
Morphological And Ecological Consequences Of Changes In Skeletal Density

Changes in skeletal mineralization have the potential to significantly alter performance and energetics of fishes. In fact, density of HA in the skeleton directly affect mechanical properties and physiological performance. There is a well-established correlation between skeletal mineralization and resistance to deformation from loads experienced during swimming. Higher mineral content in the cartilage leads to increased stiffness and strength of the skeleton, and in fact, fishes that reach high speeds during locomotion generally possess a stiffer and stronger skeleton that allows them to transfer energy more effectively. In little skates, vertebral mineralization increased by 10-20% with acidification, but warming had an opposing effect and decreased mineralization by 17-21%. Therefore, an increase in HA mineralization caused by acidification alone, in absence of warming, could theoretically support an increase in mechanical load that elasmobranch using their axial skeleton during locomotion would experience at higher speeds. Most batoids however, use mainly their pectoral fins to swim across a narrow range of speeds (optimally about 1-1.5 body lengths (BL)/s) and rarely engage in any speed below or beyond cruising because these are metabolically taxing. Even though mineralization of the vertebrae increased with simulated ocean acidification, HA density did not increase in pectoral fins. Instead, wing mineralization was lower at the high temperature and acidification tested than control conditions (Fig. 2). Previous work on skates suggests that a large portion of costs of locomotion during swimming at high speeds (>2 BL/s) is derived by the necessity to stiffen the wing through creation of a transversal arch (or a notch) on its margin. As a consequence, we would expect that metabolic costs of locomotion might increase even further with fins that are less stiff and need active deformation.

On the other hand, at low speeds skates prefer to walk on the substratum using modified fins, the crura. Macesic and Summers (2012) found that the stiffness of the cartilage in the crura was a good predictor of the ability of batoids to walk. In fact, skates with denser crura were also the most likely to exhibit this behavior. In the present study, HA density in the crura increased by 11-30% with ocean acidification. These results suggest that skates may experience an advantage and so be even more prone to walk rather than swim especially at low and intermediate speeds under low pH scenarios. The advantages acquired during punting however need to be weighed with the consequences of denser, and hence heavier, skeleton. As the tessellated cartilage becomes more mineralized, buoyancy would decrease thus reducing locomotor efficiency. Ecological studies have reported that batoid fishes with denser skeletons tend to remain on the bottom of the ocean, and are much less active than those with a lower cartilage mineral content. It is possible that the observed sluggish behavior of benthic elasmobranchs may be a consequence of the high metabolic costs of swimming incurred with a less buoyant and heavier skeleton. Rays and sharks in fact lack a gas bladder, and they need to actively push water downwards to create hydrodynamic lift. Interestingly, an increase in metabolic costs during escape responses has already been reported for elasmobranchs under ocean acidification and warming, and the present study provides an additional mechanism to explain increased costs of locomotion under simulated future ocean conditions.

Benthic fish species are expected to move to deeper waters to find thermal refugia. These deeper cooler waters are characterized by generally higher CO₂ concentrations and may

therefore exacerbate the effect of climate change (through lower pH) on skeleton mineralization. The most intriguing aspect of the results from this study is that ocean acidification and warming have unanticipated consequences on morphology and, consequently, ecology of marine fishes. We now know that ocean acidification and warming are not only affecting the skeleton of carbonate systems, such as shell-producing invertebrates, but also of phosphate systems, and in particular fishes. Collectively, ecophysiological studies on the effect of climate change on ectotherms have demonstrated that many fish species are unlikely to fare well in the near future, especially when they need to cope with a combination of stressors such as warming, acidification, hypoxia, pollution, habitat destruction, overfishing, which can all reduce the likelihood of resilience in future scenarios.

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