

Ontogenetic and positional variation in denticle morphology of *Metacarcinus magister* (Dungeness crab)

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Abstract

Decapod crustaceans, specifically crabs, use specialized feeding appendages called chelae for a range of functions, the foremost of which is prey capture and handling. The gross morphology of the chelae and denticles, the tooth-like structures along the pincher fingers, may provide information about prey selection and foraging behavior. We measured the aspect ratio (height/width) and radius of curvature (radius of the tooth tip) of the denticles on the chelae of Dungeness crab, *Metacarcinus magister*. Our specimens were collected from Friday Harbor in the San Juan Islands, Washington and varied in size from 6-21 cm carapace length. We examined denticle morphological changes in an ontogenetic series as well as along the length of the immobile finger, propus. We found that as *M. magister* matures, their denticles became overall taller and pointier as represented by higher aspect ratio morphology. Variation in denticle morphology in the ontogenetic series appears to be directly related to shifts in diet with age. Along the propus length, denticles were broad and molariform in the center and more pointed nearest the fulcrum and tip. The layout of various shaped denticles along the propus indicates that both crushing as well as peeling or piercing feeding techniques are used by *M. magister*. This study prompts further research into the effect of predatory feeding appendages on prey populations and morphologies.

Introduction

The morphology of predators' feeding structures can provide insight into foraging behavior, prey selection and subsequent effects of predation on prey populations (Yamada and Boulding, 1998). In the case of decapod crustaceans, particularly crabs,

predation involves the use of multifunctional pinching appendages called chelae, or claws. Denticles, small tooth like projections located along the movable dactyl finger and the fixed propus of the chelae, provide both prying and crushing power (Fig 1D).

There is evidence that morphological adaptations in chelae influence both prey morphology and prey population structure (Vermeij, 1977, Yamada and Boulding, 1998). For example, changes in the design of the shells of prey organisms are associated with shifts in predator chelae structure. Paleobiological studies hypothesize that the shells of molluscs increased in thickness and surface complexity in response to durophagy and the rise of decapod crustaceans, and their chelate appendages, in the Early Cretaceous (Vermeij, 1977; Schweitzer and Feldman, 2010). Current studies also indicate that changes in the morphology of predators' feeding structure can lead to shifts in prey population structure. For instance, crabs with small chelae and limited gape are restricted to consuming snails with thin shells. Thus, in populations where these crabs are the dominant predators, there is a significant phenotypic shift towards thicker shelled snails (Pakes and Boulding, 2010).

Claw size and gape are not the only aspects of chelae morphology that can influence performance; prey selection can also be influenced by denticle shape. Previous studies of a range of crab species demonstrate a qualitative correlation between the structure of denticles and diet. Crabs with fine, sharp denticles tend to be omnivorous, eating algae, snails and seed oysters while crabs with blunt molariform denticles consume hard-shelled prey such as barnacles, snails and mussels (Yamada and Boulding, 1998).

Different types of prey items can be consumed by a single species, and dietary shifts may be observed though the lifespan. Dungeness crabs, *Metacarcinus magister*,

are opportunistic omnivores that consume both soft prey items, such as annelid worms, nematodes and carrion, as well as hard-shelled molluscs and barnacles (Yamada et al., 2010). Their chelae are monomorphic, of equal size, with a staggered denticle alignment designed for cutting, shearing and crushing (Brown et al., 1979; Yamada et al., 2010). Additionally, diet has been shown to vary depending on the size or age of the crab (Pauley et al., 1989). During development, juvenile *M. magister* molt approximately 12 times before reaching sexual maturity, each time increasing in carapace length and biomass (Pauley et al., 1989). Since *M. magister* consume a diversity of prey, both as a mature adult as well as through ontogeny, how does this affect denticle morphology?

Denticle morphology is quantified by measuring the aspect ratio (AR), which is the tooth height/width, and the radius of curvature (RoC), which is the radius of a circle fitted to the denticle's point (Fig 2B). Denticles with a high AR and small RoC will be longer and more pointed, a morphology more associated with softer prey items. Conversely, broad molariform teeth used to crush hard prey items would have a lower AR and larger RoC.

