Single vs. successive hot summers in a high intertidal barnacle bed community

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Questions

This experiment set out to test how temperature shapes the composition of intertidal algal and invertebrate communities. While the experiment was initially designed to investigate this broad question through the lens of herbivory-temperature interactions, high temperatures and disturbance regimes at the site prevented our original methodology from working, and subsequently we instead asked: how do single vs. successive hot summers affect this same community?

Hypotheses

1. Barnacle bed communities that are exposed to hotter tempertures during summer, even for a single year, will have lower diversity (species richness, Shannon-Weiner diversity, evenness) than those that are exposed to ambient/cooler conditions during the same period.
2. There will be an interactive effect between the temperature treatments of the first and second summer on the same response metrics. Previously 'cool' communities, since they have more established, larger barnacle beds with a more diverse array of microhabitats and thermal refugia, will experience a smaller decline in diversity when exposed to warm temperatures than previously 'warm' communities that have less structural complexity (fewer barnacles). Meanwhile, previously 'warm' communities will increase substantially in diversity when allowed to recover in 'cool' conditions as recruitment and successional processes occur normally. Thus, diversity of communities after a second summer will fall in the order: cool-cool (highest diversity); cool-warm; warm-cool; warm-warm.

Materials & Methods

Site description This experiment was completed at Ruckle Provincial Park on the southeast-facing, semi-exposed sandstone shore of Salt Spring Island, located in British Columbia within the Salish Sea (Fig. 1). Relative to the rest of the southern Gulf Islands, this site receives more substantial wave exposure and cooler water temperatures, being positioned more towards the Strait of Juan de Fuca, and is positioned away from the Fraser River plume, meaning the seawater remains quite salty year-round. Thus, the intertidal community at this site is substantially more diverse than neighbouring islands. However, like the rest of the Gulf Islands, this island's intertidal zone is a "hot spot" in the region due to its mid-day summer low tides coupled with relatively clear, sunny weather during the summer.

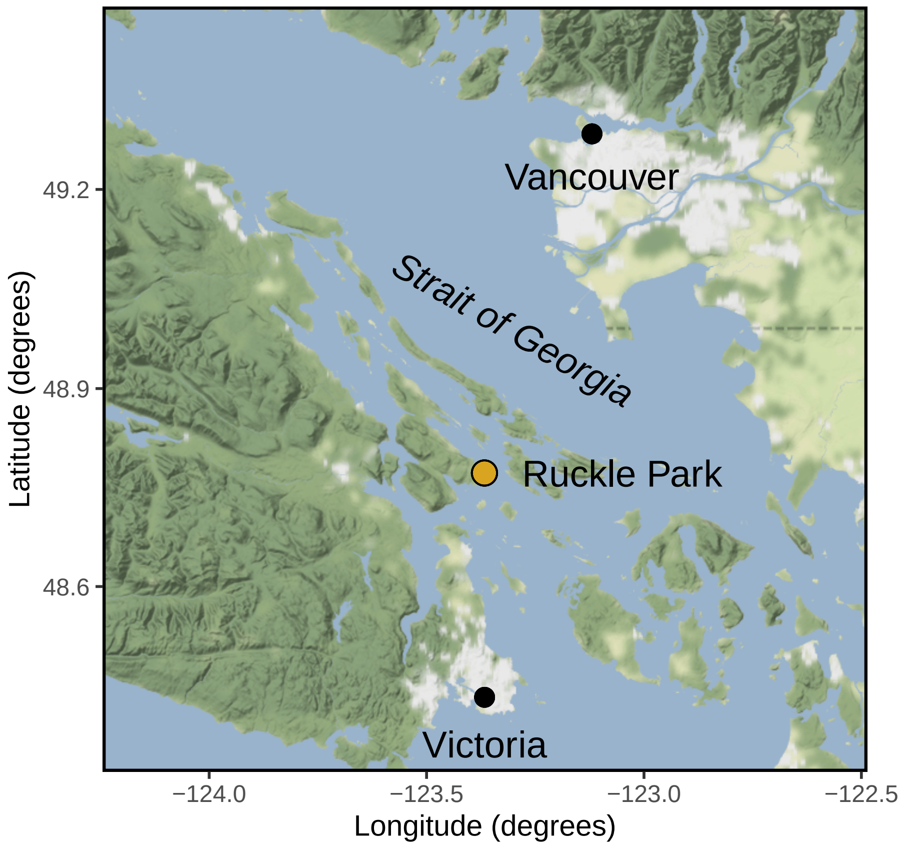

Figure 1. Study site at Ruckle Park on Salt Spring Island (latitude: 48.77229, longitude: -123.36686) within the Strait of Georgia in British Columbia's Salish Sea.

