A Tail of Two Sexes: Sexual Disparity in Brachyuran Crustaceans and Its Impact on Arthropod Trunk Evolution

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Abstract

Arthropods are well known for being rampantly speciose. Variation of form and niche-occupation in arthropods relies on specialized appendages and regionalization of a common bauplan. The specialization of particular body regions leads to displays of sexual dimorphism. Cases of intraspecies morphotypes and sexual dimorphic characters reflect larger trends of morphological variation in all major arthropod clades. Here, I report a morphospace of sexually dimorphic brachyuran crustaceans from the San Juan Islands in the Pacific Northwest and discuss inter- and intraspecies variation as it pertains to marine arthropods as whole. Abdominal shape changes in sexes of *Cancer* and *Hemigrapsus* were evaluated using geometric morphometrics and Principal Components Analysis (PCA). Traditional morphometrics, measuring the dimensions of the carapace were also incorporated. The abdominal and body shape disparity between genders of both genera is found to be statistically significant through an analysis of variance (ANOVA) statistical comparison test. Sexual dimorphism is not conserved in interspecies or in intraspecies relationships. *Hemigrapsus* specimens exhibit a higher degree of sexual dimorphism than *Cancer* specimens. The morphological results reveal ecological effects and macroevolutionary trends resulting from sexual dimorphism of the arthropod bauplan.

INTRODUCTION

Reproductive characters and sexual dimorphism in malacostracan decapods is well known (Orensanz et al. 1995, Spotte 1997, Booksmythe 2011). However, sexual disparity over the entire body shape is seldom quantified. With a quick observation of the abdomen on the underside of most crabs even a non-specialist can distinguish genders; a tapering, triangular, abdomen indicates a male, whereas females have a broadening, curved abdomen typically used for brooding eggs. Although sexual dimorphism in Crustacea as a whole is becoming understood (Baltanás 2002), the extent to which gender-based character morphology varies within Decapoda remains unreported. Therefore, the relationship between sexual dimorphism and ecological and macroevolutionary effects within decapod clades remains uncertain (Shine 1989).

Potential shape overlap of decapod males and females could result in sneaker males or cases where females with a relatively narrow abdomen and individual males with a relatively wide abdomen could be mistaken for the wrong gender. The disparity displayed between sexes and between species may not be limited to the abdomen. Sexual dimorphism displayed in the posterior segments may produce gender-identifying characters in other body regions, including the cephalon or thorax. If sexual disparity is observed across the entire body shape, one may be able to predict genders when abdominal characters are not present. Body regionalization patterns at all levels of Arthropoda (Minelli 2001, Hughes 2007) are of macroevolutionary interest (Abzahanov 2000, Adamowicz et al. 2008).

Pacific Northwest coastal marine arthropods commonly include groups of crabs, shrimp, isopods, and barnacles. Members of Brachyura or true crabs, yield the most compact form of the decapod body plan. Like other decapods, the cephalon and thorax are combined into a single carapace called the cephalothorax. Unlike other decapods, however, the abdomen is not used for locomotion, but instead is tucked underneath the rest of the body. In some cases, abdominal segments are fused. Within the true crabs, members of the families Grapsidae and Cancridae appear frequently in the intertidal

Salish Sea (Cowles 2005). Therefore, members of the genera *Hemigrapsus* and *Cancer* are of statistical and ecological importance to the area. Here, I analyze biometric sexual dimorphism exhibited between genders of *Cancer* and *Hemigrapsus* crabs from the San Juan Islands in Washington and consider the patterns of abdominal disparity within those groups.

METHODS

I compiled a dataset consisting of the intertidal crabs *Cancer productus, Cancer magister, Cancer gracilis, Cancer oregonensis*, and *Hemigrapsus nudus*. *Cancer* specimens were collected opportunistically from various sites on the San Juan Islands (Figure 1). *Hemigrapsus* individuals were photographed on the beach at Friday Harbor Laboratories on San Juan Island, Washington. A catch-photograph-release approach saved room in the laboratory collections, and ultimately enabled access to more specimens in a shorter time frame. Dorsal and ventral photographs (Figure 2) along with carapace measurements were obtained of the organisms. A standard orientation was implemented, allowing for the diagnostic features to be at a level plane parallel to the camera lens.

