ELEMENTA
Science of the Anthropocene

Busch, DS and McElhany, P 2017 Using mineralogy and higher-level taxonomy as indicators of species sensitivity to pH: A case-study of Puget Sound. *Elem Sci Anth,* 5: 53, DOI: https://doi.org/10.1525/elementa.245

RESEARCH ARTICLE

Using mineralogy and higher-level taxonomy as indicators of species sensitivity to pH: A case-study of Puget Sound

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Information on ecosystem sensitivity to global change can help guide management decisions. Here, we characterize the sensitivity of the Puget Sound ecosystem to ocean acidification by estimating, at a number of taxonomic levels, the direct sensitivity of its species. We compare sensitivity estimates based on species mineralogy and on published literature from laboratory experiments and field studies. We generated information on the former by building a database of species in Puget Sound with mineralogy estimates for all $CaCO_3$-forming species. For the latter, we relied on a recently developed database and meta-analysis on temperate species responses to increased CO_2. In general, species sensitivity estimates based on the published literature suggest that calcifying species are more sensitive to increased CO_2 than non-calcifying species. However, this generalization is incomplete, as non-calcifying species also show direct sensitivity to high CO_2 conditions. We did not find a strong link between mineral solubility and the sensitivity of species survival to changes in carbonate chemistry, suggesting that, at coarse scales, mineralogy plays a lesser role to other physiological sensitivities. Summarizing species sensitivity at the family level resulted in higher sensitivity scalar scores than at the class level, suggesting that grouping results at the class level may overestimate species sensitivity. This result raises caution about the use of broad generalizations on species response to ocean acidification, particularly when developing summary information for specific locations. While we have much to learn about species response to ocean acidification and how to generalize ecosystem response, this study on Puget Sound suggests that detailed information on species performance under elevated carbon dioxide conditions, summarized at the lowest taxonomic level possible, is more valuable than information on species mineralogy.

Keywords: Puget Sound; calcium carbonate mineralogy; ocean acidification; ecosystem-based management; global change; species inventory

1. Introduction

Marine ecosystems are reorganizing in response to anthropogenically driven global changes, such as climate change, ocean acidification, nutrient and chemical pollution, and habitat alteration. Living marine resource managers are challenged to manage resources sustainably and responsibly through this change, while still meeting society's needs for ecosystem services (Busch et al., 2016). Doing so is especially difficult in data-poor systems, where there is limited knowledge of species composition and response to projected future conditions. In these circumstances, uncertainty is amplified by lack of knowledge.

Ecosystem-based fisheries management is currently considered the best practice for simultaneously managing multiple living marine resources, especially as they respond to global change (Link, 2016). Estimates of species vulnerability to environmental change and projections of future species and ecosystem states based on them can be used to inform ecosystem-based fisheries management and, thus, are an important tool for sound marine resource management. Options exist for developing the scientific basis for ecosystem-based management even in data-poor situations, such as integrated ecosystem assessments based on qualitative conceptual models, threat maps developed using expert opinion, generic indicators, and information on trends (Tallis et al., 2010) though acknowledging uncertainty in this information, a key principle of ecosystem-based management, is especially important (Long et al., 2015).

Incorporating the impacts of ocean acidification into ecosystem-based fisheries management plans is currently challenging given the limited evidence available on this relatively newly recognized phenomenon. Available

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information on the potential impacts of ocean acidification suggests variation in the sensitivity of individual species (Kroeker et al., 2013; Busch and McElhany, 2016) and compelling evidence of the potential for ecosystem change (Hall-Spencer et al., 2008; Fabricius et al., 2014; Dutkiewicz et al., 2015; Enochs et al., 2015; Marshall et al., 2017). Ocean acidification could push marine ecosystems prone to tipping points into alternate states given that some species groups that structure ecosystems display sensitivity to carbonate chemistry conditions in both laboratory and field investigations. For example, coral-reef systems have been observed to transition into macroalgae-dominated systems at carbon dioxide vent sites (i.e., Enochs et al., 2015). Ocean acidification could similarly tip the balance between oyster reefs/pelagic food web-dominated ecosystems and kelp/urchin-dominated ecosystems given the generally positive influence of acidified conditions on primary producers and negative influence of acidified conditions on calcifiers (Kroeker et al., 2010; Gao et al., 2012; Kroeker et al., 2013; Wittmann and Pörtner, 2013; Busch and McElhany, 2016).

Here we explore ways to build ecosystem-level information on species sensitivity to ocean acidification. We consider Puget Sound, a semi-urbanized estuary in the northwest continental USA, as a case study. We consider this relatively well-studied ecosystem because we have enough information on it to compare two techniques for assessing species sensitivity to changing carbonate chemistry: estimates of the mineralogy of species that live in Puget Sound (mineralogy-related sensitivity based on species-mineralogy database) and a meta-analysis of published literature on species sensitivity to carbonate chemistry conditions tailored to the Puget Sound (survival-related sensitivity based on a species-response database). We focus these analyses on sensitivities at the species level, as previous work has explored the response of the Puget Sound food web to ocean acidification, climate change, and tidal power development (Busch et al., 2013a, 2013b). Considering this relatively well-studied ecosystem may yield results informative to those building understanding about the potential impacts of ocean acidification in more poorly studied locales.

