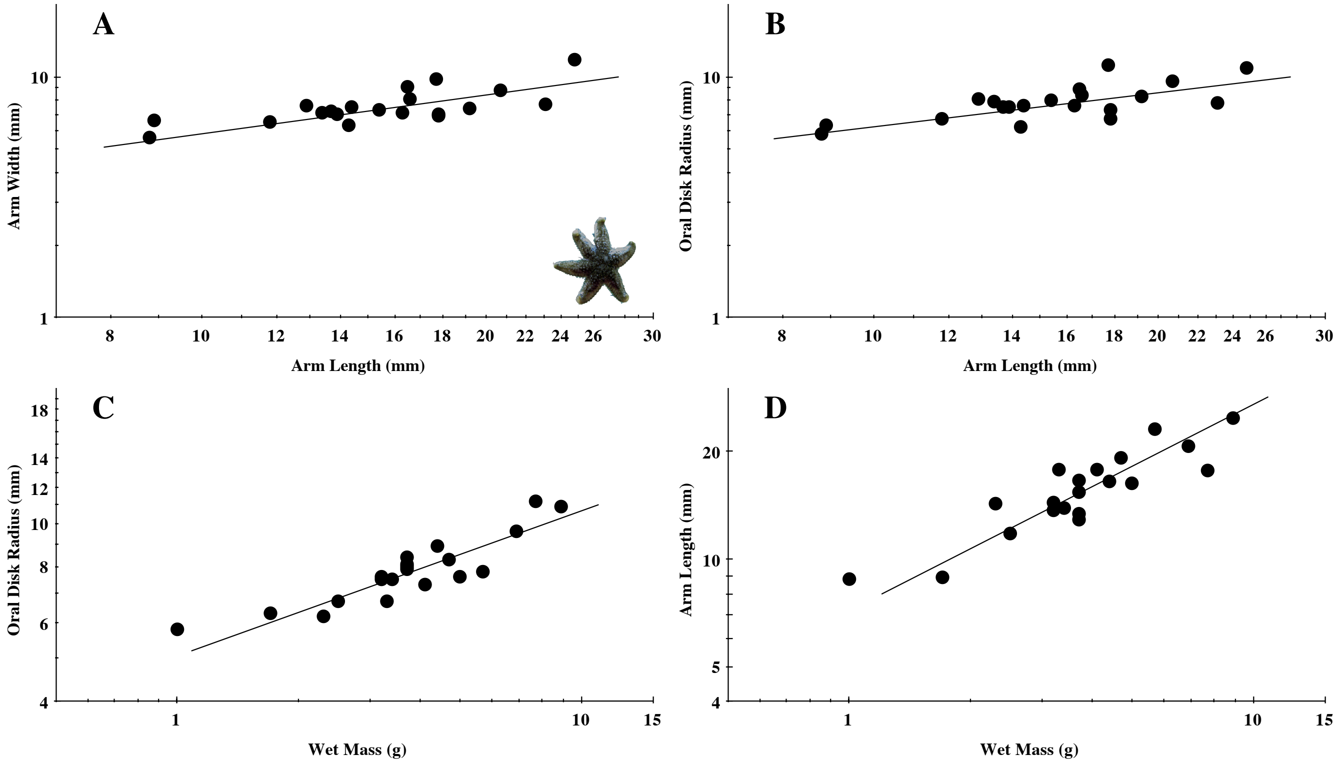

Figure 2.6A-D. Scaling relations in the six-armed sea star *Leptasterias hexactis*. Linear regressions were performed on $\log_{10}$-$\log_{10}$ transformed size data for scaling analysis. See Table 2.6 for scaling statistics and tests.

Figure 2.7A-F. Oral surfaces of Northeast Pacific sea stars. Arrows indicate ambulacral grooves – the areas that contain the hydraulic podia used for locomotion and feeding. **A)** *Pycnopodia helianthoides*. **B)** *Solaster stimpsoni*. **C)** *Dermasterias imbricata*. **D)** *Patiria miniata* [5-armed]. **E)** *Leptasterias hexactis* **F)** *Patiria miniata* [6-armed]. Scale bars in each photo indicate 20mm.

Chapter 3

Scaling of locomotion in Northeast Pacific sea stars

3.1 Introduction

As a general rule, larger animals move at faster absolute speeds than smaller individuals of the same species (Schmidt-Nielsen, 1975). This trend has been documented in phyla ranging from Cnidaria to Chordata and is independent of locomotion mechanism (Taylor *et al.*, 1970; Schmidt-Nielsen, 1975; McHenry and Jed, 2003). Larger-bodied animals achieve greater absolute speed through reduced stride/stroke/pulse frequencies but longer stride lengths that enable them to travel farther with reduced energy input (Taylor *et al.*, 1970; Schmidt-Nielsen, 1975; McHenry and Jed, 2003). Relative speed (size-specific, body lengths per s), however, may decrease with increasing body size even though absolute speed increases (Epp and Lewis, 1984). Such relations reveal valuable insights into biomechanical and energetic size-specific costs to locomotion and have been observed in taxa as diverse as rotifers and terrestrial mammals (Epp and Lewis, 1984; Diaz, 2002).

Despite the nearly universal positive relationship between locomotion speeds and body size, this relationship in echinoderms is much less clear. Larger-bodied individuals of the sea urchin *Paracentrotus lividus* crawl with faster absolute speeds (Domenici *et al.*, 2003) as do larger individuals of the five-armed sea star *Arcaster typicus* (Mueller *et al.*, 2011). In contrast, crawling speeds in the sea stars *Linckia laevigata*, *Acanthaster planci*, and *Protoreaster nodosus* are independent of body size (Mueller *et al.*, 2011). Even more surprisingly, in the bat star *Patiria miniata*, larger individuals actually crawl at slower absolute speeds (Montgomery and Palmer, 2012). Echinoderms all utilize a hydraulic system of tube feet and a water vascular system for feeding and locomotion (Lawrence, 1987). Given this shared locomotion mechanism, the variation among sea stars in the size-dependence of crawling speeds is puzzling.

Body shape and arm number vary greatly among the Asteroidea (Lambert, 2000). Therefore, these differences might provide clues about why the relationship between body size and crawling speed varies so much among sea stars. In addition, some species add arms as they grow (*size-dependent arm number*) whereas arm number is independent of body size in most species (*fixed arm number*). Arm-number effects have briefly been examined in *Patiria miniata* (Montgomery and Palmer, 2012) but I am not aware of any similar studies. Sea stars also vary quite a bit ecologically; some are particle feeders, some are herbivores and some are voracious predators (Lambert, 2000). These ecological differences might also have some bearing on the size-dependence of crawling speed in different species. Why, therefore, do larger-bodied sea stars crawl faster in some species but not in others?

I tested the effects of body size and shape on crawling speed in five species of Northeast Pacific sea stars: two sun stars with size-dependent arm number (*Pycnopodia helianthoides, Solaster stimpsoni*) and three fixed-arm species

(*Dermasterias imbricata, Patiria miniata,* and *Leptasterias hexactis*). These species range from five arms (*D. imbricata*, and *P. miniata*) to 24 arms (*P. helianthoides*) and span three orders of magnitude in body mass. Arm shapes (aspect ratio: arm length / arm width) also vary greatly among all five species. Montgomery and Palmer (2012) utilized a predator escape response as a way to ensure maximum crawling speeds in *P. miniata*. Here, I used the same predator (*Solaster dawsoni*) to trigger escape-response speeds in *P. helianthoides, S. stimpsoni, D. imbricata,* and *L. hexactis*. Speed and size-scaling data for *P. miniata* were obtained from Montgomery and Palmer (2012). I also tested the effect of natural versus artificial substrate on crawling performance in *P. helianthoides, S. stimpsoni*, and *D. imbricata* as the influence of substrate on movement speed is controversial among sea stars (Mueller *et al*., 2011).

3.2 Methods

3.2.1 Collection and morphological measurements

Sea stars were collected, housed in running seawater, and measured as described in Chapter 2.

3.2.2 Crawling speed trials

3.2.2.1 Pycnopodia helianthoides, *Solaster stimpsoni, Dermasterias imbricata*

Experiments were conducted in a fixed-volume sea table with a working area of 1m long by 60 cm wide by 10 cm deep at the Bamfield Marine Sciences Centre. No external seawater flow was present during crawling trials. Fresh seawater was used and the bottom of the tank scrubbed for each test to avoid bias from residual chemical cues of previous individuals (as per Montgomery and Palmer, 2012). All individuals were fasted for three days prior to testing to ensure the stomach would be properly retracted.

The voracious, predatory sea star *Solaster dawsoni* has previously been used to generate repeatable maximum crawling speeds in *Patiria miniata* (Montgomery and Palmer, 2012). *S. dawsoni* also triggers similar escape responses in *Pycnopodia helianthoides*, *Solaster stimpsoni, Dermasterias imbricata* (Van Veldhuizen and Oakes, 1981). To generate "forward" crawling in the current study, I briefly exposed stationary individuals to *S. dawsoni* at one end of the working area to encourage them to crawl away from the perceived threat. I ensured equal levels of "fright" within and among species by standardizing the contact time each individual had with the predator and using the same *S. dawsoni* individual (226g) for all crawling trials. Before each trial, I allowed the tip of the arm directly left of the madreporite of *S. dawsoni* to touch a single arm tip at the "back" of a stationary sea star for 10 seconds. I began filming the escape response as soon as this 10-second contact was complete. The initial orientation of crawling sea stars (relative to the madreporite) was haphazardly controlled to prevent any speed effects that might have resulted from arm preferences (Ji *et al.*, 2012; Montgomery and Palmer, 2012).

The camera was mounted on a tripod directly above the first half of the working area to give a birds-eye view of each crawling trial. A meter stick was placed parallel to the working area to provide scale for the subsequent video analysis. During each crawling trial, sea stars were visible in the center of the camera field of view and moved parallel to the meter stick. All videos were recorded at standard resolution (720x480) and 30fps.

3.2.2.2 Leptasterias hexactis

Crawling tests were conducted in a plexiglass aquarium with dimensions 30 cm long by 10 cm wide by 20 cm deep at the Friday Harbor Laboratories. The smaller working area was quite sufficient because of the smaller size of *L. hexactis*. Trials were conducted in stationary seawater and fresh seawater was used for each trial as above. As above, sea stars were fasted for three days before testing.

Due to time and locality constraints, a predator escape response was not used for *Leptasterias hexactis* crawling trials. Instead, I took advantage of this species' natural preference for dark spaces to stimulate crawling behaviour (Menge, 1972). A white paper was placed on the underside of the central 50% of the aquarium. During trials, *L. hexactis* consistently fled the brighter center and crawled to the dark corners of the aquarium. I considered this motion to be analogous to the predator escape response used to stimulate repeatable crawling behaviour in the other sea star species. Initial sea star orientation was haphazardly controlled as above.