The goals of this study were 1) to quantify denticle morphology in an ontogenetic series of *M. magister*, and 2) to determine how denticle morphology changes with position along the length of the propus. Since larger crabs have chelae with a greater propal height (proxy for closing force), we expected AR to decrease and RoC to increase linearly with increasing age, as these older crabs should be able to break hard-shelled prey items. As the design of the chelae is such that the greatest mechanical advantage is focused nearest the fulcrum where the dactyl and propus articulate, dentition in this region should be low and sturdy to minimize breakage (Seed and Hughes, 1995). Thus,

we predicted the shape of the denticles would be broader and blunter (low AR, high RoC) nearest the fulcrum and sharper (high AR, low RoC) near the chelae tip.

Methods

Study Organism

M. magister is a member of the family Cancridae and the infraorder Brachyura which are commonly referred to as true crabs. During October of 2012, we collected 29 *M. magister* specimens using five box crab pots deployed off the north shore subtidal zone of Brown Island in Friday Harbor, Washington (48.5° N, 123.0° W). Pots were baited with chicken legs and were collected, emptied and reset during a period of 24 hours to two days. Specimens were held in sea tables supplied with a constant flow of seawater and were fed biweekly. Our collection of crabs included both males and females ranging in carapace length from 6-21 cm.

Morphological Measurements

Morphological measurements of each individual were taken within five days of capture. For each crab, digital photographs of the carapace and chelae were taken and analyzed using NIH ImageJ64 software (1.46 release). Carapace length was measured using a straight line extending across the carapace ending inside the lateral spines (Fig. 1A). We used the right chela of each crab for all denticle and propus measurements. The height and base width of each denticle was measured to determine AR (height/width), and a circle fitted to the denticle tip provided the area from which RoC was calculated (Fig. 1B). The number of denticles on the propus was also recorded. Placement of each

denticle was calculated by dividing the distance along the propus from the fulcrum to the tip (L_1) by the distance from the fulcrum to the middle of the denticle (L_2) and multiplying by 100 (Fig 1C).

Statistical Analysis

All statistical analyses were performed using JMP Statistical Discovery software version 10.0 from SAS (Cary, NC). Since our measurements were concerned with chelae morphology, we used propus length as a proxy for ontogenetic growth. To identify ontogenetic changes, we used linear regression to analyze how AR and RoC changed between individuals of different sizes.

Denticle variation along the length of the propus was also analyzed using linear regression to determine if there was a change with distance from the fulcrum. To detect differences in AR and RoC and describe variation in denticle morphology, we performed a 1-way ANOVA and grouped the denticles based on their location along the propus.

Results

Ontogenetic series

As the length of the propus increased, the number of denticles on the propus increased ($p=0.0211$) (Fig. 2C). The positive correlation between propus and carapace length allowed us to use propus length to assess age ($p=0.005$) (Fig. 2A). Using propus length as a proxy for age, we found that AR significantly increased as propus length increased ($p=0.0138$), but RoC showed no significant correlation with propus length ($p=0.4865$) (Fig. 3A,B). However, when comparing AR to RoC for all

specimens, denticles showed a significant negative correlation; as AR increased, RoC decreased ($p < 0.0001$) (Fig. 2B).

Variation along propus

We found a significant positive correlation between AR and position along the propus ($p < 0.0001$) (Fig 4A). Although the RoC of the denticles did not correlate significantly with position along the propus, there was a trend showing decreasing RoC with increasing distance from the fulcrum ($p = 0.0553$) (Fig 4B).

A 1-way ANOVA provided a more detailed characterization of denticle shape along the propus. AR was significantly higher in the denticles in the 0-20% range, dropped to its lowest value from 21-40% and was highest again at the propus tip from 91-100% (Fig. 5A). RoC was significantly lower in the 0-20% range, highest from 21-80% and was lowest again from 81-100% (Fig 5B).

Discussion

As hypothesized, the morphology of the dentition along the chelae of *M. magister* varies within an ontogenetic series as well as along the length of the propus. The increase in denticle aspect ratio (AR) as crabs mature suggests distinct shifts in prey preference with ontogeny and may also be related to denticle formation (Fig 3A). The insignificant correlation between propus length and radius of curvature (RoC) may be due to the asymmetry in our data caused by lack of smaller juvenile *M. magister* (Fig. 3B). However, as there was a significant negative correlation between AR and RoC, we predict that RoC would potentially decrease with increasing age, if our ontogenetic data

were more diverse (Fig. 2B). The significant increase in AR and trend of decreasing RoC with distance from the fulcrum indicate durophagous foraging behavior in our crab specimens (Fig. 4A). One unanticipated result of our study was the placement of sharper (high AR, low RoC) dentition nearest the chelae fulcrum and tip (Fig. 5). This chelae design may be indicative of the specific prey handling technique and feeding tactics of *M. magister*.