Previous meta-analyses have found that, in general, species with calcium carbonate structures are likely to be impacted negatively by the chemistry changes associated with ocean acidification; although meta-analyses have also indicated that factors related to taxonomy and life history can influence sensitivity and that non-calcifying species can also express sensitivity (Kroeker et al., 2010; Gao et al., 2012; Kroeker et al., 2013; Wittmann and Pörtner, 2013; Nagelkerken and Connell, 2015; Busch and McElhany, 2016). Furthermore, calcium carbonate minerals differ in dissolvability, with the ranking from most soluble to least soluble as: 1) amorphous calcium carbonate, 2) high-Mg calcite (>7% mol $MgCO_3$) 3) aragonite, and 4) low-Mg calcite (Ries et al., 2009); however, biogenic calcium carbonate has considerable variation in the solubility of each type of mineral depending on its exact composition and structure. Early research on ocean acidification hypothesized that sensitivity to carbonate chemistry conditions would correlate with the solubility of the mineral form of calcium carbonate produced by the organism (e.g., Fabry et al., 2008). This hypothesis is based, in part, on the fact that the geologic record suggests that the response of calcifying species to ocean acidification depends partially on mineralogy, the extent to which organic tissues cover calcium carbonate structures, and physiological control over the chemistry of the calcification site (Knoll et al., 2007; Hautmann et al., 2008; Pörtner, 2008; Ries et al., 2009). As a specific test of this idea, we hypothesize that species in Puget Sound that make structures from more soluble forms of calcium carbonate are more sensitive to the negative effects of increased CO_2 than species that make structures from less soluble forms of calcium carbonate.

Here we compare and contrast the estimates from two methods for assessing the potential response of Puget Sound species to ocean acidification to determine whether they give similar information. We built a database of species that inhabit Puget Sound, including their taxonomy, and estimated calcium carbonate mineralogy for the early and adult life stages of all calcifiers (herein called the species-mineralogy database). We used species rankings based on estimates of mineral solubility as one potential estimate of species sensitivity to ocean acidification (which we term the mineralogy-related sensitivity). The carbonate-chemistry sensitivity of Puget Sound species was evaluated in a second way using a recently developed database of information from published studies of experiments and field observations on temperate species response to carbonate chemistry conditions (the species-response database; Busch and McElhany, 2016). The approach used to estimate species sensitivity from this species-response database incorporates information on the value of each published study relative to the question of how pH affects the survival of species in Puget Sound (termed the survival-related sensitivity, described in more detail below; Busch and McElhany, 2016). Information on the comparative performance of these two methods of estimating sensitivity builds understanding of how the Puget Sound ecosystem might change under future ocean conditions and is useful input for exercises that attempt to project the influence of ocean acidification on Puget Sound's communities, both biological and human.

2. Materials and methods

2.1 Species-mineralogy database

To generate the species-mineralogy database, a database of species in Puget Sound (including the Strait of Juan de Fuca, excluding the Strait of Georgia) was built using both published and unpublished lists of species either collected from or observed living in the wild (Dataset S1, References S1). Taxonomy for each species was taken from the Integrated Taxonomy Information Service (ITIS, www.itis.gov) for animals and protozoa or AlgaeBase (www.algaebase.org) for plants and algae or, if not available at these sources, from the World Register of Marine Species (http://www.marinespecies.org/). This database excludes microbes and viruses.

For species with calcium carbonate structures, mineralogy was assigned to both early life stages and adult forms. For some species, mineralogy was known from species-specific studies conducted in the Puget Sound region or elsewhere within the species' global distribution. For other species, mineralogy was assigned based on the pattern of mineralogy in its genus, family, order, or class, using information from the lowest taxonomic level possible. For many species, assigning mineralogy was challenging and required assumptions about patterns of mineralogy within a taxon based on little documented research and/or on distantly related species. When species mineralogy was unclear, the species of interest was assumed to have the most soluble mineralogy form present in the taxon. Similarly, early life stages were assigned the most soluble mineral form produced during development. This approach uniformly assigns species to the mineralogy category likely to be the most vulnerable to the effects of acidification. The mineralogy of biominerals in vertebrates was not assigned because of their strong control over internal chemistry and the predominance of non-carbonate minerals. The method used to assign mineralogy at both early life and adult stages for each species in the database is detailed in Dataset 1, including, if applicable, the taxonomic level on which mineralogy assignments were based.

2.2 Species-response database

We relied, with some modification, on the meta-analysis presented in Busch and McElhany (2016) to estimate the relative sensitivity of Puget Sound species to decreases in seawater pH. For the 2016 meta-analysis, we built a database of all studies published before January 1, 2015, on the response of temperate species to carbonate chemistry treatment conditions (S1 and S2 Databases in Busch and McElhany (2016)). We then evaluated the relevance of each study to the question of how decreased pH will affect the survival of functional groups in the California Current Ecosystem, where a functional group is a collection of species with similar trophic roles regardless of taxonomy. The result was a "relative survival scalar" for each functional group that ranged from a value of −1 for the functional groups most negatively affected by decreased pH to positive values for functional groups expected to be most positively affected by a decrease in pH.

For the analysis herein, we modified the approach presented in Busch and McElhany (2016) by calculating survival scalars by taxonomic groups rather than by functional groups. Another slight modification was shifting the focal geographic target for calculation of the survival scalars from the California Current to Puget Sound (Table S1). Focusing the analysis on taxonomic groups allowed us to assign pH sensitivity values to individual Puget Sound species based on taxonomic relatedness. The use of relatedness for assigning pH sensitivity is similar to the approach taken in assigning mineralogy. Direct experimental data were available for only 56 Puget Sound species so pH sensitivity was assigned to species lacking direct experimentation by looking at the sensitivity of taxonomically higher groupings. We calculated survival scalars for each family, order, and class in Puget Sound. Conducting the analysis at these higher taxonomic levels allowed us to develop sensitivity estimates for a large portion of the Puget Sound marine community (**Table 1**) and to compare species sensitivity estimates when estimates were developed at different taxonomic levels.

