Crab Signatures: Differentiating species-specific crab repair scars on mollusc prey for reconstructing crab abundance through time

by

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We acknowledge and respect the Lekwungen peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̲SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

Crustacean fisheries are increasing in economic importance globally, with crab fisheries being the most valuable fishery in BC in 2021. As these fisheries grow in importance, their sustainable management also becomes increasingly important. However, assessing the sustainability of BC's crab fisheries is challenging due to the scarcity of baseline data on crab populations. Scars left by crabs on their prey, known as "repair scars", provide an alternative source of data to reconstruct past crab abundances. However, it is unknown if repair scars can be used to determine species-specific crab abundances that could help determine species-level baselines of past or present crab populations. This would allow for improved management of each crab fishery, rather than treating them as one multispecies fishery, as different species may respond differently to various environmental impacts. Here I conducted controlled manipulative feeding experiments in which individuals of Dungeness crabs (*Metacarcinus magister*), red rock crabs (*Cancer productus*), and European green crabs (*Carcinus maenas*), were allowed to attack snails. Resulting repair scar-type shell damage was photographed and landmarked for geometric morphometric analyses to determine any differences in damage shape amongst species. Red rock damage was significantly deeper and larger than the other two species. Damage left by Dungeness and European green crabs was visually distinct, but statistical power was limited by sample size and repair scar shape variability. The findings of this study are an important step towards using repair scars to track individual crab species populations through time and space, providing population abundance baselines allowing for improved management as well as providing a cost-effective means of detecting European green crab invasions.

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Acknowledgements

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Introduction

Fisheries are valuable socioeconomic and food resources in coastal environments (Lowitt, 2013; DFO, 2023). Thus, sustainable fishery management is crucial to ensure the long-term health of these resources. Sustainable fishery management will become more important in the coming decades as there is a larger shift to the ocean for food/protein and as these resources are increasingly threatened by human activity and climate change (IPCC, 2022). However, lack of fisheries data is very common around the world, including in Canada where close to 50% of fisheries are considered understudied (Baum and Fuller, 2016). This lack of information about fishery health makes managing these resources challenging, potentially leading to population declines or collapses. For example, the Atlantic cod fishery, once one of the world's most productive fisheries, faced collapse and official closure in 1992 after overfishing due to a lack of reliable information of past and current population health led to a significant decline in the cod population (Myers et al., 1997; Haedrich and Hamilton, 2000). The Atlantic cod population has never recovered enough for the return of a large commercial fishery, with increasing ocean temperatures being a possible cause that will likely continue to limit cod productivity in the future (Sguotti et al., 2019).

Records of historical population abundances provide baselines critical to identify how fisheries are changing over time in response to factors such as increased commercial fishing, climate change, increased pollution, and the introduction of invasive species (McClenachan et al., 2012; Toniello et al., 2019). However, most records, when kept, only go back decades, especially for shellfish (non-finfish), which limits our understanding of how these populations change over time and will change in the future (Fitzgerald et al., 2018, 2019). Alternative sources of long-term records can fill in the critical gaps and provide missing baselines to understand the current state of valuable fisheries, allowing for improved management. For example, population dynamics of cod in the eastern Baltic Sea have been determined back to the 1920s using historical ecology (historical information recovered from a variety from sources), knowledge which has contributed to revision of this fishery's management (MacKenzie et al., 2011). Chong-Montenegro et al. (2022) used catch data drawn from historical newspapers to reconstruct catch rates of the Australian east coast barramundi, a popular fish for recreational fishers, from 1869 to 1952. The archeological remains of California sheephead along with isotopic data were used to discover that over approximately the past 10,000 years the relative abundance these fish has varied and declined overall in addition to experiencing a reduction of some size frequencies, providing critical information for fishery management (Braje et al., 2017). Pacific herring abundance and distribution records only date back to the mid 20th century so McKechnie et al. (2014) used archaeological herring bones from Alaska, British Columbia, and Washington to obtain Pacific herring abundance and distribution baselines prior to industrial fishing to aid management efforts of this fishery. One of the few applications of alternative data sources to crustacean fisheries is Ban et al.'s (2017) study, which used First Nation interviews to obtain historical records of Dungeness crab abundances. However, alternative data source use remains limited for crustacean fisheries compared to that used for finfish.

Commercial crab fishing has expanded rapidly since the 1980s in part due to declines of teleost and finfish species (Pauly et al., 2000; Anderson et al., 2011; Boenish et al., 2021). In 2021, crabs were the most valuable fishery in British Columbia (BC), yielding over $150M (DFO, 2022b). However, records of crab populations in BC were not collected consistently before the expansion of commercial crabbing in recent decades (Ban et al., 2017). Crabs also represent significant Food, Social, and Ceremonial (FSC) resources for many Indigenous communities in BC, and any negative impacts to crab populations infringe on their constitutionally protected rights to access these crab resources (Frid et al., 2016, Ban et al., 2017). Ban et al. (2017) interviewed elders from First Nations communities along the coast of BC to identify declines in Dungeness crab abundances since the 1950's and found increases in commercial fishing as a major contributing factor to these declines. Despite their importance, long-term records of BC's crab populations are scarce beyond these accounts, making it difficult to assess the precise impacts of increased commercial fishing and climate change on the sustainability of these species. To extend the record of past crab abundances beyond the length of a human lifespan to pre-commercial or even pre-industrial times to look at their long-term changes and human impacts, we need an alternative source of data, such as archaeological or palaeontological data like those used to study finfish fisheries. However, crabs themselves have a poor preservation potential due to their thin chitinous exoskeleton meaning that typically only claw tips, if anything, are preserved in the fossil record. Instead, we can look at their prey, such as clams or snails for evidence of crab presence in the form of predatory scars known as repair scars.

Repair scars are marks left by crushing predators, such as crabs, on their shelled prey following an unsuccessful attack attempt (Vermeij et al., 1981). When hunting, shell-crushing crabs use their claws to pinch their prey's shell in an attempt to crush it. Occasionally the crabs are unable to crush the shell instead only breaking small pieces off resulting in a characteristic wedge-shaped scar that forms as the shell heals (Stafford et al., 2015b). In paleoecology, repair scars are an important tool to study predation and its evolutionary impacts through time (Vermeij et al., 1981; Alexander and Dietl, 2003). For example, Vermeij et al. (1981) examined fossilized shells of various gastropod species from the Pennsylvanian to recent historical times for repair scars to determine that shell-crushing predators became a more important driver in gastropod selection part way through the Mesozoic. However, repair scars have also been used in modern applications. Molinaro et al. (2014) found that repair scar frequency increases with decreasing wave energy which suggests that repair scar frequency is driven mainly by crab abundance rather than success/failure rates since crabs are known to be more abundant at low wave energy sites. Stafford et al. (2015a) found similar results, surveying crab abundance to confirm that repair scar frequency was tracking crab abundance accurately. Tyler et al. (2019) found that patterns of repair scars (repair frequency higher at sites where predators are more abundant) in *Tegula funebralis* populations along an environmental gradient in Bamfield, BC were the same before and after ecological disturbances (sea star wasting disease, sea surface marine heatwave, harmful algal blooms) showing that repair scars provide a robust signals of crab abundance on a scale of decades or more despite recent environmental disturbances. Barclay and Leighton (2022) compared repair scars on living *T. funebralis* and repair scars on fossil *T. funebralis* from the Pleistocene from the same locations in California to discover that today's gastropods have fewer repair scars, indicating a decline in crab abundance since the Pleistocene. Repair scars therefore offer an alternative method of reconstructing historical crab abundances and assessing potential impacts of human activity on their populations. However, it is currently unknown if repair scars can be used to determine species-specific crab abundances that would allow for species-level baselines of past/present crab populations would improve management of each fishery, rather than treating them as one multispecies fishery, as each may experience different responses to fishing pressure, climate change and invasive species (Fitzgerald et al., 2018, 2019).

Here, I focus on three of the most socioeconomically important crabs in BC: Dungeness crabs (*Metacarcinus magister*), red rock crabs (*Cancer productus*), and the invasive European green crabs (*Carcinus maenas*) (Fig. 1, Table 1). These crab species are all known to be shell crushing predators (Behrens Yamada et al., 2010; Edgell and Hollander, 2011; Schaefer and Zimmer, 2013). Dungeness and red rock crab fisheries in BC are currently managed by retention limits on size and sex (males only), and a limited number of commercial crabbing licenses (DFO, 2022a).

