Results of a study examining how foundation species loss alters multiple ecosystem functions based on community surveys and biogeochemical sampling of tidepools in the Otter Rock Marine Reserve (ORMR) and Marine Garden, Oregon USA from June to August 2019

Website: https://www.bco-dmo.org/dataset/878413
Data Type: Other Field Results
Version: 1
Version Date: 2022-09-07

Project
» CAREER: Predicting ecosystem metabolism of rocky intertidal communities in warming and acidifying oceans. (TIDES)

Contributors	Affiliation	Role
Silbiger, Nyssa	California State University Northridge (CSUN)	Principal Investigator
Fields, Jennifer	California State University Northridge (CSUN)	Contact
Heyl, Taylor	Woods Hole Oceanographic Institution (WHOI BCO-DMO)	BCO-DMO Data Manager
Rauch, Shannon	Woods Hole Oceanographic Institution (WHOI BCO-DMO)	BCO-DMO Data Manager

Abstract
This dataset investigates how foundation species loss alters multiple ecosystem functions. This study was conducted within 32 tidepool communities from the Oregon Department of Fish and Wildlife's (ODFW) Otter Rock Marine Reserve (ORMR) and Marine Garden, Oregon USA.

Table of Contents

Coverage

Spatial Extent: **Lat**:44.752528 **Lon**:-124.066111
Temporal Extent: 2019-06 - 2019-08

Methods & Sampling

We selected 32 tide pools within the Oregon Department of Fish and Wildlife's (ODFW) Otter Rock Marine Reserve (ORMR) and Marine Garden, Oregon USA (44°45'09.1"N 124°03'58.0"W) during the months of June to August 2019. One mussel species (*M. californianus*) and two surfgrass species (*P. scouleri* and *P. torreyi*) were present at the site. Of the 32 tide pools, 16 were dominated by the California mussel (*M. californianus*) and 16 were dominated by surfgrass (*Phyllospadix spp.*; 10 pools contained *Phyllospadix scouleri* and six pools had both *Phyllospadix scouleri* and *Phyllospadix torreyi*). Percent cover of foundation species ranged from 45.3 to 98.9% in the mussel pools and 49.5 to 100% in the surfgrass tide pools. Some tide pools had both mussels and surfgrasses; however, the presence of a second foundation species did not exceed 7.2% of the remaining

tide pool cover. Tide pools were located in the mid to low intertidal zone ranging from 0.71 meters to 1.77 meters above mean lower-low water. At this tide height, tide pools were isolated for 4-6 hours during summer low tides.

A Before-After-Control-Impact (BACI) design was used to account for changes in ocean chemistry, timing of low tide, and variability within tide pools throughout the experimental period. The BACI design consisted of two 29-day time periods (before and after removal) with control and removal tide pools (Stewart-Oaten et al. 1986) where foundation species were removed from removal tide pools (n = 8 per foundation species) between the before and after removal periods. The before-removal period occurred June to mid-July 2019 and the after-removal period occurred mid-July to August 2019. Tide pools were selected for control or removal groups using a random number generator while accounting for the surface area to percent cover of foundation species. Removal of all foundation species from removal tide pools occurred in mid-July 2019 and tide pools had a one-week recovery period before any surveys or samples were taken. Rhizomes were also removed in surfgrass removal pools due to their ability to alter nutrient cycling (Terrados & Williams 1997). During each time period, we characterized physical parameters (pool volume and tide height), community composition, light, temperature, and biogeochemical fluxes (e.g., dissolved oxygen, pH, nutrients) in each tide pool.

Tide pool physical parameters included tidal height (location within intertidal) and tide pool volume (size of pool). Tide heights for each pool were surveyed with a laser level and stadia rod (DeWalt, Towson, MD, USA). Tide pool volume (V) was determined using a dye method (Pfister 1995) and measured with a SmartSpec3000 spectrophotometer (Bio-Rad Lab, Hercules, CA, USA). Water volume in the tide pools changed by 0 - 20% between the two timepoints due to removal of foundation species. To account for the slight effect of changing biomass on volume, volume was re-measured post-removal and the average between both time periods were used in statistical analyses.

We conducted two rounds of community composition surveys for sessile percent cover and mobile organism counts: three-weeks before removal and one-month post-removal. We temporarily removed seawater from the tide pool and placed a flexible mesh quadrat (Nielsen 2001) with demarcations in 10 x 10 cm squares over the bottom of each pool to survey the entire community (pools ranged from 58 to 754 squares). We measured percent cover for sessile organisms and counted mobile organisms, identifying down to the lowest possible taxonomic unit in the field (usually genus level). We normalized the sum of non-foundation species sessile cover to 100% cover per tide pool, including the opposite foundation species if present (e.g., mussel cover within surfgrass pools was also normalized to 100% cover). Each foundation species cover in their respective tide pools remained the raw percent cover and did not exceed 100%. Both sessile and mobile organisms were grouped into larger functional groups based on their ecological role for data visualizations. All tide pool characterization and community composition methods were completed at least 24 hours before any water sampling event to allow the pools to be flushed at least twice by the ocean before measurements.