The upper intertidal zone at this site is dominated by acorn barnacles (*Balanus glandula* and *Chthamalus dalli*), with sporadic beds of the perennial brown alga *Fucus distichus* and patches of the crustose phase of *Mastocarpus* sp.. Ephemeral algae can be found primarily in the winter when temperatures less stressful, namely the green ephemeral species *Ulothrix* sp. and *Ulva* sp., the red ephemeral *Pyropia* sp., and the brown *Petalonia fascia*. Herbivores are relatively plentiful at this shore level, though some more thermally sensitive species migrate down shore with the onset of summer temperatures (Hesketh, personal observation). These include the littorine snails *Littorina scutulata* and *L. sitkana* and the limpets *Lottia paradigitalis* and congeners *L. digitalis*, *L. pelta*, and *L. scutum*.

Experimental design Measurements in this experiment were made at the level of individual tiles deployed in the intertidal zone (Fig. 2). These tiles were manufactured as in previous studies employing the same passive warming method Kordas et al. (2015). In short, tiles consisted of two units made from high-density polyethylene (HDPE) plastic, a lower unit composed of thicker white HDPE (9.5 mm) anchoring the tile to the underlying bedrock, and an upper unit made of thinner HDPE (6.4 mm) that was either white (cool temperature treatment) or black (warm temperature treatment). A thin layer of Sea Goin' poxy putty was spread in the central 6.9 x 6.9 cm area of the top unit to generate a settlement surface. To enhance fine-scale heterogeneity of the surface, finely ground epsom salts were pressed into the putty as it dried, and dissolved with water after drying to leave behind fine pock marks. When tile colour was altered for a subset of tiles during the second year of the study, this was accomplished using heavy-duty tape, either white or black in colour (Gorilla Tape), with adhesion enhanced by the application of super glue.