Dungeness crabs are the most economically valuable commercial crab species in BC (DFO, 2022b). They range from Alaska to Mexico, and typically can be found from the intertidal to a depth of about 90 meters (Pauley et al., 1986; Rudy and Rudy, 1983). They prefer to live in areas where the substrate is mud, sand, or eelgrass with mud (Rudy and Rudy, 1983). Dungeness crabs typically feed on crustaceans, small clams, and also scavenge (Rudy and Rudy, 1983). Their carapace is generally purpleish to light reddish brown in colour and measures to around 120.7mm in length and 177.8 mm in width for adult males (Rudy and Rudy, 1983). Their underparts and claws are generally light in colour (Rudy and Rudy, 1983). Mating usually occurs in the fall after the female has molted (Rudy and Rudy, 1983). Fertilization is internal and females carry the eggs until they hatch in the spring (Rudy and Rudy, 1983).

Red rock crabs are a common coastal crab and an important recreational fishery. They range from Alaska to Baja, California and can be found from the intertidal to a depth of about

35 meters, overall shallower than Dungeness crabs (Rudy and Rudy, 1983). Red rock crabs typically inhabit semi-protected shores that have hard bottoms with either rocky or gravel substrate in addition to tidepools and eelgrass beds (Rudy and Rudy, 1983). They hunt predominately at night but are also active during the day with a diet consisting of barnacles, other crabs, molluscs and polycheate worms, however they are also scavengers (Rudy and Rudy, 1983). Red rock crabs are dark red above, lighter below, and have dark claw tips (Rudy and Rudy, 1983). Red rock crab carapaces are typically around 157.5 mm in width and 97 mm in length (Rudy and Rudy, 1983). Red rock crabs mate from June to August when females are soft (Rudy and Rudy, 1983). Females then extrude the eggs around December or January which then hatch usually by early April.

European green crabs are native to European and North African coasts however they have successfully invaded coasts along North America, South Africa, Australia and Eastern South America. They were first discovered on the west coast of North America in San Francisco Bay, California in 1989 (Cohen et al., 1995; Klassen and Locke, 2007). They continued northward in 1993, being found in Oregon in 1997, and then Washington in 1998 (Klassen and Locke, 2007). European green crabs were found in British Columbia in 1999, specifically Vancouver Island (Klassen and Locke, 2007; Behrens Yamada and Gillespie, 2008). European green crabs can be found commonly from the high tide level to a depth of 6 meters but have also been found to depths of at least 60 m (Cohen et al., 1995). On the west coast of North America, they typically prefer protected coasts that have muddy or sandy substrates (Cohen et al., 1995). European green crabs consume a wide variety of prey but prefer molluscs and crustaceans (Grosholz and Ruiz, 1996). They are typically dark green in colour and the carapace of adult male individuals on the west coast of North America generally ranges from 65 to 75mm in width (Grosholz and Ruiz, 1996). European green crabs also display handedness with one claw being significantly larger than the other one. European green crabs are quickly spreading through BC where they negatively impact native ecosystems by destroying eelgrass habitats and outcompeting the juveniles of native Dungeness crabs (McDonald et al., 2001; Behrens Yamada et al., 2010; Howard et al., 2019).

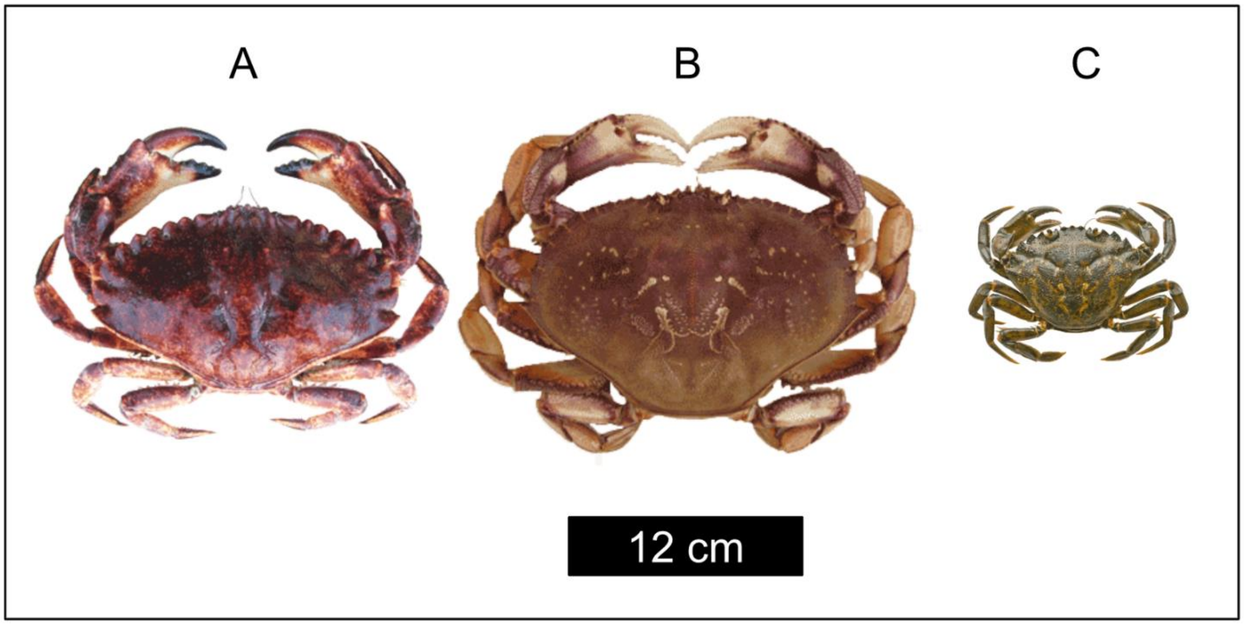

Figure 1. Three socioeconomically important crab species in British Columbia. A: Red rock crab (*Cancer productus*), B: Dungeness crab (*Metacarcinus magister*), C: European green crab (*Carcinus maenas*).

Geometric morphometrics is a useful method for quantitatively evaluating changes in shape between organisms or features, thus, rendering this a useful method to investigate variations in repair scar shape. In both 2D and 3D landmark-based geometric morphometrics, morphological features of interest are denoted by a series of analogous points (landmarks), allowing for spatial comparison of features between specimens (Webster and Sheets, 2010). Landmark configurations can then be analyzed to determine how these landmarks change between specimens or groups (Webster and Sheets, 2010). As such, geometric morphometric analyses provide a concrete method for quantifying variation in shape between specimens or groups. For example, geometric morphometric analysis on the jaw bones of various marmot species was used to show that Vancouver Island marmots, while genetically similar, are very morphologically distinct from other marmot species, demonstrating the applicability of using these techniques alongside molecular methods to determine if populations are evolutionarily distinct and relevant for conservation considerations (Cardini et al., 2009). Geometric morphometric analyses are also used to investigate the link between form and function of various structures as done by Borgard et al. (2020) where they used geometric morphometrics to determine that four rodent genera had statistically distinct shaped larygeal cartilages that could potentially help to explain the differential vocalizations of these species. Analyses based on geometric morphometric techniques can therefore be applied to determine if there are any species-level differences in the shapes of repair scars left by BC's most common shell crushing crabs.

This thesis aims to identify whether three of BC's most common and valuable crab species, Dungeness (*Metacarcinus magister*), red rock (*Cancer productus*) and invasive European green crabs (*Carcinus maenas*) (Fig. 1, Table 1), produce repair scars that are significantly different in size and shape. My null hypothesis is that repair scar shape does not vary significantly between species of crabs. The alternative hypothesis is that repair scar shape will vary significantly between crab species. I predict that repair scar shape on snail shells will be unique for each species of crab, with: 1) scars made by European green crabs being smaller compared to those made by Dungeness and red rock crabs since they have smaller claws; 2) scars caused by Dungeness crabs being shallower and narrower since their claws are narrower and not as strong compared to red rock crabs (Taylor, 2000); and 3) scars made by red rock crabs being deeper and larger than the other two species since they have the strongest claws. Differently shaped repair scars among crab species would allow for species-specific reconstructions of crab populations since pre-human times, providing new information for improved fishery management and a cost-effective early detection method for European green crab invasions.

Table 1. Taxonomy of three of the most socioeconomically important crabs in British Columbia and one of their common prey items. These species were used in the experimental trials of this research.