The camera was mounted directed above the aquarium and the field of view was set to see both the crawling sea stars and the ruler placed inside the aquarium running parallel to the length. Video data were collected at standard definition (720x480) and at 30fps.

3.2.2.3 Patiria miniata

Speed data were obtained directly from Montgomery and Palmer (2012) and correlated with the new size measures calculated in Chapter 2. Speed-size curves present data for both 5- and 6-armed *P. miniata* since there was no difference in crawling between them (Montgomery and Palmer, 2012).

3.2.2.4 Pisaster ochraceus

Crawling trials were also attempted on the common five-armed sea star *Pisaster ochraceus*, but they were not successful. This species is known to escape from *Solaster dawsoni* (Van Veldhuizen *et al.*, 1989). However modifications to the methodology for crawling trials will be required before accurate crawling speeds can be obtained for this species. In the lab, *P. ochraceus* is exceedingly difficult to move from a holding tank to a testing arena because it attaches so firmly. As a result, the level of stress the animals experienced before crawling was much greater than all other studied species and the response to *S. dawsoni* was minimal at best. Future studies should consider running crawling trials in the field to eliminate the challenges associated with handling *P. ochraceus* in the lab.

3.2.2.5 Substratum tests

A smooth, plastic poster-board was used for the standard crawling trials of *Pycnopodia helianthoides, Solaster stimpsoni,* and *Dermasterias imbricata*. This substratum was also used in Montgomery and Palmer (2012) for crawling trials of *Patiria miniata*. The crawling trials of *Leptasterias hexactis* were conducted on plexiglass because they were done at a different research facility.

Fine sand was collected from Pachena Beach, Bamfield, BC and sieved to reach a grain diameter of 0.125mm - 0.25mm for the natural substrate trials of *Pycnopodia helianthoides, Solaster stimpsoni,* and *Dermasterias imbricata* (Wentworth Scale). The sand was hand-packed to a depth of 3 cm in the working area of the same sea table used for the standard crawling trials.

3.2.3 Kinematics measurements

Video data were imported using *QuickTime* software. Individual frames were extracted and digitized at a rate of one frame per second of film using *ImageJ* (Rasband, W. S., U. S. National Institutes of Health, Bethesda, MD, http://rsb.info.nih.gov/ij/, 1997–2010). To quantify absolute speeds the madreporite (or an easily identifiable fixed position on the oral disk) was marked and tracked over time. Instantaneous speed was calculated as the distance this fixed point traveled over a 10 second interval. Average instantaneous speed was obtained from the plateau phase of each speed-time curve as per Montgomery and Palmer (2012)[see Figure 3.1]. This average instantaneous speed was converted into size-specific speed for each species where a body length was defined as: 2*arm length + oral disk diameter.

3.2.4 Statistical analyses

Statistical analyses were performed using *R* (64-bit client for Macintosh, R Development Core Team, 2008) and VassarStats online (Lowry, R., 1998- 2013, USA). Linear regression analyses were used to quantify the relationship between crawling speed and measures of body size for each species. One-way analysis of covariance (ANCOVA) was used to compare the slopes and intercepts (with the effect of slope removed) of these regressions on artificial substrate and sand for *Pycnopodia helianthoides, Solaster stimpsoni,* and *Dermasterias imbricata*.

3.3 Results

3.3.1 Kinematics on artificial substrate

Absolute crawling speed (mm/s) increased with increasing size for all measures of body size in both sun-star species, *Pycnopodia helianthoides* [wet mass ($p < 0.001$), arm length ($p < 0.001$), arm width ($p = 0.003$), and oral disk radius ($p = 0.002$); Fig. 3.2A-D] and *Solaster stimpsoni* [wet mass ($p < 0.001$), arm length ($p = 0.048$), arm width ($p = 0.026$), and oral disk radius ($p = 0.012$); Fig. 3.3A-D]. In contrast, absolute crawling speed decreased with increasing size for all measures of body size in the three fixed-arm species, *Dermasterias imbricata* [wet mass ($p = 0.016$), arm length ($p = 0.039$), arm width ($p = 0.002$), oral disk radius ($p = 0.012$); Fig. 3.4A-D], *Patiria miniata* [wet mass ($p = 0.028$), arm length ($p = 0.040$), arm width ($p = 0.129$), oral disk radius ($p = 0.033$); Fig. 3.5A-D], and *Leptasterias hexactis* [wet mass ($p = 0.009$), arm length ($p = 0.004$), arm width ($p = 0.008$), oral disk radius ($p = 0.082$); Fig. 3.6A-D], although these declines were not significant statistically in two cases (oral disk radius in *P. miniata* and *L. hexactis*).

Size-specific crawling speed (body lengths/s) also varied with body size in different ways in different species. It decreased with increasing body mass in one sun-star species, *Pycnopodia helianthoides* ($p = 0.009$, Fig. 3.7A), but increased with increasing body mass in the other, *Solaster stimpsoni* ($p = 0.086$, Fig. 3.7B). In all three fixed-arm species, though, size-specific crawling speeds decreased with increasing body mass: *Dermasterias imbricata* ($p = 0.003$, Fig. 3.7C), *P. miniata* ($p < 0.001$, Fig. 3.7D), and *Leptasterias hexactis* ($p < 0.001$, Fig. 3.7E).

3.3.2 Kinematics on fine sand

Size-specific crawling speeds on fine sand for *Pycnopodia helianthoides, Solaster stimpsoni* and *Dermasterias imbricata* showed the same relations with wet body mass as on artificial substrate (Fig. 3.7). Relative crawling speed still decreased with increasing body mass in *P. helianthoides* and *D. imbricata* (p

<0.001, $p = 0.007$ respectively, Fig. 3.8A, C). There was no difference in speed magnitude between sand and plastic for either *P. helianthoides* (ANCOVA [slope] $p = 0.13$, [intercept] $p > 0.99$) or *D. imbricata* (ANCOVA [slope] $p = 0.42$, [intercept] $p = 0.86$). In contrast, *S. stimpsoni* crawled slower overall on fine sand and relative speed increased with increasing body mass (ANCOVA [slope] $p > 0.99$, [intercept] $p = 0.007$, Fig. 3.8B).

3.4 Discussion

The crawling speeds of all studied sea star species varied significantly with at least three of the four body-size measures tested (Figs. 3.2-3.6). These results differ from those of Mueller *et al*. (2011) who observed a size-dependence of crawling speed in only one of four sea star species: *Arcaster typicus*. This difference likely resulted from the different stimuli used. I used a predator cue (*P. helianthoides, S. stimpsoni, D. imbricata* and *P. miniata*) or unfavourable conditions (*L. hexactis*) to stimulate crawling behaviour. In contrast, Mueller *et al*. (2011) took measurements of crawling speed in naturally moving individuals in the field. When animals encounter a negative stimulus (either a predator or an environmental trigger), they presumably flee at the fastest speed possible as it could affect their survival (Van Veldhuizen and Oakes, 1981). In addition, biomechanical constraints to locomotion are likely have a stronger effect at maximum crawling speeds as animals are pushing their energetic and physical limitations to extremes (Daniel and Meyhöfer, 1989). Thus movement associated with escape responses may be more accurate in describing the true impact of body size on locomotion.

As a general rule, larger animals (within species) move at faster absolute speeds (Schmidt-Nielsen, 1975). The sun stars with size-dependent arm number (*Pycnopodia helianthoides* and *Solaster stimpsoni*) both exhibited this same trend relative to wet mass (g), arm length (mm), arm width (mm), and oral disk radius (mm) (Figs. 3.2, 3.3). However, the average speed differed greatly between these two species despite their physical similarities: 8 mm/sec (*P. helianthoides*) compared to 1 mm/sec (*S. stimpsoni*).

Both species also increase their arm number as they grow (Lambert, 2000), which means that larger diameter individuals have proportionally more podia. Because podia are used for locomotion in sea stars, this numerical increase in *Pycnopodia helianthoides* and *Solaster stimpsoni* likely enables larger individuals to crawl faster than their smaller counterparts. But arms are not added in the same way in these two species: *P. helianthoides* can double its arm number over time (from 12 to 24 at larger body sizes) whereas *S. stimpsoni* only adds a few (from 8 to 11) (Lambert, 2000; Lamb and Hanby, 2005). Therefore the arm-number differences between these two species may partially explain the eight-fold difference in the magnitude of their crawling speeds.

Differences in body density may also explain the difference in absolute crawling speeds observed in *Pycnopodia helianthoides* and *Solaster stimpsoni* (Full and Tu, 1991). Buoyancy is an important component to locomotion in aquatic systems (Vogel, 2008). *P. helianthoides* and *S. stimpsoni* with the same arm length do not have comparable wet masses: at a comparable arm length of 56mm *P. helianthoides* is nearly twice as heavy (mass = 110g vs. 58g). This mass difference is likely due to the increased arm number of *P. helianthoides.* The aboral tissue of *P. helianthoides* is rich with mucus and appears to drape loosely over the ossicles during crawling (pers. obs.). In contrast, the aboral surface of *S. stimpsoni* is made almost entirely of calcified plates and is quite rigid. So, although wet mass of *P. helianthoides* is greater at a given diameter, its body density may be much lower since the mucus-rich aboral surface is composed of presumably more buoyant tissue than the heavy ossicle plates of *S. stimpsoni*. A reduced density would enable *P. helianthoides* to crawl more easily in water because less mass would need to be supported per individual tube foot. A comparison of wet and immersed weights (which estimate the weight of the denser calcareous ossicles in the skeleton) in a future study could be informative in this regard.

In contrast to the sun stars, the fixed-arm species *Dermasterias imbricata*, and *Leptasterias hexactis* did not follow the general trend seen among animals: larger individuals of these species actually crawled more slowly (Figs. 3.4-3.6), as seen in an earlier study of *Patiria miniata* (Montgomery and Palmer, 2012).

Such a relationship between body size and crawling speed might have been expected for *D. imbricata* given that its body shape is similar to *P. miniata* (low aspect ratio, “webby” arms). However, *L. hexactis* has more slender arms than the other two fixed-arm species. In addition, body shape changes with size in different ways in *D. imbricata, P. miniata,* and *L. hexactis* (Chapter 2). Given these differences, why does crawling speed decline with increasing size in all three species?