2.3 Comparing survival-related sensitivity to mineralogy-related sensitivity

We describe patterns in species sensitivity to carbonate chemistry based on results from survival-related sensitivity estimates and mineralogy-related sensitivity estimates. We considered using an ordered ANOVA to compare the distribution of survival scalars by species mineralogy at a variety of taxonomic levels. However, we decided against this approach because taxonomy was used to assign mineralogy categories in the database of Puget Sound and, due to the fact that species physiology can control mineralogy, taxonomy and mineralogy are confounded. Thus, we believe that such a statistical analysis is inappropriate.

3. Results

3.1 Mineralogy-related sensitivity

The species-mineralogy database includes 3,059 entries (2,992 defined at the species level) in 31 phyla that have been collected from or sighted in Puget Sound (**Table 2**, Dataset S1). In comparison, the species-response database includes 240 species in 18 phyla. The five dominant phyla in Puget Sound in terms of species number are the Annelida, Arthropoda, Chordata, Mollusca, and Rhodophyta.

Thirty percent of the species that live in Puget Sound form calcium carbonate structures and less than ten percent form structures out of materials other than calcium carbonate (e.g., silica-based minerals; **Figure 1**). About half of the species do not form hard structures, and 14% are vertebrates that form calcium phosphate bones (fish make otoliths from calcium carbonate, which we chose

Table 1: Contents by taxonomic level for the species-mineralogy and species-response databases, with matches between databases. DOI: https://doi.org/10.1525/elementa.245.t1

Database contents	Taxonomic level[a]					
	Phylum	Class	Order	Family	Genus	Species
Species-mineralogy database	31	72	256	760	1,645	2,992
Species-response database	18	32	94	158	213	240
Matches between databases[b]	17(55%)[b]	28(39%)	73(29%)	92(12%)	85(5%)	56(2%)
Number of Puget Sound species captured when databases matched by taxonomic level[b]	2,990(98%)[b]	2,519(83%)	1,912(63%)	615(20%)	268(9%)	56(2%)

[a] Number of entries.
[b] Percentages given are the percent of Puget Sound taxa in the species-response database.

Table 2: Number of classes, orders, families, genera, and species in each phylum in the species-mineralogy and species-response databases. DOI: https://doi.org/10.1525/elementa.245.t2

Kingdom	Phylum	Class	Order	Family	Genus	Species
Species-mineralogy database						
Animalia	Arthropoda	5	22	137	289	487
Plantae	Rhodophyta	4	23	53	187	482
Animalia	Annelida	2	6	45	219	465
Animalia	Chordata	7	48	123	283	463
Animalia	Mollusca	6	33	123	222	336
Chromista	Ochrophyta	4	14	29	77	179
Plantae	Chlorophyta	5	11	27	53	139
Animalia	Cnidaria	3	14	48	76	98
Chromista	Bacillariophyta	3	26	35	47	84
Animalia	Bryozoa	2	3	34	46	65
Animalia	Echinodermata	4	13	27	40	64
Chromista	Miozoa	2	8	16	24	40
Animalia	Porifera	3	8	18	21	23
Animalia	Nemertea	2	3	8	14	20
Plantae	Tracheophyta	2	2	4	4	9
Animalia	Platyhelminthes	2	1	5	6	7
Animalia	Kamptozoa	1	2	3	4	6
Animalia	Sipuncula	2	2	2	4	5
Animalia	Chaetognatha	1	2	2	4	4
Animalia	Brachiopoda	1	1	2	3	3
Protozoa	Ciliophora	2	5	8	9	3
Animalia	Ctenophora	1	2	2	2	2
Animalia	Phoronida	0	0	0	2	2
Protozoa	Protozoa	2	2	2	2	2
Plantae	Charophyta	2	2	2	2	1
Protozoa	Craspedophyta	1	1	1	1	1
Animalia	Hemichordata	1	0	1	1	1
Animalia	Priapulida	0	0	1	1	1
Chromista	Cryptophyta	1	1	1	1	0
Chromista	Haptophyta	1	1	1	1	0
Animalia	Nematoda	0	0	0	0	0
Species-response database						
Animalia	Mollusca	3	11	20	35	49
Animalia	Arthropoda	2	8	22	27	42
Animalia	Echinodermata	4	15	23	32	36
Animalia	Chordata	3	11	17	17	19
Plantae	Rhodophyta	1	3	8	15	17
Animalia	Cnidaria	1	3	8	11	12
Chromista	Ochrophyta	3	5	8	12	11
Chromista	Bacillariophyta	3	14	16	20	8
Plantae	Chlorophyta	2	4	7	8	8
Chromista	Miozoa	1	5	5	8	7
Animalia	Porifera	1	4	5	6	7
Plantae	Tracheophyta	1	1	5	6	7
Chromista	Haptophyta	1	5	5	6	6
Protozoa	Protozoa	1	1	4	5	5
Animalia	Annelida	2	2	2	2	3
Animalia	Bryozoa	1	1	2	2	2
Animalia	Xenacoelomorpha	1	1	1	1	1
Chromista	Cryptophyta	1	0	0	0	0

not to capture in the database because otolith mineralogy is not a good representation of the animals' dominant mineralogy). Slightly more species in Puget Sound form calcium carbonate structures as adults (984 species, 32%) than in their early life stages (911 species, 30%; **Figure 2a, b**). The type of calcium carbonate mineral formed at each life stage is largely dependent on phylogeny. Molluscs typically form amorphous calcium carbonate structures with some aragonite in early life stages and aragonite structures as adults. Crustacea form high-Mg calcite structures with some amorphous calcium carbonate both in early and adult life stages. Echinoderms form