Temperature (°C) and light intensity (lumens m-2) were recorded continuously every 15 minutes for 29 days during each time period using HOBO® Pendant loggers bolted facing up on the flattest part of the tide pool on a level platform in the interstitial spaces of the foundation species (Onset® HOBO® Pendent Light Intensity Data Logger MX2202, Bourne, MA, USA). Light intensity (lumens m-2) was converted to photon flux density (PFD; µmol photons m-2 s-1) following Long et al. (2012) field experiment values. We measured the change in maximum temperature between the before and after removal period (i.e., the average of the daily hottest temperature from 7/18/2019 – 8/16/2019 minus the average daily hottest temperature from 6/16/2019 – 7/15/2019) and the percent change in maximum light (i.e., the average maximum light from 7/18/2019 – 8/16/2019 minus the average maximum light from 6/16/2019 – 7/15/2019 divided by the average maximum light from 6/16/2019 – 7/15/2019 multiplied by 100). For the causal model, maximum temperature was extracted from the logger data for the specific dates and times of water collection for comparison with biogeochemistry and ecosystem metabolism measurements. Hourly ocean temperatures over the experimental period were extracted from a nearshore ODFW Marine Reserve mooring sensor at 1 meter depth within ORMR to descriptively compare tide pool temperatures to the local ocean.

To determine biogeochemistry fluxes and ecosystem metabolism (NEC and NEP) before and after removal of foundation species, we collected daytime and nighttime water samples during low tide. We used a block design for water sampling with two daytime and two nighttime sampling events due to the timing of low tide and time restraints of sampling, where n = 16 pools (n=8 per foundation species) were measured on separate day and night sampling events. Each sampling event had an equal number of pools per foundation species and treatment group (removal or control: n = 8 pools). In situ temperature, DO, salinity, pH, and discrete samples for dissolved inorganic nutrients ($NH4+$, $NO2- + NO3-$, $PO43-$) were collected hourly over a four-hour period in each pool and the adjacent ocean following methods by Silbiger & Sorte (2018). Temperature, DO, and salinity were measured with a calibrated multi-parameter pro meter directly in each pool (YSI Pro 2030, Lot #18B100763, Yellowsprings, OH, USA). For pH, nutrients, and TA, we collected 400 mL discrete water samples

into a sealed Erlenmeyer flask using a vacuum hand pump (Mityvac, St. Louis, MO, USA) from the deepest part of the pool. Discrete samples (~250mL) for total alkalinity (TA) were taken four times over the low tide period. To compare tide pool conditions to the open ocean, ocean measurements were taken from the surface adjacent to the site.

pHT was measured within one hour of water collection from the sealed Erlenmeyer flask using an Orion Star Multiparameter Meter with a ROSS Ultra glass electrode (Thermo Scientific, USA, accuracy = ±0.2 mV, resolution = ±0.1, drift < 0.005 pH units per day) and a traceable digital thermometer (5-077-8, accuracy = 0.05 °C, resolution = 0.001 °C; Control Company, Friendswood, TX, USA) following Dickson SOP 6 (Dickson et al. 2007). The glass electrode measured millivolts (mV) and was calibrated within 48 h of each sampling event using a multipoint calibration to a tris standard solution from the Dickson Lab at Scripps Institution of Oceanography following Dickson SOP 6a (Dickson et al. 2007). TA seawater samples were placed in 250 mL Nalgene bottles with 100 µl of 50% saturated HgCl2 to preserve the water within five hours of collection. Seawater samples for nutrient analysis were filtered through GF/F filters (0.7µm) with a syringe into designated 50 ml centrifuge tubes and frozen within five hours of collection. All sampling and storage containers were soaked in 10% HCl for 24 hours, rinsed with MilliQ water, and rinsed three times with sample water before sampling events.

In situ pH was calculated using the seacarb package in R (Gattuso et al. 2018) by correcting for the in situ temperature in each tide pool from a multi-parameter pro meter. Total alkalinity seawater samples were processed using open-cell potentiometric titrations on a Mettler-Toledo T5 auto-titrator (Columbus, OH, USA) following Dickson SOP 3b (Dickson et al. 2007). A certified reference material (CRM) from the Dickson Lab at the Scripps Institution of Oceanography was used at the beginning of each sample group run. The accuracy of the CRM never exceeded ± 0.79% (precision = 5 µmol kg-1) from the standard value and TA samples were corrected for deviations from the standard value. Dissolved inorganic nutrients (NH_4^+, $NO_2^- + NO_3^-$, PO_4^{3-}) were analyzed at Moss Landing Marine Laboratory using a Lachat Quickchem 8000 Flow Injection Analyzer (± 1.21% NH_4^+, ± 0.26% $NO_2^- + NO_3^-$, ± 3.57% PO_4^{3-} instrument precision; Hach, Loveland, CO, USA). After processing nutrients, one mussel control pool (Pool ID 30) was removed from all resource flux analyses due to abnormally high values of ammonium compared to other pools (4290 ± 188.1 µmol g-1), likely due to contamination, on one sampling day leaving n = 7 control pools.

