The effect of single versus successive warm summers on an intertidal community

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Questions

This experiment set out to test how temperature shapes the composition of intertidal barnacle bed communities, asking the question: how do single vs. successive hot summers affect this same community?

Hypotheses

1. Barnacle bed communities that are exposed to hotter temperatures during summer, even for a single year, will have lower diversity (species richness, Shannon-Weiner diversity, evenness, beta diversity) than those that are exposed to ambient/cooler conditions during the same period.
2. Warming will exert a persistent effect through time (i.e., warming in year one will stil affect communities in year two) mediated by changes in the cover of biogenic habitat.
3. Previously 'cool' communities, since they have more established, larger barnacle beds with a more diverse array of microhabitats and thermal refugia, will be less perturbed by warming than previously 'warm' communities that have less structurally complex biogenic habitat. That is, the effect of warming in year two will be contigent upon warming in year one.

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. Relative to the rest of the southern Gulf Islands, this site receives more substantial wave exposure and cooler, saltier water, being positioned more towards the Strait of Juan de Fuca and away from the Fraser River plume. 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.

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 alga *Pyropia* sp., and the brown alga *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. 1). 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 (Permalite Plastics) was spread in the central 6.9 x 6.9 cm area of the top unit to generate a settlement surface. To enhance the 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 1. 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 randomly 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. 2), 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 2. 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, signaling that their grazing activity 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. 3). 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.

Figure 3. 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). Differences in barnacle cover after the first year are quite evident in this photograph.

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 6 x 6 cm area with the aid of a small wire quadrat, while mobile species were enumerated on the entire upper face of the tile.

Tiles were destructively 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 counted under a dissecting microscope.

Data dictionary

Raw data */design*

SVSWS_satellite_temps.nc: This .nc file is downloaded from the Copernicus Climate Data Store from the ERA5 Land hourly surface temperature dataset. It is used here as an auxiliary variable for multiple imputation of temperature

SVSWS_daylight_hours_pst.rtf: This raw text file includes sunset and sunrise times for the entire duration of the experiment, for the exact lat/long of the field experiment, using the National Research Council of Canada Sunrise/Sunset calculator (https://nrc.canada.ca/en/research-development/products-services/software-applications/sun-calculator/)

SVSWS_species_conversions.csv: These tabular data allow conversion between shorthand species/taxon notation in survey data and actual scientific names

- sp_abbrev: shorthand species abbreviation
- species_full: scientific name of taxon

SVSWS_survey_times.csv: These tabular data associate survey identifier (key) with the date surveys occurred on.

- date: YYYY-MM-DD, date of survey
- survey_no: survey number, a key to associate with other dataframes

SVSWS_tides.csv: These tabular data contain tide predictions for Fulford Harbor, BC, the nearest tide station to the field site.

- column 1: YYYY-MM-DD, date associated with tide prediction
- column 2: HH:MM, 24 hour time associated with tide prediction
- column 3: either PST or PDT, time zone associated with tide prediction
- column 4: predicted level of tide in metres, relative to Canadian chart datum

SVSWS_tilelevels.csv: Estimated height of individual tiles, as approximated by temperature traces for rapidly rising summer tides.

- new_block: block associated with individual tile
- new_number: number associated with individual tile, within the given experimental block
- tile_height_1, 2 and 3: three numeric estimates of the shore level of the tile above Canadian chart datum.

SVSWS_tilesetup.csv: Information related to the placement of tiles and design considerations (e.g., treatment in year one and year two)

- original_block: Original block (letter, A-E), prior to change in design to six blocks in response to log damage (occurred June 2019)
- original_no: Original number (integer, 1-20), prior to change in design to six blocks in response to log damage (occurred June 2019)
- original_angle: In degrees, numeric angle of tile relative to a flat surface (0^o), prior to change in design to five blocks in response to log damage (occurred June 2019)
- original_herb_trt: Original herbivore manipulation attempted, abandoned in August 2019. ldig = Lottia digitalis, lpdig = Lottia paradigitalis, lsc = Littorina scutulata, lsi, Littorina sitkana, NA = control
- original_shore_level: Original shore level (numeric, in metres) relative to Canadian chart datum, prior to change in design to five blocks in response to log damage (occurred June 2019)
- new_block: Final block (letter, A-F), after change in design to six blocks -new_no: Final number (letter, 1-16), after change in design to six blocks

- new_angle: In degrees, numeric angle of tile relative to a flat surface (0^o), after change in design to five blocks
- new_compass: In degrees, compass direction towards which tile surface was oriented after change in design to five blocks
- new_shore_level: Shore level (numeric, in metres) relative to Canadian chart datum, after change in design to five blocks. Shore levels are very rough, as only a few per block were measured using a laser level. See SVSWS_tilelevels.csv for more accurate estimates.
- colour_y1: Color of tile (white or black) during year one of the experiment (prior to 3 April 2020)
- colour_y2: Color of tile (white or black) during year two of the experiment (after 3 April 2020)
- survived: Did the tile persist through the entire experiment (y/n)?
- treatment: Code representing the thermal history treatment of each tile, either C or W (if tile did not persist until year two), or CC, CW, WC, or WW.
- tile_id: Unique numeric identifier associated with each tile, used as key to associate with other dataframes.