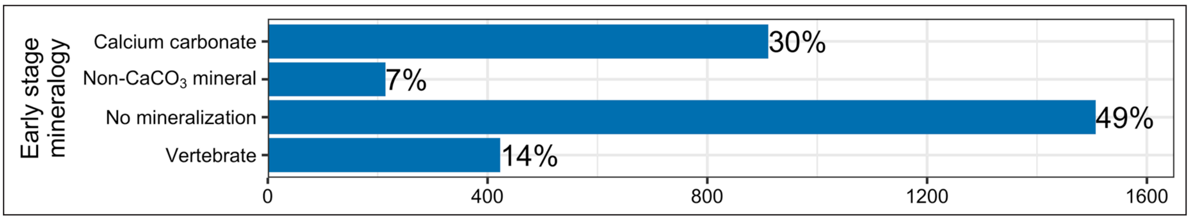

Figure 1: Summary of Puget Sound species mineralogy. Number of Puget Sound marine species with and without hard structures of various mineralogy in the early life stages. DOI: https://doi.org/10.1525/elementa.245.f1

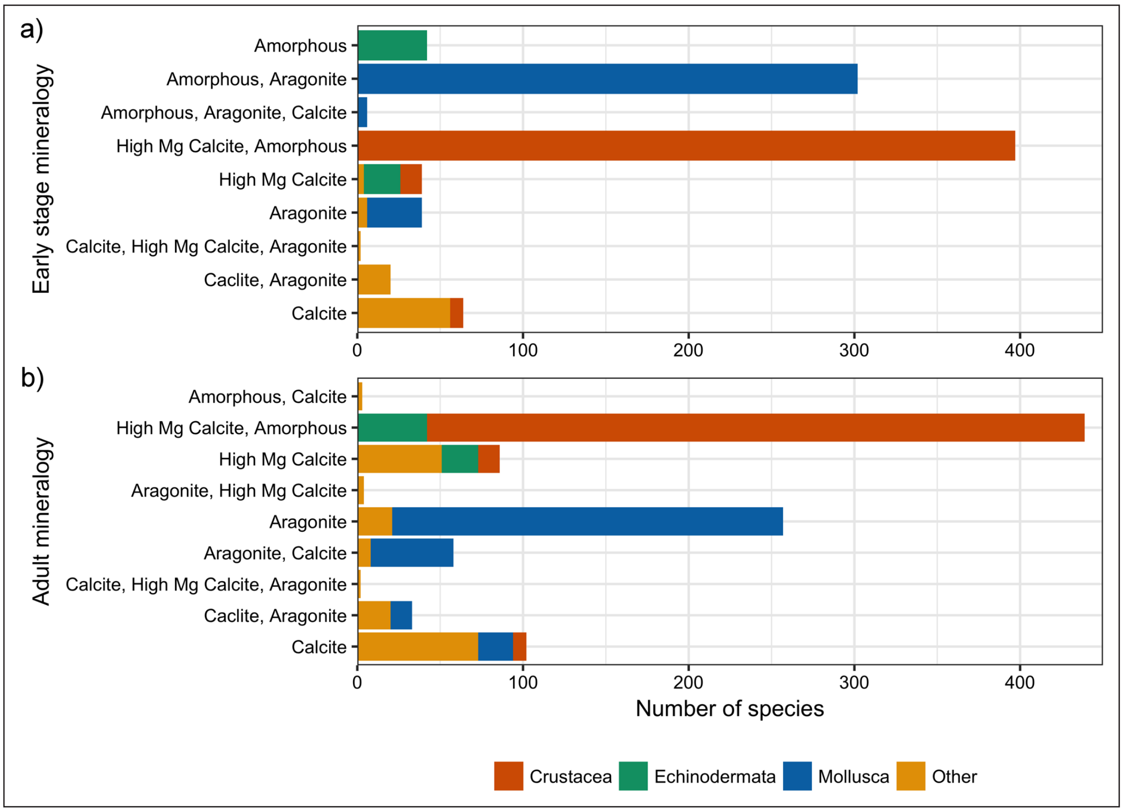

Figure 2: Mineral type by taxonomy and life stage for Puget Sound calcifiers. Mineralogy of species that form calcium carbonate in the early life **(a)** and adult **(b)** stages, with different colors depicting broad taxonomic group. DOI: https://doi.org/10.1525/elementa.245.f2

amorphous calcium carbonate or high-Mg calcite structures in early life stages and high-Mg calcite structures as adults. Other types of species, such as brachiopods, some algae, and some flatworms, form high and low-Mg calcite structures. In general, early life stages form structures with more soluble forms of calcium carbonate than adults. The number of species that form biominerals from minerals other than calcium carbonate is approximately the same in early (215 species) and adult life stages (226 species). Most autotrophs are non-calcareous as adults.

3.2 Survival-related sensitivity

When grouped by class (26 classes assessed), the three classes most sensitive to increased CO_2 as derived from the survival-based sensitivity estimates were, in order, Bivalvia (e.g., mussels, clams), Gastropoda (e.g., snails, abalone), and Malacostraca (e.g., crabs, krill; **Figure 3**). Most of the classes in the bottom third (i.e., most negatively affected) and middle third of survival scalar scores include species that calcify. No species in the classes in the top third of survival scalar scores (i.e., positively affected) calcify. Of the ten classes that are primary producers, three were in bottom third of survival scalar scores, and the remaining six were in the top third of survival scalar scores.