Ontogenetic series

As *M. magister* progresses through ontogeny, there are distinct changes in the morphology of the carapace, propus and denticles (Fig. 2A, 3). As propus and carapace length positively correlate, increasing propus length indicates greater maturity. We observed that juvenile crab chelae dentition is broad and molariform (low AR) while that of mature crabs is tall and sharp (high AR). This trend may be the result of variation in the denticle microstructure, crab diet, or chelae closing speed throughout ontogeny.

The design of individual denticles and the process of dentition formation may account for the observed changes in tooth morphology with age. The orientation of the cuticle layers, or laminar geometry, of the denticles differs from that of the surrounding chelae cuticle (Waugh et al., 2006). There is an infolding of cuticle material along the lateral margins of each denticle suggesting that new cuticle forms beneath the old prior to molting. These infolds are the result of denticles which have not yet fully expanded (Waugh et al., 2006). Thus, as younger crabs are molting more frequently, their denticles may still be emerging and expanding, which may account for their low AR. In addition, the design of a tooth is such that low AR dentition is structurally stronger and less

susceptible to breakage (Freeman and Lemen, 2007). The low AR denticles of our juvenile specimens may be an evolutionary adaptation which ensures minimal breakage while the crab is in its vulnerable state of development.

Alternatively, ontogenetic changes in diet may also account for variation in denticle morphology. Stevens et al. (1982) observed a significant shift in *M. magister* diet with age. First year juveniles feed primarily on bivalves, molluscs and crustaceans (Stevens et al., 1982; Pauley et al., 1989). *Crangon* spp. shrimps are the primary food source for second year crabs, and teleost fishes comprise the bulk of the diet for third year crabs (Stevens et al., 1982). It is hypothesized that this trend is the result of increasing body size and the subsequent changes in the mechanics of prey handling (Pauley et al., 1989; Stevens et al., 1982). As dentition is fundamental in determining prey handling, we propose that the low AR of juvenile denticles may be linked to the durophagous diet of these young crabs while the high AR of our more mature specimens' teeth reflects their need to penetrate flesh rather than crush.

Finally, the ontogenetic variation in denticle morphology may relate to chelae closing speed. Some crab species possess dimorphic chelae, where one claw is a smaller 'cutter' claw and the other is a large 'crusher' claw. It has been found that, although weaker, the 'cutter' claw is faster than the powerful but slow 'crusher' claw (Schenk and Wainwright, 2001). These distinct chelae morphologies are similar to those of the claws of *M. magister* at different ontogenetic stages and this trade-off between strength and speed may explain the variation in denticle morphology that we observed. The sharper denticles (high AR) of mature *M. magister* are typical of a 'cutter' claw and are ideal for the capture of elusive, active prey such as shrimp and fish (Fig. 3A). Similarly, the

molariform denticles (low AR) of the younger specimens are characteristic of a ‘crusher’ claw modeled for strength rather than speed. This design is ideal for the juvenile crab’s crustacean based diet.

Variation along propus

Variation in tooth morphology along the length of the propus is indicative of specialization in chelae function and may allow us to characterize the foraging behavior of *M. magister*. As suspected, denticles in the proximal regions of the chelae were generally blunter and broader than those in the distal regions (Fig 4). This correlation indicates that the dentition of our specimens is designed for both durophagy as well as cutting or puncturing.

Previous studies examining denticle morphology reveal a similar trend between tooth type and chelae function. The denticle ridge of the crusher chela of *Carcinus maenas* is significantly broader near the fulcrum, which creates a grinding surface ideal for durophagy (Yamada et al., 2010). We hypothesize that the similar design of *M. magister* chelae indicates a shelled prey diet. The high AR of denticles at the propus tip suggests that the function of our crabs’ chelae is not exclusively durophagous. As sharper teeth are designed for efficient penetration or piercing, the placement of these teeth near the propus tip may indicate diversity in *M. magister* diet and the need for feeding tactics such as peeling and pinching (Freeman and Lemen, 2007).

A closer analysis of denticle morphology along the propus length revealed an interesting trend. The placement of fine, sharp denticles near the fulcrum (0-20%) where mechanical advantage and force production is greatest indicates *M. magister*’s feeding

strategy. Many molluscivorous crabs possess a dactylar tooth or enlarged, pronounced denticle near the fulcrum which provides both shearing and compressive forces (Seed and Hughes, 1995). This specialized peg is used for peeling and prying apart the outer lip of the prey's shell aperture (Seed and Hughes, 1995). The similar design of the *M. magister* chelae suggests that their primary mode of attack involves prying away the protective structure of the prey rather than outright crushing.