We used the total alkalinity anomaly technique (Chisholm & Gattuso 1991) to calculate net ecosystem calcification (mmol $CaCO_3$ m^{-2} hr^{-1}) where total alkalinity values were divided by 1000 to convert from µmol kg^{-1} to mmol kg^{-1}. ΔTA/2 is the salinity-normalized and nutrient-corrected TA (mmol kg^{-1}) between each time point (n = 2−3 values per pool) divided by 2, where one mole of $CaCO_3$ is formed per 2 moles of TA times ρ is the density of seawater (1023 kg m^{-3}) times V is the volume of water in the pool at each time point (m^3) divided by SA is the bottom surface area of the tide pool (m^2) and t is the time between sampling points (h). and net ecosystem production rates (mmol C m-2 hr-1) were calculated from differences in dissolved inorganic carbon (DIC), calculated from pHT and TA (error propagation = 7.09 ± 0.06 mmol kg -1) with the seacarb package in R (Gattuso et al. 2018), using Gattuso et al. 1999's equation: NEP = ΔDIC is the difference in salinity-normalized DIC (mmol kg^{-1}) between each time point (around n = 3 values per pool) times density of seawater times the volume of the tide pool divided by the surface area of the tide pool and the time between sampling. NEC is subtracted to account for changes in DIC by the precipitation or dissolution of $CaCO_3$, and FCO_2 (mmol m^{-2} h^{-1}) is the air−sea flux of CO_2, which was subtracted to account for the flux in CO_2 from the air−sea exchange. FCO_2 is k is the gas transfer velocity (m h^{-1}) calculated from wind speed (Ho et al. 2006) using the closest weather station, around 10 miles south of Otter Rock (NOAA Station NWPO3: 44° 36' 46.8" N, 124° 04' 01.2" W) multiplied by s (the solubility of CO_2 in seawater calculated from in situ temperature and salinity (Weiss 1974) times CO_2 (µatm) in water is calculated from pHT and TA values minus CO_2 in the air was 410 µatm based on concurrent measurements at the Mauna Loa Observatory (Tans & Keeling 2019).

Known Issues:

- Tide pool 30 was removed because of high nutrient values in the after period. All time period 5 data were removed from analysis due to issues with sampling with the incoming tide.
- Missing 8 samples from nutrient analysis out of 612 samples: N_17_5_BC was lost before taking nutrients, D_24_1_BC, N_24_1_BC, N2_Ocean_5_BC, D_1_2_AI, D_16_2_AI, D_4_3_AI, N_20_3_AI were missing from lab analyses. We removed time points that nutrients were missing. N_26_1_BC has very low phosphate that yields it to be an outlier in later analysis could be a typo or the tide pool was just exposed from the ocean during sampling so time point was removed.
- Tide pool 18 was removed from mobile community composition analysis.

Data Processing Description

Data Processing:
We conducted separate statistical analyses for surfgrass and mussel tide pools for all response variables due to the difference in effects that each foundation species has on the ecosystem. Change in foundation species loss between the before and after removal periods varied continuously across treatment groups from -27.5% to 100% change in cover in the surfgrass tide pools and -10.4 to 98.5% change in cover in the mussel pools (Fig. S1, Fields & Silbinger 2022), with negative values indicating there was an increase in foundation species cover between time points. Therefore, we investigated foundation species loss as a continuous gradient rather than using categorical ANOVA-style design typical for BACI studies (Smith 2002).

Multivariate plots and analyses were used to assess how community composition and biogeochemistry parameters changed between time periods. We used a principal coordinate analysis (PCoA) in the vegan package (Oksanen et al. 2007) to visualize how the gradient of percent foundation species loss altered the change (after – before removal periods) in the cover of sessile organisms and counts in mobile organisms by functional group. Mobile community data were square root transformed to reduce the effect of rare values. One surfgrass control tide pool (Pool ID 18) was removed from the mobile community analysis because of outlier values of limpets and littorine snails. A PERMANOVA was used to test if foundation species loss altered functional community composition, with tide height and tide pool size included as covariates. For the biogeochemistry data, principal component analyses (PCA) were used to reduce the dimensionality and visualize the multivariate data. Data was centered and standardized before visualizing the PCA. Specifically, shifts between the before and after-removal period in biogeochemistry (DO, nutrients, and pH) and temperature mean, maximum, and variance of n = 8 (four day and four night) time points were visualized to observe differences for local tide pool conditions and the adjacent ocean from water sampling events.

We used general linear models to test the effect of foundation species loss on change (after – before removal periods) in species richness, percent maximum light, and maximum temperature in tide pools, with tide height and tide pool volume as covariates. Model assumptions for general linear models were verified by investigating residual plots of the model for homogeneity of variance and normality and data that did not meet assumptions were transformed. Multi-collinearity was tested with Pearson correlations between each predictor. All data was processed and analyzed using R statistical program (v 4.0.2; R Core Team 2020).

