

Burying efficiency and sediment preferences reveal complexities in habitat choice for Dungeness (*Metacarcinus magister*) and red rock (*Cancer productus*) crabs

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Particle size distribution is a key physical factor in determining where organisms live in sedimentary marine habitats because it strongly influences the mechanical properties of the medium and thus the energy required to move through it. We examined burying efficiency in and preference among five natural sediments for two crab species – *Metacarcinus magister* (the Dungeness crab), a habitat specialist and *Cancer productus* (the red rock crab), a habitat generalist. Crab burial speeds and sediment stiffnesses were measured at five field sites. Dungeness crabs buried equally well in less stiff, well-sorted sands and more stiff, poorly-sorted mud/cobble mixtures. At all sites they buried more quickly than red rock crabs whose performance decreased with increasing heterogeneity of the sediment. These results are contrary to expectations based on reported habitat specificity of the two species. Burial speed decreased with increasing carapace size especially for red rock crabs. The burial success and speed of Dungeness crabs is associated with the relatively larger surface area of their propoduses and the sharper angle formed by the posterior border of the carapace and abdomen. In replicate mesocosms, crabs explored five substrates and then buried in one. Dungeness crabs tended to select well-sorted sediments similar to where we found them in the field. In contrast, red rock crabs were least likely to bury in the mud/cobble sediment in which they had the most difficulty burying although this sediment was typical of the field site where they were most common. The discrepancies among burial performance, sediment preference, and natural distribution reveal the complexity of habitat use between these co-occurring species and are in contrast to the pattern shown by burying fish and some other crab species.

Introduction

For soft-bottom benthic organisms, the sediment is a feeding ground as well as a refuge from predators and currents (Arnold and Weihs, 1978; Gibson and Robb, 2000; Cook, 1985, Nel *et al.*, 1999; Nel *et al.*, 2001). The mechanical properties of sediment control the efficiency of burying and predation success (Dorgan *et al.*, 2008; Wright *et al.*, 2000; Tanda, 1990). The primary factor that determines the mechanical properties of the sediment is the distribution of particle sizes within it (Stoner and Ottmar, 2003; Moles and Norcross, 1995). Well sorted medium grain-sized sediments resist compaction and readily 'liquefy' compared to poorly sorted sediments where small particles fill the interstices between grains and impede the movement of grains relative to each other (Nel *et al.*, 2001).

Coarser sediments and compacted fine sediments require more energy to erode or manipulate (Nel *et al.*, 2001).

Organisms across a size series may be uniquely suited for specific habitats due to their differing body sizes and burying abilities. Moles and Norcross (1995) found that larger fish could exert more force and bury in coarser sediments than smaller fish and often preferred those sediments. Juvenile starry flounder, for instance, selected for fine sediment when offered a choice of pebbles, coarse sand and fine sand whereas adult starry flounder chose larger grain sizes (Moles and Norcross, 1995). Similarly, large yellowfin sole selected mud significantly more often than smaller sole (Moles and Norcross, 1995). Furthermore, Tanda (1990) found a positive correlation between sediment preferences and natural distribution, suggesting flatfish actively choose sediments in the wild where they can bury most easily.

Despite the broad implications of marine species preferentially choosing their habitats as a result of particle size distribution, few studies have been conducted on the burying capabilities and sediment selection of benthic organisms other than fish. This study was conducted to explore the size-related differences in burying efficiency and sediment preferences of benthic crabs in various particle sizes. While Dugan *et al.* (2000) reported on the burying ability of various crab species across a wide size range, little is known about the relationship between burial ability and size within individual species.

To this end, burial rates in size series of two sympatric brachyuran species were compared across a wide range of sediment types. *Metacarcinus magister* (formerly *Cancer magister*), or the Dungeness crab, is a large crab native to the west coast of North America.

M. magister lives almost exclusively in sandy bottoms and eel grass habitats (Pauley *et al*, 1986) and buries in a manner similar to that of *Blepharipoda occidentalis*, a sand crab, suggesting that it specializes to its sandy environment (McGaw, 2005). In contrast, *Cancer productus* (the red rock crab) has many characteristics that suggest it is more of a generalist. It inhabits a wider variety of habitats including rock bottoms, gravel, mud and sand (McGaw, 2005; Carroll and Winn, 1989, Schmitt, 1921). Additionally, *C. productus* has, on average, a greater number and diversity of epibionts per organism (McGaw, 2006; Becker, 1996; Becker and Wahl, 1996).

We compared burial speeds of both species in a variety of natural sediments with the expectation that *C. productus* would have similar but perhaps slower burial speeds across a range of sedimentary habitats compared to the sediment specialist. We anticipated that *M. magister* would bury more efficiently in the sand sediments typical of eelgrass beds (Koch, 2001). Additionally, we expected 1) that smaller crabs would bury more efficiently than large crabs in fine grains as reported by Dugan *et al.* (2000) and 2) that crabs would select sediments where they buried most efficiently – similar to sediment selection in flatfish (Tanda, 1990). *M. magister* and, to a lesser extent, *C. productus*, are economically crucial to the fisheries of California, Oregon and Washington (Hankin and Warner, 2001; Parker, 2001). Therefore, identifying the factors that determine habitat choice in these species may have important implications for conserving marine habitats and maintaining a sustainable fishery.