The presence of sharp teeth in the distal region (91-100%) of the propus may indicate the need for dexterous, fine-tuned prey handling. In order to strategically focus the application of force on the prey's body, crabs will reorient prey in their claw until the weakest region has been exploited (Seed and Hughes, 1995). We suggest that the placement of fine dentition near the propus tip is most ideal for this adroit grasping and manipulation of prey items. Also, fine denticles near the tip may be ideal for a feeding technique observed in *Callinectes sapidus* crabs which involves chipping the posterior edge of a mussel shell, prying the valve open and severing the adductor muscle (Seed and Hughes, 1995). Although dexterity is important, *M. magister* may also rely on the sturdier low AR, high RoC denticles along the majority of the propus for crushing power.

These molariform teeth indicate that durophagous feeding is also a significant part of *M. magister*'s foraging behavior. If a prey item is particularly heavily armored, and peeling or chipping is unsuccessful, outright crushing may be necessary. This technique involves extended periods of repeatedly loading the shell and thus requires strong low AR, high RoC dentition. We hypothesize that the placement of these crushing teeth along the middle section of the propus maximizes surface area and minimizes the force required

to successfully crush the prey. Evaluating these results in an ecological context provides insight into predator-prey interactions and introduces topics for future study.

Implications and Future Study

We suggest that future projects expand this study temporally in order to include a broader range of maturity levels of *M. magister*, specifically more juveniles. With a broader ontogenetic series, it would be possible to draw parallels between diet and denticle morphology. We also recommend examining the contents of crab stomachs in order to further explore how feeding structure morphology is related to prey selection. By furthering our understanding of the relationships between predator and prey and the morphologies involved in these interactions, we can better understand the ecology.

Pakes and Boulding (2010) suggest that ontogenetic changes in feeding structure morphology impact the selection differential exerted on the prey. In populations where young crabs dominate, there are significant phenotypic shifts in the prey population's shell thickness. This shift is due to the morphology of the chelae restricting the crab's diet to thin shelled prey. As our study suggests a similar connection between denticle morphology and diet preferences, there is the possibility of quantifying how ontogenetic variation in *M. magister* chelae morphology affects prey morphology.

Identifying the mechanism of the selection differential exerted on prey items has significant implications in population management. By manipulating the predator populations based on denticle morphology, there is the possibility of controlling the phenotypic selection of the prey population (Pakes and Boulding, 2010). Thus, our characterization of variation in denticle shape with ontogeny and position provides

valuable insight into the foraging behavior of this species. This study prompts further research into the effects of chelae morphology of *M. magister* and other crab species on prey population dynamics.