We conducted a piecewise structural equation model (SEM) using PiecewiseSEM 2.1.0 (Lefcheck 2016) understand how mussel and surfgrass percent loss and tide pool physical characteristics affected community changes, physical environmental conditions, biogeochemistry, and ecosystem metabolism of tide pool communities. Piecewise SEMs combine multiple linear models into a single causal framework (Shipley 2009, Lefcheck 2016). Because the model is pieced together with local estimation, it is more flexible than traditional SEMs and allows for inclusion of non-normal distributions, random effects, nested models, and smaller sample size within the causal model network (Lefcheck & Duffy 2015). Specifically, we tested direct and indirect pathways of surfgrass and mussel percent loss on ecosystem metabolism (NEC and NEP) mediated by changes in micro/macroalgae cover, temperature, nutrients (dissolved nitrogen to phosphate ratio), pH, and physical parameters of the tide pool. We conducted a multigroup analysis to test if each path varied by day and night, as expected from previous tide pool studies (Kwiatkowski et al. 2016, Bracken et al. 2018, Silbiger & Sorte 2018, Wolfe et al. 2020). The fit of each model was determined with a Shipley's test of d-separation, which verifies there are no missing inferences from the model using a Fisher's C statistic, where $p>0.05$ indicates that the model is a good fit for the data (Shipley 2009). However, since our study's ratio of total number of samples (16) to the number of variables (9) is 1.78 versus the recommended 5 (Grace et al. 2015, Lefcheck 2016), the smaller sample size could influence the goodness of fit of the model. Path coefficients were standardized allowing for comparisons of the magnitude of effect among groups.

For all model components, we averaged values over the low tide period (n=3 - 4 values per tide pool for pH, nutrients, and temperature; n= 2 - 3 values for NEC and NEP), and then calculated the difference between the before and after removal time period (n = 16 pools for the surfgrass model and n =15 pools for the mussel model). Positive values indicate an increase, zero indicates no change, and negative indicates a decrease in that parameter after the removal period. For the community composition components of the model, we used the sessile community metrics that changed the most between the before and after removal period, including, surfgrass, mussel, and non-surfgrass, non-calcifying producers (all fleshy micro and macroalgae). We excluded coralline algae from the analysis due their different functional roles within the tide pool (e.g., calcification and production and to reduce the number of pathways in our analysis). Tide pool size, represented as volume, and tide pool height was used as a covariate in all models because physical parameters can affect temperature and biogeochemistry (Legrand et al. 2018, Wolfe et al. 2020).

Due to the collinearity between nutrient species, the dissolved nitrogen to phosphate ratio ([nitrite + nitrate +

ammonium]: phosphate) was used as the measurement for nutrients in the SEM models. Because temperature and light were highly correlated and change in light was zero in most pools at night, only maximum temperature was used with the SEM framework (Fig. S3, Fields & Silbinger 2022). We used existing knowledge of intertidal systems to create hypothesized paths within each of the models (Grace 2008, Grace et al. 2012):

Micro/macroalgal cover ~ Foundation species loss + Volume + Tide height [1]

Model 1 represents the hypothesis that loss of surfgrass and mussel cover would increase producer cover by increasing free space for fast colonizers, with the volume of the pool and tide height as a covariates (Dethier 1981, 1984).

Maximum Temperature ~ Foundation species loss + Volume + Tide height [2]

Model 2 tests the understanding that temperature will increase with surfgrass and mussel loss (Stephens & Bertness 1991, Shelton 2010), with size of the pool and tide height as covariates.

N:P ~ Foundation species loss + Volume + Tide height [3]

Model 3 represents the hypothesis that the N:P ratio will increase with surfgrass loss because the loss of dominant producers will lead to less nitrogen uptake (Terrados & Williams 1997, Ramirez-Garcia et al. 2002). We hypothesized that the N:P ratio will decrease with mussel loss due to the mussels' ability to recycle nitrogen (Nielsen 2003, Bracken & Nielsen 2004, Pfister 2007, Pfister & Altabet 2019). N:P ratio may be affected by the size of the tide pool due to diffusive properties of tide pools (Hurd 2000) and tide height due to emersion time.

NEP ~ Maximum temperature + Micro/Macroalgal Cover + N:P + Tide Height;

NEP~ N:P + Micro/Macroalgal Cover + Tide Height [4]

Model 4 represents the different mechanisms that influence NEP. NEP is increased by producer cover, temperature, and nutrients (N:P) and affected by tide height (Pfister 2007, Kwiatkowski et al. 2016, Takeshita et al. 2016, Bracken et al. 2018, Duarte & Krause-Jensen 2018, Silbiger & Sorte 2018, Pfister & Altabet 2019, Wolfe et al. 2020). Surfgrass and mussel loss were both correlated with most of the components of the NEP model and were therefore excluded from the NEP model. Since volume was already accounted for in the calculation of NEP, it was removed from the model equation. Maximum temperature and N:P were correlated within mussel pools, so N:P ratio was used because there is more background knowledge on mussels' effect on production via altering nutrients (Pfister 2007, Pfister & Altabet 2019).

pH ~ NEP + Foundation species loss + Volume + Tide height [5]

Model 5 represents our understanding that there is a positive relationship between NEP and pH (Silbiger & Sorte 2018). Production increases pH, while respiration decreases pH due to the uptake and release of CO_2 respectively. Foundation species loss, size of tide pool, and tide height may also affect pH. Foundation species loss was also included within the pH model as a missing link determined by tests of directed separation.