Materials and Methods

Sixty *Metacarcinus magister* and sixty *Cancer productus* were collected throughout June, 2014 from a variety of locations on San Juan Island, Washington. Crabs were collected via trap, hand, trawl and seine methods. Collection locations were Argyle Lagoon, Jackson Beach, Friday Harbor Laboratory (FHL) Docks and False Bay (Figure 1) and varied in substrate from rocky cobbles and gravel to fine sand and mud. A broad size series was collected for both *M. magister* and *C. productus* but young-of-the-year (for both species) were difficult to find. Crabs were maintained in FHL lab sea tables on natural light cycles at 12°C and fed biweekly on salmon and mussels.

Calipers were used to measure the carapace width of each individual and sex was also noted. Carapace width was taken from the widest point on the shell – the 10th tooth on *M. magister* and the 8th tooth on *C. productus*. Only crabs with all of their limbs intact were kept for experiments. After behavioral and morphometric analysis crabs were returned to the field.

Material properties of sediment and particle size composition

To quantify the mechanical properties of sediment, we used a penetration test that is analogous to measuring stress (force/unit area) and strain (displacement of the material when placed under a stress) and therefore describing stiffness or the characteristic yield of a material when placed under a force. Stiffness was measured at five field locations (Fig. 1), three in False Bay and two in Argyle Lagoon, by measuring the penetration of a 3.6mm diameter steel rod which was held at shoulder height and released vertically into the sediment. The depth the rod penetrated for a given weight was recorded. Additional

weights were added to the rod and penetration depth was recorded for weights up to 700 grams. Five replicates of twenty weights were run at each of the five field locations.

Sediment cores were collected with a 10cm diameter copper pipe to a depth of 10cm to analyze sediment composition at each of the five sites. Cores were sieved through a nine piece set (8mm, 4mm, 2mm, 1mm, .5mm, .25mm, .125mm, .063mm and <.063mm). The separated sediment was collected in tins, dried for at least 24 hours at 73°C in a drying oven and weighed.

Field tests of burial speed in different sediments

Burial speeds were tested *in situ* and under water to present the animals with the mechanical conditions under which burial would normally occur. Twenty-five individuals of each species were taken to each location. Crabs were transported in the dark in a cooler after being wrapped in damp cloth to keep them moist and prevent fighting. At each location, crabs were individually placed feet-down in water-covered sediment and a video camera was used to record their burial. In all cases, videotaping was continued until a crab had finished burying and remained motionless for twenty seconds or until three minutes had been exceeded without the crab attempting to bury. The time it took for each crab to bury was recorded from these video tapes.

Morphometric analysis

Morphological measurements were taken across a size series of organisms in order to pinpoint the anatomical differences between *C. productus* and *M. magister* (Figure 2). Calipers were used to measure chela length and width as well as primary pereopod length.

The lengths, widths and depths of the propodus, the second distal-most segment on the anterior and posterior pereopods, were also measured in both species. Segment width and length were multiplied to get an approximate estimate of surface area on the “face” of the posterior and anterior legs since these are the limbs that seem to be used most in burial. The posterior angle made by the conjunction of the carapace and abdomen forms the leading edge of the body during entry of the body into the sediment. This angle was photographed in a size series of each species and measured with ImageJ (Figure 3). In order to make this measurement repeatable, the angle was constructed from the same three points on every individual – the posterior side of the third pereopod’s attachment joint to the abdomen, the most posterior point of the carapace and the peak of the carapace directly above the largest tooth on the margin of the carapace (8th tooth in *C. productus*, the 10th in *M. magister*) (Figure 3).

Preference tests

Sediments were collected from each of the five field locations and placed in plastic bins in flow-through microcosms at Friday Harbor Laboratories. This procedure maintained the characteristic particle size distribution of each test site. We did not measure the stiffness of these translocated sediments. Arenas were divided into six identical sections (in a 2 x 3 array). Five bins contained sediment from the field sites (one type of sediment per bin) and an empty one was used as an entrance platform on which a single crab was placed at the initiation of a test. Crabs were divided into three size classes (>150mm, 80-150mm and <80mm) and assigned to different sized bins to ensure that crabs had enough room to bury while also increasing the likelihood that a crab would

explore sediments in multiple bins. The largest group of crabs was placed in bins approximately 30cm x 20cm, the middle group in bins sized 15cm x 10cm, and the smallest group in bins sized 10cm x 8cm. In each case, the sizes of the microcosms were altered so that the each sediment comprised approximately 1/6th of the microcosm. The crabs were allowed 24 hours to bury in the offered sediments and fresh seawater flowed through the arenas throughout the test period. Crab locations were checked in two hour intervals for the first six hours, at midnight and again in early morning to ensure that each crab moved around the test arena and encountered the various sediments at some point. Final locations were recorded.

Sediments remained submerged at all times and were replaced with fresh sediment every two days. Individual organisms were chosen in order to maximize size range. Additionally, equal numbers of crabs from each species were run each day to avoid variation in preference based on sediment age.

Data analysis

We compared the distribution of test weights used in evaluating the stiffness of sediments of each site with Wilcoxon rank sum tests. The replicate data were compiled for each location and linear regressions of weight and sediment penetration were used in conjunction with Wilcoxon rank sum tests to analyze the distribution of penetration data. Additionally, the slopes, or stiffness values, were averaged for each location and plotted against each other.

