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Ocean acidification leads to altered micromechanical properties of the mineralized cuticle in juvenile red and blue king crabs

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ABSTRACT

Ocean acidification (OA) adversely affects a broad range of marine calcifying organisms. Crustaceans, however, exhibit mixed responses to OA, with growth or survival negatively affected in some species, but unaffected or positively affected in others. In crustaceans, the mineralized cuticle resists mechanical loads, provides protection from the environment, and enables mobility, but little is known about how OA or interactions between OA and temperature affect its structure or function. Here, the effects of OA on the mechanics, structure, and composition of the cuticle in two Alaska king crab species was assessed. Juvenile blue king crabs (*Paralithodes platypus*) were exposed for a year to three pH levels, 8.1 (ambient), 7.8 and 7.5. Juvenile red king crabs (*Paralithodes camtschaticus*) were exposed for ~6 months to two pH levels, 8.0 and 7.8, at three temperatures: ambient, ambient + 2 °C, and ambient + 4 °C. Cuticle microhardness (a measure of resistance to permanent or plastic mechanical deformation), thickness, ultrastructure, and elemental composition were assessed in two body regions, the carapace and the crushing chela (claw). In both species tested, OA reduced endocuticle microhardness in the chela, but not in the carapace. There was no effect of pH or temperature on total procuticle thickness of the chela or carapace in either species. Reductions in microhardness were not driven by reduced calcium content of the shell. In fact, calcium content was significantly elevated in the carapace of blue king crabs and in the chela of red king crabs exposed to lower than ambient pH at ambient temperature, suggesting that calcium content alone is not a sufficient proxy for mechanical properties. Reduced chela microhardness, indicative of more compliant material, could compromise the utility of crushing chelae in feeding and defense.

1. Introduction

Within the past ~200 years, atmospheric carbon dioxide (CO_2) levels have increased from ~280 µatm prior to the Industrial Revolution to over 400 µatm today (Dlugokencky and Trans, 2016; IPCC, 2001; Raven, 2005). Projections based on "business-as-usual" emission scenarios suggest a further doubling of atmospheric CO_2 from today's levels by the end of this century (Orr et al., 2005; IPCC, 2001). Absorption of increased levels of atmospheric CO_2 by the world's oceans has and continues to reduce oceanic pH levels, a process known as ocean acidification (OA). The pH of global surface waters has dropped by 0.1 pH units since the industrial revolution and is projected to drop a further 0.3–0.5 pH units by the year 2100 (Caldeira and Wickett, 2003; Doney et al., 2009). The decrease in pH is likely to be extreme in high latitude waters due to increased solubility of CO_2 in colder waters and local upwelling of CO_2 rich waters (Orr et al., 2005; Mathis et al., 2015). Co-occurring with this reduction in pH is an increase in sea surface temperatures. The average temperature of global sea surface waters has already increased by ~0.4 °C (Roemmich et al., 2012) since the industrial revolution and is projected to increase by an additional 2–4 °C by the end of the century (IPCC, 2014).

While an increase in atmospheric CO_2 and a decrease in seawater pH appears to be inevitable, the extent to which OA will affect marine organisms, particularly in the long term (many months to years), remains an area of active investigation. Meta-analyses of OA literature have highlighted a generally large and negative effect of ocean acidification on marine organisms that build a calcified shell (Kroeker et al., 2010; Kroeker et al., 2013). When all taxa were assessed together, Kroeker et al. (2013) found a significant negative effect of OA on survival, calcification, growth, development, and abundance. When

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taxa were analyzed separately, however, responses varied considerably among major groups of calcifying organisms. In particular, among crustaceans, there was not a significant average effect on survival, calcification, growth or abundance (Kroeker et al., 2013). Although some crustacean species show reduced growth upon exposure to conditions that emulate OA (Long et al., 2013a; Kurihara et al., 2008), others show no effect (Carter et al., 2013; Hauton et al., 2009; Kurihara and Ishimatsu, 2008; Small et al., 2010) or even enhanced growth under OA conditions (McDonald et al., 2009; Ries et al., 2009).

Little is known about the functional responses of decapod crustaceans to OA, specifically in terms of how OA may affect the structure and mechanical properties of the mineralized exoskeleton. OA has the potential to affect both uptake of Ca^{2+} and HCO_3^- after molting and precipitation of $CaCO_3$ within the exoskeletal compartment, which requires a pH slightly above that of the hemolymph (Whiteley, 2011). The decapod exoskeleton, or cuticle, fulfills many functions including resistance to mechanical loads (e.g. those from predators and prey items), protection from the environment (including desiccation), and structural support for mobility (Chen et al., 2008; Raabe et al., 2006). Therefore, alterations in the structural or mechanical properties of the exoskeleton due to OA may significantly affect the fitness of decapod species.

The decapod exoskeleton is multilayered, consisting of an outer epicuticle, a procuticle composed of an outer exocuticle and inner endocuticle, and a thin membranous inner layer (Travis, 1963). The mineralized exo and endocuticle are composed of chitin-protein nanofibrils grouped into fibrous bundles (Chen et al., 2008; Giraud-Guille, 1984; Raabe et al., 2005; Raabe et al., 2006). These chitin-protein bundles arrange into planes, which are stacked on top of one another, with the direction of each plane shifted slightly with respect to the last. This regular shifting of horizontal planes results in a helicoidal "twisted plywood" or "Bouligand" structure, with each 180° turn of the helix referred to as a "Bouligand layer" (Giraud-Guille, 1984; Raabe et al., 2006). Within an individual procuticle, the thickness of Bouligand layers tends to be greater in the endocuticle than in the exocuticle, resulting in denser packing of Bouligand layers in the exocuticle (Hegdahl et al., 1977; Raabe et al., 2005; Raabe et al., 2006). Amorphous calcium carbonate or nanocrystalline magnesian calcite is embedded within the chitin-protein matrix (Boßelmann et al., 2007; Dillaman et al., 2005; Roer and Dillaman, 1984).