Common Name	Scientific Name
Red rock crab	*Cancer productus*
Dungeness crab	*Metacarcinus magister*
European green crab	*Carcinus maenas*
Black turban snail	*Tegula funebralis*

Materials and Methods

Crabs

All crabs were housed in the Outdoor Aquatic Unit at the University of Victoria with a continuous water supply and an air stone. Red rock crabs (*Cancer productus*) were caught using bait-loaded casting crab traps deployed off the fishing pier in Sidney, BC between May and September 2022. European green crabs (*Carcinus maenas*) were obtained from Coastal Restoration Society by boat in the Sooke region as part of their European green crab trapping program. Dungeness crabs (*Metacarcinus magister*) were already being housed in the Outdoor Aquatic Unit at the time the other crabs were collected but were originally collected from the Victoria area. Despite differences in collection location and method for each crab species, all crabs were equally "naïve" to the prey species used in this experiment, which is not found on the south or east sides of Vancouver Island. Crabs of each species were uniquely labelled using numbered wire markers affixed to the right anterior side of the carapace using aquarium safe marine glue. For each crab, maximum carapace width as well as left and right claw heights, measured as the height of the propodus directly behind the dactyl, were measured using digital calipers (± 0.01 mm). Carapace width range from 130.27 mm – 162.03 mm, 71.36 mm – 80.2 mm, and 191.71 mm- 205.54 mm for red rock, European green, and Dungeness crabs, respectively (Table A1). Red rock crab claw height ranged from 33.43 mm – 42.41 mm, Dungeness crab claw height ranged from 37.83 mm – 40.61 mm, and European green crab claw height ranged from 16.39 mm – 28.99 mm (Table A1). Dungeness and red rock crabs were put on a reduced feeding schedule and fed once per week during the course of the experiment to increase hunger and interest in prey offered during the experiments. European green crabs were fed three times a week throughout the experiment since they are a smaller crab that need to eat more frequently.

Prey

Three-hundred black turban snails (*Tegula funebralis*) (Table 1) were collected from Eagle (Scott's) Bay in Bamfield, BC on September 26, 2022. Black turban snails can live to around 30 years of age (Frank, 1975), during which time they can obtain repair scars. They can have shell heights of about 10 to 30 mm in the area from which they were collected (Stafford et al., 2015a). Their shells are quite round, relatively smooth and typically a dark purpleish black colour except for where the shell is worn down at the top exposing a white pearly or orange layer beneath (Fig. 2). Black turban snails prefer moderately exposed cobble beaches or rocky intertidal habitat (Frank, 1975). Black turban snails were chosen for these experiments since they are a common prey item for crabs and have been well studied in terms of the relationship to repair scars and crabs (Molinaro et al., 2014; Stafford et al., 2015a; Tyler et al., 2019; Barclay and Leighton, 2022). Each snail was uniquely labelled using lettered and numbered wire markers affixed to the shell opposite the aperture using aquarium safe marine glue so that each snail had a unique ID. The maximum height (measured from apex to lowest point on aperture) and width (maximum width across the shell perpendicular to the axis of coiling) of each snail was measured using digital calipers (± 0.01 mm). The snails ranged from 11.19 mm – 26.93 mm in height and 12.36 mm – 24.54 mm in width. Snails were kept in a tank with continuous water flow and an air stone and continuous access to kelp for food.

Figure 2. Black turban snail (*Tegula funebralis*), a common crab prey. The red arrow denotes a prominent repair scar, the result of a non-lethal attack from a shell-crushing crab predator.

Trials

Controlled manipulative feeding trials were conducted, in which individual crabs of each species were allowed to attack black turban snails and produce predation traces that could become repair scars. Prior to each experimental trial, a crab was placed in the 175 L experimental tank for a 20 minute acclimatization period in the dark tank. Snails were chosen for particular trials to account for size difference within each crab species; Smaller snails were used in trials with smaller crabs. A stopwatch was started at the beginning of each trial when the snails were placed, evenly spaced, in the tank. The time at which a crab made contact with a snail was recorded as well as the strategy (crush or peel) used by the crab to try and get into the shell. The snail was taken from the crab after the first notable break in the shell. A snail was also removed from the tank if the crab left it after an attack and there was notable shell damage. If the crab successfully crushed the shell, it was left to consume the snail tissue as to not disturb the crab more than necessary. Shell pieces were removed from the tank once the crab consumed all the tissue and moved away from the attack site. A trial was ended either when the crab caused damage to all the snails or had gone more than around 40 minutes without attacking a snail or showing interest in hunting. After each trial, all snails that acquired shell damage from the crab were photographed: three replicate photos each of the snail positioned with the aperture facing left (apertural view). For each set of photo replicates, the one with the most consistent alignment was selected for analysis.

Data Analysis

The software tpsUtil (Rohlf, 2015) was used to convert the folder containing all images with the apertural view of snails with shell damage into a TPS file package used in landmarking and digitizing specimens. This TPS file was loaded into tpsdig2 (Rohlf, 2015) and the scale of all images was set (to account for any minor differences in focal length of the camera) and four landmarks were placed on the image. Landmark one was placed where the top of the shoulder/aperture met the left edge of the shell; this was a consistent landmark between all damaged shells. Landmark two was placed at the top of where the deepest damage met the original apertural edge. Landmark three was placed on the deepest point of the largest chip/peel. Landmark four was placed at the bottom of where the deepest damage met the original apertural edge. The landmarked photos were saved as a new TPS file that was uploaded into tpsRelw (Rohlf, 2015) to obtain the consensus configuration (least-squares Procrustes average) of all specimens. After the consensus configuration was determined, partial and then relative warp analyses were conducted. The relative warp analysis produces axes scores that indicate how each component (warp) contributes to overall changes in shape, (i.e., to evaluate how landmarks for each specimen differed from the consensus configuration). A generalized linear model (GLM), performed in Rstudio with R version 4.2.2 (R core team 2022) was then used to determine if the axis scores were significantly different between any of the crab species. To aid in visualizing shape change of the major axes, thin plate splines were then generated using the software tpsSplin (Rohlf, 2015). These thin plate splines are a visual tool used in conjunction with relative warp analyses that depicts the landmarks on a grid, showing how each specimen differs from the consensus configuration, with the grid distorting along the major axes of shape change.

Results

The primary relative warp axis (Axis 1) accounted for 59.85% of the total observed shape variation of the shell damage and described a change in depth of the damage (largest distance from where the apertural edge was prior to damage to the current apertural edge after damage) (Fig. 3, Fig. 4). The secondary relative warp axis (Axis 2) accounted for 27.81% of the total observed shape variation of the shell damage and depicts a change in the position of the shell damage along the edge of the apertural whorl (Fig. 4, Fig. A1). The tertiary and quaternary relative warp axes accounted for 8.57% and 3.77% of the total observed shape variation of the shell damage, respectively. The tertiary and quaternary relative warp axes did not show any obvious visual patterns in shell damage shape. In geometric morphometric analyses, axes that describe a comparatively small percentage of the total observed shape variation (usually anything other than the first two axes, or anything describing less than 10% of the shape change), are typically ignored. We therefore only focus on the first two axes, which account for 87.66% of the overall shape change. The relative warp scores for all axes can be found in Table A2.