NEC ~ pH + Maximum temperature + Tide Height [6]

Model 6 represents our understanding that NEC increases with pH and temperature and may be affected by the tide height (Kwiatkowski et al. 2016, Silbiger & Sorte 2018, Wolfe et al. 2020). Since volume was already accounted for in the calculation of NEC, it was removed from the model equation. Foundation species loss was correlated with both pH and maximum temperature and therefore was excluded from the model.
R statistical program (v 4.0.2; R Core Team 2020)

BCO-DMO Processing Description:
- Adjusted field/parameter names to comply with BCO-DMO naming conventions
- Added a conventional header with dataset name, PI names, version date

[table of contents | back to top]

Data Files

File
data_fields.csv(Comma Separated Values (.csv), 128.81 KB) MD5:a7590c20146977f86814425be9a2a29a Primary data file for dataset ID 878413

[table of contents | back to top]

Related Publications

Bracken, M. E. S., & Nielsen, K. J. (2004). DIVERSITY OF INTERTIDAL MACROALGAE INCREASES WITH NITROGEN LOADING BY INVERTEBRATES. Ecology, 85(10), 2828–2836. doi:10.1890/03-0651
Methods

Bracken, M. E. S., Silbiger, N. J., Bernatchez, G., & Sorte, C. J. B. (2018). Primary producers may ameliorate impacts of daytime CO2 addition in a coastal marine ecosystem. PeerJ, 6, e4739. doi:10.7717/peerj.4739
Methods

Chisholm, J. R. M., & Gattuso, J.-P. (1991). Validation of the alkalinity anomaly technique for investigating calcification of photosynthesis in coral reef communities. Limnology and Oceanography, 36(6), 1232–1239. doi:10.4319/lo.1991.36.6.1232
Methods

Dethier, M. N. (1981). Heteromorphic algal life histories: The seasonal pattern and response to herbivory of the brown crust, Ralfsia californica. Oecologia, 49(3), 333–339. https://doi.org/10.1007/bf00347594 https://doi.org/10.1007/BF00347594
Methods

Dethier, M. N. (1984). Disturbance and Recovery in Intertidal Pools: Maintenance of Mosaic Patterns. Ecological Monographs, 54(1), 99–118. Portico. https://doi.org/10.2307/1942457
Methods

Dickson, A.G.; Sabine, C.L. and Christian, J.R. (eds) (2007) Guide to best practices for ocean CO2 measurement. Sidney, British Columbia, North Pacific Marine Science Organization, 191pp. (PICES Special Publication 3; IOCCP Report 8). DOI: https://doi.org/10.25607/OBP-1342
Methods

Duarte, C. M., & Krause-Jensen, D. (2018). Greenland Tidal Pools as Hot Spots for Ecosystem Metabolism and Calcification. Estuaries and Coasts, 41(5), 1314–1321. https://doi.org/10.1007/s12237-018-0368-9
Methods

Fields, J. (2022). jenniferfields/EcoFunORTidepools: DOI 10.3354 (Version DOI10.3354) [Computer software]. Zenodo. https://doi.org/10.5281/zenodo.7039052
Software

Fields, J., & Silbiger, N. (2022). Foundation species loss alters multiple ecosystem functions within temperate tidepool communities. Marine Ecology Progress Series, 683, 1–19. https://doi.org/10.3354/meps13978
Results

Gattuso J-P, Epitalon J-M, Lavigne H, Orr J (2018) Seacarb: seawater carbonate chemistry. R package version 3.2.10.
Software

Gattuso, J.-P., Frankignoulle, M., & Smith, S. V. (1999). Measurement of community metabolism and significance in the coral reef CO 2 source-sink debate. Proceedings of the National Academy of Sciences, 96(23), 13017–13022. https://doi.org/10.1073/pnas.96.23.13017
Methods

Grace, J. B. (2008). Structural Equation Modeling for Observational Studies. Journal of Wildlife Management, 72(1), 14–22. https://doi.org/10.2193/2007-307
Methods

Grace, J. B., Scheiner, S. M., & Schoolmaster Jr, D. R. (2015). Structural equation modeling: building and evaluating causal models: Chapter 8.
Methods

Grace, J. B., Schoolmaster, D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M., & Schweiger, E. W. (2012). Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere,

3(8), art73. doi:10.1890/es12-00048.1 https://doi.org/10.1890/ES12-00048.1
Methods

Hurd, C. L. (2000). WATER MOTION, MARINE MACROALGAL PHYSIOLOGY, AND PRODUCTION. Journal of Phycology, 36(3), 453–472. Portico. https://doi.org/10.1046/j.1529-8817.2000.99139.x
Methods

Kwiatkowski, L., Gaylord, B., Hill, T., Hosfelt, J., Kroeker, K. J., Nebuchina, Y., Ninokawa, A., Russell, A. D., Rivest, E. B., Sesboüé, M., & Caldeira, K. (2016). Nighttime dissolution in a temperate coastal ocean ecosystem increases under acidification. Scientific Reports, 6(1). https://doi.org/10.1038/srep22984
Methods

Lefcheck, J. S. (2015). piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution, 7(5), 573–579. Portico. https://doi.org/10.1111/2041-210x.12512 https://doi.org/10.1111/2041-210X.12512
Methods