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Figures and Legends

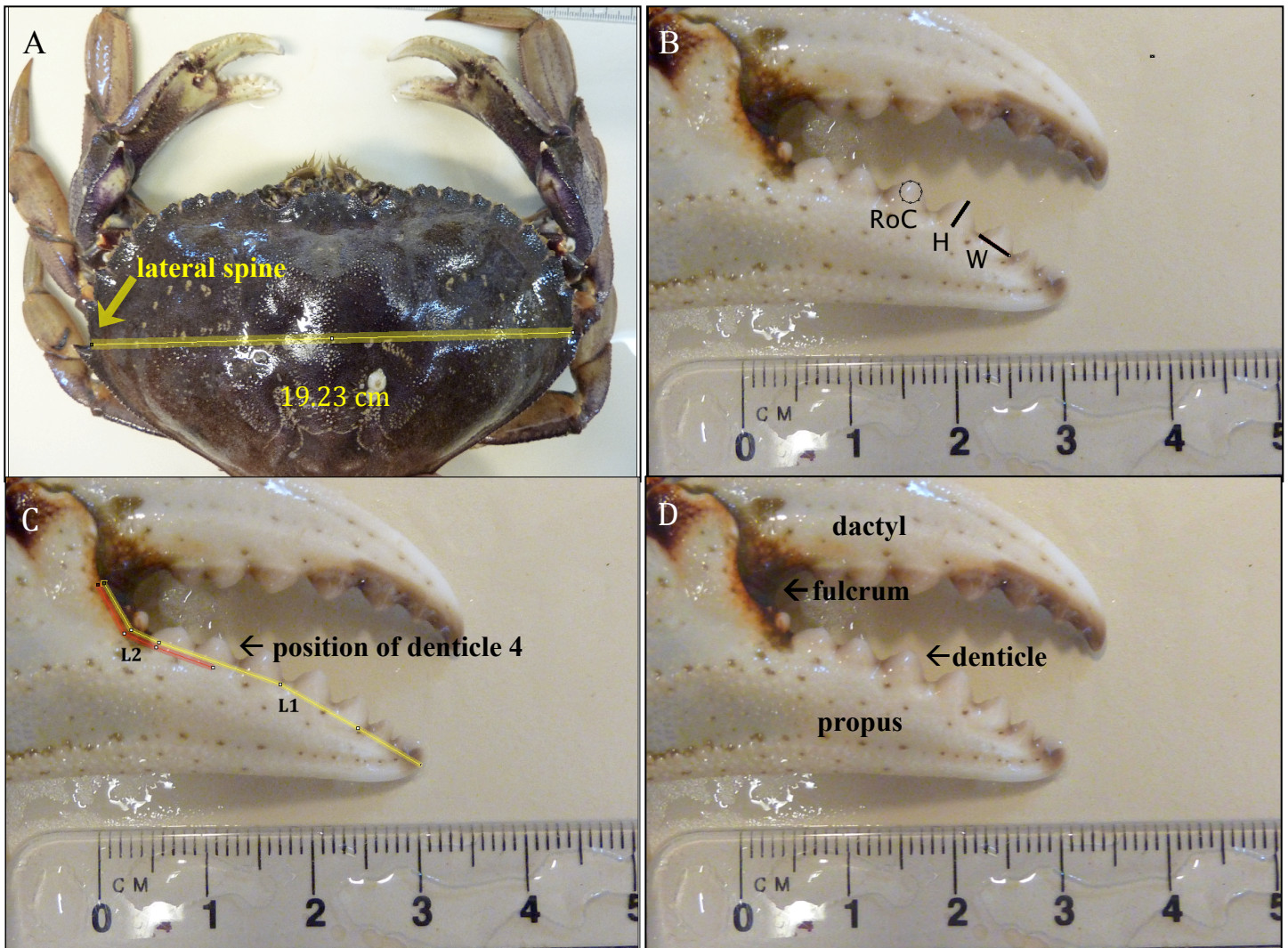


Figure 1: Chelae anatomy and measurement techniques used in ImageJ. (A) Carapace length was measured with a straight line extending across the body and inside the lateral spines. (B) A circle fitted to the denticle tip represents radius of curvature (RoC) and height (H) and width (W) were measured with straight lines. (C) Denticle position= $(L_1/L_2)*100$ where L_1 is the total propus length and L_2 is the distance from the fulcrum to the center of each denticle. (D) Labeled picture of chelae anatomy.