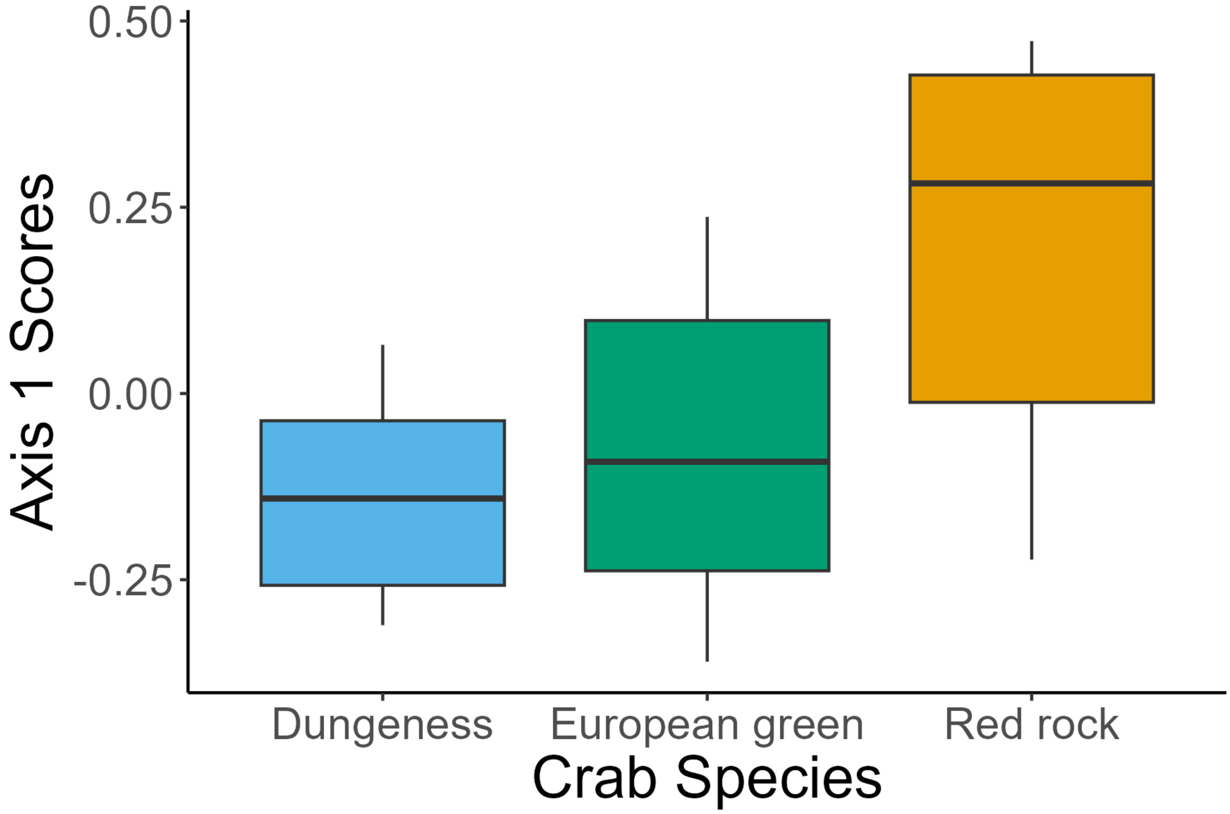

Figure 3. Boxplot of relative warp scores of Axis 1 for snails damaged by each crab species. Axis 1 accounted for 59.85% of the total observed shape variation of the shell damage and depicts a change in depth of the damage. Relative warp scores were calculated from the landmarked photos of shell damage using the software tpsRelw. Damage caused by red rock crabs is significantly deeper than the other two crab species.

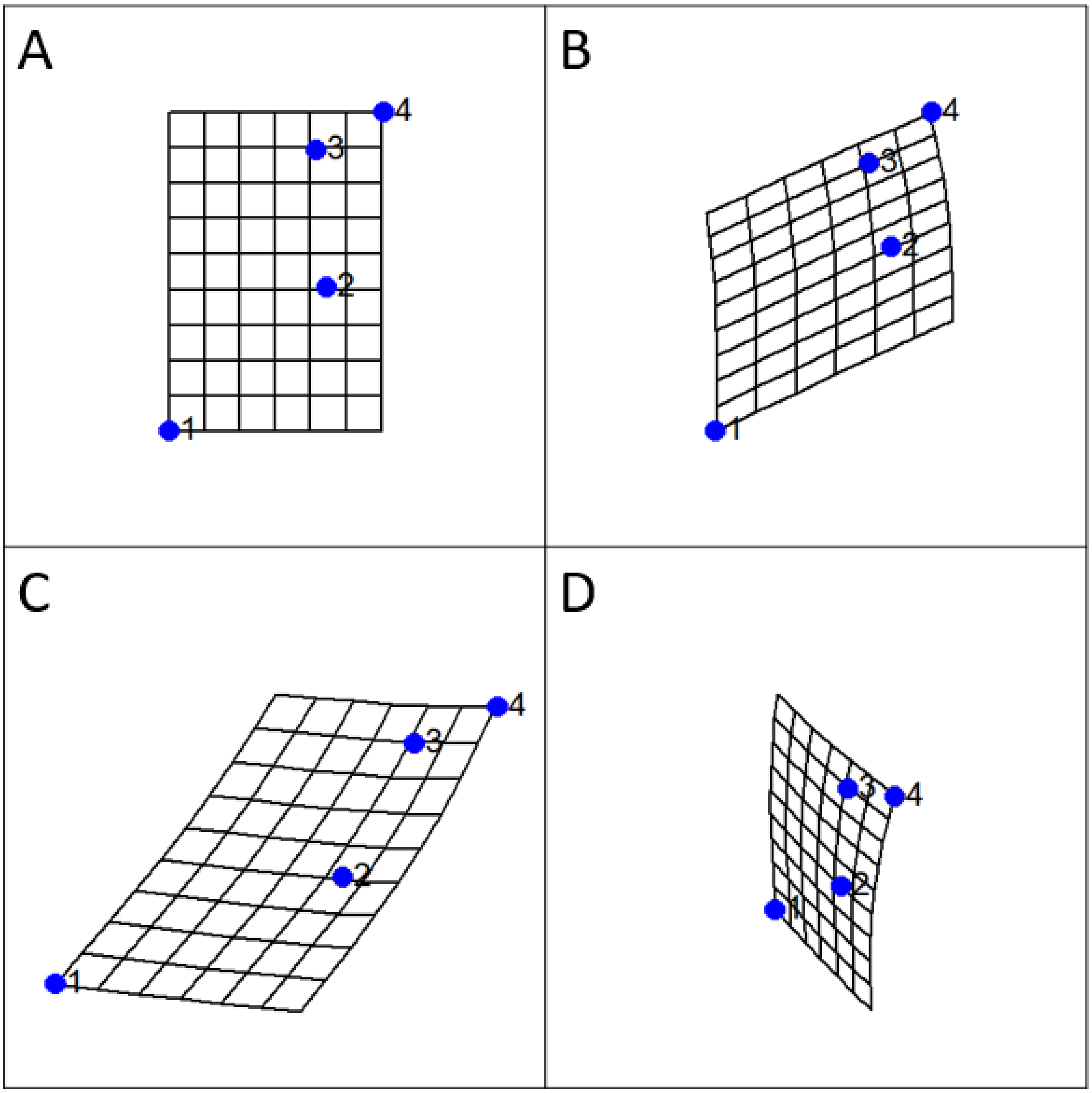

Figure 4. Average shell damage shape change for each species from the consensus of all landmarks as expressed by thin plate splines. A: consensus (average) of all shell damage, B: average shell damage shape change for Dungeness crabs compared to the overall consensus, C: average shell damage shape change for European green crabs compared to the overall consensus, D: average shell damage shape change for red rock crabs compared to the overall consensus. Landmark one was placed where the top of the shoulder/aperture met the left edge of the shell; this was a consistent landmark between all damaged shells. Landmark two was placed at the top of where the deepest damage met the original apertural edge. Landmark three was placed on the deepest point of the largest chip/peel. Landmark four was placed at the bottom of where the deepest damage met the original apertural edge.