The taxonomic level at which we calculated survival scalars for the Puget Sound marine community had a large effect on estimates of species sensitivity to carbonate chemistry. Some classes had considerable variation in sensitivity estimates at the order and family levels, such as Gastropoda and Florideophyceae, while others, such as Ulvophyceae and Demospongiae, had little. For example, in the Gastropoda, some orders tended toward no response to carbonate chemistry conditions (e.g., survival scalar score near zero), while others responded negatively to high CO_2 conditions (e.g., negative survival scalar score). For only two classes, Florideophyceae and Anthozoa, both of which have calcifying and non-calcifying species, did some orders respond negatively and some positively

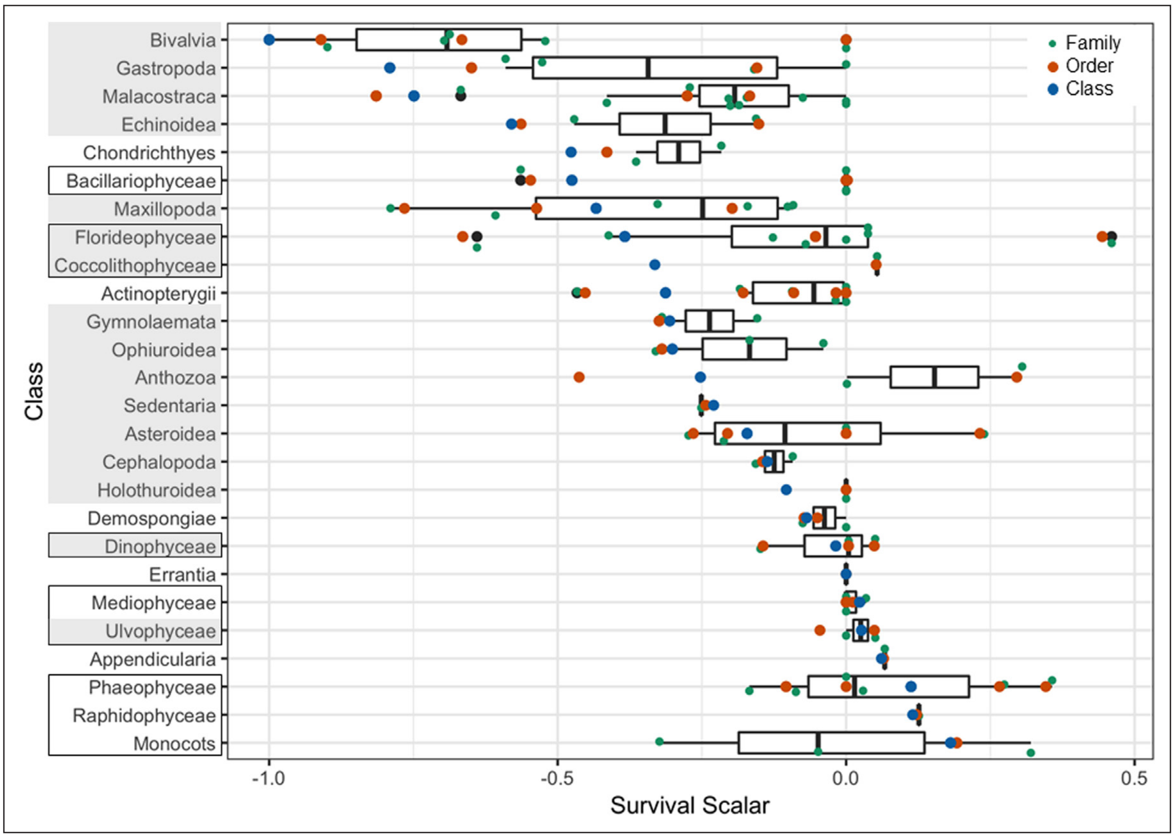

Figure 3: pH sensitivity survival scalar for various taxonomic groups in Puget Sound. A negative survival scalar indicates a negative effect of decreasing pH on survival and a positive scalar indicates a positive effect on survival. The blue points show scalars by class, the orange points are by order, the green points and box plots are by family. Each row of the chart shows the values for taxonomic groups in the given class and the chart is sorted by class level scalars. Classes that calcify are shaded in gray. Outlined classes are primary producers. At each taxonomic level, we applied the method of Busch and McElhany (2016): the scalars were estimated for every taxonomic group in Puget Sound for which we could find matching taxonomy in the literature review database of Busch and McElhany (2016) and for which the total "evidence score" was greater than 1. The evidence score would be less than 1 if their literature contains only a few experimental responses (generally ≤3) that are not of high relevance to survival of species in Puget Sound. The family-level box plot shows the median of the distribution (line), the 25–75% quartiles (box), 1.5 times the interquartile range (Tukey, 1977), and the outliers (black points). DOI: https://doi.org/10.1525/elementa.245.f3

to high CO_2 conditions (i.e., classes contain orders with survival scores greater than 0.25 and less than –0.25). This result indicates that, in general, the response of orders within most classes tends to lean in just one direction.

All but one of the classes in the bottom third group of survival scalar scores had family survival scalar scores with a higher median and central tendency than the class score (e.g., median and two central quartiles had higher survival scalar scores than the class scalar score; top portion of **Figure 3**). This result suggests that grouping species by class may overestimate the CO_2 sensitivity of the most sensitive classes. In particular, Florideophyceae families have a distribution that trends towards neutral and positive effects of high CO_2 conditions, even though the class has a quite negative survival scalar score (~–0.4). Agreement among the class, order, and family survival scalar scores was better for the classes in the middle and top third group of survival scalar scores (middle and bottom portion of **Figure 3**) than for the classes in the bottom third group of survival scalar scores (top portion of **Figure 3**).