The number and flexibility of podia are thought to have direct consequences on crawling ability in sea stars (Santos *et al.*, 2005; Montgomery and Palmer, 2012). Tube feet are added at the arm tip as arm length increases and broader arms are thought to improve podia range-of-motion within the ambulacral grooves (Lawrence, 1987). Given these growth patterns, species with relatively narrow ambulacral grooves may experience more biomechanical constraints to locomotion because the tube feet may collide with one another during movement or not be able to reach as far. This seems particularly likely for longer-armed *Dermasterias imbricata* that also had proportionally wider oral disk radii relative to arm length and thus more body mass per unit area of tube feet (though this relation did not pass a sequential Bonferroni correction; Chapter 2, Fig. 2.7, Table 2.7). A similar situation may occur in *Patiria miniata* where total oral surface area has been previously reported to increase with positively allometry relative to arm length (Montgomery and Palmer, 2012). Arm length and arm width both increased isometrically in *D. imbricata* and *P. miniata* relative to mass and arm length respectively. But little is known about how podia numbers and sizes scale with other measures of sea star body size (Montgomery and Palmer, 2012). If the tube feet in *D. imbricata* and *P. miniata* grow allometrically in stem width or disk diameter relative to ambulacral groove area, crowding could occur at larger body sizes (Lawrence, 1987; Montgomery and Palmer, 2012). As a result, tube foot size and ambulacral groove area will be important features to address in future studies of sea star locomotion.

Arm width and length scale differently in *Leptasterias hexactis* but the effect of body size on crawling speed is the same as for *Dermasterias imbricata* and *Patiria miniata*: larger individuals crawl at slower absolute speeds (Fig. 3.6). Larger *L. hexactis* had proportionally skinnier arms relative to arm length but proportionally much longer arms relative to wet mass (Chapter 2, Table 2.7). Reduced tube foot flexibility associated with narrower arms at larger arm lengths may impair the ability of larger *L. hexactis* to move more rapidly. This is particularly surprising for *L. hexactis* where the proportional increase in podia number presumably provided by proportionally longer arms at larger body masses appears not to be sufficient to overcome the proportional narrowing of arms (relative to arm length). These data suggest that arm width may have a greater impact on the ability of a sea star to crawl effectively at larger body sizes and that arm width, not length, may act as the critical length in sea stars (Schmidt-Nielsen, 1975; Montgomery and Palmer, 2012).

Arm aspect ratio (arm length / arm width; a measure of arm slenderness) is clearly a key feature of overall sea star shape (Montgomery and Palmer, 2012). As both arm width and arm length appear to affect locomotion in the fixed-armed species (*Dermasterias imbricata, Patiria miniata,* and *Leptasterias hexactis*) the ratio between them may also be relevant to locomotion. Arm number alone does not seem sufficient to explain why these fixed-arm species crawl more slowly at larger sizes because the five-armed star *Arcaster typicus* crawls faster at larger body sizes (Mueller *et al.* 2011). However, arm aspect ratio appears to become highly informative when *A. typicus* is added to the analysis (Fig. 3.9). There appears to be a critical point aspect ratio around 2.0 (arms are twice as long as wide) below which sea star species switch from the typical pattern of size-dependence (larger animals move faster) to the opposite (larger animals crawl slower). The proportion of the arms made up of ambulacral groove area in different species may confound this trend, because groove width appears to make up a greater proportion of arm width in species with narrower arms (higher aspect ratios; Chapter 2, Fig. 2.7). Future studies of locomotion in sea stars will need to examine this relationship in more detail.

Size-specific crawling speed decreased with increasing body size in four of the five species studied: *Pycnopodia helianthoides*, *Dermasterias imbricata, Patiria miniata,* and *Leptasterias hexactis* (Figs. 3.7A, C-E). This association necessarily arises in species that crawl at slower absolute speeds with increasing size (*D. imbricata, P. miniata,* and *L. hexactis*). The negative association in *P.*

helianthoides is also not that surprising, because in many other species where absolute speed increases with increasing body size, relative speed (body lengths moved per unit time) decreases at larger body sizes (Schmidt-Nielsen, 1975; Diaz, 2002). *Solaster stimpsoni* appears to be unusual compared to the other sea stars studied because larger *S. stimpsoni* travel more body lengths per second than their smaller counterparts (Fig. 3.7B). However, this association is not significant statistically so more data are required before attempting to interpret its significance.

The effect of substrate type on crawling in sea stars is controversial. Ferlin (1973) found increased crawling ability on sand whereas Schiebling (1981) found that substrate made no difference to crawling sea stars. The present study suggests that the effect of substrate may depend on the species studied. *Pycnopodia helianthoides* and *Dermasterias imbricata* both crawled with the same relative crawling speeds on both artificial substrate and fine sand (Figs. 3.8A, C) whereas *Solaster stimpsoni* crawled more slowly on fine sand compared to artificial substrate (Fig. 3.8B). When crawling on artificial substrate, both *P. helianthoides* and *S. stimpsoni* adopted a similar body posture and oriented their arms in similar angular placements (Fig. 3.10). *P. helianthoides* was able to replicate this crawling posture on sand but *S. stimpsoni* seemed to be unable to orient the arms in the "correct" pattern (Fig. 3.10). This suggests there may be an optimal orientation for sun-stars that enables the most effective crawling speeds. No such pattern was observed in *D. imbricata* but this may mean the angular organization of arms during crawling in species with few arms may not need to be as precise (Fig. 3.10). Tube feet have been shown to attach to rough surfaces preferentially (Santos *et al*., 2005b). The fine sand had much more texture than the artificial plastic substrate and likely enabled better attachment and balance for crawling. Future studies should include other substrates as different species may be designed to crawl differentially on different textures.

A compelling pattern emerges when speed and body size (mass) are correlated across a wide range of phyla and locomotive mechanisms: heavier species generally move faster (Schmidt-Nielsen, 1975; Vogel, 2003). This trend also appears to hold among the sea stars in the current study (Fig. 3.11) despite the within-species dependence of crawling speed on body size. The Asteroidea are therefore an important group to continue to examine the relationship between body size and locomotion speed both within and among species. Many factors that may influence crawling in sea stars require further scrutiny. In particular, detailed study of tube-foot scaling (number, size, shape), and tube-foot movement during the crawling process, could prove valuable to further unraveling the puzzles of sea star locomotion.

3.5 References

Daniel, T. L., and Meyhöfer, E. (1989). Size limits in escape locomotion of carridean shrimp. *J. Exp. Biol.* **143,** 245-265.

Diaz-Iriarte, J. (2002). Differential scaling of locomotive performance in small and large terrestrial mammals. *J. Exp. Biol.* **205,** 2897-2908.

Domenici, P, Gonzalez-Calderon, D. and Ferrari, R. S. (2003). Locomotor performance in the sea urchin *Paracentrotus lividus*. *J. Mar. Biol. Ass. U.K.* **83,** 285-292.

Epp, R. W., and Lewis Jr., W. M. (1984). Cost and speed of locomotion for rotifers. *Oecologia* **61,** 289-292.

Ferlin, V. (1973). The mode of dislocation of *Astropecten aranciacus*. *Helgol. Mar. Res.* **24,** 151-156.

Full, R. J. and Tu, M. S. (1991). Mechanics of a rapid running insect: Two-, four- and six-legged locomotion. *J. Exp. Biol.* **156,** 215-231.

Ji, C., Wu, L., Zhao, W., Wang, S. and Lv, J. (2012). Echinoderms have bilateral tendencies. *PLoS ONE* **7,** 1-6.

Lamb, A., and Hanby, B. P. (2005). *Marine Life of the Pacific Northwest*. Harbour Publishing: Madeira Park, British Columbia.

Lambert, P. (2000). *Sea Stars of British Columbia, Southeast Alaska, and Puget Sound*. UBC Press: Vancouver, British Columbia.

Lawrence, J. M. (1987). *A Functional Biology of Echinoderms*. Croom Helm, London.

McHenry, M. J., and Jed, J. (2003). The ontogenetic scaling of hydrodynamics and swimming performance in jellyfish (*Aurelia aurita*). *J. Exp. Biol.* **206,** 4125-4137.

Menge, B. A. (1972). Competition for food between two intertidal starfish species and its effects on body size and feeding. *Ecology* **53,** 635-644.

Montgomery, E. M., and Palmer, A. R. (2012). Effects of body size and shape on locomotion in the bat star (*Patiria miniata*). *Biol. Bull.* **222,** 222-232.

Mueller, B., A. Bos, R. Graf, G., and Gumanao, G. S. (2011). Size-specific locomotion rate and movement pattern of four common Indo-Pacific sea stars (Echinodermata; Asteroidea). *Aquat. Biol.* **12,** 157-164.

Santos, R., Haesaerts, D., Jangoux, M. and Flammang, P. (2005). Comparative histological and immunohistochemical study of sea star tube feet (Echinodermata, Asteroidea). *J. Morphol*. **263,** 259-269.

Santos, R., Gob, S., Jamar, V. and Flammang, P. (2005b). Adhesion of echinoderm tube feet to rough surfaces. *J. Exp. Biol.* **208,** 2555-2567.

Scheibling, R. E. (1981). Optimal foraging movements of *Oreaster reticulatus* (Echinodermata: Asteroidea). *J. Exp. Mar. Biol. Ecol.* **81,** 173-185.

Schmidt-Nielsen, K. (1975). Scaling in biology: The consequences of size. *J. Exp. Biol.* **194,** 287-308.

Taylor, C. R., Schmidt- Nielsen, K. and Raab, J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Amer. J. Physiol.* **4,** 1104-1107.

Van Veldhuizen, H. D., and Oakes, V. J. (1981). Behavioural responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni*. *Oecologia* **48,** 214-220.

Vogel, S. (2003). *Comparative Biomechanics: Life's Physical World*. Princeton University Press, New Jersey, USA.

Vogel, S. (2008). Modes and scaling in aquatic locomotion. *Int. Comp. Biol.* **48,** 702-712.