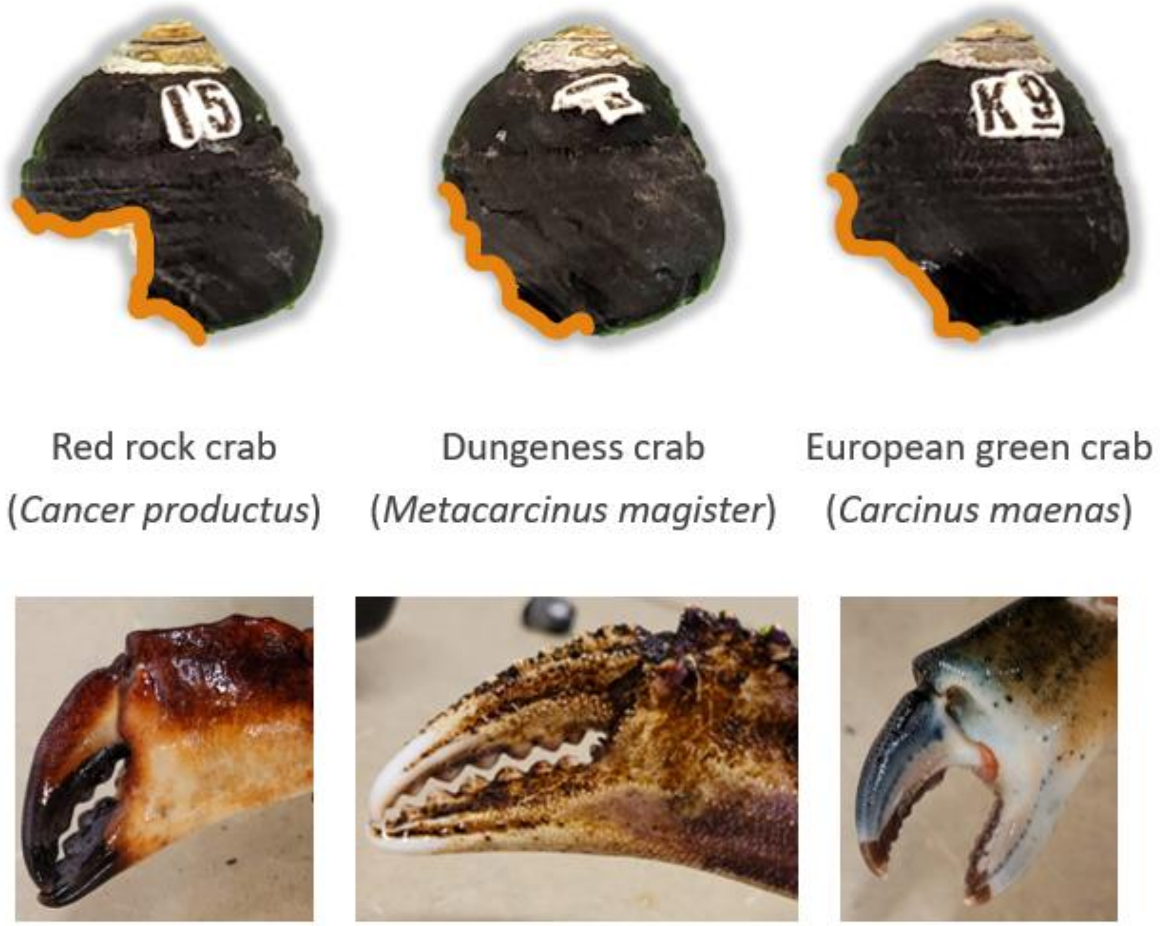

Figure 5. Claw shape and typical shell damage caused by each crab species. Red rock crabs have bulky, robust claws, Dungeness crabs have large, slender claws, and European green crabs have small claws and show handedness. Red rock crabs typically caused the deepest damage of all three crab species. Differences in the shape of shell damage is likely due to differences in claw shape, size, and strength.

Shell damage caused by red rock crabs was significantly deeper than that caused by both other species based on their Axis 1 scores (GLM, red rock versus Dungeness, p = 0.0001, red rock versus European green, p = 0.0003) (Fig. 3, Table 2). Damage caused by European green crabs was not significantly different from damage caused by Dungeness crabs based on their Axis 1 scores (GLM, p = 0.3317, Table 2). Axis 2 scores were not significantly different between any crab species (Fig. A1, Table A3).

Shell damage caused by red rock crabs was visually larger and more triangular than the other two species which is reflected in the thin plate splines (Fig. 3, Fig. 4, Fig. 5, Fig. A2, Fig. A3). Although not statistically significant damage caused by Dungeness and European green crabs was visually different, with damage caused by Dungeness crabs having more small individual chips along the edge of the aperture whereas damage from European green crabs was shallower, wider, and more rectangular (Fig. 3, Fig. 5, Fig. A3-A5).

Table 2. Generalized linear model (GLM) results comparing Axis 1 relative warp scores from the relative warp analysis. Relative warp scores are based on the distance of each set of landmarks from the consensus configuration. Coefficients for each crab intercept are shown, along with paired species comparisons to show relationships between all crabs. Bolded p-values indicate significance at a significance level of $p < 0.05$. Axis 1 depicts a change in depth of the damage, thus damage caused by red rock crabs was significantly deeper than that caused by Dungeness and European green crabs.

GLM of Axis 1 Scores, AIC= -14.154 (family=gaussian)				
Coefficients				
	Estimate	Std. Error	t value	P value (Pr>|t|)
Intercept (RRC)	0.19525	0.05101	3.827	**0.000406**
Intercept (DC)	-0.13885	0.05957	-2.331	**0.024413**
Intercept (EGC)	-0.06666	0.04311	-1.546	0.129227
RRC vs. EGC	-0.26191	0.06679	-3.921	**0.000305**
RRC vs. DC	-0.33410	0.07843	-4.260	**0.000106**
EGC vs. DC	-0.07218	0.07354	-0.982	0.331659

Observations

None of the three crab species appeared to chemically or visually detect the snails at the start of the trial since they did not usually exhibit hunting behaviour (sweeping legs out then towards their mouth while walking) when the snails were first placed in the tank. Instead, crabs typically moved around the tank, would accidentally run into a snail and decide to attack it once they tactilely recognized it as potential prey (Barclay et al., 2020). After the crab had encountered one snail it was more likely to display explicit hunting behaviour. Red rock crabs commonly attacked the snail that was dropped closest to it. Red rock and Dungeness crabs moved mostly along the edges of the tank when not actively attacking a snail. European green crabs moved across the middle of the tank much more commonly than the other two species.

Red rock and European green crabs both seemed to be able to tactilely detect the snails and recognize them as prey items relatively easily. Dungeness crabs seemed to have a harder time tactilely identifying the snails as prey and were commonly seen walking over the snails or kicking them without recognizing them. Dungeness crabs also occasionally grabbed a snail and investigated it very briefly before dropping it and moving on. To identify a snail as a prey item, red rock crabs seem to need to touch the snail with at least two walking legs, whereas Dungeness crabs mainly determined a snail was a prey item only when they touched it with one of their claws. European green crabs seemed to only need to touch a snail with one leg to determine it was prey as long as the crab was actively hunting.

When a crab did determine a snail to be prey it typically dropped on top of it using its walking legs and scooped the snail towards its claws and mouth. All crab species used their mouth parts at some point to help position the snail in their claws. Crushing was typically the starting strategy for all crab species.

Red rock crabs often switched to trying to crush the apex of the shell if they were unable to crush the entire snail before switching to peeling. To peel, red rock crabs grabbed the apertural lip with one claw inserted into the aperture. The crab would then try to grab the apertural lip with the other claw either in front or behind the first claw. From there the crab usually stabilized the snail against the ground and with the first two pairs of walking legs while flexing their claw arms in an attempt to break the apertural lip off. Red rock crabs typically had a firm hold on the snail and therefore stayed mostly in one place while trying to crush or peel the snail. They also were commonly actively trying to crush or peel for a longer period of time than European green or Dungeness crabs.

It was mainly red rock crabs that tried to peel with both claws grasping the apertural lip, however Dungeness crabs also showed a peeling type motion but most times they still had one claw grabbing around the entire snail and one claw grasping the apertural lip. Dungeness crabs also mostly used only their claws to attack the snail and only sometimes used their first pair of walking legs. Once Dungeness crabs made contact with the snails they seemed to have a hard time grasping them and manipulating them in their claws. They often dropped the snails underneath themselves and had a hard time grabbing them again. Dungeness crabs typically did not take any longer than 10 minutes trying to attack any one snail. European green crabs did not appear to peel; instead they attempted to crush across the apertural lip with their claw around and parallel with the apertural lip since their claws were typically not big enough to try and crush the entire shell. They sometimes used their first set of legs to help stabilize or position the snail. European green crabs did not spend very long for each attack attempt. Often they would try to crush a snail and realize they could not so they left it and tried to attack another snail, sometimes returning to the previous snail.

Dungeness crabs often left snails by themselves in under 10 minutes and near the end of the trial, and sometimes left almost immediately. European green crabs almost always left the snails by themselves and were observed often extending their claw away from their body before dropping the snail or pushing the snail away as they left it. Red rock crabs typically only found a maximum four or five of the six snails before becoming disinterested in hunting. European green crabs usually made contact with five or six snails quite quickly. Dungeness crabs only typically made contact with a maximum of three snails before becoming disinterested in hunting or simply sitting still.

Discussion

The major finding of my experiments is that the shape of shell damage caused by red rock crabs differs significantly from damage caused by Dungeness and European green crabs. These differences in shell damage shape are most likely due to differences in claw shape, size and strength among the various crab species. This shell damage is sublethal so when the snail heals its shell the damage will form a repair scar. Thus, my results demonstrate that it is possible to distinguish between repair scar shape based on the crab species that caused the initial damage, which has major implications for reconstructing and monitoring crab populations spatially and temporally. In BC, my results minimally indicate that in the past (prior to European green crab invasions), red rock and Dungeness crab populations can be tracked separately, which has important implications for the management of these fisheries. Furthermore, we can monitor for European green crab invasions using repair scar surveys by looking for the characteristic shape of the shell damage they cause, particularly in environments where there are no or few Dungeness crabs.