Traditional morphometric data included length and width dimensions of the carapace (Figure 3, A). Length measurements were taken from the tip of the rostrum to the center point of the carapace posterior. Maximal width was measured between the tips of the posterior-most spine. Landmarks for geometric analysis of the abdominal outline (n=9) were chosen based on common morphological points between the male and female species that captured maximal disparity. The landmarks surround the ultimate (telson), penultimate and antepenultimate segments of the abdomen (Figure 3, B).

Raw images were corrected for contrast, brightness and color in PhotoShop CS6. ImageJ was used to digitize landmark data with the software plug-in Point Picker (Abramoff 2004). Data points and measurements were collected and organized in Microsoft Excel before being exported via text file to MorphoJ (Klingenberg 2011).

MorphoJ was used for primary morphological analysis. After applying a procrustes fit to the landmark data, I generated a covariance matrix in MorphoJ. The procrustes fit removed variations in size, translation, and rotation between the specimens. With the covariance matrix, I conducted a principal components analysis (PCA) on each of the species individually and each sex separately. A calculated procrustes distance from average shape was obtained for each specimen and compared to respective carapace dimensions of length and width. Lastly, analysis of variance (ANOVA) tested for statistical variance between sexes (primary classifier effect) and species (additional main effect).

RESULTS

I report comparative morphological results from *Cancer productus*, *Cancer oregonensis*, and *Hemigrapsus nudus*. Principal components analysis was used to assess sexual dimorphism in all three species. Principal Component 1 (PC1) accounts for 90.1% of shape variation between the genders of specimens. Together, PC1 and PC2 make up more than 97% of the total variation. Plots of PC1 and PC2 effectively distinguished sexes of *C. productus*, *C. oregonensis*, and *H. nudus*. PCA of both *Cancer* and *Hemigrapsus* not only separate the organisms by species but also by sexes within the species. Procrustes ANOVA found the sexual disparity between species to be highly significant ($p > 0.0001$, Table 1.). Positive correlation between average procrustes distance and carapace dimensions could be found in females of all three species, but not in any of the males. Complete results on all measured specimens can be found in Table 2.

DISCUSSION

I have quantitatively shown that male and female brachyuran crustaceans are morphologically different. While the proving the presence of sexual dimorphism is trivial, quantifying the disparity between sexes of different species is of ecological and evolutionary interest. Sexual dimorphism displayed in *Hemigrapsus* is significantly greater than that displayed in *Cancer*. However, the abdominal disparity within *Hemigrapsus* sexes is noticeably less than that of either *C. productus* or *C. oregonensis*. In other words, *Hemigrapsus* males and females are quite distinct from each other, but morphological variation within each sex is relatively low. In observed *Cancer* specimens, on the other hand, sexual dimorphism is barely recorded in *C. oregonensis* but present to some degree in *C. productus*. I conclude that intraspecies variation is strongest in *H. nudus* and weakest in *C. oregonensis* (Figure 4).

Interspecies variation, as evident in the PCA, uniquely favors a correlation of male abdominal forms. The male morphologies are more similar to each other than the female forms. This may suggest that the male morphotype was a precursor evolutionarily to the female form. Alternatively, if the forms evolved contemporaneously, the variations in female form may represent some ecological factor.

The sampled organisms are taxonomically and geographically related, however, the two genera occupy very different nice spaces in the intertidal. *Hemigrapsus* are found fairly high in the intertidal and are found in high population density (evident by the opportunistically-collected sample distribution) than *Cancer* crabs. *C. productus* and *C. oregonensis* are found lower in the intertidal and in seldom found in large groups. If population size is a driving factor in sexual dimorphism, female *Hemigrapsus* may rely on the morphological disparity to be identified as reproductively mature under a crowded rock. Links between sexual dimorphism and reproductive success are not so far fetched. Ecologically, *Cancer* crabs are essential members of the intertidal food web as predators, scavengers, and generally sloppy feeders. A uniform morphology may favor ecological success in *C. productus* and *C. orgeonensis*, thus minimizing sexual dimorphism. The reasons behind sexual dimorphism are many and vary greatly between clades, but the effects acting on the brachyuran crabs may provide insight into other arthropod clades.