Lefcheck, J. S., & Duffy, J. E. (2015). Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. Ecology, 96(11), 2973–2983. https://doi.org/10.1890/14-1977.1
Methods

Legrand, E., Riera, P., Pouliquen, L., Bohner, O., Cariou, T., & Martin, S. (2018). Ecological characterization of intertidal rockpools: Seasonal and diurnal monitoring of physico-chemical parameters. Regional Studies in Marine Science, 17, 1–10. https://doi.org/10.1016/j.rsma.2017.11.003
Methods

Nielsen, K. J. (2003). Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Sciences, 100(13), 7660–7665. https://doi.org/10.1073/pnas.0932534100
Methods

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. A. S. S. (2007). The vegan package. Community ecology package, 10(631-637), 719. http://vegan.r-forge.r-project.org/
Software

Pfister, C. A. (1995). Estimating Competition Coefficients from Census Data: A Test with Field Manipulations of Tidepool Fishes. The American Naturalist, 146(2), 271–291. https://doi.org/10.1086/285798
Methods

Pfister, C. A. (2007). INTERTIDAL INVERTEBRATES LOCALLY ENHANCE PRIMARY PRODUCTION. Ecology, 88(7), 1647–1653. doi:10.1890/06-1913.1
Methods

Pfister, C. A., & Altabet, M. A. (2019). Enhanced microbial nitrogen transformations in association with macrobiota from the rocky intertidal. Biogeosciences, 16(2), 193–206. https://doi.org/10.5194/bg-16-193-2019
Methods

R Core Team (2020) R: A language and environment for statistical computing.
Software

Ramírez-García, P., Terrados, J., Ramos, F., Lot, A., Ocaña, D., & Duarte, C. M. (2002). Distribution and nutrient limitation of surfgrass, Phyllospadix scouleri and Phyllospadix torreyi, along the Pacific coast of Baja California (México). Aquatic Botany, 74(2), 121–131. https://doi.org/10.1016/s0304-3770(02)00050-5 https://doi.org/10.1016/S0304-3770(02)00050-5
Methods

Shelton, A. O. (2010). Temperature and community consequences of the loss of foundation species: Surfgrass (Phyllospadix spp., Hooker) in tidepools. Journal of Experimental Marine Biology and Ecology, 391(1–2), 35–42. https://doi.org/10.1016/j.jembe.2010.06.003
Methods

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. Ecology, 90(2), 363–368. https://doi.org/10.1890/08-1034.1
Methods

Silbiger, N. J., & Sorte, C. J. B. (2018). Biophysical feedbacks mediate carbonate chemistry in coastal ecosystems across spatiotemporal gradients. Scientific Reports, 8(1). https://doi.org/10.1038/s41598-017-18736-6

Methods

Smith EP (2002) BACI design. Encyclopedia of Environmetrics 1:141–148.
Methods

Stephens, E. G., & Bertness, M. D. (1991). Mussel facilitation of barnacle survival in a sheltered bay habitat. Journal of Experimental Marine Biology and Ecology, 145(1), 33–48. https://doi.org/10.1016/0022-0981(91)90004-g https://doi.org/10.1016/0022-0981(91)90004-G
Methods

Stewart-Oaten, A., Murdoch, W. W., & Parker, K. R. (1986). Environmental Impact Assessment: "Pseudoreplication" in Time? Ecology, 67(4), 929–940. Portico. https://doi.org/10.2307/1939815
Methods

Takeshita, Y., McGillis, W., Briggs, E. M., Carter, A. L., Donham, E. M., Martz, T. R., … Smith, J. E. (2016). Assessment of net community production and calcification of a coral reef using a boundary layer approach. Journal of Geophysical Research: Oceans, 121(8), 5655–5671. doi:10.1002/2016jc011886 https://doi.org/10.1002/2016JC011886
Methods

Tans P, Keeling R (2019) Trends in atmospheric carbon dioxide. NOAA Earth Systems Research Laboratory, Boulder, CO
Methods

Terrados, J., & Williams, S. (1997). Leaf versus root nitrogen uptake by the surfgrass Phyllospadix torreyi. Marine Ecology Progress Series, 149, 267–277. doi:10.3354/meps149267
Methods

Weiss, R. F. (1974). Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Marine Chemistry, 2(3), 203–215. doi:10.1016/0304-4203(74)90015-2
Methods

Wolf-Gladrow, D. A., Zeebe, R. E., Klaas, C., Körtzinger, A., & Dickson, A. G. (2007). Total alkalinity: The explicit conservative expression and its application to biogeochemical processes. Marine Chemistry, 106(1–2), 287–300. https://doi.org/10.1016/j.marchem.2007.01.006
Methods

Wolfe, K., Nguyen, H. D., Davey, M., & Byrne, M. (2020). Characterizing biogeochemical fluctuations in a world of extremes: A synthesis for temperate intertidal habitats in the face of global change. Global Change Biology, 26(7), 3858–3879. Portico. https://doi.org/10.1111/gcb.15103
Methods

[table of contents | back to top]