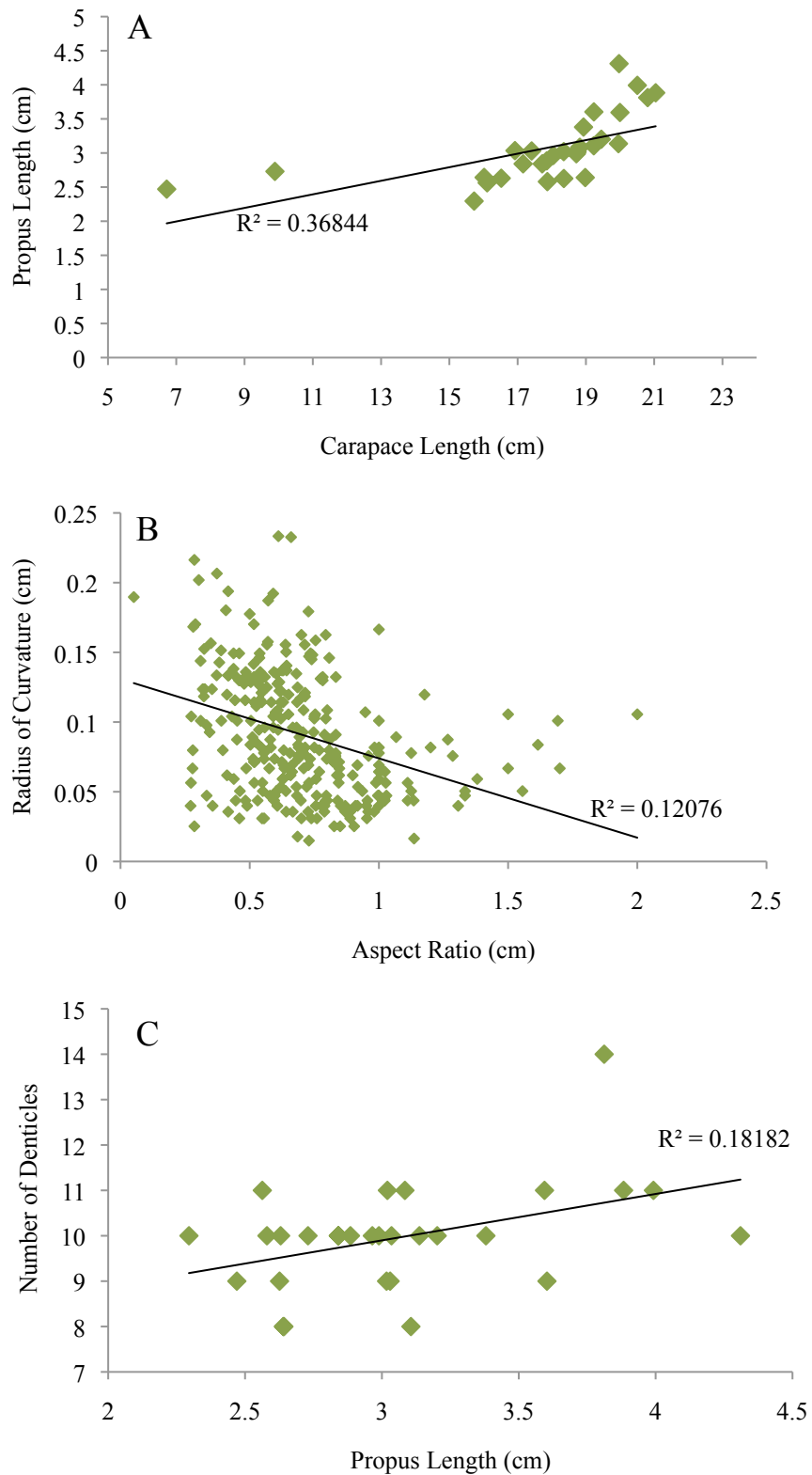


Figure 2: Relationships between chelae and denticle morphometric measurements. (A,C) Each data point represents an individual crab. (B) All denticles on the right propus of every crab were included. (A) Increasing carapace length correlated significantly with increasing chelae propus length ($p=0.005$). (B) There was a significant negative correlation between AR and RoC ($p<0.001$). (C) The number of denticles on the propus increased significantly as propus length increased ($p=0.0211$).