/epifauna

SVSWS_20200914_epifauna.csv: Epifauna data obtained from destructive sampling in September 2020

- block: same as new_block in SVSWS_tilesetup.csv, experimental block (A-F) in which tile was located
- number: same as new_number in SVSWS_tilesetup.csv, identifying number within block of the tile sampled
- taxon: name of taxon identified within epifauna sample
- abund: integer, abundance of organisms within the identified taxon
- notes: observations or caveats associated with identification process

SVSWS_20210224_epifauna.csv: Same as above, for destructive sampling that occurred in Feburary 2021.

taxonomic_codes.csv: Tabular data for repairing and unifying taxonomic categories

- taxon: originally identified taxon
- sp_code: original four-five character alphanumeric code
- taxon_repaired: corrected spelling/identification or unified name for similar lumped taxa
- unified_code: code derived from corrected/unified taxon

/temperature

These tabular files are all labeled as SVSWS_block_number_temp_date.csv and contain hourly (or every-two-hourly) temperature data recorded by embedded iButton loggers within tiles or on adjacent bedrock.

- block: the experimental block where the tile was located, either the old or new block within SVSWS_tilesetup.csv depending on the date of collection
- number: the tile's unique identifyin number within the experimental block, either the old or new number within SVSWS_tilesetup.csv depending on the date of collection

- date: the date on which the temeperature logger was retrieved

Each file has the same basic structure. There is a descriptive header containing information about the time of mission start and end. The data to be extracted are contained within three columns.

Date/Time: The date and time associated with each logged temperature, in format DD/MM/YY HH:MM:SS. Time is 12-hour, with either AM or PM following.

Unit: The unit of temperatures collected, always C for degrees Celsius

Value: Numeric data, the recorded temperature in degrees Celsius

/tile_surveys

SVSWS_barnacle_mortality.csv: These tabular data contain data on the abundance of dead barnacles (lateral plates remaining, even partially; not single basal plates), for timepoints where full photographic series of tiles exist.

- date: Date, format YYYY-MM-DD, date on which photograph was taken of tile
- block: Experimental block in which tile was located (same as new_block in SVSWS_tilesetup.csv)
- number: Number of tile identifying it within the experimental block (same as new_block in SVSWS_tilesetup.csv)
- number_dead: integer, number of dead barnacles

SVSWS_barnacle_recruit.csv: These tabular data contain abundance data for barnacles, both recruits and adults, beginning in June 2020 when we began to distinguish between adults and recruits.

- block: Experimental block in which tile was located (same as new_block in SVSWS_tilesetup.csv)
- number: Number of tile identifying it within the experimental block (same as new_block in SVSWS_tilesetup.csv)
- species: Species of barnacle identified, either B. glandula or C. dalli
- size: Either adult or recruit
- count: Integer, number of barnacles within species and size category that were counted on the tile surface.
- date: Date, format YYYY-MM-DD, of tile survey

SVSWS_barnacle_size.csv: These tabular data contain data on the size (basal diameter) of live and dead barnacles, for timepoints where full photographic series of tiles exist.

- date: Date, format YYYY-MM-DD, date on which photograph was taken of tile
- treatment: Character, code representing the treatment of the tile at the time the photograph was taken (C, W, CC, CW, WC, or WW)
- basal_diameter_mm: Numeric, basal diameter in millimetres of barnacle in photograph
- Experimental block in which tile was located (same as new_block in SVSWS_tilesetup.csv)
- number: Number of tile identifying it within the experimental block (same as new_block in SVSWS_tilesetup.csv)

- status: Character factor, either “alive” or “dead” depending upon whether the measured barnacle was alive or dead at the time the photograph was taken.