3.6 Figures and Tables

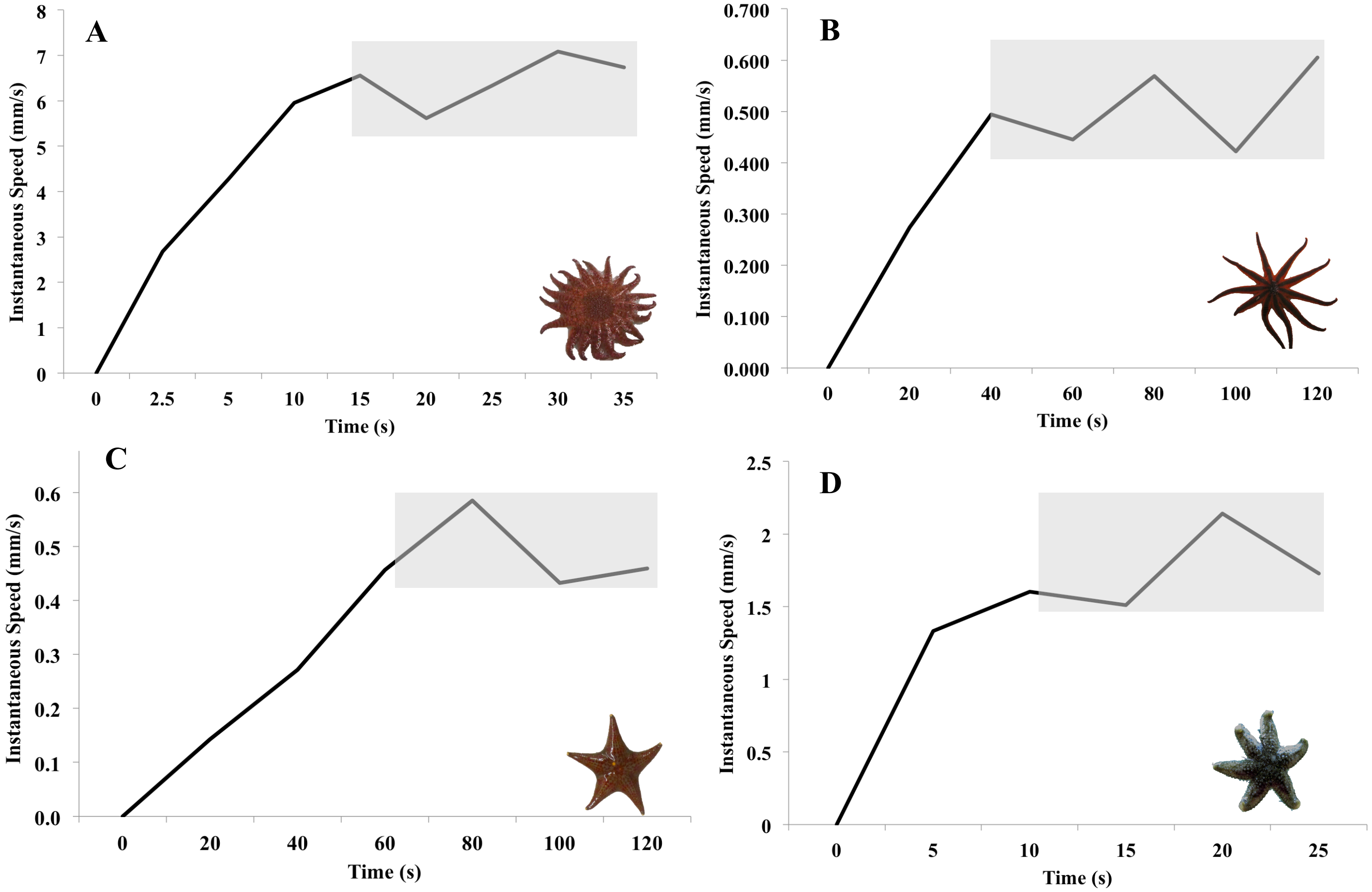

Figure 3.1A-D. Representative instantaneous crawling speeds (mm/s) versus time (s) in sea star locomotion trials on artificial substrate. Maximum average speed was calculated from the plateau phase (shaded region). For *Patiria miniata* see Montgomery and Palmer (2012). **A)** *Pycnopodia helianthoides* (146g). **B)** *Solaster stimpsoni* (431g). **C)** *Dermasterias imbricata* (55g). **D)** *Leptasterias hexactis* (3.2g).

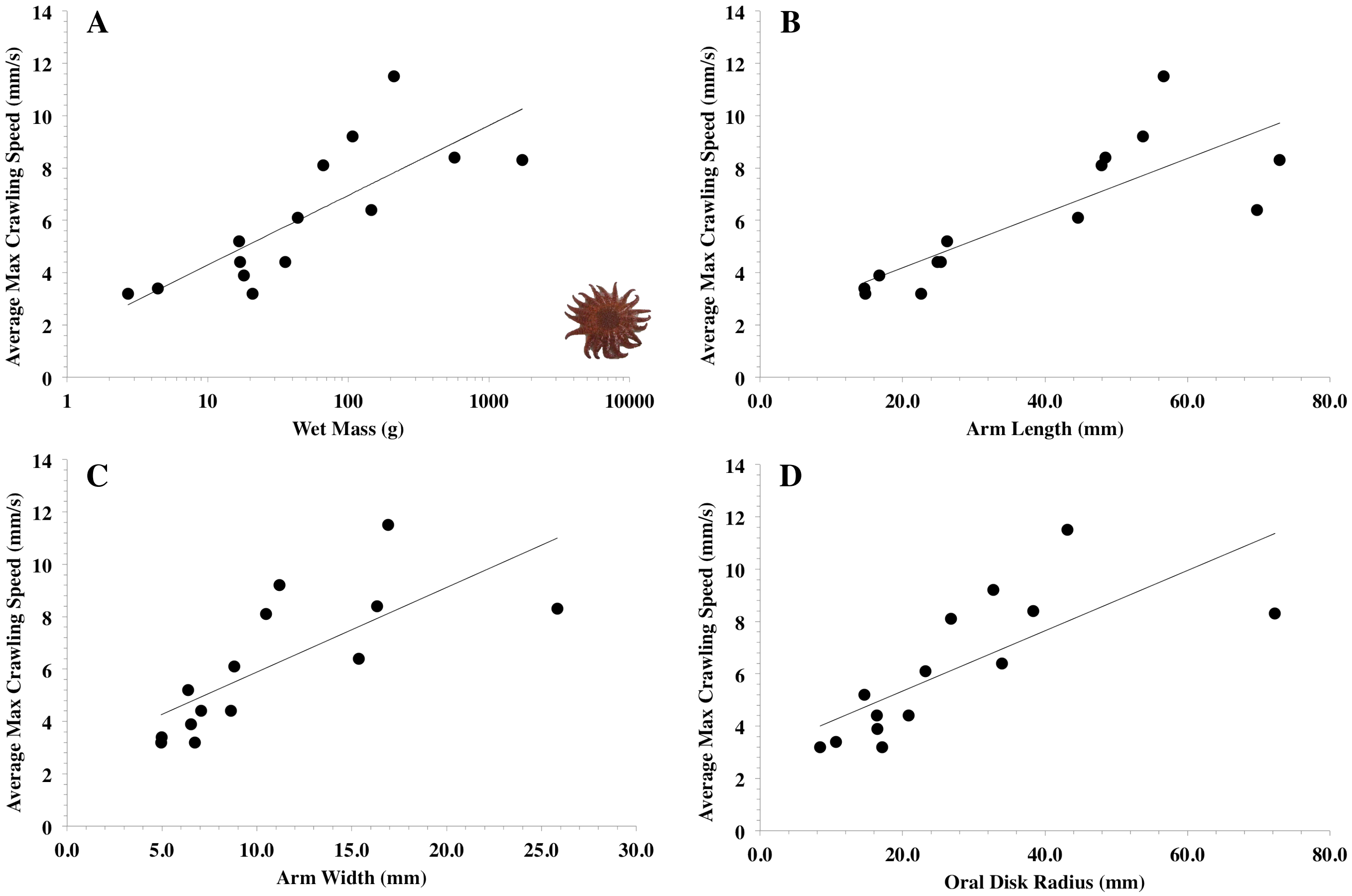

Figure 3.2A-D. Crawling speed (mm/s) on artificial substrate versus measures of body size in the multi-armed sea star *Pycnopodia helianthoides*. **A)** $\mathbf{y} = 2.67(\pm 0.599)\mathbf{x} + 1.62$, $R = 0.789$, $p < 0.001$. Wet mass (g) was Log_{10} transformed for regression analysis. **B)** $\mathbf{y} = 0.10(\pm 0.022)\mathbf{x} + 2.10$, $R = 0.810$, $p < 0.001$. **C)** $\mathbf{y} = 0.32(\pm 0.086)\mathbf{x} + 2.65$, $R = 0.737$, $p = 0.003$. **D)** $\mathbf{y} = 0.12(\pm 0.030)\mathbf{x} + 3.03$, $R = 0.741$, $p = 0.002$. Each point represents an individual sea star. N = 14 for all models.