Red rock crabs

Red rock crabs caused the most distinct damage/repair scars that were typically very large and triangular in shape. These results are unsurprising, given that red rock crabs have stronger, bulkier claws than the other two species for their size (Taylor, 2000). Since European green crabs were not present in British Columbia prior to 1999, repair scars on shells from before that time including those from historical, archaeological and fossil collections would be from either red rock or Dungeness crabs (Gillespie et al., 2007). Thus, repair scars could be used to obtain species-level estimates of past crab abundances for red rock and Dungeness crabs.

Repair scars on shells from historical collections could be used to estimate independent red rock and Dungeness crab abundances from before and after the commercialization of crab fishing. These species-specific crab abundance baselines could be used to investigate how both red rock and Dungeness crab abundances have responded to the commercialization of crab fishing and if Dungeness crabs have been more impacted since they are a commercial fishery, whereas red rock crabs are a recreational fishery. For example, we might expect to see greater declines in Dungeness crabs compared to red rock crabs since the start of commercialized crab fishing.

Similarly, relative crab abundances prior to European colonization could be established from repair scars on shells from archaeological collections to explore the relationship between Indigenous communities and crabs. For example, the relationships between crabs and actively maintained clam gardens could be examined by comparing modern/historical and archaeological material. Early Indigenous communities often excluded other predators, such as sea otters, from areas where they harvested shellfish (Slade et al., 2022), and the same could be true for crabs. If humans were actively removing crabs from the clam gardens there would be fewer repair scars on prey within the clam garden compared to the surrounding area or compared to those same inactive clam gardens today.

Data of repair scars on fossilized snails could be compared to data from archeological and historical time periods to gain a broad understanding of how humans have impacted red rock and Dungeness crab populations through time. Seeing how red rock and Dungeness crab abundances change over time and if their abundances are different at different times could give insight into possible causes affecting their productivity such as increased commercial or recreational fishing, climate change, pollution, and/or competition from invasive species. If differences in red rock and Dungeness crab abundance patterns exist this may indicate the need for management of the fisheries individually as management of this multispecies fishery may mask declines in one species' abundance if the other species' abundance is on this rise.

European green crabs

Shell damage caused by European green crabs was also distinct from damage caused by red rock crabs. The shape of damage caused by European green crabs was shallow and wide and was visually different compared to damage caused by Dungeness crabs which consisted of many small triangular chips along the apertural lip of the shell (Fig. 3). This finding has important implications for the monitoring effort of the invasive European green crab, particularly in intertidal habitats or areas where there are no known Dungeness crab populations. Surveys of repair scars in the intertidal would likely capture European green crab invasions since European green crabs and red rock crabs are more abundant in the intertidal (Rudy and Rudy, 1983; Klassen and Locke, 2007). Rather than starting with costly trapping surveys, initial repair scar surveys could be a preliminary method to look for the presence of European green crabs in areas suspected of their invasion. If repair scars surveys in those areas find repair scars known to be caused by European green crabs, then additional trapping methods could follow to further investigate the extent to which green crabs have invaded that area. These first repair scar surveys could be done at low tides since European green crabs are typically found from the high intertidal line to a depth of five meters. Surveys at low tides would also reduce the need for divers to look for repair scars subtidally which could be as expensive as trapping methods. For areas where European green crabs are known to be established repeated repair scar surveys over time could be used to track their abundance over time. Repair scar surveys that calculate the proportion of repair scars caused by red rock crabs compared to European green crabs could also be used to obtain insight into the effect of this invasive species on the native red rock crabs and the ability of red rock crabs to keep European green crab numbers in check through predation (Hunt and Behrens Yamada, 2003).

Dungeness crabs

While damage caused by Dungeness crabs was distinct from damage caused by red rock crabs, the differences between damage caused by Dungeness and European green crabs were more subtle and difficult to distinguish statistically. Visually, it appears that Dungeness crab damage is similar in shape to damage caused by red rock crabs (triangular), but that caused by Dungeness is much less deep (Fig. 3). Distinguishing between damaged caused by Dungeness and European green crabs statistically was likely limited given the small sample size and the variation in damage shape within each crab species (Fig. A2-A5). It was difficult to obtain data points (shell damage) for Dungeness crabs as they appeared to have a hard time detecting the black turban snails tactilely. During the experimental trials the Dungeness crabs would often brush against the black turban snails but not detect them as easily as the red rock and European green crabs. Given the size differences between Dungeness and the snails, it is also possible that Dungeness may not see these snails as a high value prey. However, repair scars can also be seen on bivalves such as clams, a common prey item for Dungeness, and it is likely that those repair scars would also differ in shape by crab species since the difference in repair scar shape is likely due to differences in claw shape and strength.

Limitations

My findings may be limited by my relatively small sample size of snails with damage for each crab species which may be why, despite the visual differences (Fig. 3, Fig. A2-A5), damage caused by Dungeness and European green crabs was not found to be statistically significant. The variation in the shape of the shell damage within crab species may have been an added factor to why this difference was not found to be statistically significant despite visual differences in the damage caused by these two crab species (Fig. A2-A5). Furthermore, the fact that only adult crab specimens were used to assess the differences in repair scar shape among species may also limit these results since juveniles may also cause damage to these species. However, juvenile crabs would likely still have differences between the shape of repair scar they cause since the juveniles would still vary in claw shape. The choice to use average-sized adult male crabs for each species in my experiments not only reflects the average type of repair scar expected in any prey population, but it also reflects those Dungeness and red rock crabs most likely impacted by fisheries that have minimum size requirements for adult males. Finally, the applicability of my findings may be limited to the prey type used since only black turban snails were used to assess differences in repair scar shape among crab species. As black turban snails are only found on the west coast of Vancouver Island this could limit the use of repair scar surveys on this species of snail to monitor European green crab invasions in this area.

However, there are other snail and mollusc species that inhabit broader locations that would be preyed upon by these crab species such frilled dogwinkles (*Nucella lamellosa*) or butter clams (*Saxidomus gigantea*). Based on my results, differences in repair scar shape among crab species are driven by the differences in claw shape, size, and strength of these crab species and thus repair scars on other mollusc species would likely also show differences in repair scar shape for various crab species. Differences in prey shell strength may also help demonstrate differences in the repair scar shape on other crab species. For example, only repair scars from European green crabs would likely be seen on smaller snail species such as the Northern striped dogwinkle (*Nucella ostrina*) since red rock crabs would crush these smaller snails (Mendonca, 2020).

Future Research

A first step to further investigate the differences in shape of the repair scars caused by Dungeness and European green crabs would be to identify if the lack of statistical significance between damage caused by these species was only the result of a small sample size, or if it is a true biological signal. Based on the visual differences I observed, I predict that an increase in sample size would indicate a difference in shell damage between Dungeness and European green crabs. However, given the variation in shell damage shape obtained in this research (Fig. A2-A5), another avenue of study could investigate if there are confidence levels/scores that could be used to aid in identifying repair scars to certain species. Future research could also examine the shape of the damage to see if there are angles or measurements that surveyors could use to determine the crab species the repair scar was caused by in the field (i.e. by using a protractor), or to assign confidence levels/scores in the identification of the crab that caused the repair scar. Species-level repair scar survey accuracy could also be checked by pairing repair scar surveys and trapping surveys for European green crabs. Studies could also use the same methods used in this research to identify if the same trends in shell damage shape appear when other prey items such as butter clams (*Saxidomus gigantea*) or frilled dogwinkles (*Nucella lamellosa*) are used. Finding similar trends in shell damage shape on other prey items would broaden the applicability of the use of repair scars to monitor European green crab invasions and assess changes in past abundances of Dungeness and red rock crabs.

Another application of this research would be to use repair scars to examine Dungeness and red rock populations separately through time. Historical accounts from Indigenous communities or fishermen could be compared to relative abundances of Dungeness and red rock crabs estimated using repair scars to identify the accuracy of the species-level repair scar method to determine changes in past relative crab abundances. More broadly, researchers could use these results to investigate changes to Dungeness and red rock crab abundances through deep time to examine the impacts of human activity and climate change on each species since pre-human times. Additionally, these results could be used to establish relative population abundance baselines and assess current population health of both Dungeness and red rock crabs to improve the sustainable management of both these species.