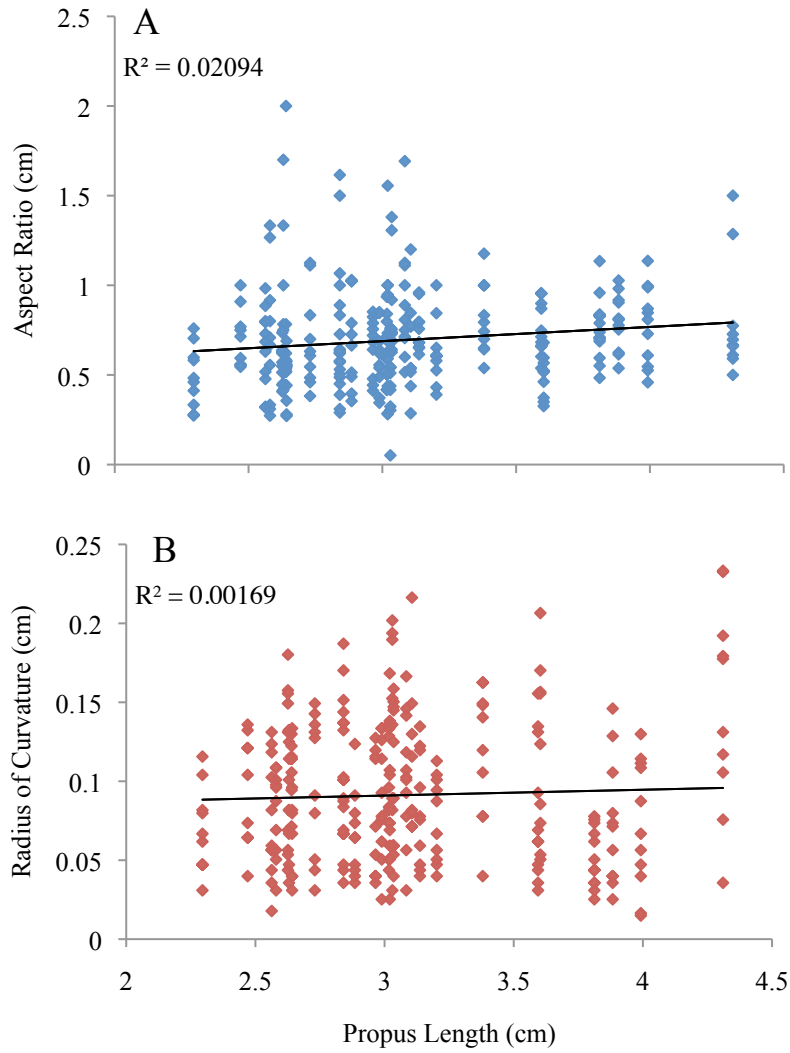


Figure 3: Linear regressions of AR and RoC in relation to propus length. Each data point represents one denticle. (A,B) As the length of the propus increased, AR significantly increased ($p=0.0138$), while RoC showed no significant correlation ($p=0.4865$).

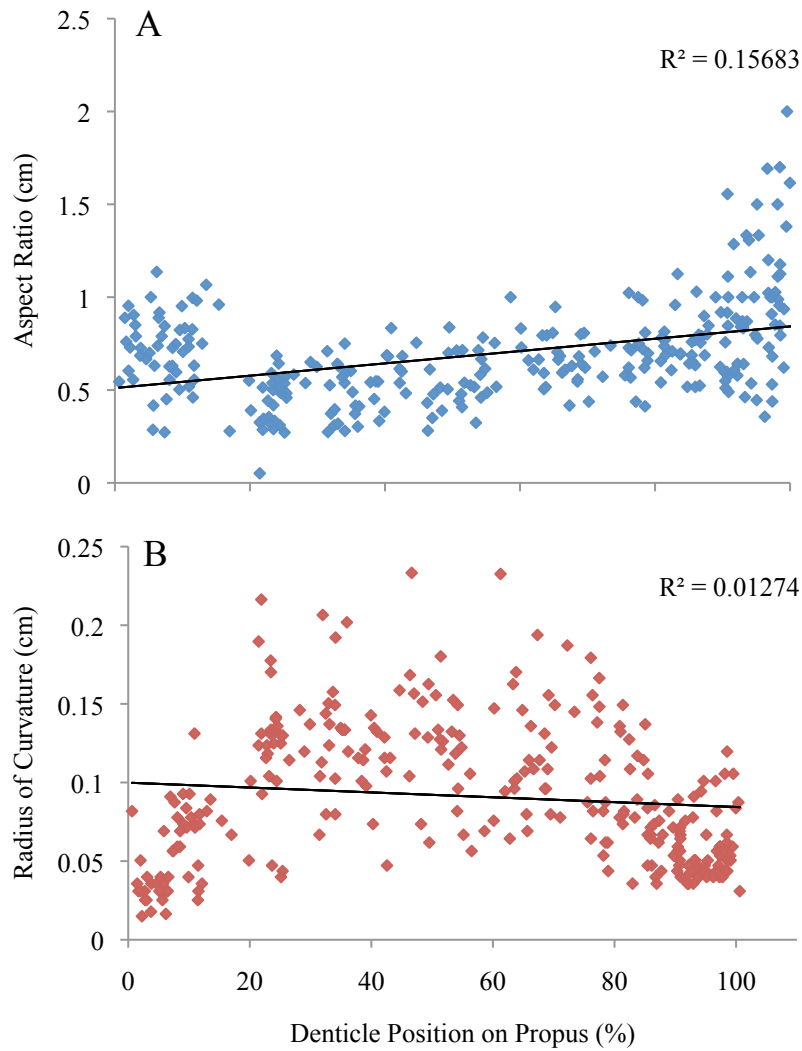


Figure 4: Linear regressions of AR and RoC in relation to the position of each denticle on the propus. Each data point represents one denticle. Denticle position is denoted by percent: 0% is closest to the fulcrum, and 100% is at the chela tip. (A) Denticle AR increased significantly with increasing distance from the fulcrum ($p < 0.0001$). Although not significant, there was a trend of decreasing RoC with distance from the fulcrum ($p = 0.0553$).