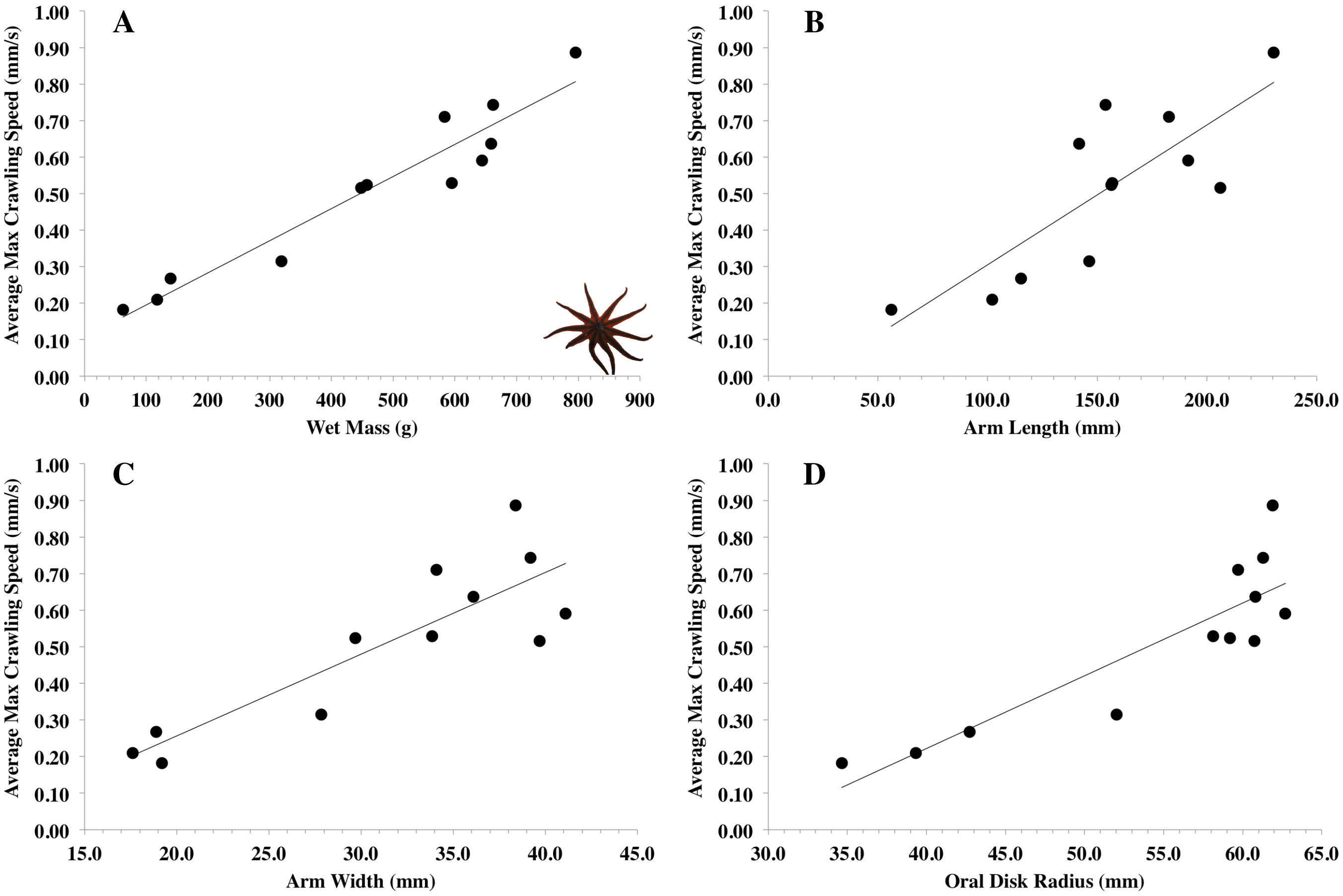

Figure 3.3A-D. Crawling speed (mm/s) on artificial substrate versus measures of body size in the multi-armed sea star *Solaster stimpsoni*. **A)** $\mathbf{y} = 8.22E\text{-}4(\pm1.9E\text{-}4)\mathbf{x} + 0.24$, R = 0.742, $p < 0.001$. **B)** $\mathbf{y} = 0.003(\pm0.002)\mathbf{x} + 0.16$, R = 0.439, p = 0.048. **C)** $\mathbf{y} = 0.02(\pm0.007)\mathbf{x} + 0.10$, R = 0.539, p = 0.026. **D)** $\mathbf{y} = 0.02(\pm0.005)\mathbf{x} - 0.14$, R = 0.591, p = 0.012. Each point represents an individual sea star. N = 17 for all models.

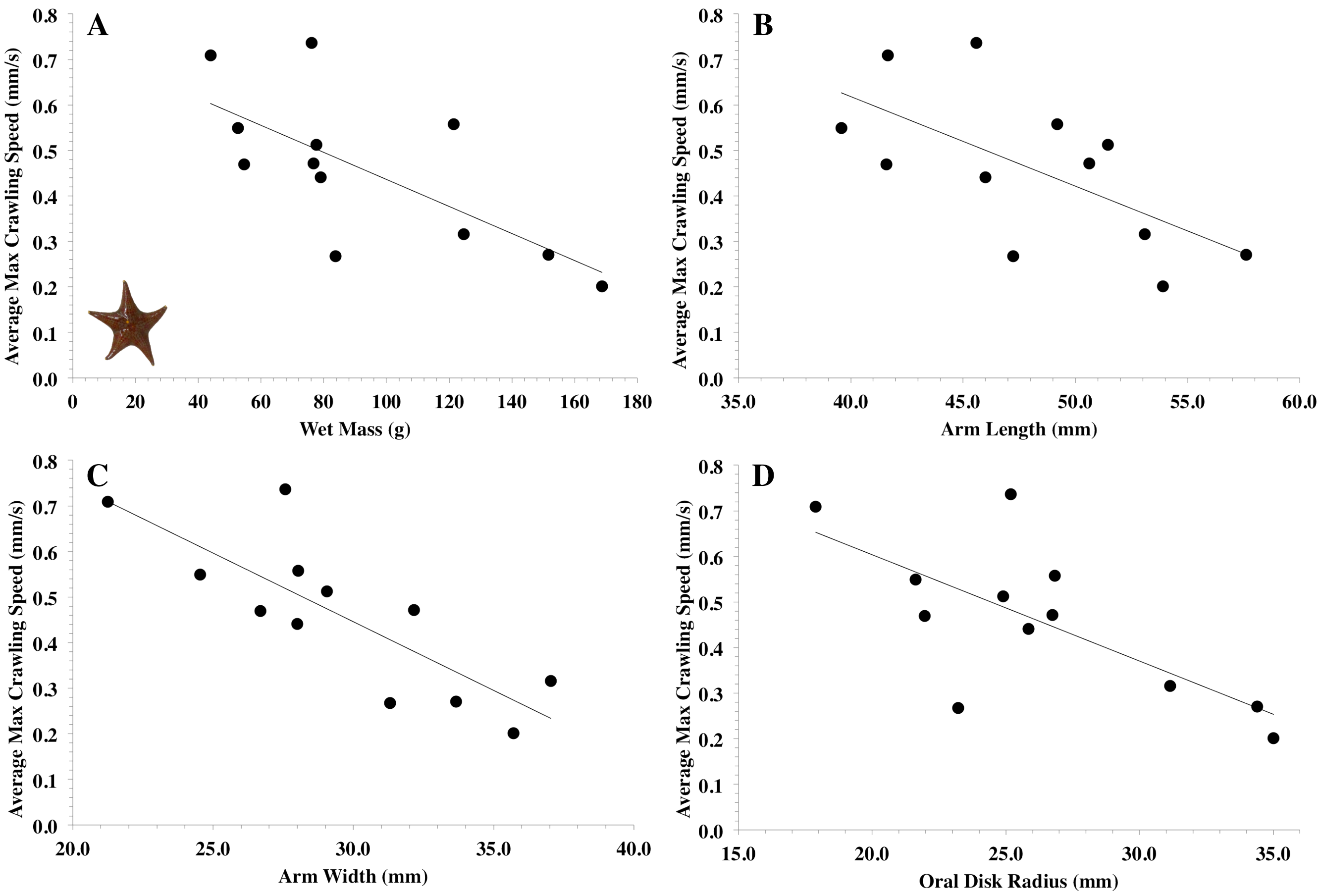

Figure 3.4A-D. Crawling speed (mm/s) on artificial substrate versus measures of body size in the primarily five-armed sea star *Dermasterias imbricata*. **A)** **y** = -0.003(±9.5E-4)**x** + 0.71, R = 0.675, p = 0.016. **B)** **y** = -0.02(±0.007)**x** + 1.31, R = 0.600, p = 0.039. **C)** **y** = -0.03(±0.007)**x** + 1.29, R = 0.800, p = 0.002. **D)** **y** = -0.02(±0.007)**x** + 1.04, R = 0.702, p = 0.011. Each point represents an individual sea star. N = 12 for all models.

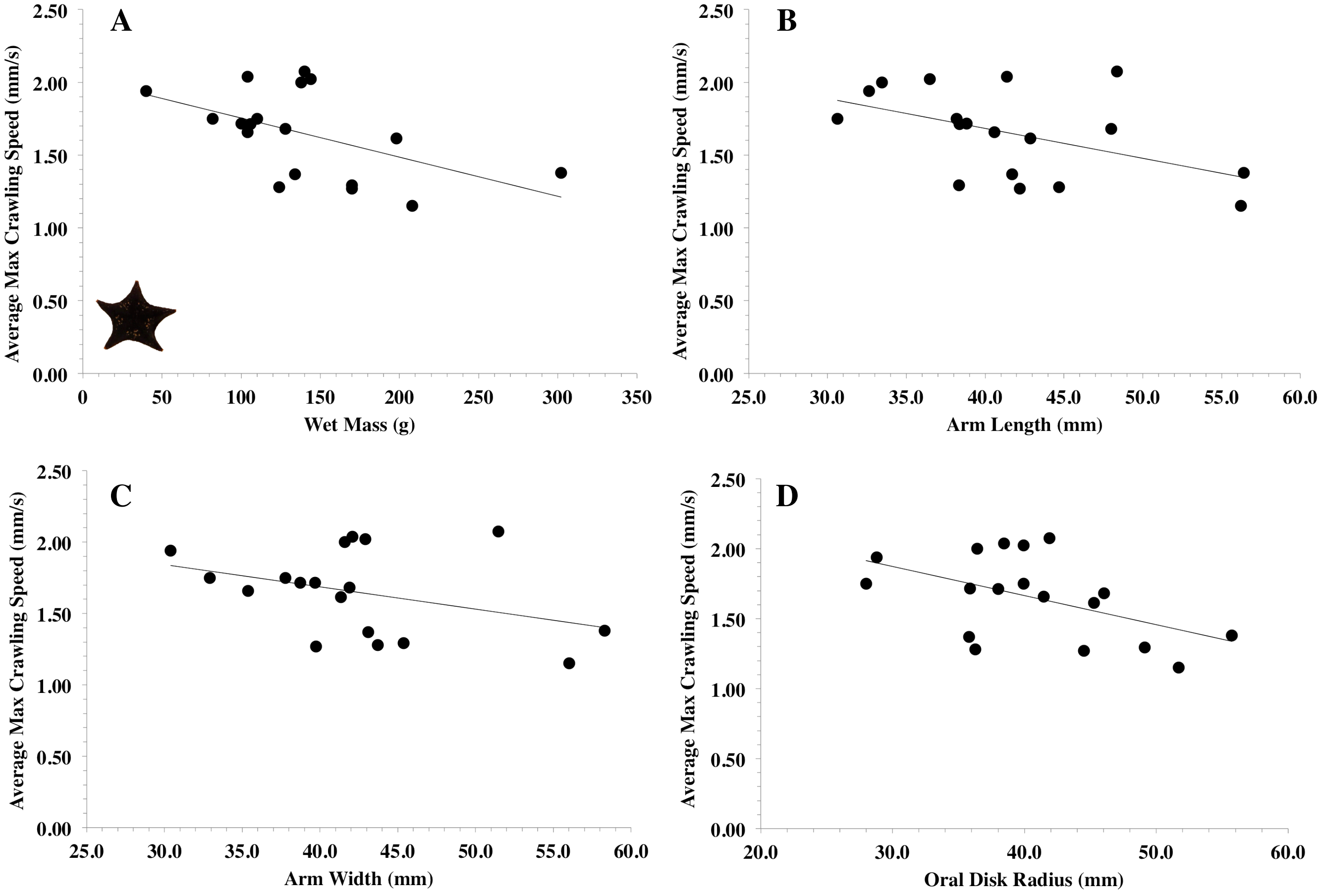

Figure 3.5A-D. Crawling speed (mm/s) on artificial substrate versus measures of body size in the primarily five-armed sea star *Patiria miniata*. **A) y** = -0.003(±0.001)**x** + 2.02, R = 0.518, p = 0.028. **B) y** = -0.02(±0.009)**x** + 2.50, R = 0.487, p = 0.040. **C) y** = -0.02(±0.010)**x** + 2.31, R = 0.372, p = 0.129, N.S. **D) y** = -0.02(±0.009)**x** + 2.56, R = 0.504, p = 0.033. Each point represents an individual sea star. N = 18 for all models.