Conclusions

My honours research aimed to determine if there are differences in the shape of repair scars caused by three of BC's most socioeconomically important crabs: Dungeness, red rock, and European green crabs. My results show that the shell damage caused by red rock crabs is significantly deeper than shell damage caused by Dungeness and European green crabs. These findings are consistent with my hypothesis that repair scars made by these three crab species will differ in shape and is consistent with my prediction that repair scars made by red rock crabs will be larger than those made by the other two species since red rock crabs have stronger claws than Dungeness and European green crabs. The thin plate splines for each species also show the trends in shape differences among damage caused by each species. Although not statistically significant Dungeness and European green crabs made damage that visually looks distinct with shell damage caused by Dungeness crabs consisting of small typically triangular chips and damage caused by European green crabs typically being shallow, rectangular damage along the apertural lip. Biological differences in the shape of repair scars made by these two species may be revealed with a larger sample size. Finding that the repair scars made by different crab species do differ in shape has implications for the management of these crab fisheries and the monitoring efforts of invasive European green crabs. Repair scars could be used to obtain species-level baselines for red rock and Dungeness crab abundance and to investigate if these two species relative abundance changes differently over time. This would allow for better management of these fisheries and help to determine if these species respond to various environmental factors differently and potentially indicate if they would better be managed as two individual fisheries rather than as a multispecies fishery. Repair scar surveys could also be used as an initial step in assessing whether European green crabs have invaded a new area or for monitoring their abundances in areas where they have already invaded.

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Appendix

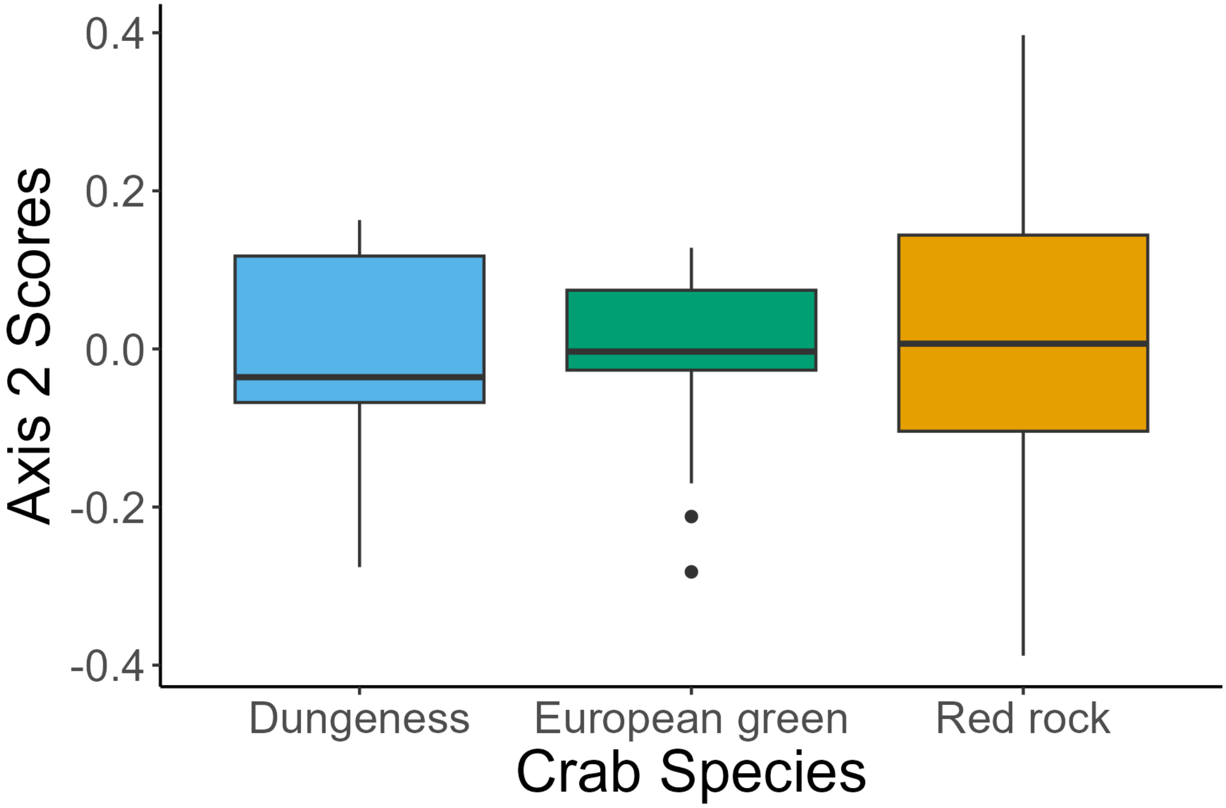

Figure A1. Boxplot of relative warp scores of Axis 2 for snails damaged by each crab species. Axis 2 accounted for 27.81% of the total observed shape variation of the shell damage and depicts a change in the position of the shell damage along the edge of the apertural whorl. No crab species' Axis 2 score was significantly different than any other crab species.

Figure A2. Black turban snails (*Tegula funebralis*) that were damaged by red rock crabs (*Cancer productus*). The placement of the landmarks that were used to calculate relative warp scores are shown by the blue dots.

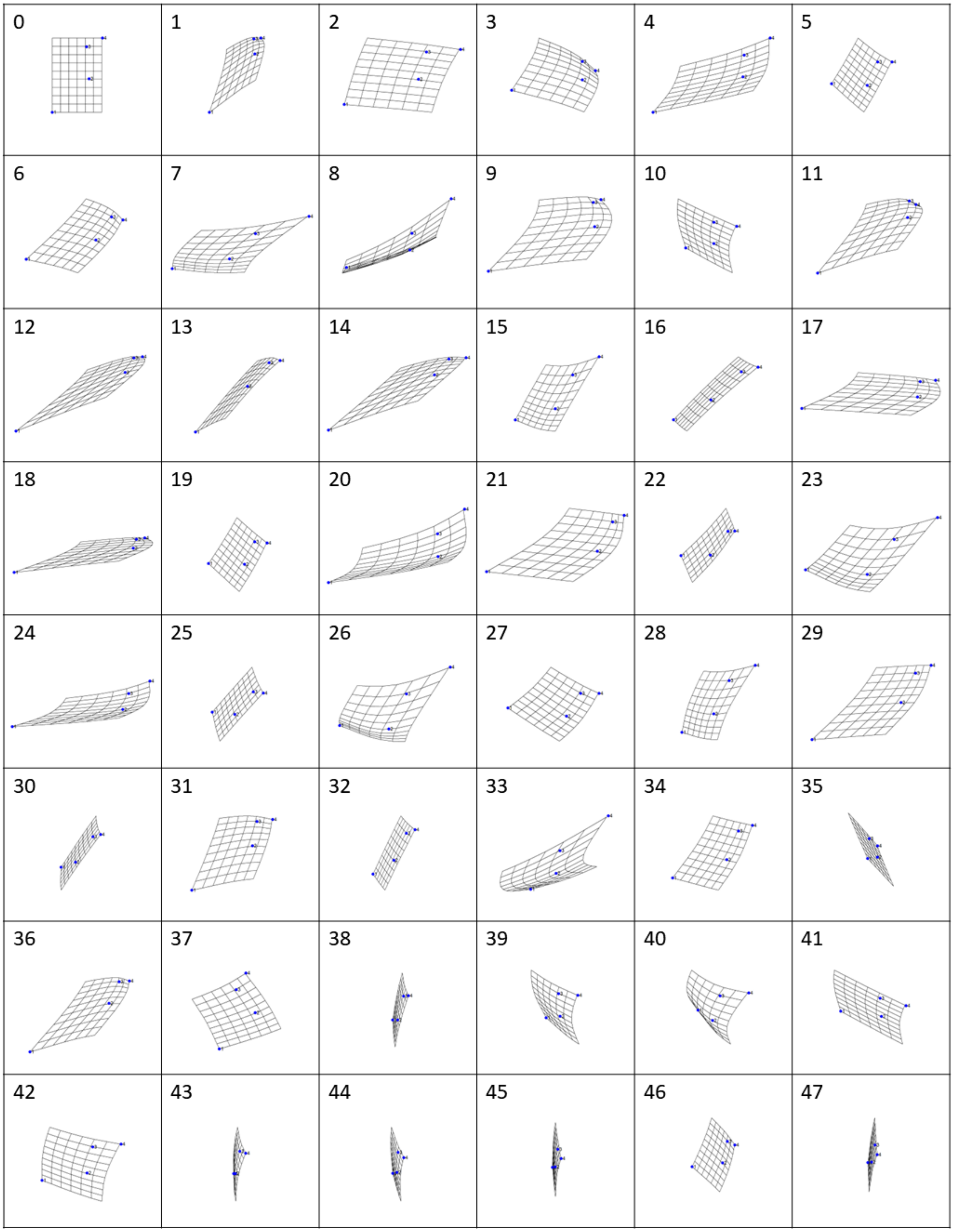

Figure A3. Thin-plate splines for all data points. Panel 0 is the consensus configuration (average) of all data points. Panels 1 to 11 are changes in the positions of the four landmarks of damage caused by Dungeness crabs compared to the consensus configuration. Panels 12 to 32 are changes in the positions of the four landmarks of damage caused by European green crabs compared to the consensus configuration. Panels 33 to 47 are changes in the positions of the four landmarks of damage caused by red rock crabs compared to the consensus configuration.