Wilcoxon rank sum tests were conducted to ensure that the distribution of carapace widths of crabs that buried were similar in each test location. Analyses of covariance

(ANCOVAs) were used to check for significant differences in the relation between burial speed and carapace size for species illustrating homogeneity in variance. For species without homogeneous relations between burial time and carapace size, ANOVA's were used to analyze differences in average burial times between species and across sites in conjunction with Tukey-Kramer post-hoc tests.

Chela length and width, anterior pereopod length, posterior angle and the length, width and depth of the anterior and posterior prodopuses were plotted against carapace width to compare rates of change of various body parts. Linear regression analysis was used to compare the slopes and, in cases where they were equal, a nonparametric ANCOVA (Wilcoxon rank sum) test was used to compare whether the response variable was different among groups.

Results

Material properties of sediment and particle size composition

Distribution of weights used in stiffness testing were not significantly different between the five sites ($\chi^2 = 5.3449$, d.f. = 4, $p > 0.05$). The stiffest sediments were found in Sites 1 and 2 in False Bay, followed by Site 3 (Figure 4). These three sites also harbored the highest proportion of particles smaller than 0.063mm – which are positively correlated with sediment stiffness (Figure 5) (Crane and Merz, 2012). Sites 1 and 2 were similar in composition and were poorly sorted with Site 1 having slightly more particles sized 0.125mm and 0.25mm and a slightly lower percentage of particles smaller than 0.063mm. Site 3 had a higher percentage of particles sized 0.125mm – a size which is negatively correlated with stiffness (Crane and Merz, 2012) – and a higher percentage of 0.25mm

particles (no correlation). The sediments from Sites 4 and 5 (Argyle Lagoon) were similar in their stiffness values with Site 4 being slightly stiffer and more poorly sorted than Site 5 and both being less stiff than any of the False Bay locations. Site 4 had a rocky bottom with cobbles comprising 65% of the weight whereas Site 5 had very high proportions of 0.25mm and 0.5mm sized particles. Both sites were composed of smaller proportions of particles smaller than 0.063mm. The stiffness values in all locations were within the range provided by previous experimentation (Crane and Merz, 2012).

Stiffness readings at Sites 1, 2 and 4 were not significantly different from each other (Sites 1 and 4, $p = 0.1377$, Sites 2 and 4, $p = 0.3310$, Sites 1 and 2, $p = 0.9940$). Site 3's stiffness was significantly different than all other sites ($p < 0.001$ for all comparisons) and Site 5 also showed statistical difference from all other sites ($p < 0.001$ for all comparisons).

Burial description

Dungeness and red rock crabs appear to bury using the same stereotypic motions. First, the rear pereopods (number 5, Fig. 2) are inserted into the sediment behind the crab at an angle and curled medially, anchoring the abdomen to the sediment. The third and fourth (numbers 3 and 4, Fig. 2) pairs of limbs are inserted vertically into the sediment and also curl medially. The primary pereopods (the second pair of limbs) (number 2, Fig. 2) are inserted in a similar manner but, after curling medially beneath the abdomen, push forward towards the chelae and sweep outwards. This motion sweeps sediment from beneath the abdomen and is completed one side at a time. Immediately following the pereopod sweep, the chela (number 5, Fig. 2) on the corresponding side pushes forward the sediment left by the pereopod. At this point, the anchoring legs (numbers 3, 4, 5, Fig. 2)

are moved vertically in the sediment in a stomping motion believed to fluidize the sand beneath the abdomen and create space beneath the crab (Maltman and Bolton, 2003). The crab is forced backwards and down by the chelae pushing forwards and the stomping pereopods. This cycle of sweeping, pushing and stomping repeats until the posterior angle is beneath the sediment. At this point, the crab rocks forward and backwards several times, which jets the liquefied sand out from beneath its abdomen and onto its carapace.

Dungeness crabs were more easily observed burying in part because their limbs seemed to extend further from beneath their carapace and their limbs were wider and flatter. Red rock crabs, while using the same stereotypic movements, were more difficult to track due to their thinner and rounder pereopods. The fastest Dungeness crabs in any of the locations buried in 7.6 seconds and the fastest red rock buried in 12.7 seconds. Overall, Dungeness crabs buried in an average time of 24.97 ± 11.58 seconds while red rock crabs buried, on average, in 42.54 ± 22.00 seconds which is slightly faster than reported by McGaw (2005, *M. magister* 26.8 ± 3.1 seconds, *C. productus* 59.5 ± 7.5 seconds). Across five locations, there were 103 successful Dungeness crab burials and 78 successful red rock crab burials out of a total of 125 trials for each species.

Field tests of burial speed in different sediments

The Dungeness and red rock crabs tested were not significantly different in regards to carapace width at any of the sites (L1, $Z = -0.4209$, $n_{cp} = 21$, $n_{mm} = 24$, $p = 0.6738$; L2, $Z = -1.1432$, $n_{cp} = 14$, $n_{mm} = 23$, $p = 0.2530$; L3, $Z = -1.0457$, $n_{cp} = 17$, $n_{mm} = 19$, $p = 0.2957$; L4, $Z = -0.6267$, $n_{cp} = 12$, $n_{mm} = 16$, $p = 0.5308$; L5, $Z = -0.9596$, $n_{cp} = 14$, $n_{mm} = 21$, $p = 0.3372$).