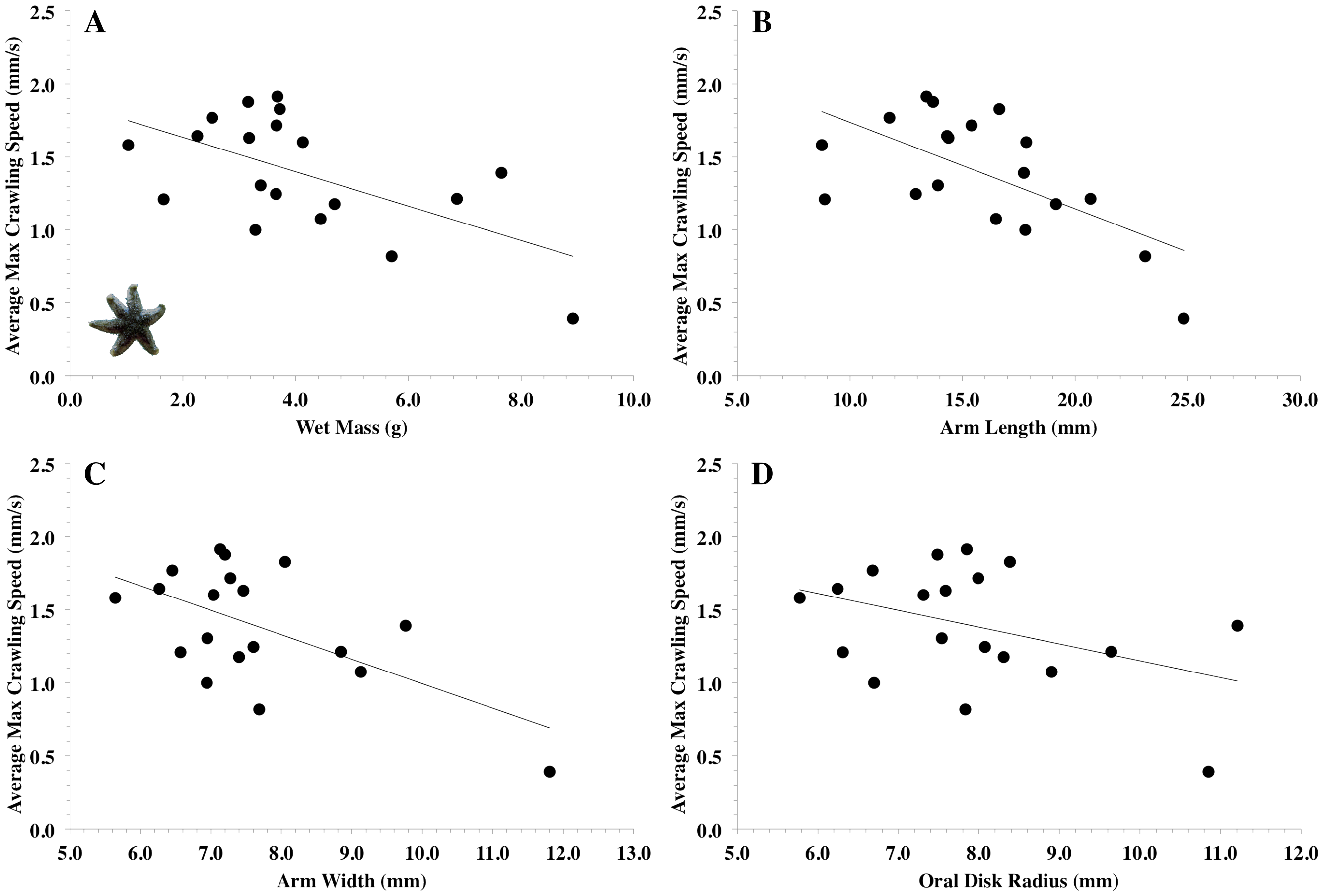

Figure 3.6A-D. Crawling speed (mm/s) on artificial substrate versus measures of body size in the primarily six-armed sea star *Leptasterias hexactis*. **A) y** = -0.12(±0.039) **x** + 1.86, R = 0.583, p = 0.009. **B) y** = -0.06(±0.018)**x** + 2.33, R = 0.632, p = 0.004. **C) y** = -0.16(±0.055)**x** + 2.64, R = 0.586, p = 0.008. **D) y** = -0.11(±0.061)**x** + 2.28, R = 0.409, p = 0.082, NS. Each point represents an individual sea star. N = 19 for all models.

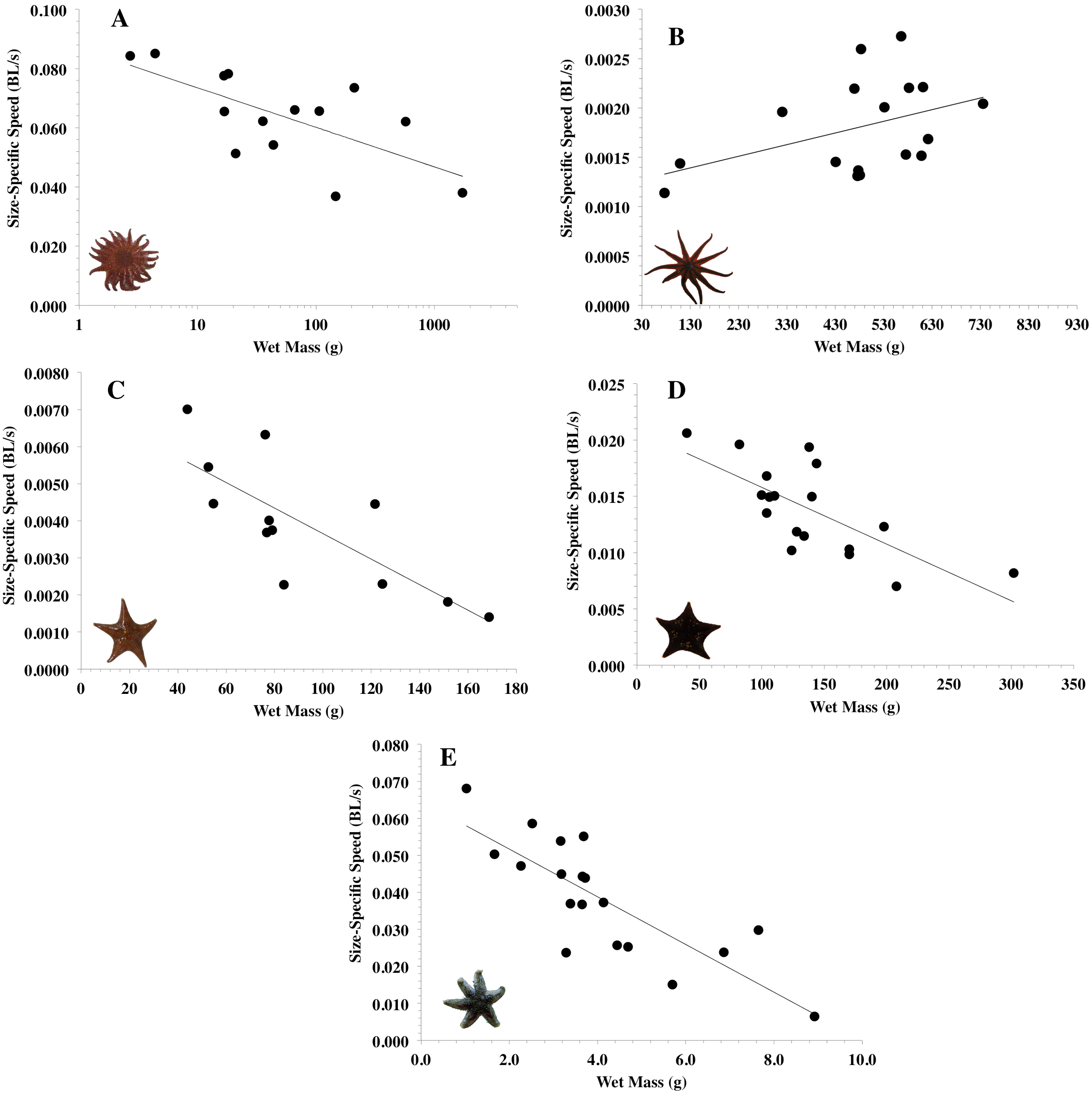

Figure 3.7A-E. Size-specific crawling speed (body lengths /s) on artificial substrate versus wet mass (g) in five Northeast Pacific sea stars. **A)** *Pycnopodia helianthoides*: $\mathbf{y} = -0.01(\pm 0.004)\mathbf{x} + 0.09$, $R = 0.670$, $p = 0.009$, $N = 14$. Mass (g) was Log_{10} transformed for linear regression. **B)** *Solaster stimpsoni*: $\mathbf{y} = 1.2\text{E-}6(\pm 6.4\text{E-}7)\mathbf{x} + 0.001$, $R = 0.429$, $p = 0.086$, $N = 17$. N.S. **C)** *Dermasterias imbricata*: $\mathbf{y} = -3.43\text{E-}5(\pm 8.8\text{E-}6)\mathbf{x} + 0.007$, $R = 0.778$, $p = 0.003$, $N = 12$. **D)** *Patiria miniata*: $\mathbf{y} = -5.27\text{E-}5(\pm 1.2\text{E-}5)\mathbf{x} + 0.021$, $R = 0.735$, $p < 0.001$, $N = 18$. **E)** *Leptasterias hexactis*: $\mathbf{y} = -0.006(\pm 0.001)\mathbf{x} + 0.06$, $R = 0.806$, $p < 0.001$, $N = 19$. Each point represents an individual sea star.