Because the abdominal dimorphism is striking, it may betray other aspects of sexual disparity that have been overlooked. This would be a valuable tool for determining genders of arthropods with missing abdomens, fossil cases where the abdomen is not preserved, or ancient clades where the gender is unknown. For example, in the stem group arthropods, the trilobites, gender morphologies are unresolved. Similarly, eurypterids possess definitive sex appendages but it is unclear which appendage belongs to which gender, although progress is being made rapidly on this front (Vrazo 2011). Interspecies and intraspecies sexual disparity in trilobites and eurypterid is anticipated to be as significant as that of recent brachyurans. By comparing the average procrustes distance to carapace dimensions in the brachyuran crustaceans, I found a strong positive correlation in females and absent in males (Figure 5). As the abdomen leans more toward the female morphotype, effects are seen across the carapace length and width. The correlation may suggest a link between the evolution of the female abdomen and its effect on the cephalothorax; a link is not observed in males. Sexual dimorphism and its effect on regionalization of the arthropod body plan are of macroevolutionary importance and should be investigated in future reports.

Error caused by movement of living specimens in relation to the plane of the camera lens was minimized with multiple photographs per specimen (n>6). Human error caused by consistent selection of landmark points across data files was minimized with high-resolution (18 megapixels) images. Additional assessment of experimentation along with improvements will be considered in this paragraph. The dataset would greatly benefit from the addition of more brachyuran clades, particularly, families Majidae and Portunidae. Given more time and opportunity to collect, I would incorporate specimens of these groups. Nevertheless, Grapsidae and Cancridae were morphologically compelling while representing ecologically important roles that enabled the successful completion of this project.

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TABLE 1. ANOVA results table with sexes as the primary classifier effect and species as the additional main effect overall N=121 specimens.

Source	SS	d.f.	MS	F-Score	P-Value
JW000	2.11822	9	0.23535	5.32	<0.001

TABLE 2. Specimen dataset (N=121) used for analysis.

JW###	Name	Location	Sex	Length	Width	Procrustes Distance
JW001	Cancer productus	Lab 3	F	7.8	12.6	24.21
JW002	Cancer productus	Lab 3	M	8.4	15.3	13.96
JW003	Cancer productus	Lab 3	M	5.9	9.5	14.98
JW004	Cancer productus	Lab 3	M	6.1	10.1	11.83