Parameters

Parameter	Description	Units
Pool_ID	tide pool id	unitless
Id_code	day or night, tide pool id, sampling period, and if it's in the before (BC) or after (AI) foundation species removal period	unitless
Time_Point	Time point of sampling (1-4)	unitless
Foundation_spp	mussel (Mytilus) or surfgrass (Phyllospadix) tide pool	unitless
Before_After	Before or after foundation species removal	unitless
Removal_Control	Removal pools that had foundation species removed in the after period or control	unitless
Day_Night	Day or night sampling	unitless
Group	Combination or Before/After and Removal/Control	unitless
TADeltaTime	Change in total alkalinity over sampling time points (2-1, 3-2, 4-3)	mmol kg_1

DICDeltaTime	Change in dissolved inorganic carbon over sampling time points (2-1, 3-2, 4-3)	mmol kg_1
DeltaTime	change in time between sampling periods	hrs
DeltaNN	Change in NO2_ + NO3_ over sampling time points (2-1, 3-2, 4-3)	µmol/L
DeltaNH4	Change in NH4+ over sampling time points (2-1, 3-2, 4-3)	µmol/L
DeltaPO	Change in PO43 _ over sampling time points (2-1, 3-2, 4-3)	µmol/L
DeltapH	Change in pH over sampling time points (2-1, 3-2, 4-3)	unitless
DeltapCO2	Change in pCO2 over sampling time points (2-1, 3-2, 4-3)	µatm
DeltaDO	Change in dissolved oxygen over sampling time points (2-1, 3-2, 4-3)	mg/L
SurfaceArea	surface area of tide pool	m2
Vol	volume of tide pool via dye method	m3
SAtoV	ratio of surface area to volume	m
TideHeight	tide height of tide pools	m
SamplingVolume	sampling volume from water sampling	mL
AdjSamplingVolume	sampling volume from water sampling included collection error	mL
DeltaTA_N_Norm	Change in total alkalinity over sampling time points (2-1, 3-2, 4-3) normalized with nutrients	mmol kg_1
NEC	net ecosystem calcification rates	mmol CaCO3 m_2 hr_1
Temp	mean temperature over time points	degrees celsius (°C)
pCO2	mean of pCO2 between time points	µatm
Salinity	mean salinity between time points	ppt
Wind	mean wind between time points	m h_1
pH	mean pH between time points	unitless
DO	mean dissolved oxygen between time points	mg/L
NN	mean NO2_ + NO3_ between time points	µmol/L
NH4	mean NH4+ between time points	µmol/L
PO	mean PO43- between time points	µmol/L
K	gas transfer velocity	m h_1
dpCO2	difference btween air and seawater pCO2 pCO2_water - pCO2_atm	µatm
a	CO2 solubility constant according to Weiss (1974) solubility	mmol L^-1 atm^-1 or mmol m^-3 uatm^-1
F_CO2	CO2 flux	mmol m_2 hr_1
NEP	Net ecosystem production rates	mmol C m-2 hr-1
AdjMusselCover	percent cover of mussels adjusted to be proportional to 100%	percent
AdjSurfgrassCover	percent cover of surfgrass adjusted to be proportional to 100%	percent
MusselCover	raw percent cover of mussels	percent
SurfgrassCover	raw percent cover of surfgrass	percent
allCCA	percent cover crustose coralline and coralline algae	percent
macroalgae	percent cover of algae	percent

macrophytes	percent cover algae + surfgrass	percent
macroCCA	percent cover all macroalgae + all CCA	percent
consumers	percent cover consumers (e.g. barnacles)	count
allconsumers	percent cover consumers (e.g. barnacles) + mussel cover	percent
prodphyllodom	percent cover macroalgae - all consumers	percent
allproddom	percent cover producers - all consumers	percent

[table of contents | back to top]

Instruments

Dataset-specific Instrument Name	Mettler-Toledo T5 auto-titrator
Generic Instrument Name	Automatic titrator
Generic Instrument Description	Instruments that incrementally add quantified aliquots of a reagent to a sample until the end-point of a chemical reaction is reached.

Dataset-specific Instrument Name	FisherBrand™ Traceable™; Model 5-077-8
Generic Instrument Name	digital thermometer
Generic Instrument Description	An instrument that measures temperature digitally.

Dataset-specific Instrument Name	Lachat Quickchem 8000 Flow Injection Analyzer (Hach)
Generic Instrument Name	Flow Injection Analyzer
Generic Instrument Description	An instrument that performs flow injection analysis. Flow injection analysis (FIA) is an approach to chemical analysis that is accomplished by injecting a plug of sample into a flowing carrier stream. FIA is an automated method in which a sample is injected into a continuous flow of a carrier solution that mixes with other continuously flowing solutions before reaching a detector. Precision is dramatically increased when FIA is used instead of manual injections and as a result very specific FIA systems have been developed for a wide array of analytical techniques.

Dataset-specific Instrument Name	Orion Star Multiparameter Meter
Generic Instrument Name	Multi Parameter Bench Meter
Dataset-specific Description	Orion Star Multiparameter Meter with a ROSS Ultra glass electrode (Thermo Scientific; accuracy = +/- 0.2 mV, resolution = +/-0.1 mV, drift < 0.005 pH units d−1)
Generic Instrument Description	An analytical instrument that can measure multiple parameters, such as pH, EC, TDS, DO and Temperature with one device.