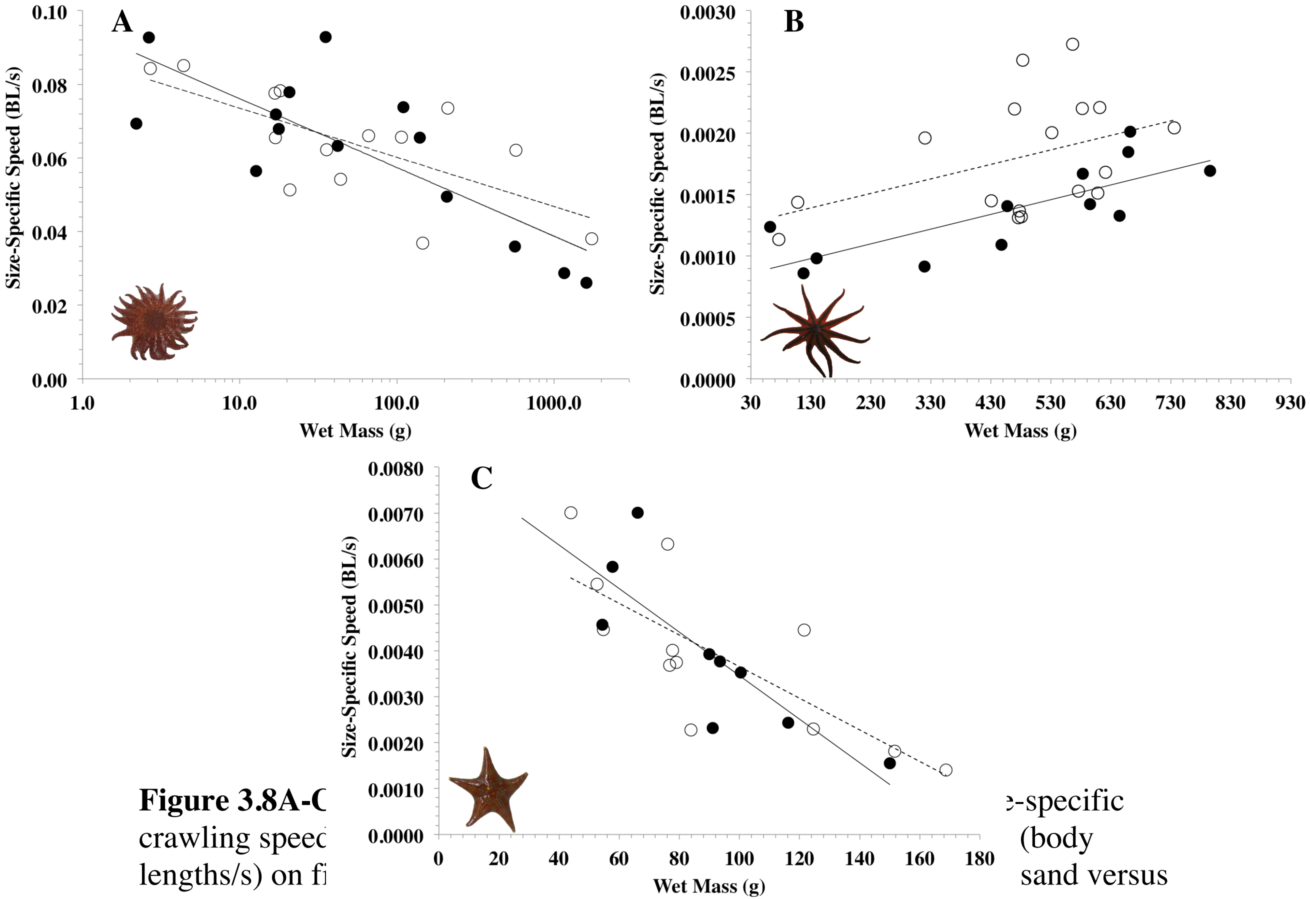

Figure 3.8A-C e-specific crawling speed (body lengths/s) on fi sand versus wet mass (g) in three Northeast Pacific sea stars. Speed trials on fine sand (black circles) are compared to crawling trials on artificial plastic substrate from Figure 3.7A-C (open circles). **A)** *Pycnopodia helianthoides*: **y** = -0.02(±0.004)**x** + 0.09, R = 0.792, $p < 0.001$, N = 14. Mass (g) was Log_{10} transformed for linear regression. [ANCOVA (slope) p = 0.13, (intercept) $p > 0.99$]. **B)** *Solaster stimpsoni*: **y** = 1.17E-6(±3.0E-7)**x** + 8.3E-4, R = 0.780, p = 0.003, N = 12. [ANCOVA (slope) $p > 0.99$, (intercept) p = 0.007]. **C)** *Dermasterias imbricata*: **y** = -4.72E-5(±1.2E-5)**x** - 0.008, R = 0.822, p = 0.007, N = 9. [ANCOVA (slope) p = 0.42, (intercept) p = 0.86]. Each point represents an individual sea star.

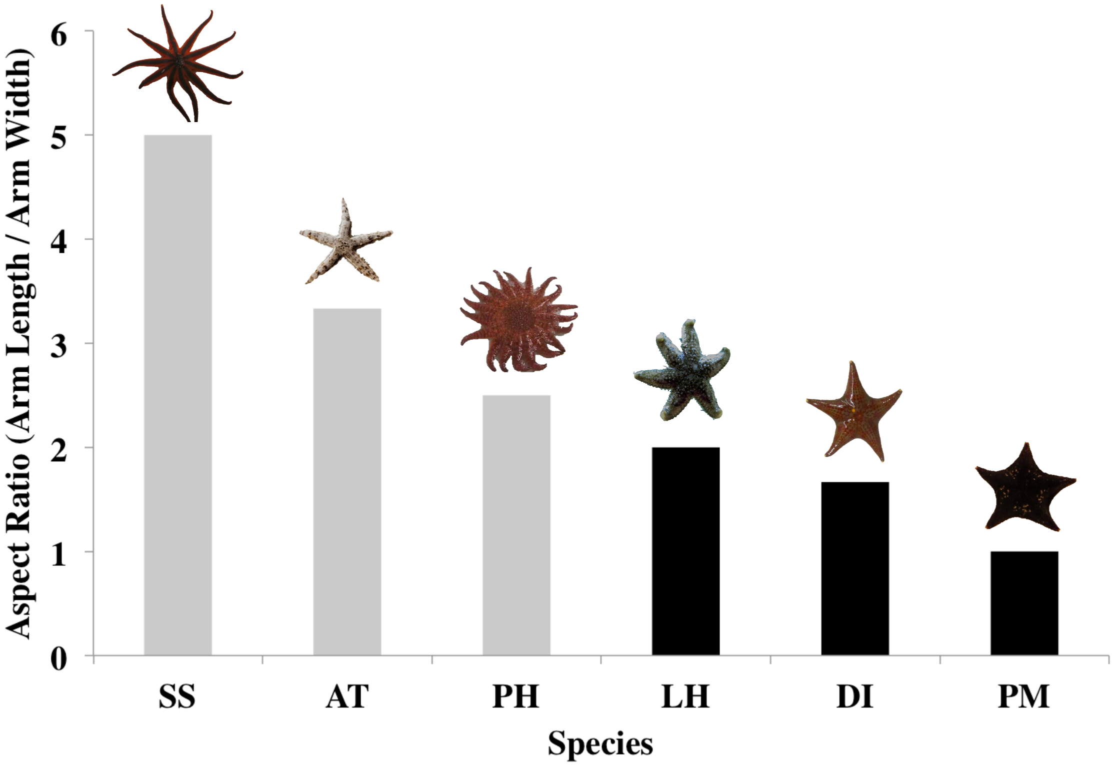

Figure 3.9. Average arm aspect ratios (arm length / arm width) in six species of sea stars. SS = *Solaster stimpsoni*. PH = *Pycnopodia helianthoides*. AT = *Arcaster typicus* (velocity data from Mueller *et al*., 2011). LH = *Leptasterias hexactis*. DI = *Dermasterias imbricata*. PM = *Patiria miniata*. Bar shading indicates the relationship between body size and crawling speed for each species: grey = larger individuals crawl faster, black = larger individuals crawl slower. Sea star images not to scale.

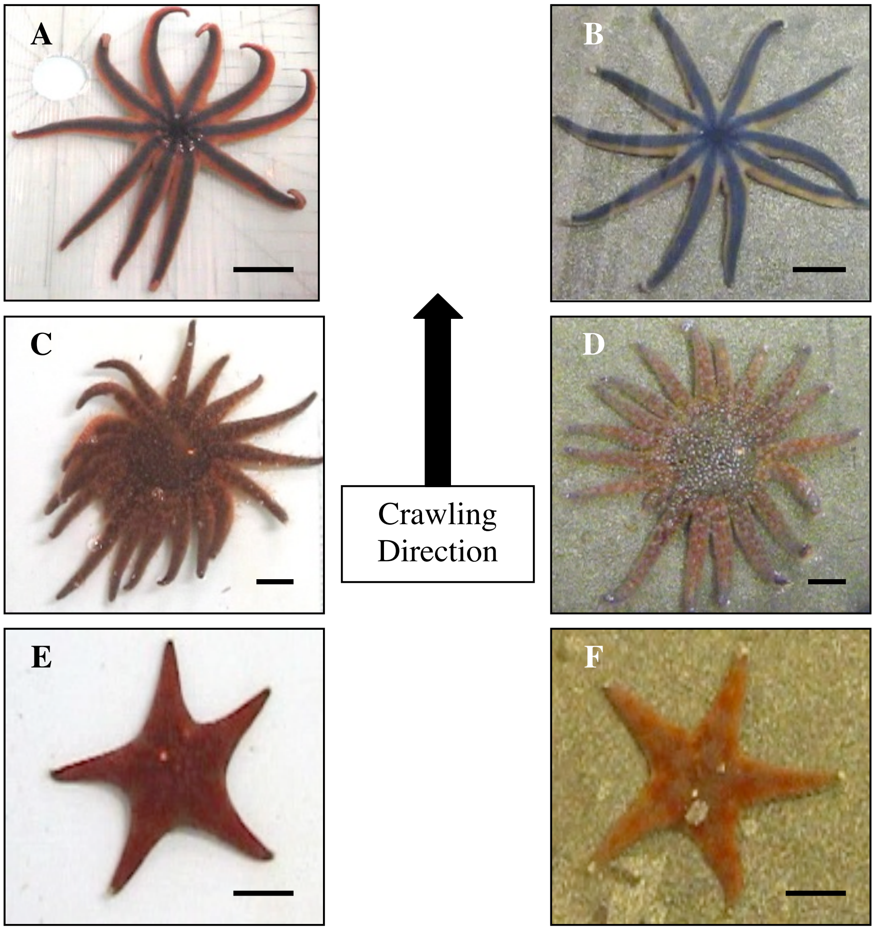

Figure 3.10A-F. Crawling body-form on artificial substrate (A, C, E) and fine sand (B, D, F) in three species of Northeast Pacific sea star. **A-B)** *Solaster stimpsoni*. **C-D)** *Pycnopodia helianthoides*. **E-F)** *Dermasterias imbricata*. The arrow indicates crawling direction. Scale bar indicates 50mm.