The goal of this study was to assess the extent to which OA alone or in combination with increased seawater temperature affects functional properties of the mineralized cuticle in two commercially harvested Alaska crab species. It was hypothesized that microhardness of the cuticle, a measure of resistance to permanent or plastic mechanical deformation, would be reduced under low pH or elevated temperature and that those changes would be driven by altered structure or reduced mineral content. To test this hypothesis, juvenile blue king crabs (*Paralithodes platypus*) were exposed for a full year to three levels of pH, an ambient level of 8.1 and reduced levels of 7.8 and 7.5 (predicted global averages in surface waters for the years ~2100 and ~2200, respectively: Caldeira and Wickett, 2003). Juvenile red king crabs (*Paralithodes camtschaticus*) were exposed for ~6 months to two levels of pH, an ambient level of 8.0 and a reduced level of 7.8, at three levels of temperature, ambient, ambient + 2 °C and ambient + 4 °C. In both cases, individual crabs underwent several molts during the exposure (Long et al., 2017; Swiney et al., 2017). Following exposures, microhardness, thickness, ultrastructure, and elemental content was assessed in two body regions, the carapace and crushing chela.

2. Materials and methods

The animals studied in this paper came from two distinct, though conceptually similar experiments, which examined a broad range of responses of red and blue king crabs to ocean acidification and warming; those data, including survival, growth, and morphology, have been published elsewhere (Long et al., 2017; Swiney et al., 2017). The response variables reported here were opportunistically made post hoc. Given the similarity of the experiments, data collected on the mineralized cuticles from these experiments were combined into this paper. Although the experiments were not identical, and therefore explicit statistical comparisons between the studies cannot be done, the comparisons between the two species are informative and thus have been combined into this manuscript.

2.1. Animal collection and experimental exposure

Juvenile blue king crabs, *Paralithodes platypus*, were reared from larvae at the Alaska Fisheries Science Center's Kodiak Laboratory seawater facility in Kodiak, Alaska, as described by Long (2016), from broodstock captured in commercial pots near St. Matthew Island in the winter of 2010. Thirty juvenile blue king crabs at the first crab stage (C1) stage were randomly assigned using a random number generator to each of three pH treatments (90 crabs total): 1) ambient (8.1), 2) 7.8, or 3) 7.5. The experiment began on June 17, 2011 and was ended on June 14, 2012 (363 days).

Juvenile red king crabs, *Paralithodes camtschaticus*, were also reared from larvae at the Kodiak Laboratory seawater facility from an ovigerous female collected in Bristol Bay, Alaska, in June 2011 and shipped live to the laboratory; because only one female was used, this likely represents a limited range of genetic and phenotypic diversity compared to the Bristol Bay population as a whole. Thirty juvenile red king crabs were randomly assigned using a random number generator to one of two levels of pH (ambient (8.0) or 7.8) at one of three levels of temperature (ambient, ambient + 2 °C, and ambient + 4 °C). This fully-crossed design yielded six experimental treatments each with 30 crabs for a total of 180 crabs. A pH treatment lower than pH 7.8 was not included in this study because in a previous study 100% mortality was observed for young-of-the-year red king crabs exposed to pH 7.5 waters after 95 days (Long et al., 2013a). The juvenile red king crab experiment began August 5, 2012 and was ended on February 4, 2012 (184 days).

Crabs were reared in tubs (53 (L) × 38 (W) × 23 (H) cm) that were placed randomly in the experimental area and which received flow-through water at the appropriate pH from head tanks as described below. One tub was used per treatment in each experiment. Juveniles were reared in individual inserts (one crab per insert) constructed from PVC pipe 40 mm inner diameter with 750 μm mesh attached to the bottom and the inserts were placed inside the treatment tub on top of a grid that was raised off the bottom of the tubs so that the tops of the inserts were just out of the water. These inserts were large enough to ensure that neither growth nor survival would be affected (Swiney et al., 2013). Water was delivered into each insert within each tub via a submersible pump connected to a manifold. Flow rates were checked visually each day for each insert and adjusted to ensure equal flow rates (each insert had its own flow valve). Three times a week, crabs were feed ad libitum a gel diet of Gelly Belly (Florida Aqua Farms, Inc., Dade City, FL, USA) enhanced with Cyclop-eeze powder (Argent Laboratories, Redmond, WA, USA), pollock bone powder (US Department of Agriculture, Agricultural Research Service, Kodiak, AK, USA), and astaxanthin. Excess food was cleaned from each insert prior to feeding. Each insert was checked daily for molts and mortalities. Exuvia and mortalities were recorded and removed.

2.2. Seawater chemistry

Seawater acidification followed the methods described in Long et al. (2013b). Sand filtered seawater was pumped into the Kodiak Laboratory seawater facility. A 160 l tank of pH 5.5 was established by bubbling CO_2 into ambient seawater. This pH 5.5 water was then mixed with ambient seawater in 160 l treatment head tanks (one per pH treatment) to the nominal pH via peristaltic pumps controlled by

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