JW005	Cancer gracilis	Lab 3	F	6	8.7	53.64
JW006	Cancer productus	Lab 3	F	6.1	9.9	50.63
JW007	Cancer productus	Lab 3	M	9.6	16.4	35.78
JW008	Cancer productus	Lab 3	F	7.5	11.6	29.81
JW009	Cancer productus	Lab 3	F	6.7	10.6	23.53
JW010	Cancer productus	Lab 3	F	5.9	9.5	21.5
JW011	Cancer productus	Lab 3	F	5.2	7.8	18.2
JW012	Cancer productus	Lab 3	F	8	11.7	76.65
JW013	Cancer productus	Lab 3	M	7.5	11.7	19.61
JW014	Cancer magister	Lab 3	M	6.7	10.8	48.79
JW015	Cancer productus	Lab 3	M	5.6	8.8	14.39
JW016	Cancer productus	Lab 3	F	5.6	9	21.02
JW017	Hemigrapsus nudus	FHL Beach	M	2.2	2	40.04
JW018	Hemigrapsus nudus	FHL Beach	M	1.2	1.3	35.1
JW019	Hemigrapsus nudus	FHL Beach	M	1.7	2	25.77
JW020	Hemigrapsus nudus	FHL Beach	M	1.8	2	12.81
JW021	Hemigrapsus nudus	FHL Beach	F	1.5	1.75	10.36
JW022	Hemigrapsus nudus	FHL Beach	M	1.5	1.7	14.84
JW023	Hemigrapsus nudus	FHL Beach	F	1.6	1.8	13.34
JW024	Hemigrapsus nudus	FHL Beach	F	1.3	1.5	6.75
JW025	Hemigrapsus nudus	FHL Beach	F	1.5	1.7	7.89
JW026	Hemigrapsus nudus	FHL Beach	F	1.65	2	12.94
JW027	Hemigrapsus nudus	FHL Beach	F	1.2	1.4	11.96
JW028	Hemigrapsus nudus	FHL Beach	F	1.7	2	11.61
JW029	Hemigrapsus nudus	FHL Beach	M	1.6	1.8	23.65
JW030	Hemigrapsus nudus	FHL Beach	F	1.3	1.55	14.22
JW031	Hemigrapsus nudus	FHL Beach	F	1.25	1.4	6.41
JW032	Hemigrapsus nudus	FHL Beach	M	2	2.2	15.95
JW033	Hemigrapsus nudus	FHL Beach	M	1.6	1.7	13.2
JW034	Hemigrapsus nudus	FHL Beach	F	1.4	1.6	8.77
JW035	Hemigrapsus nudus	FHL Beach	F	1.55	1.7	4.87
JW036	Hemigrapsus nudus	FHL Beach	F	1.5	1.7	5.35
JW037	Hemigrapsus nudus	FHL Beach	M	1.9	2.15	8.27
JW038	Hemigrapsus nudus	FHL Beach	F	1.4	1.65	5.53
JW039	Hemigrapsus nudus	FHL Beach	F	1.7	1.95	7.87
JW040	Hemigrapsus nudus	FHL Beach	M	1.6	1.7	12.04
JW041	Hemigrapsus nudus	FHL Beach	F	1.45	1.6	13.43
JW042	Hemigrapsus nudus	FHL Beach	F	1.85	2.2	8.85
JW043	Hemigrapsus nudus	FHL Beach	F	1.6	2	11.17
JW044	Hemigrapsus nudus	FHL Beach	M	1.3	1.5	12.22
JW045	Hemigrapsus nudus	FHL Beach	M	1.4	1.6	7.15
JW046	Hemigrapsus nudus	FHL Beach	F	1.4	1.5	11.43
JW047	Hemigrapsus nudus	FHL Beach	F	1.4	1.7	3.43
JW048	Hemigrapsus nudus	FHL Beach	M	1.2	1.4	15.24
JW049	Hemigrapsus nudus	FHL Beach	F	1.7	1.9	6.21
JW050	Hemigrapsus nudus	FHL Beach	F	1.4	1.7	4.65
JW051	Hemigrapsus nudus	FHL Beach	F	1.55	1.8	10.89
JW052	Hemigrapsus nudus	FHL Beach	M	1.8	1.9	16.59
JW053	Hemigrapsus nudus	FHL Beach	M	1.3	1.4	11.83
JW054	Hemigrapsus nudus	FHL Beach	M	1.5	1.6	14.1
JW055	Hemigrapsus nudus	FHL Beach	M	1.4	1.6	12.84
JW056	Hemigrapsus nudus	FHL Beach	M	2	2.3	10.05
JW057	Hemigrapsus nudus	FHL Beach	F	1.3	1.4	12.24
JW058	Hemigrapsus nudus	FHL Beach	M	1.4	1.6	8.36
JW059	Hemigrapsus nudus	FHL Beach	F	1.4	1.6	5.96
JW060	Hemigrapsus nudus	FHL Beach	F	1.6	1.95	6.65