Analysis of burial speed revealed three main patterns. First, at every site, *M. magister*

buried more quickly than *C. productus* (L1, $x^2 = 16.2169$, d.f. = 1, $p < 0.0001$; L2, $x^2 = 10.0042$, d.f. = 1, $p = 0.0016$; L3, $x^2 = 4.5749$, d.f. = 1, $p = 0.0337$; L4, $x^2 = 8.5539$, d.f. = 1, $p = 0.0034$; L5, $x^2 = 7.0770$, d.f. = 1, $p = 0.0082$)(Figure 6), Second, burial time increased with increasing carapace size in both species. Finally, the rate of change in burial time with increasing carapace size differed between species at each location.

Specifically, *M. magister* and *C. productus* regressions at Site 1 were not significantly different in regards to slope (t ratio = 0.35, d.f. = 44, $p = 0.7278$) but were significantly affected by carapace width (t ratio = 5.46, $p < 0.0001$) and species (ANCOVA t ratio = 5.16, $p < 0.0001$). Similarly, at Site 2, the regression lines do not differ in slope (t ratio = -0.79, d.f. = 36, $p = 0.4329$) but showed significant effects of carapace width (t ratio = 5.36, $p < 0.0001$) and species (ANCOVA t ratio = 5.06, $p < 0.0001$). *C. productus* at Site 3 and Site 4 had significantly more difficulty burying with increasing carapace size than did *M. magister* (Site 3 t ratio = 3.42, d.f. = 35, $p < 0.0017$; Site 4 t ratio = 3.60, d.f. = 30, $p < 0.0012$). Rates did not differ at Site 5 (t ratio = 0.91, d.f. = 34, $p = 0.3718$) but speed of burial at the site was significantly affected by carapace width (t ratio = 5.44, $p < 0.0001$) and species (ANCOVA t ratio = 4.67, $p < 0.0001$).

Within a species, the size distributions of Dungeness crabs and red rock crabs used in burial speed tests were the same at all sites (*M. magister* $x^2 = 1.4967$, d.f. = 4, $p < 0.8272$; *C. productus* $x^2 = 0.8221$, d.f. = 4, $p < 0.9355$). Analysis of the burial speeds of *M. magister* across the sites revealed that Dungeness crabs do not bury significantly faster in any of the tested sediments (f ratio = 0.7452, d.f. = 4, $p = 0.5635$). There were, however, significant differences in burial speed among locations for *C. productus* (f ratio = 17.8834, d.f. = 5,

$p < 0.0001$). The rate of red rock burial with increasing carapace size was significantly higher at Site 4 other sites (f ratio = 5.3656, d.f. = 4, $p = 0.0008$). Additionally, homogeneity in the error variances of for red rock crabs allowed for an analysis of the rate at which burial time increases with increasing carapace size at each location (sec/mm). This analysis showed that the rates of burial for Sites 1 and 2 were equivalent and that burial rates at Sites 3 and 5 were significantly lower than at site 4.

Morphometric analysis

The chelae of *C. productus* are morphologically more robust than *M. magister*. Analysis of chela length and width reveal that *C. productus* claws are longer relative to carapace length than *M. magister* claws (ANCOVA t ratio = 3.70, d.f. = 24, $p = 0.0012$) (Table 1). Additionally, chelae widths increase with carapace size at a significantly higher rate in *C. productus* than *M. magister* (ANCOVA t ratio = 2.46, d.f. = 24, $p = 0.0224$).

Morphological measurements revealed significant differences in surface area on the prodopuses of the posterior and anterior pereopods (Figure 7). *M. magister* has significantly more surface area on its anterior prodopus at any given carapace size ($\chi^2 = 5.4697$, d.f. = 1, $p < 0.0193$) but not on the posterior prodopus ($\chi^2 = 3.4091$, d.f. = 1, $p = 0.0648$). Measurements of prodopus thickness did not reveal significant differences in posterior ($Z = -0.1232$, $n = 24$, $p = 0.9020$) and anterior limbs ($Z = -0.8325$, $n = 24$, $p = 0.4051$). The posterior angle on Dungeness crabs was significantly sharper than the posterior angle on red rock crabs ($Z = -4.069$, $n = 24$, $p = 0.0001$) (Figure 8).

Preference tests

Preference trial results were analyzed by looking at the final sediment choice of each organism after a 24 hour period. Size distributions between species in the preference trials were not different ($\chi^2 = 3.5487$, d.f. = 1, $p < 0.0596$). In neither species was there a significant preference or aversion for any particular sediment type (*C. productus* $X^2 = 7.25$, d.f. = 4, $p > 0.05$; *M. magister* $X^2 = 7.8$, d.f. = 4, $p > 0.05$). The highest ranked choice for *C. productus* was for Site 5 (9 out of 24 crabs) and only one crab selected the sediment from Site 4 (Figure 9). The lowest ranked site for *M. magister* was also the number 4 site from Argyle Lagoon, with the highest preferences shown for Sites 1 and 2 (7 of 24 crabs in sediment 1, 9 of 24 crabs in sediment 2).