Dataset-specific Instrument Name	Onset. HOBO. Pendant light intensity data logger MX2202, Bourne
Generic Instrument Name	Onset HOBO Pendant Temperature/Light Data Logger
Generic Instrument Description	The Onset HOBO (model numbers UA-002-64 or UA-001-64) is an in-situ instrument for wet or underwater applications. It supports light intensity, soil temperature, temperature, and water temperature. A two-channel logger with 10-bit resolution can record up to approximately 28,000 combined temperature and light measurements with 64K bytes memory. It has a polypropylene housing case. Uses an optical USB to transmit data. A solar radiation shield is used for measurement in sunlight. Temperature measurement range: -20 deg C to 70 deg C (temperature). Light measurement range: 0 to 320,000 lux. Temperature accuracy: +/- 0.53 deg C from 0 deg C to 50 deg C. Light accuracy: Designed for measurement of relative light levels. Water depth rating: 30 m.

Dataset-specific Instrument Name	ROSS Ultra glass electrode
Generic Instrument Name	pH Sensor
Dataset-specific Description	(Thermo Scientific; accuracy = +/- 0.2 mV, resolution = +/-0.1 mV, drift < 0.005 pH units d−1)
Generic Instrument Description	An instrument that measures the hydrogen ion activity in solutions. The overall concentration of hydrogen ions is inversely related to its pH. The pH scale ranges from 0 to 14 and indicates whether acidic (more H+) or basic (less H+).

Dataset-specific Instrument Name	Multi-parameter pro meter (YSI Pro 2030, Lot #18B100763, Yellowsprings, OH, USA
Generic Instrument Name	YSI Professional Plus Multi-Parameter Probe
Generic Instrument Description	The YSI Professional Plus handheld multiparameter meter provides for the measurement of a variety of combinations for dissolved oxygen, conductivity, specific conductance, salinity, resistivity, total dissolved solids (TDS), pH, ORP, pH/ORP combination, ammonium (ammonia), nitrate, chloride and temperature. More information from the manufacturer.

[table of contents | back to top]

Project Information

CAREER: Predicting ecosystem metabolism of rocky intertidal communities in warming and acidifying oceans. (TIDES)

Coverage: California, USA

NSF Award Abstract:
This award is funded in whole or in part under the American Rescue Plan Act of 2021 (Public Law 117-2).

The devastating impacts of global warming and ocean acidification (OA) on rocky intertidal ecosystems are expected to increase as the oceans continue to warm and acidify. Further, loss of critical foundation species as a result of anthropogenic stressors lead to changes in local conditions that alter ecosystem functioning. While data exist on the physiological response of individual organisms to OA and warming in rocky systems, far less research has been conducted on community and ecosystem-scale metabolic responses. The proposed work provides a critical step in understanding how altered environmental conditions affect ecosystem functioning in rocky intertidal systems through the combination of controlled laboratory studies, field experiments, and a synthetic modeling approach integrating experimental results with pre-existing time-series data. The proposed work is focused on the overarching question: How does shifting environmental variability and loss of foundation species interact to affect ecosystem functioning in rocky intertidal communities? The PI is integrating research with ecological and quantitative educational opportunities including classroom and hands-on training in lab/field methods in marine ecology, and data science and coding bootcamps for undergraduate students. Importantly, these opportunities financially and educationally support traditionally underrepresented students at one of the largest minority-serving institutions in the country. This project provides support for intensive mentoring and training for 35 undergraduate students (25 in data science and 10 in field/lab science, all paid), 2-3 masters students, and hands-on marine ecology opportunities in the classroom (~125 students). In addition to formal education, the PI is collaborating with an artist-in-residence to communicate science to the broader public through interactive and immersive art installations in Los Angeles.

Because rocky intertidal systems provide important ecosystem services including food production, coastal protection, and tourism, it is critical to understand how warming (both air and ocean), acidification, and altered community states affect reef-scale ecosystem metabolism. While information exists on responses of a variety of individual intertidal taxa to temperature stress, ocean acidification, and habitat loss, there is notably less on the response of ecosystem metabolism (e.g. NEP and NEC) to these stressors. This proposed work is focused on a series of conceptual knowledge gaps and tests mechanisms through which different warming regimes, lowered pH, and community disturbance lead to altered community metabolism and ultimately affect ecosystem function. Specifically, this study: 1) Describes community thermal performance curves of multiple ecosystem functions under differing pH conditions in experimental mesocosms, 2) characterizes drivers of ecosystem functioning (e.g. Net Ecosystem Production [NEP] and Net Ecosystem Calcification [NEC]) in situ using natural changes in environmental variability before and after a disturbance, and 3) integrates 16 years of publicly available community composition and environmental time-series data with lab and field data to hindcast ecosystem metabolic rates and predict how ecosystem metabolism may change in the future.

This award reflects NSF's statutory mission and has been deemed worthy of support through evaluation using the Foundation's intellectual merit and broader impacts review criteria.

[table of contents | back to top]

Funding

Funding Source	Award
NSF Division of Ocean Sciences (NSF OCE)	OCE-2044837

[table of contents | back to top]