JW###	Name	Location	Sex	Length	Width	Procrustes Distance
JW061	Hemigrapsus nudus	FHL Beach	M	1.8	2.1	20.98
JW062	Hemigrapsus nudus	FHL Beach	F	2	2.3	4.51
JW063	Hemigrapsus nudus	FHL Beach	M	1.7	1.85	11.65
JW064	Hemigrapsus nudus	FHL Beach	F	1.55	1.75	4.99
JW065	Hemigrapsus nudus	FHL Beach	F	1.65	1.8	6.9
JW066	Hemigrapsus nudus	FHL Beach	F	2.3	2.7	17.04
JW067	Hemigrapsus nudus	FHL Beach	F	1.75	2	5.32
JW068	Hemigrapsus nudus	FHL Beach	M	1.4	1.6	12.36
JW069	Hemigrapsus nudus	FHL Beach	M	1.4	1.65	20.95
JW070	Hemigrapsus nudus	FHL Beach	M	1.4	1.6	13.37
JW071	Hemigrapsus nudus	FHL Beach	F	1.4	1.55	8.49
JW072	Hemigrapsus nudus	FHL Beach	M	1.5	1.7	6.59
JW073	Hemigrapsus nudus	FHL Beach	M	2.5	2.85	5.91
JW074	Hemigrapsus nudus	FHL Beach	F	1.6	1.95	6.62
JW075	Hemigrapsus nudus	FHL Beach	F	1.85	2.15	9.38
JW076	Hemigrapsus nudus	FHL Beach	F	1.7	2	13.59
JW077	Hemigrapsus nudus	FHL Beach	F	1.55	1.8	12.13
JW078	Hemigrapsus nudus	FHL Beach	M	1.2	1.4	14.48
JW079	Hemigrapsus nudus	FHL Beach	M	1.3	1.4	18.46
JW080	Hemigrapsus nudus	FHL Beach	F	1.5	1.8	4.45
JW081	Hemigrapsus nudus	FHL Beach	F	1.6	1.95	7.43
JW082	Hemigrapsus nudus	FHL Beach	F	1.3	1.6	6.68
JW083	Hemigrapsus nudus	FHL Beach	F	1.2	1.4	19.6
JW084	Hemigrapsus nudus	FHL Beach	M	1.3	1.5	21.4
JW085	Hemigrapsus nudus	FHL Beach	F	1.65	2	6.82
JW086	Hemigrapsus nudus	FHL Beach	F	1.6	1.8	4.17
JW087	Hemigrapsus nudus	FHL Beach	M	1.7	2	9.36
JW088	Hemigrapsus nudus	FHL Beach	M	1.35	1.5	28.77
JW089	Hemigrapsus nudus	FHL Beach	F	1.4	1.7	10.42
JW090	Cancer productus	Snug Harbor	F	4.8	7.6	12.58
JW091	Cancer productus	Snug Harbor	M	4.8	7.5	13.34
JW092	Cancer productus	Snug Harbor	F	4.9	7	16.16
JW093	Cancer productus	Snug Harbor	M	4.4	6.7	18.16
JW094	Cancer productus	Snug Harbor	F	4.2	5.9	24.84
JW095	Cancer productus	Snug Harbor	F	3.8	5.8	16.7
JW096	Cancer productus	Snug Harbor	F	3.6	5.3	31.8
JW097	Cancer productus	Snug Harbor	M	3.5	5.4	11.61
JW098	Cancer productus	Snug Harbor	F	5.65	8.8	29.41
JW099	Cancer productus	Snug Harbor	M	4.7	8	11.47
JW100	Cancer productus	Snug Harbor	F	5	7.4	28.68
JW101	Cancer oregonensis	Snug Harbor	F	1.9	2.6	22.75
JW102	Cancer oregonensis	Snug Harbor	M	2.2	2.9	28.52
JW103	Cancer oregonensis	Snug Harbor	M	2.5	3.3	19.06
JW104	Cancer oregonensis	Snug Harbor	M	1.5	1.9	63.05
JW105	Cancer oregonensis	Snug Harbor	M	1.7	2.2	54.79
JW106	Cancer oregonensis	Snug Harbor	F	2.15	2.85	38.06
JW107	Hemigrapsus nudus	Snug Harbor	M	2.2	2.5	15.9
JW108	Hemigrapsus nudus	Snug Harbor	F	1.55	1.8	5.52
JW109	Cancer oregonensis	Snug Harbor	F	2.1	2.65	29.15
JW110	Hemigrapsus nudus	Snug Harbor	F	1.6	1.8	8.63
JW111	Hemigrapsus nudus	Snug Harbor	F	1.6	1.85	7.37
JW112	Cancer oregonensis	Snug Harbor	F	1.9	2.45	27.98
JW113	Cancer oregonensis	Snug Harbor	M	1.8	2.3	28.82
JW114	Cancer oregonensis	Snug Harbor	F	1.85	2.4	52.15
JW115	Cancer oregonensis	Snug Harbor	M	1.6	1.9	21.2
JW116	Cancer oregonensis	Snug Harbor	M	1.4	1.75	25.02
JW117	Cancer oregonensis	Snug Harbor	M	1.4	1.8	37.47
JW118	Cancer oregonensis	Snug Harbor	M	1.4	1.75	34.73
JW119	Cancer oregonensis	Snug Harbor	F	1.55	2.05	17.13
JW120	Cancer oregonensis	Snug Harbor	F	1.4	1.85	50.43
JW121	Cancer oregonensis	Snug Harbor	M	1.4	2	31.34