Discussion

The field-based burial trials convincingly demonstrate that *Metacarcinus magister* and *Cancer productus* are not limited in their habitat choice by their burying ability. Both species achieved burial in sediments varying in a two-fold difference in stiffness and varying composition demonstrating that they are not limited from any of these habitats because of the difficulty of burial. Similarly, the disparity between where the species are found and which sediments they prefer suggests that natural distribution is not limited by sediment preference.

Despite being found nearly exclusively in sandy habitats and eelgrass beds, *Metacarcinus magister* buried more quickly than *Cancer productus* in all sediments. The even performance in *M. magister's* burial times suggests that the Dungeness crabs should actually be considered a sediment generalist in terms of burial ability. Not only was *M.*

magister capable of burying in each sediment, it also buried at a similar rate in each sediment. Specifically, while Dungeness crabs are found primarily in sand (Pauley *et al.*, 1986), these results suggest that they can bury equally quickly in cobble-rich sediment and sediment with high fractions of mud and silt. The lack of a significant difference in burial speed between Site 2 (where the Dungeness crabs are naturally found) and the other sites (where Dungeness crabs were not found) illustrates that burial ability is not the limiting factor in their choice of habitat. Given their burial ability, we would expect to have found Dungeness crabs in all of these locations if it were merely their physical limitations that restricted their habitats. Instead, Dungeness crabs were found in only one of these possibilities.

Examining the preference trends suggests a similar story. Dungeness crabs chose to bury themselves most frequently in sediments from Sites 1 and 2 and yet were found only at Site 2. As with their burial abilities, the habitats where we actually found *M. magister* was restricted compared to the range of sediments they chose in the preference trials.

In contrast, *C. productus* buried at varying rates in different sediments and always at slower rates than *M. magister*. Notably, *C. productus* was relatively slow to bury at the cobble dominated site 4 and larger crabs took a disproportionately long time to bury there relative to other sites (Figure 3). This suggests that perhaps red rock crabs are the sediment specialists with striking differences in burial performance at different field sites despite being categorized as habitat generalists (McGaw, 2005; Carroll and Winn, 1989, Schmitt, 1921, Becker, 1996; Becker and Wahl, 1996)

In a slightly different way than with the Dungeness crabs, the natural distribution of red rock crabs is at odds with the locations where they are most efficient at burial. Notably, *C. productus* is found in rocky habitats and cobble bottoms (Carroll and Winn, 1989) and yet this is the location where their burial was slowest. Assuming that burying ability is a major factor in habitat choice, we would have expected to see red rock crabs inhabiting Sites 1, 2, 3 and 5 and avoiding Site 4. The low frequency of red rock crabs choosing sediment from Site 4 during the preference trials supports this hypothesis. However, Site 4 is instead both a habitat reported to host *C. productus* and the only site where we noticed these crabs.

This compilation of data convincingly shows that burial ability is not the only factor influencing habitat choice in Dungeness and red rock crabs. Trends in the preference data suggest that sediment preference is also likely not a controlling factor in their natural distribution. It is probable that other variables are contributing to the variance in distributions for each of these species. In the case of *M. magister*, competition for space or resources with nonindigenous crabs such as *Carcinus maenas* (the green crab) has been suggested as a possible factor restricting Dungeness crabs' distribution to sand bottoms and eelgrass (McDonald *et al*, 2001). Similarly, competition for prey or space could explain the disparity in where *C. productus* buries most efficiently and where it tends to be found.

Alternatively, habitat choice could be linked to predation indirectly. For example, rather than choosing environments where burial is easiest and used as the primary escape from predators, crabs might choose an environment with fewer predators or one where burial is not the primary escape method. Red rock crabs, for instance, may choose a rocky

habitat precisely because they bury slowly overall but are offered greater cover and better camouflage in cobble areas (Stoner and Titgen, 2003). Thus, they can compensate for their slower burial by choosing a habitat where burial is not necessary. Similarly, Dungeness crabs may choose their habitats because their carapaces are cryptic in sand backgrounds and eelgrass offers cover and protection from predation (Hovel, 2003). In these cases, it is the structural complexities of these habitats that the species would be choosing rather than the properties of the sediment. Such a pattern would prove useful for fisheries dedicated to understanding these crustaceans and is in contrast to patterns seen in other species of marine organisms.

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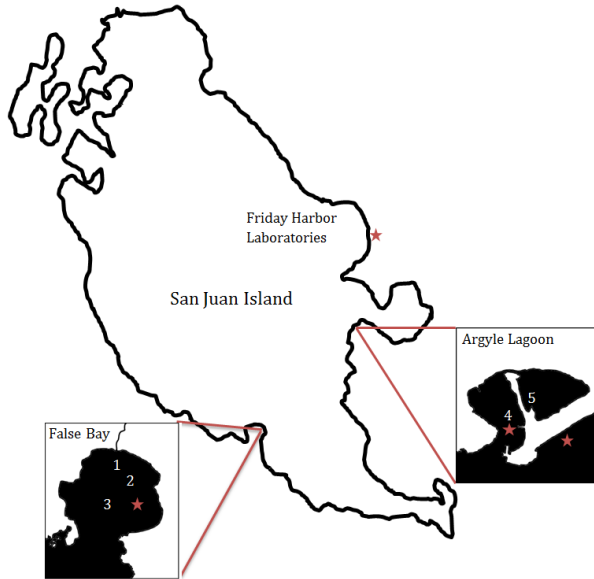
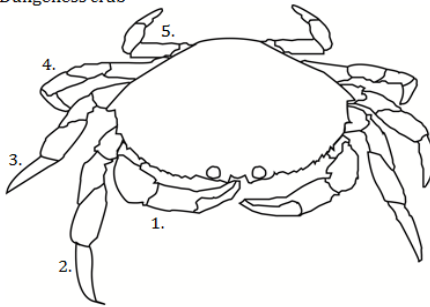