3.3 Comparing survival-related sensitivity to mineralogy-related sensitivity

Here, we discuss only data on early life stage mineralogy, given that species are thought to be more sensitive to carbonate chemistry conditions in their early life stages (Ross et al., 2011; adult data are presented in Figure S1). For each data grouping, by family, order, and class, all calcifying groups except those species that produce only calcite had negative median survival scalars and a negative central tendency of the distribution of scores (two central quartiles; **Figure 4**; non-calcifiers are the "non-$CaCO_3$ mineral", "no mineralization", and "vertebrates" groups). Of the calcifiers, species with "amorphous, aragonite" calcium carbonate structures tended to have the lowest survival scalar scores, followed by those with "amorphous, aragonite, calcite" calcium carbonate structures and those with "high-Mg calcite, amorphous" calcium carbonate structures. Species with other types of calcium carbonate structures, including those with the most soluble type of calcium carbonate (amorphous), for the most part, had

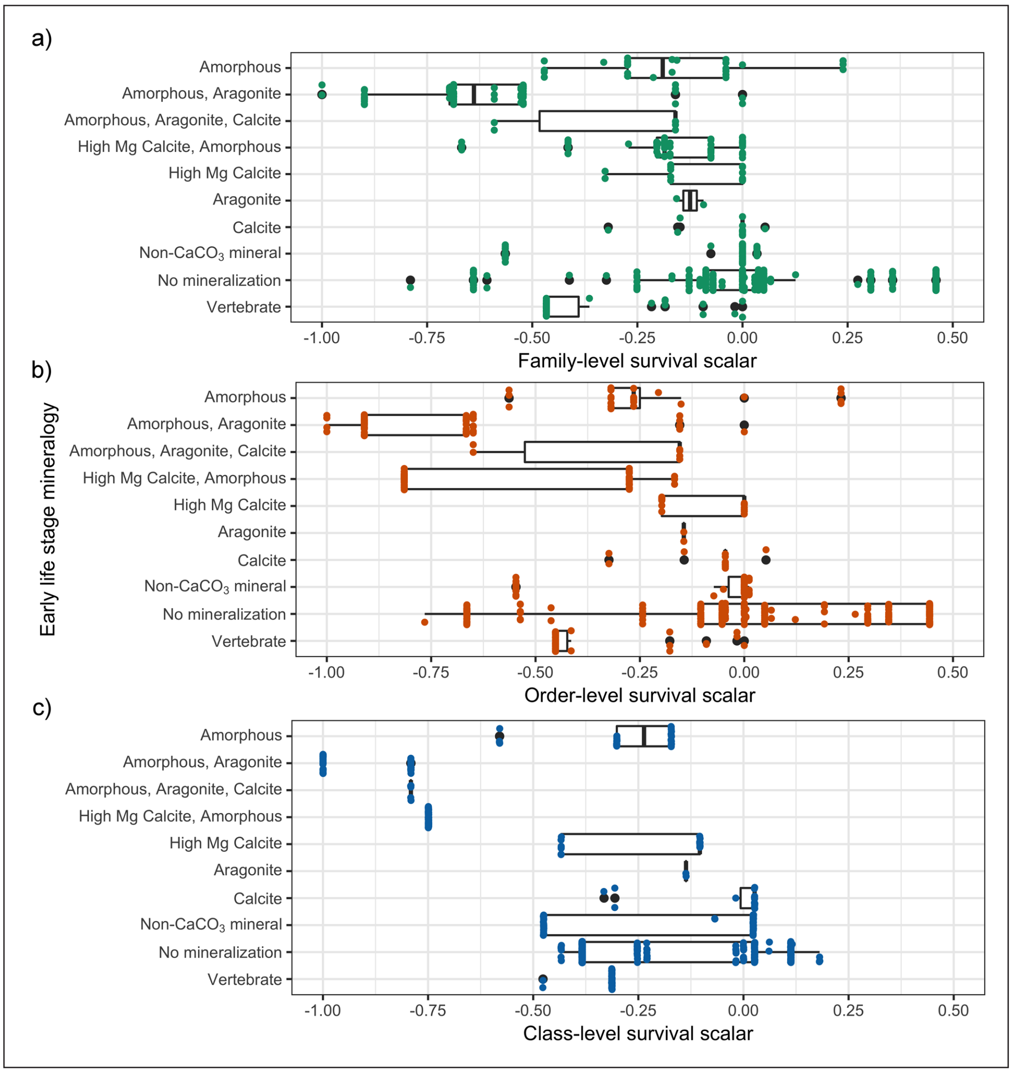

Figure 4: Estimates of pH sensitivity of Puget Sound species by early-life-stage mineralogy at different taxonomic levels. pH sensitivity survival scalars were estimated for Puget Sound species and assigned to each species at the family **(a)**, order **(b)**, or class **(c)** level. These data were organized by the calcium carbonate mineralogy of these species in early life stages. Each colored point is the survival scalar for a single species. The box plots show the median of the distribution (line), the 25–75% quartiles (box), 1.5 times the interquartile range (Tukey, 1977), and the outliers (black points). The abiotic calcium carbonate mineralogy (y-axis) is ordered from most soluble at the top to least soluble at the bottom. DOI: https://doi.org/10.1525/elementa.245.f4

higher survival scores, some of which were even positive (i.e., benefit from high CO_2 conditions).

The median and central tendency of survival scalar scores for fish species (vertebrates) and those species with non-calcium-carbonate structures were also negative. The central tendency of survival scalars for vertebrates is similar to some of the most sensitive calcifiers. The pattern of survival scalar scores for species without hard structures changed depending on how the data were organized: the central tendency of survival scalar scores was close to zero when the data were organized by family, largely positive when the data were organized by order, and negative when the data were organized by class.