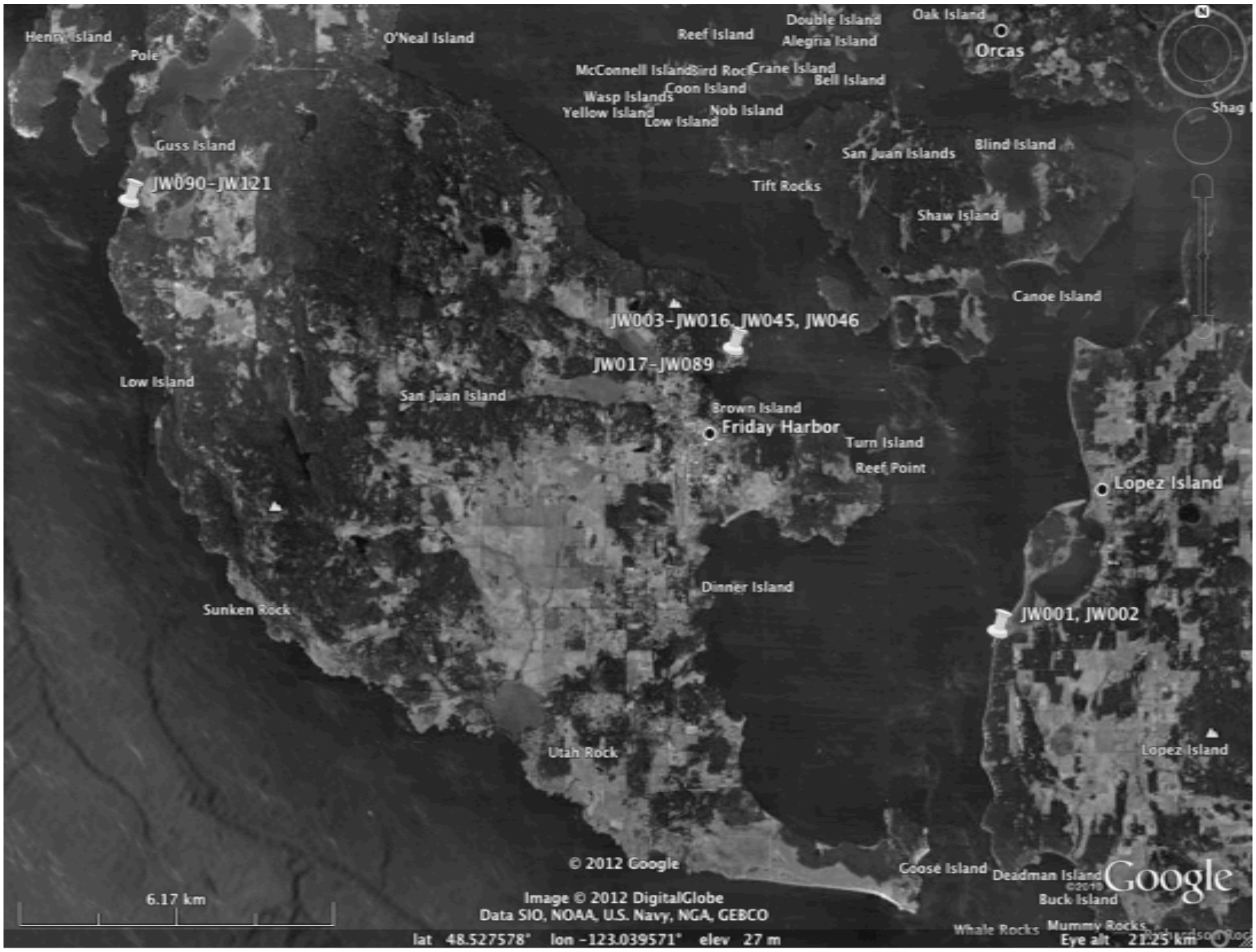

FIGURE 1. Specimen sites around San Juan Island. JW001, JW002 off Rock Point; JW003-JW0016 amassed in Lab 3 at Friday Harbor Laboratories; JW017-JW089 on Friday Harbor Beach; JW090-JW121 from Snug Harbor.