SVSWS_surveys.csv: Contain all other data resulting from visual surveys of tile surfaces date:

- block: the experimental block where the tile was located, either the old or new block within SVSWS_tilesetup.csv depending on the date of collection
- number: the tile's unique identifyin number within the experimental block, either the old or new number within SVSWS_tilesetup.csv depending on the date of collection
- species: More properly taxon, the name of the identified organism
- count: Integer value, for invertebrates species only, the number of individuals counted on the tile surface.
- percent_cover: Numeric value, for algal species only, the percentage of the tile surface covered by the observed taxon.
- notes: observations or caveats associated with identification process

Clean data SVSWS_epifauna_clean.csv: Data associated with destructive sampling

- date: Date of sample collection, format YYYY-MM-DD
- block: same as new_block in SVSWS_tilesetup.csv, experimental block (A-E) in which tile was located
- number: same as new_number in SVSWS_tilesetup.csv, identifying number (1-16) of the tile sampled within each block
- taxon: name of taxon, after being repaired
- total_abund: integer, total abundance of taxon within sample
- treatment: treatment, one of CC, CW, WC, or WW, of the tile sampled
- tile_id: unique identifier for tile based on the combination of block and number

SVSWS_species_list.csv: Tabular data dividing taxa observed into invertebrate and algal categories for analyses of diversity

- species: more properly, taxon, observed during visual survey
- type: one of alga or invertebrate, used to filter observations

SVSWS_survey_clean.csv: Tabular data associated with visual surveys, now tidy -tile_id: Unique identifier of the tile surveyed

- survey_no: Unique identifier of the survey where the observation was recorded
- species: more properly, taxon, identified during visual survey
- count: for invertebrates, the number of individuals observed
- percent_cover: for algae, the percentage cover of the taxon on the settlement surface

- block: the experimental block where the observation was recorded,at the time of the survey (letter, A-F)
- original_herb_trt: the original herbivore treatment applied during early manipulations (April to August 2019). Either ldig (Lottia digitalis), lpdig (Lottia paradigitalis), lsc (Littorina scutulata), lsi (Littorina sitkana), a combination thereof, or NA (control)
- angle: the angle of the tile surface in degrees relative to a flat surface (0^o) at the time of the survey
- new_compass: the compass bearing faced by the tile surface at the time of the survey
- shore_level: the approximate shore level of the tile's settlement surface, reported in metres above Canadian chart datum
- treatment: thermal history treatment (across both years)
- trt_y1: temperature treatment during year one of the experiment (C or W)
- trt_y2: temperature treatment during year two of the experiment (CC, CW, WC, or WW)
- notes: any notes associated with the abundance/percentage cover observation

SVSWS_temp_clean.csv: Tabular data containing all temperatures recorded by embedded iButton temperature loggers.

- block: experimental block in which tile was located at the time of recording -number: number of block within the experimental block where tile was located at the time of recording
- date_time: the date and time associated with a given temperature recording, format YYYY-DD-MM HH:MM:SS, with time in 24-hour format, rounded to the nearest hour.
- collect_date: the date on which iButton was collected from the field for temperature readings
- date: the date on which the temperature was recorded, extracted from date_time, format YYYY-MM-DD
- temp: numeric, in degrees Celsius, temperature of tile surface
- new_no: the number of the given tile within its experimental block, following change in design to six blocks
- new_block: the experimental block in which the tile was located, following change in design to six blocks
- original_no: the number of the given tile within its experimental block, before the change in design to six blocks
- original_block: the experimental block in which the tile was located, before the change in design to six blocks
- original_shore_level: the original shore level, in m, of the tile before the change in design to six blocks, in metres above Canadian chart datum.
- new_shore_level: the new shore level, in m, of the tile after the change in design to six blocks, in metres above Canadian chart datum. These values are very approximate; see raw_data/design/SVSWS_tilelevels.csv for better values. -treatment: thermal history treatment (across both years)
- tile_id: unique identifier associated with the individual tile for which temperature was recorded
- trt_y1: temperature treatment during year one of the experiment (C or W or Rock)

- trt_y2: temperature treatment during year two of the experiment (CC, CW, WC, WW, or Rock)

SVSWS_tile_treatments.csv: Tabular data containing details related to study design and tile attributes

- tile_id: Unique identifier of the tile surveyed
- survey_no: Unique identifier of the survey where the observation was recorded
- block: the experimental block where the observation was recorded,at the time of the survey (letter, A-F)
- original_herb_trt: the original herbivore treatment applied during early manipulations (April to August 2019). Either ldig (Lottia digitalis), lpdig (Lottia paradigitalis), lsc (Littorina scutulata), lsi (Littorina sitkana), a combination thereof, or NA (control)
- angle: the angle of the tile surface in degrees relative to a flat surface (0^o) at the time of the survey
- new_compass: the compass bearing faced by the tile surface at the time of the survey
- shore_level: the approximate shore level of the tile's settlement surface, reported in metres above Canadian chart datum -treatment: thermal history treatment (across both years)
- trt_y1: temperature treatment during year one of the experiment (C or W)
- trt_y2: temperature treatment during year two of the experiment (CC, CW, WC, or WW)
- notes: any notes associated with the tile at the time of a given survey

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References

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