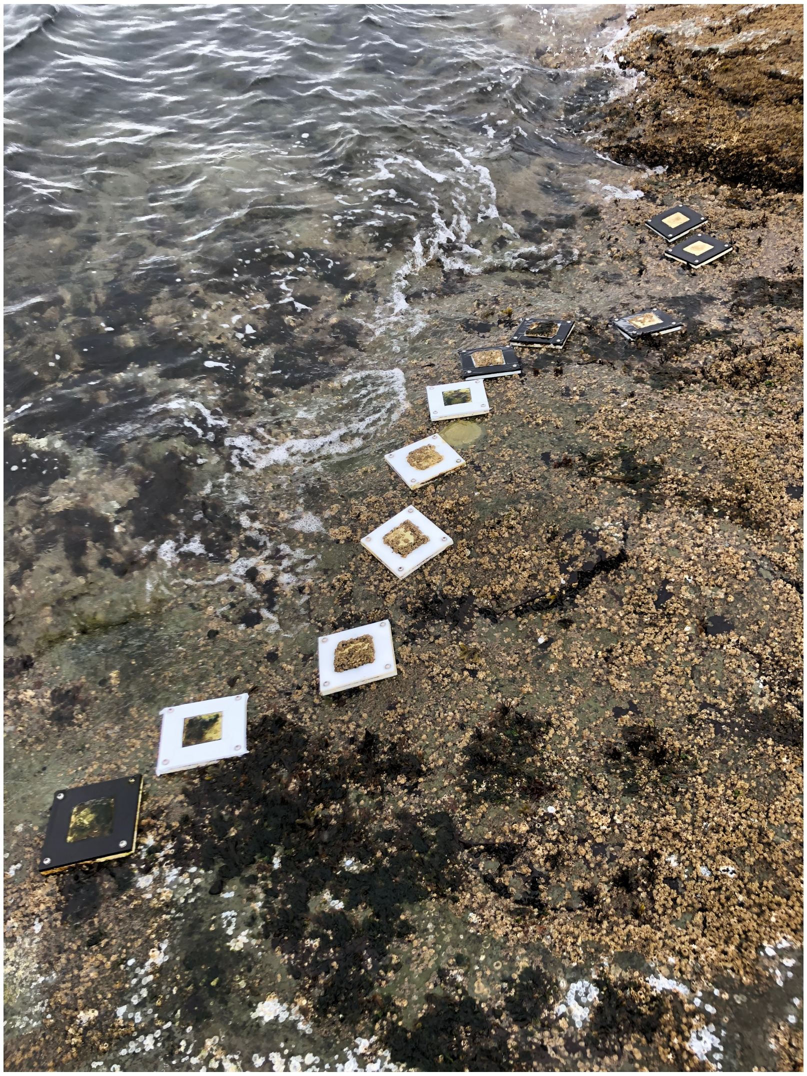

Figure 2. Experimental tiles deployed at Ruckle Provincial Park, Salt Spring Island, pictured one year after their initial installation on shore. Recruitment and growth of algae and barnacles is evident in the central settlement area of each tile, while the outer black or white area of each tile serves to passively generate the warm and cool treatments used during this experiment, respectively.

The experiment followed a stratified random design, which went through several iterations as the original herbivore manipulation changed in response to methodological complications, and then again after the final question changed.

1. **Original herbivory x warming design (March - June 2019):** In this design, we had five blocks of 20 tiles each, half of which were white and half of which were black. Copper fences were installed along the perimeter of each tile (0.511 mm thick, 3.8 cm high above the level of the tile). Each of these ten tiles had a different herbivore treatment applied: no herbivores, *L. paradigitalis* alone, *L. digitalis* alone, *L. scutulata* alone, *L. sitkana* alone, each two-way combination of herbivores, and all herbivores. Prior to treatments, we dissected a number of individuals of each species to determine the species-specific relationship between wet and dry tissue weight for each. Thus, when applying herbivores to the tiles, we attempted to standardize wet weight to ~120 mg of dry tissue weight per tile. Thus, there was one replicate of each treatment per tile, n=5 across all blocks.
2. **Updated herbivory x warming design (June 2019 - August 2019):** For this design, tiles were moved to new locations to avoid log damage, log-damaged tiles were removed, and littorine snails were removed from the herbivore treatment pool since they were dislodged or appeared in treatments so

easily due to wave action. This resulted in a new design of six experimental blocks with 16 tiles each, eight of which were black and eight of which were white. Only limpets were used in the herbivory treatments (Fig. 3), of which there were eight: no herbivores, *L. paradigitalis* alone, *L. digitalis* alone, *L. scutum* alone, each of the three two-species combinations of these, and all species. Thus, there was again a sample size of five per treatment, one replicate per block.

Figure 3. Stage 2 of experimental herbivore additions. Pictured here: *L. digitalis* (large, ribbed limpet) and *L. paradigitalis* (small limpets) added to a cool treatment tile in July 2019.

3. **Final design (August 2019-February 2021):** While the limpet manipulation worked reasonably well for *L. paradigitalis*, the other two limpet species more often than not died within two weeks of being added to tiles, presumably due to heat stress. What limpets of these species did survive were often found at the edges of the tile units, or wedged in the crack between the tile and copper fence, meaning their biological function on the tile may be minimal. Thus, at this point the copper fences were removed from all tiles, and herbivores of all species were allowed to access and leave tiles freely. In April 2020, the colour of half of these tiles were changed (white -> black or black -> white), while half were left unaltered (Fig. 4). This resulted in four treatments (cool-cool: CC; warm-warm: WW; cool-warm: CW; and warm-cool: WC) with a final sample size of 20 tiles per treatment (four per experimental block, five blocks). Some tiles were lost from this intended final number due to log damage and wave dislodgement. Final sample sizes are reported in the results section.