Figure 1. Dungeness and red rock crabs were collected from four locations (red symbols) on San Juan Island and kept in sea tables at the Friday Harbor Laboratories. Burying efficiency was tested at five field locations, three at False Bay and two at Argyle Lagoon. Stiffness measurements and sediment cores were also taken at each of these sites.

A. *Metacarcinus magister*,
the Dungeness crab



B. *Cancer productus*,
the red rock crab

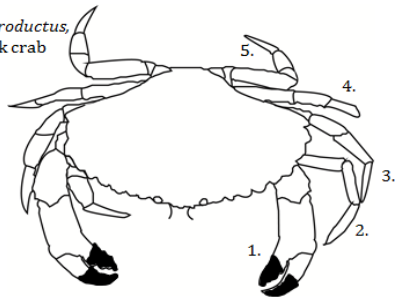


Figure 2. Outlines of the body and claw of the Dungeness crab, *Metacarcinus magister* (A. and C.) and the red rock crab, *Cancer productus* (B. and D.). Leg numbers (1-5) are associated with the description of burial behavior in the text. Both claws are shown from the frontal view; the brackets indicate the dimensions taken for the morphometric analysis (I., claw width. II., claw length).

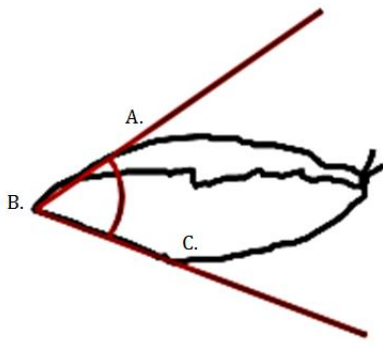


Figure 3. The angle of the posterior wedge (formed by the conjunction of the carapace and abdomen) was measured using the same three points on each crab. A., the peak of the carapace directly above the largest tooth on the margin of the carapace (8th tooth in *C. productus*, the 10th in *M. magister*), B., the most posterior point of the carapace and C., the posterior side of the third pereopod's attachment joint to the abdomen (Leg 4 from Fig. 1).

Figure 4. Average stiffness \pm standard deviation of sediments from five field locations. Stiffness was tested with a penetration test measuring the yield of each substrate when placed under force. Five replicate sets of stiffness measurements were taken at each location. * Data were omitted from the fourth site in cases where there was no penetration due to contact with a cobble.

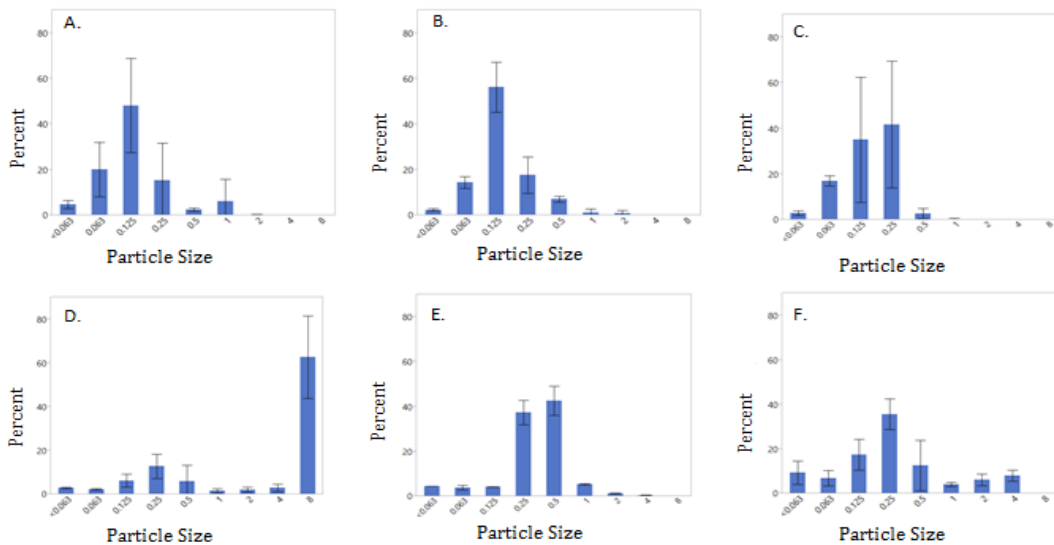
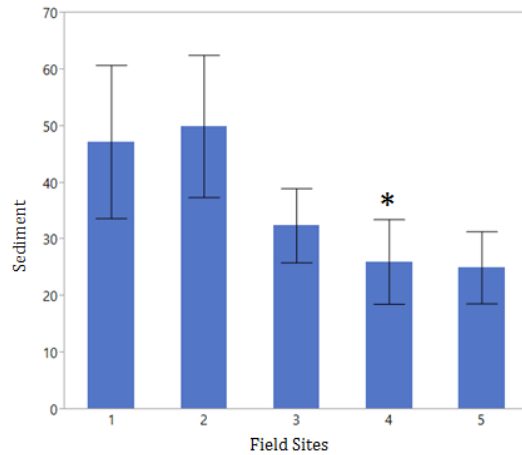


Figure 5. Frequency distributions by particle size and mean weight \pm standard deviation from three sediment cores taken at each field site. Cores were taken from False Bay Sites (A., B. and C.) and Argyle Point (D. and E.). Site D. was composed of 62.6% cobbles (particles > 2mm). F. is a modified version of D. showing composition with the largest particles removed.