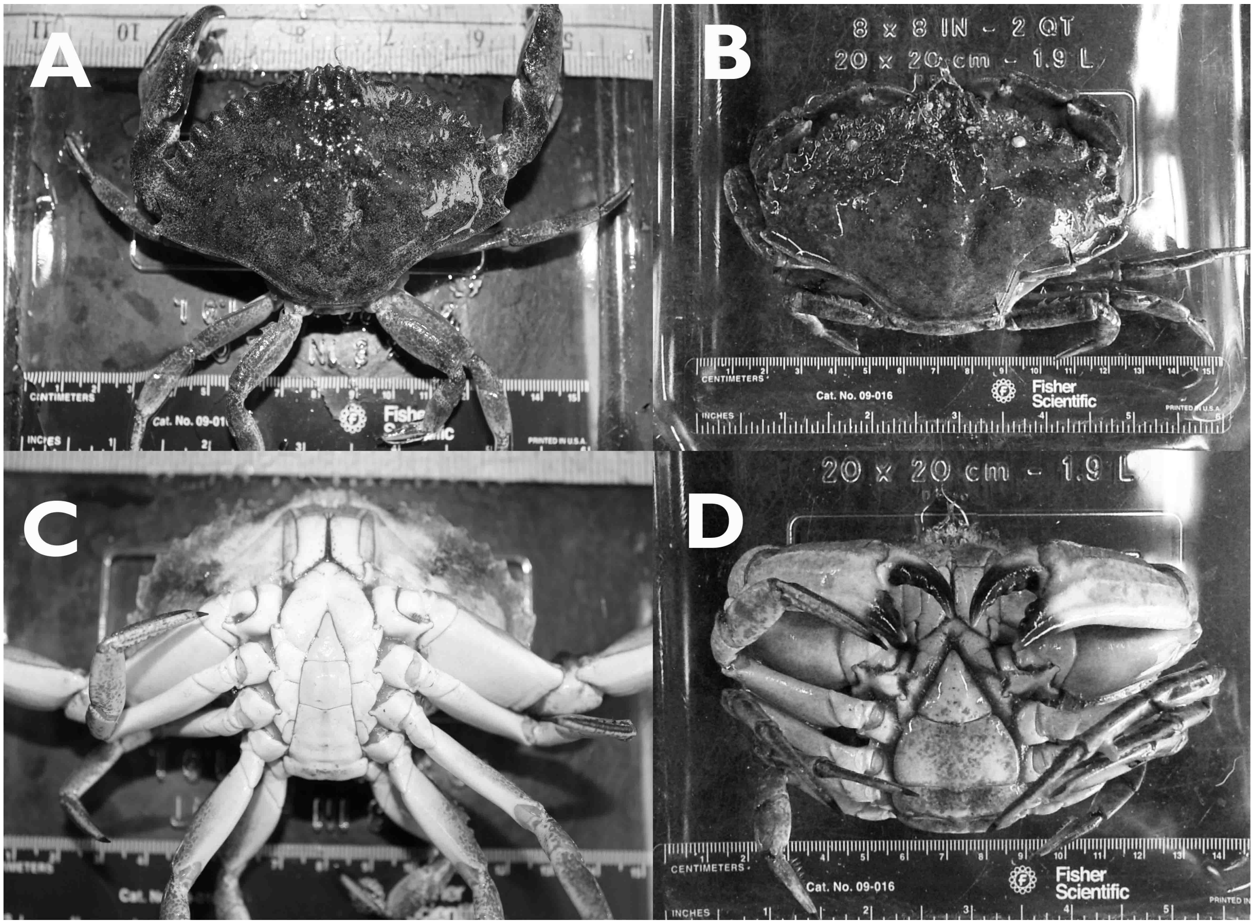

FIGURE 2. Dorsal (A,B) and ventral (C,D) photographs of male (A,C) and female (B,D) *Cancer productus* specimens; JW003 (A,C), JW016 (B,D). Photographed in Lab 3.

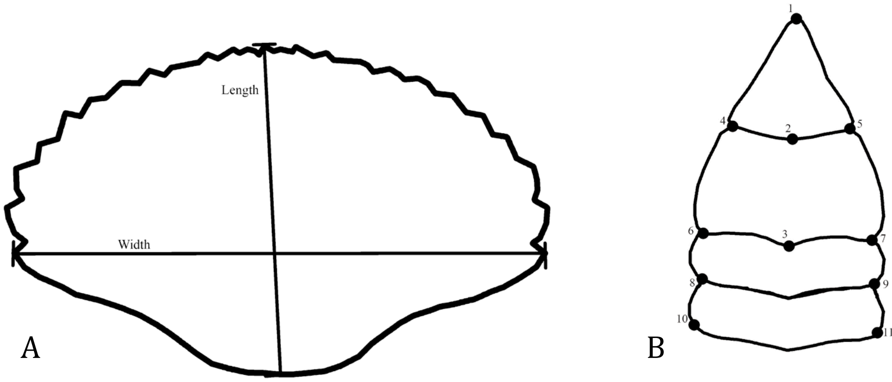

FIGURE 3. Carapace measurements (A) and landmarks (B) used to quantify specimen form. Landmarks were chosen to capture both male and female forms across all studied species.