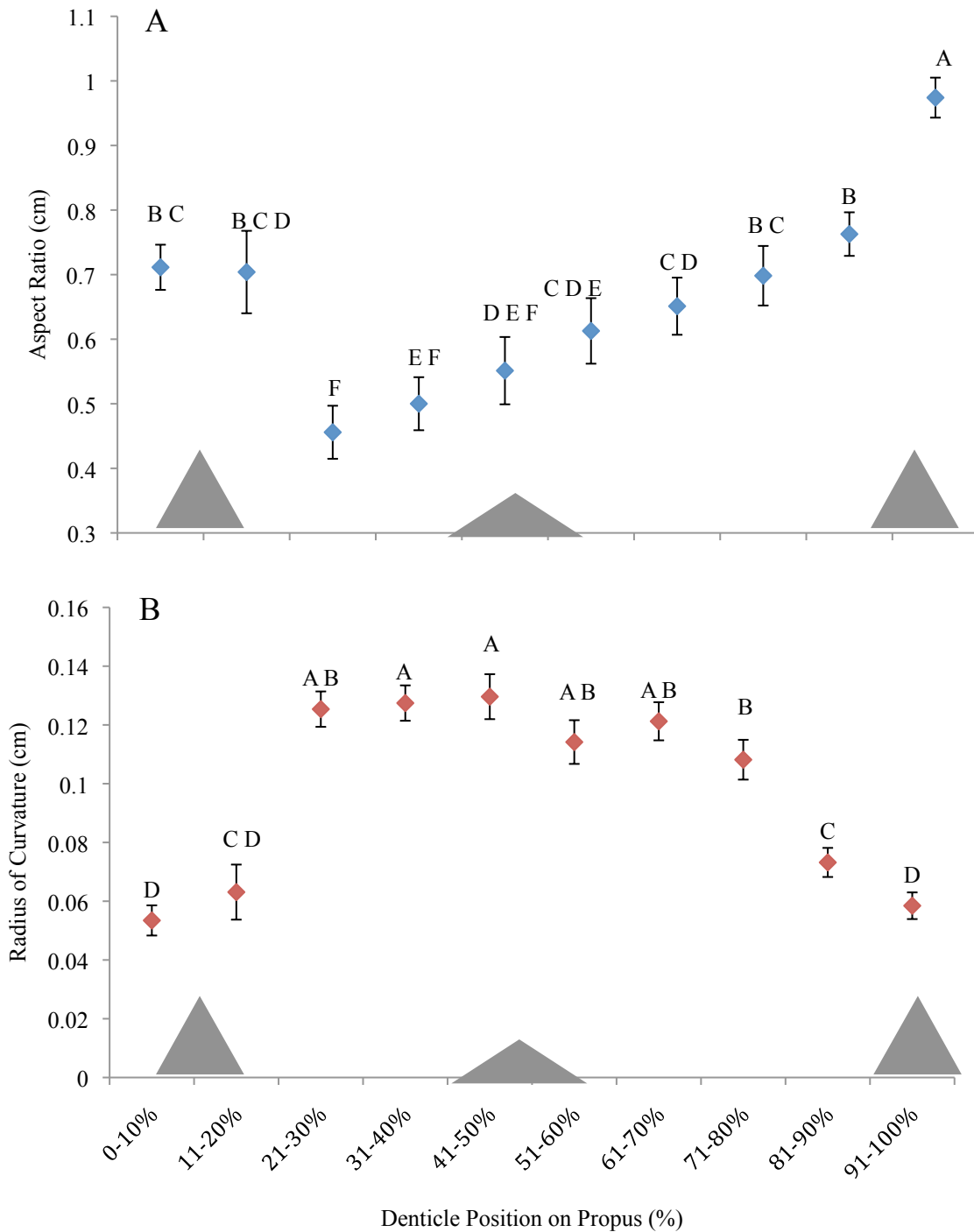


Figure 5: Variation in denticle morphology along the length of the propus. Each data point represents the mean AR or RoC for all the denticles in each position category. 0-10% is closest to the fulcrum and 91-100% is nearest the chelae tip. (A) AR is significantly higher near the fulcrum (0-20%) and near the tip (81-100%) and is low in the middle of the propus ($F_{9, 278}=17.4437$, $p<0.0001$). (B) RoC is significantly lower nearest (0-20%) and farthest (81-100%) from the fulcrum and is high in the middle of the propus ($F_{9, 278}=29.0046$, $p<0.0001$). Standard error bars are shown and the letters above each point indicate significant differences between data points. Grey triangles represent denticle shape variation along the propus.