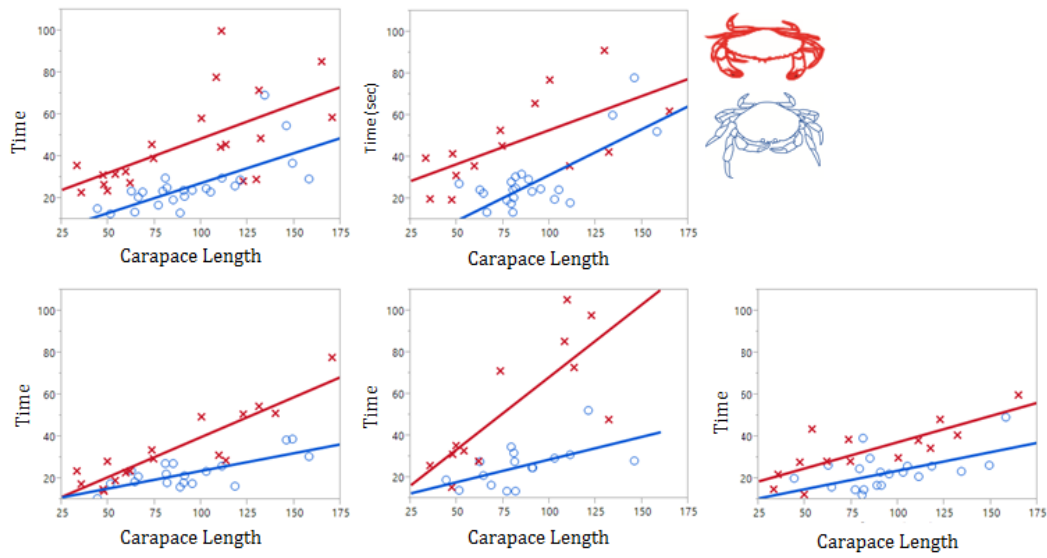


Figure 6. Burial speeds of Dungeness (blue symbols) and red rock (red symbols) crabs at five different field sites on San Juan Island, WA (see Figure 1). Crabs were transported to five field locations and given the chance to bury in the sediment. Dungeness crabs buried more quickly than red rock crabs in all five sediments. Larger crabs of each species took longer to bury than smaller ones of the same species at each site. Additionally, Dungeness crabs buried in higher numbers in each location.

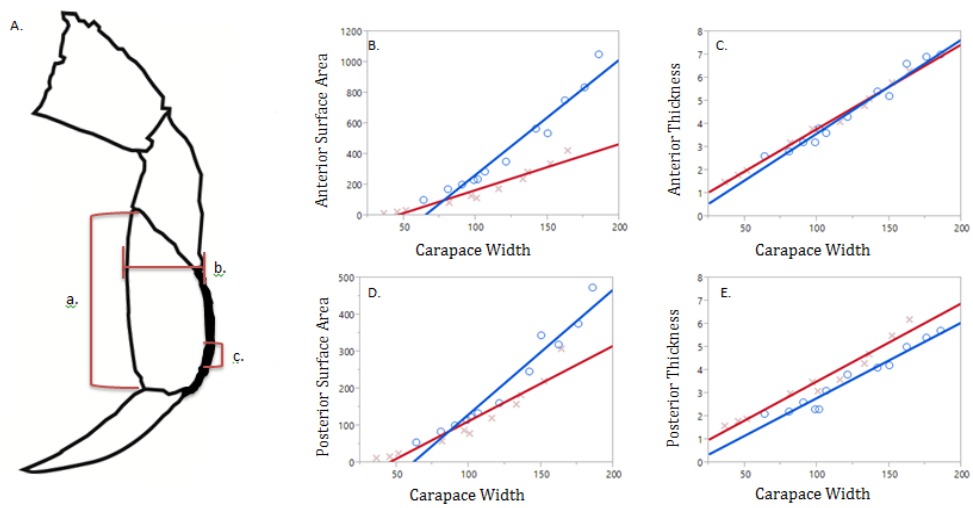


Figure 7. Comparison of the morphology of the anterior and posterior propoduses of Dungeness (blue symbols) and red rock (red symbols) crabs. A. Diagram of a leg where measurements were made (a. length, b. width, c. thickness) on the propodus (the second most distal segment of the leg). Length and width were multiplied together to get an estimate of the frontal surface area of the anterior (B) and posterior (D) propoduses which is consistently larger in Dungeness crabs. There is no difference in the thickness of the anterior propodus of the two species (C), however the rock crabs have a thicker posterior propodus (E).