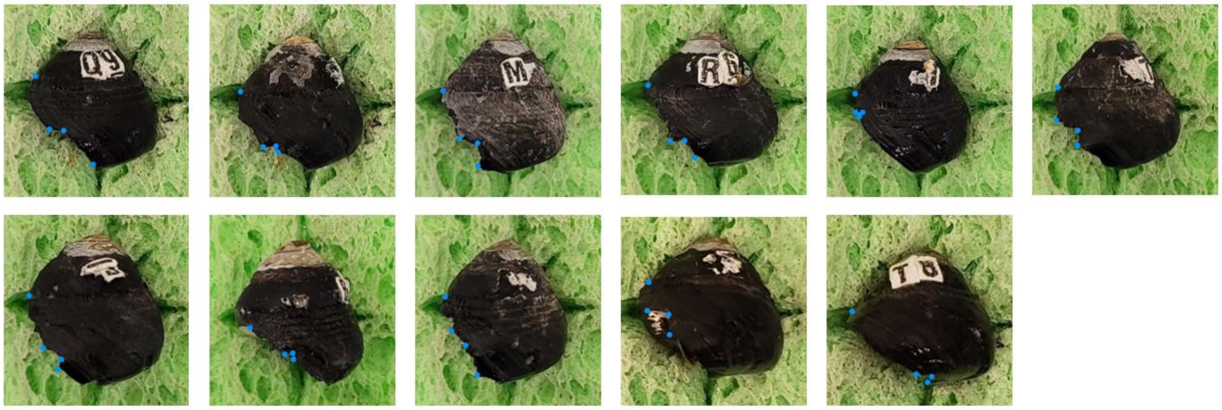

Figure A4. Black turban snails (*Tegula funebralis*) damaged by Dungeness crabs (*Metacarcinus magister*). Blue dots denote placement of landmarks that were used to calculate relative warp scores.

Figure A5. Black turban snails (*Tegula funebralis*) with damage caused by European green crabs (*Carcinus maenas*). Blue dots show the placement of the landmarks that were used to calculate relative warp scores.

Table A1. Summary of carapace width, left claw height, and right claw height for all crabs used in experimental trials. Crabs were measured with digital calipers (± 0.01 mm). RRC refers to red rock crabs (*Cancer productus*), EGC refers to European green crabs (*Carcinus maenas*), and DC refers to Dungeness crabs (*Metacarcinus magister*).

Crab species	Crab ID	Carapace width (mm)	Left Claw height (mm)	Right claw height (mm)	Handedness
RRC	1	162.03	42.41	41.8	NA
RRC	2	150.41	39.49	39.31	NA
RRC	3	130.27	34.31	35.46	NA
RRC	4	145.57	37.74	33.43	NA
RRC	5	144.35	36.03	35.58	NA
RRC	7	141.41	38.91	35.5	NA
DC	1	191.71	38.51	37.83	NA
DC	2	194.21	38.71	39.12	NA
DC	3	205.54	40.61	39.92	NA
EGC	Blue 1	75.6	19.39	25.05	R
EGC	Blue 4	73.94	23.9	18.24	L
EGC	Blue 5	76.41	19.59	26.78	R
EGC	Blue 6	74.66	19.39	26.78	R
EGC	Blue 7	76.17	20.99	28.99	R
EGC	Blue 8	74.87	20.48	26.01	R
EGC	Blue 10	80.2	27.84	20.55	L
EGC	Blue 13	75.87	24.73	17.86	L
EGC	Blue 14	71.36	22.4	16.39	L

Table A2. Raw relative warp scores for each axis for all landmarked photos of shell damage. Crab species denotes the species of crab that caused the shell damage. Each row is a photograph of individual snail with shell damage. RRC refers to red rock crabs (*Cancer productus*), EGC refers to European green crabs (*Carcinus maenas*), and DC refers to Dungeness crabs (*Metacarcinus magister*).

Crab Species	Axis 1	Axis 2	Axis 3	Axis 4
DC	-0.264	0.137	0.023	-0.0336
DC	-0.103	-0.0444	-0.0241	-0.0745
DC	-0.251	0.115	-0.095	-0.0528
DC	-0.206	-0.0476	-0.0151	0.018
DC	0.0298	-0.0357	-0.0499	0.0634
DC	-0.141	0.0914	0.0317	-0.0163
DC	0.0446	-0.241	0.0648	-0.0532
DC	-0.103	-0.276	0.000491	0.0315
DC	-0.288	0.12	-0.0314	0.0543
DC	0.0653	-0.0879	-0.166	-0.107
DC	-0.311	0.163	0.0051	-0.0232
EGC	-0.309	0.128	0.046	-0.0351
EGC	-0.111	0.0756	0.141	-0.0797
EGC	-0.256	0.0875	0.0629	-0.0738
EGC	0.0999	-0.17	0.064	0.0294
EGC	0.0782	-0.0263	0.157	-0.0482
EGC	-0.319	0.0801	-0.0187	0.00279
EGC	-0.36	0.124	0.016	-0.0162
EGC	0.0145	-0.00399	-0.0494	0.0582

EGC	-0.238	-0.0661	-0.0243	0.0799
EGC	-0.211	0.0743	0.0161	0.0653
EGC	0.0977	0.0257	0.05	0.095
EGC	0.0555	-0.212	0.0379	0.0747
EGC	-0.277	0.00562	0.00899	0.0358
EGC	0.172	-0.0179	0.0407	0.0591
EGC	0.0979	-0.282	0.0118	0.0743
EGC	-0.0916	-0.0239	-0.0372	0.0592
EGC	0.118	-0.148	0.0793	-0.0434
EGC	-0.163	0.0433	0.0415	0.0194
EGC	0.237	-0.0268	0.147	0.0258
EGC	-0.162	0.0725	0.0147	-0.0453
EGC	0.127	-0.0033	0.119	0.00411
RRC	0.132	-0.388	0.00382	-0.138
RRC	-0.0522	0.00663	0.0255	0.0433
RRC	0.378	0.292	-0.261	0.059
RRC	-0.223	0.109	0.0476	-0.0279
RRC	-0.0299	-0.0574	-0.106	0.111
RRC	0.411	-0.0048	0.13	0.0538
RRC	0.283	-0.0942	-0.175	-0.0995
RRC	0.282	-0.327	-0.129	0.023
RRC	-0.0987	-0.133	-0.191	-0.0834
RRC	0.00637	-0.114	-0.0681	-0.0343

RRC	0.473	0.0513	0.142	-0.0308
RRC	0.446	0.179	0.0239	-0.0168
RRC	0.471	0.365	-0.013	-0.0459
RRC	0.0062	0.0863	-0.0807	0.063
RRC	0.444	0.397	-0.0178	-0.0251

Table A3. Generalized linear model (GLM) results comparing Axis 2 relative warp scores from the relative warp analysis. Relative warp scores are based on the distance of each set of landmarks from the consensus configuration. Coefficients for each crab intercept are shown, along with paired species comparisons to show relationships between all crabs. Axis 2 depicts a change in the position of the shell damage along the edge of the apertural whorl.

GLM of Axis 2 Scores, AIC= -31.29 (family=gaussian)				
Coefficients				
	Estimate	Std. Error	t value	P value (Pr>|t|)
Intercept (RRC)	0.02452	0.04251	0.577	0.567
Intercept (DC)	-0.009655	0.049644	-0.194	0.847
Intercept (EGC)	-0.012556	0.035929	-0.349	0.728
RRC vs. EGC	-0.03708	0.05566	-0.666	0.509
RRC vs. DC	-0.03418	0.06536	-0.523	0.604
EGC vs. DC	0.002901	0.061281	0.047	0.962