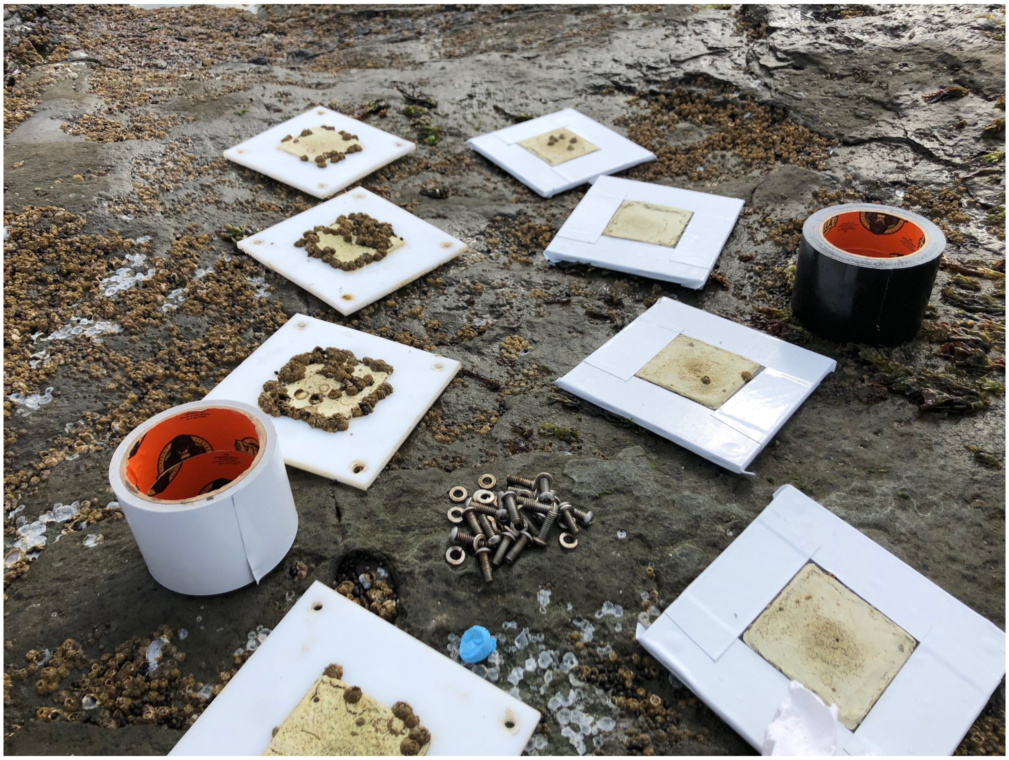

Figure 4. Stage 3 of the experimental design, when the decision was made to alter temperature for a subset of experimental tiles using heavy-duty tape. Pictured here: cool temperature tiles that were left unaltered between experiment years (CC treatment, left) and previously warm temperature tiles covered with heavy-duty white tape (WC treatment, right).

Temperature was monitored in each experimental temperature treatment using iButton temperature loggers (Maxim Integrated) embedded between the upper and lower units of tiles.

Diversity surveys Visual surveys were performed at monthly intervals during summer and every two months during winter from April 2019 (one month after experiment installation) to February 2021. During these, each species was identified and enumerated — in the case of invertebrates — or their percent cover measured — in the case of algae. Organisms were identified down to species, or in cases where this was unclear (i.e. for amphipod and isopod crustaceans), coarser taxonomic measures were instead employed. Sessile species were only measured within the central ?? with the aid of small wire quadrat, while mobile species were enumerated on the entire upper face of the tile.

Infauna were sampled to record the diversity of meiofauna in September 2020 (after summer heat stress) and in February 2021 (to allow for winter recovery). Barnacles and associated fauna were scraped from experimental tile's settlement area and identified to species (where possible) and enumerated under a dissecting microscope.

Data analysis ...

Results

1. Temperature traces to show difference between treatments
2. Community trajectories in non-metric space?
3. Infaunal diversity in September vs. April
4. Barnacle recruitment?

Acknowledgements

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References

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