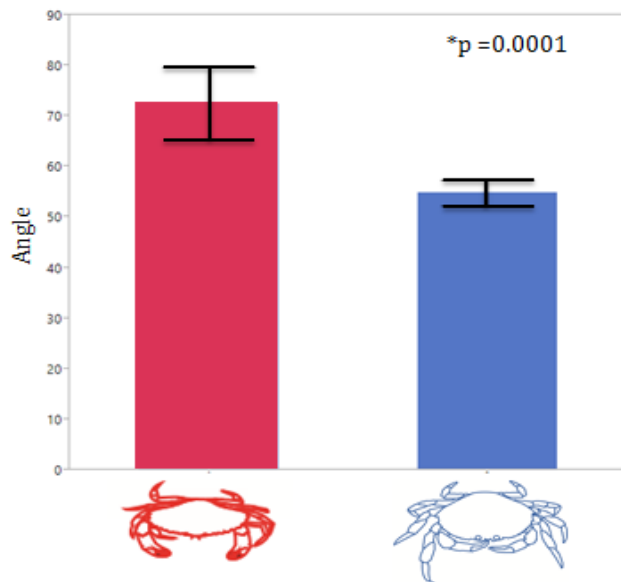


Figure 8. Average posterior angle \pm standard deviation from across a size series of Dungeness (blue) and red rock (red) crabs. Dungeness had significantly sharper angles than red rock crabs ($p=0.0001$). However, no association was found between angle sharpness and carapace width.

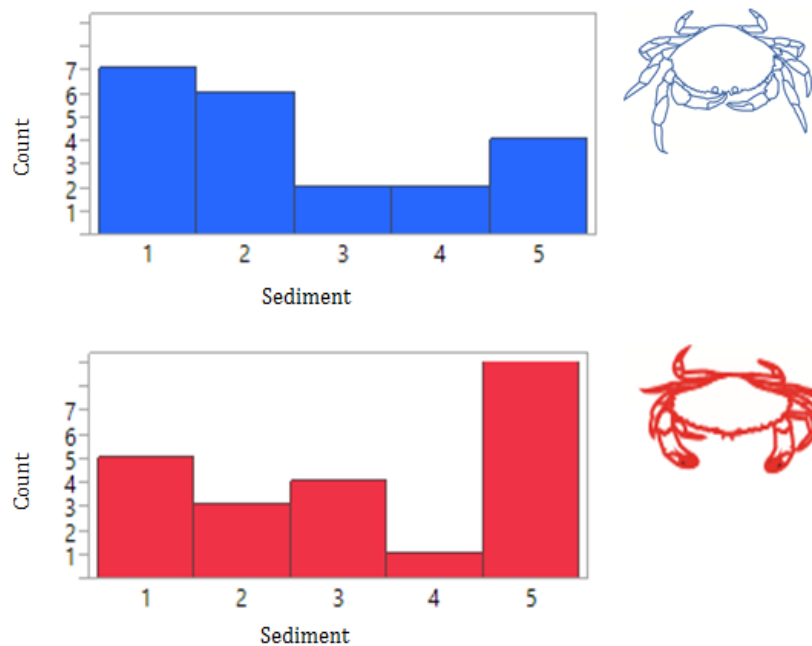


Figure 9. Sediment preferences of Dungeness and red rock crabs from microcosm experiments. Dungeness (blue) and red rock (red) crabs were given twenty four hours to explore five different sediments before their final burial location was noted. Dungeness crabs tended to prefer well sorted sediments (choices 1, 2 and 5) whereas red rock crabs tended to avoid large particles and selected against the mud/cobble mixture where they are most commonly found (choice 4). Sediments were collected from the field as indicated in Fig. 1, origin of sediment is indicated by numbers 1-5.

Measurement	<i>M. magister</i> slope	<i>C. productus</i> slope	p-value	Proposed Function	Species w/ Advantage
Chela length	0.488	0.515	ANCOVA t=3.70, df=24, p=0.0012	Claw closing (crushing)	<i>C. productus</i> *
Chela width	0.202	0.254	ANCOVA t=2.46, df=24, p=0.0224	Claw closing (crushing)	<i>C. productus</i> *
Anterior prodopus surface area	7.505	3.000	$\chi^2 = 5.4697$, df=1, p<0.0193	Moving sediment or fluid	<i>M. magister</i> *
Anterior prodopus depth	0.041	0.037	n=24, z=- 0.8325, p= 0.4051	Moving through sediment or fluid	no diff
Posterior prodopus surface area	3.377	2.037	$\chi^2 = 3.4091$, df=1, p=0.0648	Moving sediment of fluid	no diff
Posterior prodopus depth	0.033	0.034	n=24, z=- 0.1232, p= .9020	Moving through sediment or fluid	no diff
Posterior angle	$\bar{x}=54.782 \pm 2.5$ 4	$\bar{x}=72.427 \pm 7.$ 25	n=24, z=- 4.069, p= 0.0001	Leading through sediment or fluid	<i>M. magister</i> *

Table 1. Morphometric analysis comparing anatomical sizes across a size series in both species. Insignificant differences were found in the relative posterior and anterior prodopus depth and posterior prodopus surface area across a size series between the two species. *C. productus* had significantly larger chelae (both width and length) proportional to its carapace while *M. magister* had significantly more surface area on its anterior prodopus relative to its carapace size and a significantly narrower posterior angle.