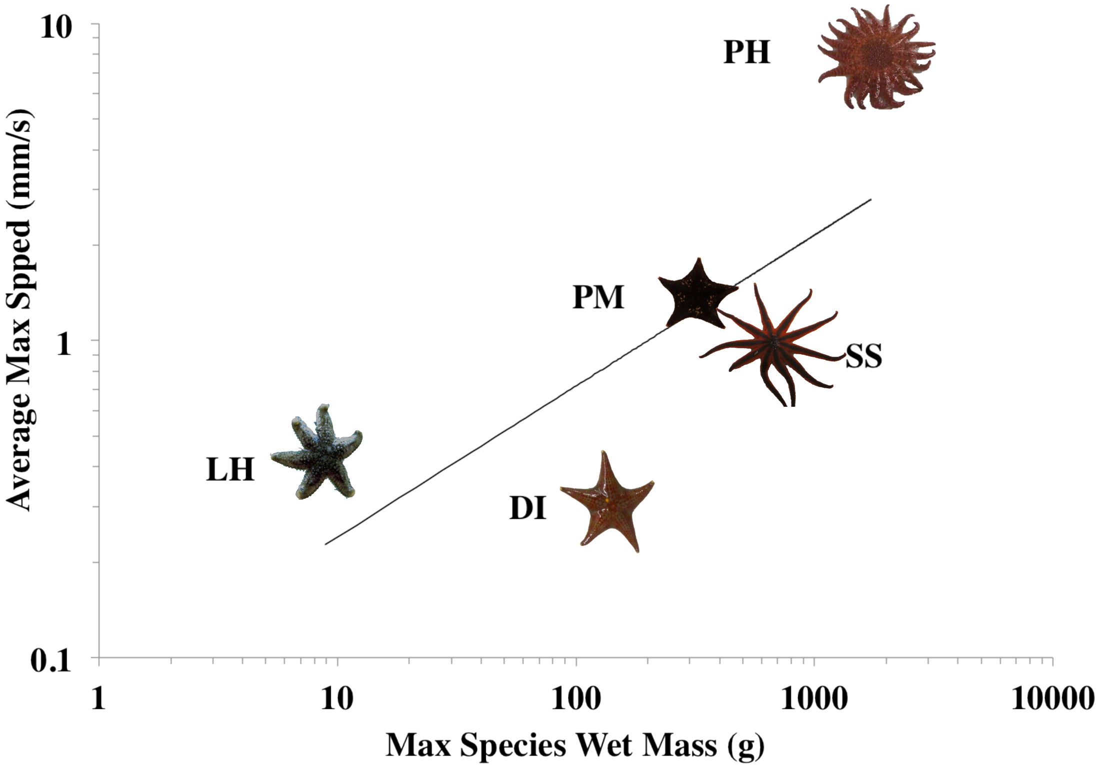

Figure 3.11. Average max speed (mm/s) versus maximum body wet mass (g) for five species of Northeast Pacific sea stars. LH = *Leptasterias hexactis*. DI = *Dermasterias imbricata*. PM = *Patiria miniata*. SS = *Solaster stimpsoni*. PH = *Pycnopodia helianthoides*. **y** = 0.005(±9.9E-4)**x** - 0.43, R = 0.937, p = 0.019, N = 5. Points represent the heaviest individual of each studied species.

Chapter 4
General conclusions

No strong allometries among body size variables were seen in *Pycnopodia helianthoides, Solaster stimpsoni, Dermasterias imbricata,* and *Patiria miniata* despite previous evidence that allometry does occur in some sea stars (Montgomery and Palmer, 2012). Unlike Mueller *et al.* (2011), all measures of size correlated with crawling speed in the studied species. While arm number and aspect ratio did not appear to affect scaling relations, the multi-armed stars with large aspect ratios crawled faster at larger body sizes while the fixed-arm species with small aspect ratios crawled slower at larger body sizes.

There was a similar dependence of body shape on size in four previously unstudied Northeast Pacific sea stars: *Pycnopodia helianthoides*, *Solaster stimpsoni*, *Dermasterias imbricata,* and *Leptasterias hexactis* (Table 2.7). This was surprising given the different arm numbers and body shapes (aspect ratios) represented among the species with size-dependent arm number (*P. helianthoides* and *S. stimpsoni*) and the fixed-arm species (*D. imbricata* and *L. hexactis*) (Mayo and Mackie, 1976; Van Veldhuizen and Oakes, 1981). But because of the strong allometries seen in *L. hexactis,* the relationships among size parameters during growth still need to be considered at the species level. This could have serious connotations for studies of size-dependent processes such as reproductive output and feeding that utilize arbitrary linear measures of body size that do not take into account proportional changes during growth (Levitan, 1991; Sommer *et al.*, 1999).

The sun star species *Pycnopodia helianthoides* and *Solaster stimpsoni* both have many more than five arms, and add arms as they grow. But the shape and number of those arms differed greatly between these two species (Lambert, 2000; Lamb and Hanby, 2005). *P. helianthoides* nearly doubles its arm number from juvenile to adult and those arms grow isometrically with increasing arm length (Table 2.7). In contrast, *S. stimpsoni* only adds a few arms as it grows but arm width still remains proportional to arm length (Table 2.7). These arm number differences appeared to have significant consequences for locomotion because *P. helianthoides* crawl on average eight times faster (8 mm/s) than *S. stimpsoni* (1 mm/s) (Fig. 3.2, 3.3). Interestingly, both of these species exhibited the typical relationship between body size and absolute locomotion speed seen within animal species (Fig. 3.2, 3.3; Schmidt-Nielsen, 1975). The fact that *P. helianthoides* and *S. stimpsoni* both increase their arm number with increasing body size appears to permit faster crawling speeds at larger body sizes as well. However arm addition is not sufficient on its own to explain why larger stars move faster because in *Arcaster typicus*, a tropical five-armed species, larger individuals also crawl faster (Mueller *et al.*, 2011).

In contrast, all three fixed-arm species, *Dermasterias imbricata*, *Patiria miniata,* and *Leptasterias hexactis*, showed a decline in crawling speed at larger body sizes (Table 2.7). *D. imbricata* and *P. miniata* both typically have five arms as adults and share similar overall body shapes (wide oral disks, short "webby" arms). In comparison, *L. hexactis* has six long, slender arms as an adult and much smaller overall body sizes (Lambert, 2000; Lamb and Hanby, 2005). Despite the similarities in shape between *D. imbricata* and *P. miniata*, there were subtle variations in scaling relations between these two species (Figure 2.7, Table 2.7). Not surprisingly, scaling in the six-armed star *L. hexactis* was completely different (Table 2.7). But since all three of these fixed-arm species crawled more slowly at larger body sizes, there must be something else beyond scaling relations that can explain this shared pattern in locomotion (Table 2.7). To address this puzzle, two important features of sea star geometry come to mind: a) the aspect ratio between arm length and arm width and b) the scaling and stride-cycle of tube feet (Montgomery and Palmer, 2012). A curious trend emerges when all of the currently available sea-star locomotion-size data is plotted with respect to arm aspect ratio (Fig. 3.9). There appears to be a critical aspect ratio (around 2.0) where the relationship between body size and speed shifts from the general trend to the inverse - where larger-bodied individuals crawl slower (Fig. 3.9). But given the small sample size (n = 5), more species data will be needed to further characterize the influence of aspect ratio on speed-size relationships in the Asteroidea. Tube foot scaling and movement during the crawling process also could provide valuable insight into the peculiarities of sea star locomotion. Longer-limbed animals are typically fasters because they take fewer, longer strides (Schmidt-Nielsen, 1975). Since the podia in sea stars have been likened to limbs in running mammals, *P. helianthoides* and *S. stimpsoni* may have proportionally longer tube feet than the three fixed-arm species and thus individual tube feet may be able to “step” farther and less frequently (Lawrence, 1987; Montgomery and Palmer, 2012).

The effect of substratum type on crawling speed seen in the three studied sea stars were curious but not surprising given earlier contradictory results (Mueller *et al*., 2011). This study suggests that the effect of substrate on crawling speed in sea stars is species-dependent and that crawling behaviour / arm orientation may play a role in determining this relationship (Fig. 3.8, 3.10). *Pycnopodia helianthoides* and *Dermasterias imbricata* crawled on sand with no change in size-specific speed (Fig. 3.8A, C). In contrast, *Solaster stimpsoni* had a harder time crawling on sand (Fig. 3.8B). The differences between the two sun-stars seem to be a result of arm positioning during crawling - *P. helianthoides,* but not *S. stimpsoni,* is able to keep the same angles between arms when crawling on sand versus artificial substrate. These differences could have fundamental implications for ecological and habitat selection studies as class-wise generalizations about substrate effects in sea stars no longer seem practical (Mueller *et al.*, 2011).

To my knowledge, the bat star *Patiria miniata* was the first animal studied to show a slower absolute rate of locomotion at larger body sizes (Montgomery and Palmer, 2012). We presumed that this deviation from the typical trend in other animals might have been the result of a unique mode of locomotion (tube feet) combined with both biomechanical restrictions (imposed by narrow ambulacral grooves) and behavioural changes to the body form at larger body sizes (Montgomery and Palmer, 2012). The discovery here that the leather star, *Dermasterias imbricata,* and the six-armed star, *Leptasterias hexactis,* are two more species that show the same departure from the typical association with size further emphasizes the peculiarity of sea stars both within the phylum Echinodermata and among all animals. Further study is needed on both size-dependent and fixed-arm species to better tease apart the parameters that drive the three different relationships observed between body size and locomotion in different sea stars: bigger means faster, size has no effect, and bigger means slower (Mueller *et al*., 2011; Montgomery and Palmer, 2012).

4.1 References

Lamb, A., and Hanby, B. P. (2005). *Marine Life of the Pacific Northwest*. Harbour Publishing: Madeira Park, British Columbia.

Lambert, P. (2000). *Sea Stars of British Columbia, Southeast Alaska, and Puget Sound*. UBC Press: Vancouver, British Columbia.

Levitan, D. R. (1991). Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* **181**, 261-268.

Mayo, P and Mackie, A. M. (1976). Studies of avoidance reactions in several species of predatory British seastars (Echinodermata: Asteroidea). *Mar. Biol.* **38**, 41-49.

Montgomery, E. M., and Palmer, A. R. (2012). Effects of body size and shape on locomotion in the bat star (*Patiria miniata*). *Biol. Bull.* **222**, 222-232.

Mueller, B., A. Bos, R. Graf, G., and Gumanao, G. S. (2011). Size-specific locomotion rate and movement pattern of four common Indo-Pacific sea stars (Echinodermata; Asteroidea). *Aquat. Biol.* **12,** 157-164.

Schmidt-Nielsen, K. (1975). Scaling in biology: The consequences of size. *J. Exp. Biol.* **194**, 287-308.

Sommer, U., Meusel, B., and Stielau, C. (1999). An experimental analysis of the importance of body-size in the seastar-mussel predator-prey relationship. *Acta. Oecol.* **20**, 81-86.

Van Veldhuizen, H. D., and Oakes, V. J. (1981). Behavioural responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni*. *Oecologia* **48**, 214-220.