4. Discussion

A third of the species in Puget Sound produce calcium carbonate structures, and calcifying animals account for almost 50% of Puget Sound's standing biomass (Harvey et al., 2010). In a high-CO_2 world, these species and potentially many non-calcifiers may face both altered energetic demands as they maintain physiological processes (e.g., Rosa and Seibel, 2008; Cohen and Holcomb, 2009; Waldbusser et al., 2013) and altered ecological interactions (e.g., Asnaghi et al., 2013; Sanford et al., 2014). Based on evidence from laboratory studies on extant species, we did not find a strong link between mineral solubility and the sensitivity of species survival to changes in carbonate chemistry, suggesting that mineralogy may play a lesser or equal role to other physiological sensitivities. For example, high CO_2 conditions can fertilize some calcifying primary producers in addition to influencing the production and maintenance of their calcium carbonate structures. We emphasize that ocean acidification also has the potential to directly affect non-calcified groups of species such as algae, fish, and squid, many of which have physiological processes sensitive to changes in carbonate chemistry (e.g., Rosa and Seibel, 2008; Tatters et al., 2013; Murray et al., 2014). For these two reasons, we suggest that mineralogy is an insufficient proxy for the sensitivity of modern species to ocean acidification conditions, and knowledge of the mineralogy of species in an ecosystem is likely a poor predictor of future ecosystem change. That said, detailed information on species mineralogy may help elucidate patterns of sensitivity within a given taxonomic group (i.e., closely related species of cold-water corals).

4.1 Using species-mineralogy database to characterize Puget Sound

The majority of calcifying species in Puget Sound produce calcium carbonate structures with relatively high solubility. This result is due to the diversity of crustaceans in the ecosystem, which produce carapaces embedded with high-Mg calcite and some amorphous calcium carbonate, and molluscs, many of which produce aragonite shells. In general, early life stages (e.g., larvae) produce forms of calcium carbonate that are relatively more soluble than the forms produced by adults (contrast **Figure 2a** with **Figure 2b**). This pattern is mainly driven by the early life stages of echinoderms, which produce amorphous calcium carbonate, and of molluscs, which produce amorphous calcium carbonate with some aragonite.

Assigning mineralogy to species at times required tenuous extrapolations based on limited literature reports from distantly related species. Even if perfect information was available on the mineralogy of each species, the relative solubility of abiotic calcium carbonate crystals does not necessarily translate to predictions of an organism's ability to produce and maintain calcium carbonate structures. For example, research on a variety of animals has indicated that energetic state can have a large influence on the ability to build and maintain calcium carbonate structures, even if food availability cannot fully erase the influence of the chemistry change in all species (Holcomb et al., 2010; Hettinger et al., 2013; Thomsen et al., 2013). These interactive effects between carbonate chemistry conditions and some other environmental parameter were not included in the survival scalar scores, though they were captured in the species-response database.

4.2 Survival-related sensitivity based on species-response database

We found that estimates of species sensitivity based on survival scalar scores were dependent on the taxonomic level at which the survival scalars were calculated. At the class level, the patterns in survival scalar scores for Puget Sound taxa were consistent with the patterns of species sensitivity found by other meta-analysis on species response to carbonate chemistry: namely, calcifying species tend to be more negatively affected than non-calcifying species (Kroeker et al., 2010; Gao et al., 2012; Kroeker et al., 2013; Wittmann and Pörtner, 2013; Nagelkerken and Connell, 2015; Busch and McElhany, 2016). However, this generalization was not universally true, as some calcifying classes, particularly the primary producers, had high survival scalar scores (e.g., classes Ulvophyceae and Dinophyceae) and some non-calcifying classes had low survival scalar scores (e.g., classes Chondrichthyes and Bacillariophyceae). While the four most sensitive classes calcify, the orders and families nested inside of these sensitive classes varied in their survival scalar scores. Some classes of calcifiers, particularly the Gastropoda and Florideophyceae, had order-level survival scalar scores that ranged widely. Of all of the most sensitive classes, family and order data presented a different understanding of species sensitivity: some lineages in each class respond negatively to high CO_2 conditions, while others seem insensitive to the changes in carbonate chemistry. In more extreme examples, family and order data for the Florideophyceae and Anthozoa suggest that lineages in these classes respond to high CO_2 conditions in opposite ways, with some increasing fitness and others decreasing fitness. The difference in results between classes, orders, and families emphasizes the importance of acknowledging variation in species response to carbonate chemistry conditions, even in closely related species (e.g., Miller et al., 2009).

In general, summarizing species sensitivity at the family level resulted in higher survival scalars scores than at the class level, suggesting that grouping results at the class level may overestimate species sensitivity. If this result is true, then other coarse-resolution meta-analyses focused on species sensitivity to ocean acidification conditions might also overestimate the sensitivity of some groups of species as they have often summarized data at the phylum level; thus, these meta-analyses could potentially yield inaccurate information about the relative sensitivity of taxa to ocean acidification. It might be that at coarse taxonomic resolution, meta-analyses can only predict the sign of response to ocean acidification (e.g., positive, negative). Results such as these raise caution about the use of coarse generalizations on species response to ocean acidification, particularly when developing summary information for a specific location. That said, we acknowledge that the study of species response to changes in carbonate chemistry is young, and our current understanding of species response is incomplete. Additional research may resolve the apparent inconsistencies in sensitivity estimates when calculated at different taxonomic levels and should yield information on the sensitivity of classes for which we currently lack data.