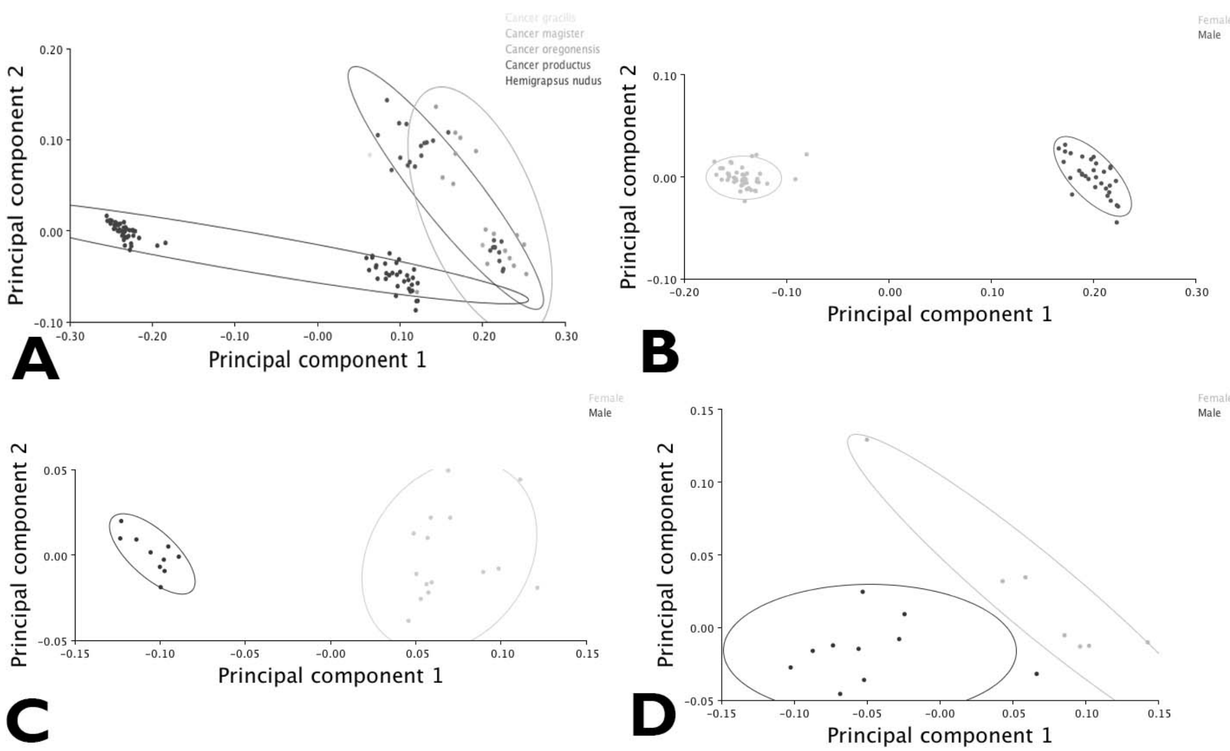

FIGURE 4. PCA of all sexes and specimens (A), *Hemigrapsus nudus* (B), *Cancer productus*, and *Cancer oregonensis* (D)

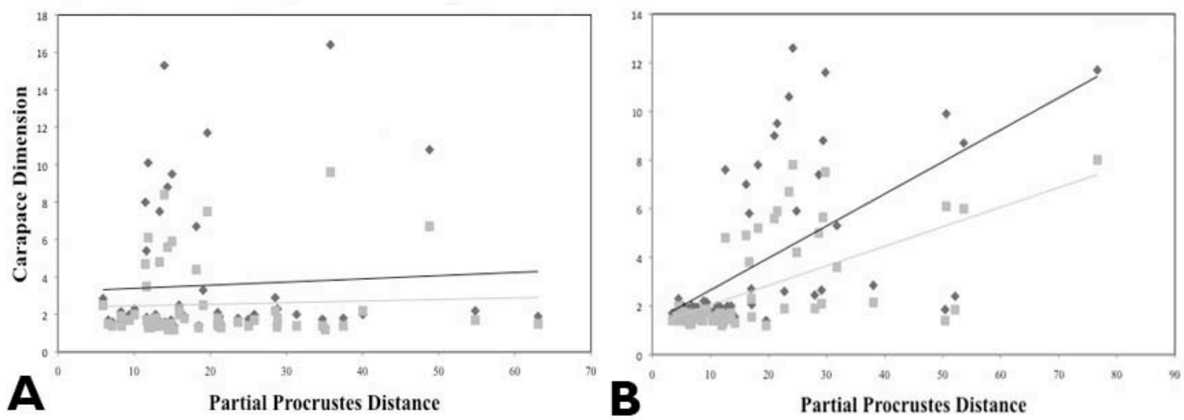

FIGURE 5. Correlation between partial procrustes distance and carapace length and width of male (A) and female (B) all specimens (N = 121). Dark diamonds mark width (Female R^2 = 0.366 Male R^2 = 0.003), grayed squares mark length (Female R^2 = 0.378, Male R^2 = 0.003).