4.3 Comparing survival-related sensitivity to mineralogy-related sensitivity

Comparison of survival-related sensitivity estimates to mineralogy-related sensitivity estimates showed the general pattern that calcifying species have negative survival scalar scores, indicating a negative survival response to exposure to high CO_2. However, we did not find the hypothesized relationship between the solubility of calcium carbonate forms and survival scalar scores. While species with structures made from some of the highly soluble forms of calcium carbonate (amorphous and aragonite; amorphous, aragonite, calcite; high-Mg calcite and amorphous) had the lowest survival scalar scores, species with structures made from amorphous calcium carbonate, the most soluble form of calcium carbonate, had scores that were similar to those for species with much less soluble forms of calcium carbonate and species that make structures out of minerals other than calcium carbonate. Similarly, species that make structures from calcite also had high survival scalars that were similar to or higher than non-calcifying species groups. Thus, we posit that mineralogy is not sufficient to assign sensitivity at the coarse scale considered here, even though it may be useful when comparing the sensitivity of very closely related species. Additionally, we found that, in Puget Sound, species mineralogy is tightly linked to taxonomy. This result suggests that in this ecosystem, and likely many others, mineralogy and phylogeny cannot be uncoupled when considering broad patterns of species sensitivity to carbonate chemistry conditions and that the influence of mineralogy on species sensitivity is confounded with other aspects of species physiology and life history.

Whether these generalizations will hold as information builds on species mineralogy and sensitivity to carbonate chemistry conditions is not certain. We expect that new research would change findings related to specific taxonomic groups, but not the general patterns of the results. The species-response database on which the survival scalar scores are based includes information from 393 manuscripts, but has a strong bias towards work on cultivated shellfish species, urchins, and coccolithophores, making it challenging to characterize the response of most members of the ecosystem. Furthermore, research in the species-response database is biased towards information on adults rather than early-life stages, which potentially results in underestimates of species sensitivity. That said, the methods used to develop survival scalar scores from the species-response database account for the amount of available evidence and the level of agreement among findings, in an attempt to characterize our level of knowledge and uncertainty. For the species-mineralogy database, we assigned each species the most soluble form of calcium carbonate that it could have, which may have masked the relationship between mineralogy and survival scalar scores. It is possible that some species have calcium carbonate structures better characterized by a less soluble form of calcium carbonate, and, if so, the relationship between highly soluble forms of calcium carbonate and survival scalar scores may be stronger than we found.

4.4 Building ecosystem-level information on species sensitivity to ocean acidification

We found that, in general, species sensitivity estimates based on the published literature suggest that calcifying species are more likely to suffer direct negative effects in response to high CO_2 conditions than non-calcifying species. However, this generalization is incomplete, as non-calcifying species also show direct sensitivity to high CO_2 conditions. Our test of the hypothesis that species sensitivity, as assigned by survival scalar scores, would correlate with species mineralogy was not supportive. Additionally, the species-mineralogy database that we built showed that mineralogy is so confounded by phylogeny that considering mineralogy on its own is not statistically valid. While we have much to learn about species response to ocean acidification and how to generalize ecosystem response, this study on Puget Sound suggests that detailed information on the performance of modern species to carbonate chemistry conditions, summarized at the lowest taxonomic level possible, is more valuable than information on species mineralogy. We encourage living resource managers to support and engage in collection of such data in laboratory and field settings and to turn to this knowledge set and ecological modeling exercises based on it for guidance when engaging in ecosystem-based fisheries management.

Data Accessibility Statement

The database of Puget Sound species and their mineralogy (the species-mineralogy database) is included as a supplement to this manuscript, and the database on the sensitivity of temperate species to changes in carbonate chemistry (the species-response database) is included as a supplement to Busch and McElhany (2016). Both databases are also archived by the NOAA Ocean Acidification Data Stewardship Project.

Supplemental Files

A database of Puget Sound species including their mineralogy is available online in the supplementary material (Dataset S1), as is a list of the references cited in the database (References S1). Figure S1 shows family, order, and class-level survival scalars by adult calcium carbonate mineralogy. Table S1, which is a modified version of Table 1 in Busch and McElhany (2016), details the scoring system used to define the relevance of a response to informing sensitivity of Puget Sound species to changes in survival with decreased ocean pH.

The supplemental files for this article can be found as follows:

- **Dataset S1.** Puget Sound species-mineralogy database. DOI: https://doi.org/10.1525/elementa.245.s1
- **References S1.** References for the manuscripts included in Dataset S1. DOI: https://doi.org/10.1525/elementa.245.s2
- **Figure S1.** Estimates of pH sensitivity of Puget Sound species by adult mineralogy at different taxonomic levels. DOI: https://doi.org/10.1525/elementa.245.s3
- **Table S1.** Scoring system used to define relevance of response to decreased ocean pH. DOI: https://doi.org/10.1525/elementa.245.s4

Acknowledgements

Jaysen Niedermeyer, Naomi Yoder, Karen Avery, Danielle Perez, and Caitlin O'Brien contributed to the development of the Puget Sound species database. Chris Harvey and Jameal Samhouri provided helpful comments to improve this manuscript. Funding for this project was provided by the NOAA Ocean Acidification Program and the Northwest Fisheries Science Center.

Funding information

DSB and PM were funded by the National Oceanic and Atmospheric Administration's Ocean Acidification Program and Northwest Fisheries Science Center.

Competing interests

The authors have no competing interests to declare.

Author contributions

- Contributed to conception and design: DSB, PM
- Contributed to acquisition of data: DSB, PM
- Contributed to analysis and interpretation of data: DSB, PM
- Drafted and/or revised the article: DSB, PM
- Approved the submitted version for publication: DSB, PM

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How to cite this article: Busch, DS and McElhany, P 2017 Using mineralogy and higher-level taxonomy as indicators of species sensitivity to pH: A case-study of Puget Sound. *Elem Sci Anth,* 5: 53, DOI: https://doi.org/10.1525/elementa.245

Domain Editor-in-Chief: Jody W. Deming, University of Washington, US

Associate Editor: Julie E. Keister, University of Washington, US

Knowledge Domain: Ocean Science

Part of an *Elementa* Special Feature: Advances in Ocean Acidification Research

Submitted: 30 March 2017 **Accepted:** 05 August 2017 **Published:** 12 September 2017

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