Species cover in 15 permanent survey plots in the lower intertidal zone of Tatoosh Island, Makah Reservation, Washington, USA 2012-2022

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Project
» Eco-Evolutionary Response to the Scale of Temporal Environmental Fluctuation (Eco Evolutionary Response)
» Effects of Demography and Genetics on Extinction in Small Populations: Experiments with an Exploited Kelp (Experiments with an Exploited Kelp)
» Field Parameterization and Experimental Tests of the Neutral Theory of Biodiversity (Neutral Theory of Biodiversity)
» LTREB: Ecological Dynamics in an Experimentally-Tractable Natural Ecosystems (LTREB Ecological Dynamics)

Program
» Long Term Research in Environmental Biology (LTREB)

Contributors	Affiliation	Role
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Abstract
To document dynamics on lower tidal levels of rocky shores, a set of 15 permanent 50 x 50 cm quadrats were established in 2012 on Tatoosh Island, Makah Reservation, Washington, USA. Diagonal corners of each quadrat site were marked with a pair of different stainless steel screws allowing precise determination and orientation of the quadrat in subsequent annual sampling. Quadrats where subdivided with 10 monofilament lines in both top-down and side-side directions. In 2012, each quadrat was sampled visually under each point where monofilament lines crossed, both for the species first encountered from above, and for the species occupying the rock surfaces. Beginning in 2014, plots were documented annually through digital photographs of both the undisturbed plot, and the plot with overstory kelp moved to reveal understory organisms as much as possible. Photographs were analyzed for the percentage of area covered by mussels (Mytilus californianus) from 2014-2022, and for the percentage area covered by all identifiable organisms to the lowest taxonomic level possible in 2014 and 2019, using the 121 squares defined by the monofilament lines and the outer frame of the quadrat. The data can be useful for exploring changes in this ecosystem through time, particularly in the context of changes in populations of the sea star Pisaster ocraceus in response to Sea Star Wasting Disease epidemic in late 2014.

Table of Contents

Coverage

Location: Tatoosh Island, Makah Reservation, Washington, USA. Eastern Pacific rocky intertidal shoreline.
Spatial Extent: **N**:48.3952 **E**:-124.7326 **S**:48.3782 **W**:-124.7411
Temporal Extent: 2012-06-16 - 2022-07-31

Methods & Sampling

Permanent quadrats (50 x 50 cm) were established in the lower intertidal zone (below the lower limit of beds of the mussel *Mytilus californianus*) by embedding two stainless steel screws of two types (1 hex-head, 1 Phillips-head) into Rawl plug wall anchors located at diagonal corners of each plot. The two types of screws allowed the quadrat to be positioned and oriented in the same location in subsequent sampling years to document dynamics without confounding spatial variation. Quadrats were constructed out of 1/4" schedule 80 PVC pipe connected with 90^{o} joints at the corners. Each pipe had a series of 10 equidistant holes drilled through them, which were strung with heavy duty 40 lb test monofilament line, creating a grid of sampling squares., and each line was designated with either a letter (top to bottom) or number (left to right) to allow spatial information to be collected. Plots were established in 2012 and subsequently surveyed from 2014-2026 (except in 2020), with surveys still ongoing. In 2012, plots were visually surveyed by identifying the taxon of individual first encountered below each point where monofilament lines crossed, and then by identifying the taxon of individual adhering to the rock located under each sample point, with the aid of a pen/pencil to carefully move the overstory away. Beginning in 2014, plots were digitally photographed annually for later analysis on computers in the lab. Two photographs, with the quadrat filling the frame as much as possible, were taken: 1) the plot without any disturbance and 2) the plot with all overstory kelp blades moved to the side as much as possible without destructive manipulation. At present, photographs from 2014 through 2022 have been analyzed for the percentage of area covered by mussels, aided by the 121 squares defined by the 10 monofilament lines plus the edges of the quadrat. Additionally, photographs from 2014 and 2019 have been analyzed for percent cover of all identifiable species to the lowest taxonomic level possible from non-destructive photographs. Data are likely to be updated as subsequent analysis of the photographs from other years is carried out. Tide height of plots was determined using a rotary laser level, referenced to permanent markers of known tide height. Latitude and longitude were determined by GPS.

Data Processing Description

The original data are digital photographs (see quadrat_photos.zip). Values for the associated data table (1006607_v1_quadrat-species.csv) were extracted from the photographs through visual inspection of photos on computer screens with the aid of Adobe Photoshop or Apple Preview software.

Note: Blank values in the species category columns of 1006607_v1_quadrat-species.csv indicate that category was not assessed. A zero value indicates it was assessed but no quadrat squares were occupied by that species category.

BCO-DMO Curation Notes

Curation Actions Performed on Data

The following supplemental files were created from provided files and metadata:

Supplemental file "category_taxon_information.csv":
* Columns from the originally provided file "Lower Intertidal Quadrat BCODMO.csv" that were identification categories were extracted and added to column "identifications" in this table, a corresponding column "lowest_identificable_taxon" was added with just the taxonomic names corresponding to the categories. Names were matched to the World Register of Species (WoRMS) on 2026-08-08. All names matched exactly to known names there, however some are currently unaccepted synonyms. Accepted names change over time so the identifiers in this table can be used in the future to reference WoRMS for up to date information about the name. More could be added to "lowest_identifiable_taxon" for categories like "Crustose Red Algae" or "Colonial Hydroid."

Supplemental file quadrat_photos.zip
* All files provided to BCO-DMO within the originally named folder "Amy Quadrat Photos BCODMO" were included in this zip package in addition to two additional photos described below as being part of that collection

with additional notes. The notes were added to a "comment" column in the supplemental quadrat_photo_inventory.csv:
IMG_7566.jpeg = 2025 photo of quadrat 14, untouched
IMG_7567.jpeg = 2025 quadrat 14, kelp moved

quadrat_photo_inventory.csv
* This supplemental file was made by listing all the jpg files provided (included in quadrat_photos.zip and getting their size and checksum from command-line find and md5sum operations.

quadrat_locations.csv
* This table was made by taking the unique set of Quadrat,Site,Latitude,Longitude records included in the originally supplied file "Lower Intertidal Quadrat BCODMO.csv"

The provided data tables were loaded into the processing pipeline described below and the following curation actions were taken:

- Loaded quadrat_locations.csv, containing quadrat identifiers with associated latitude/longitude
- Loaded category_taxon_information.csv, containing taxonomic reference information for species categories
- Loaded LowerIntertidalQuadPhotoMeta.csv as table photo_metadata, containing photo metadata for quadrat surveys
- Loaded quadrat_photo_inventory.csv, containing an inventory of quadrat photos
- Loaded "Lower Intertidal Quadrat BCODMO.csv" as table 1006607_v1_quadrat-species, containing quadrat species/category counts; a fully blank unnamed header column was identified and ignored during load
- Set missing value markers to empty string for all loaded tables (indicating blanks are missing data values).
- Updated column metadata (descriptions, supplied units) on the quadrat-species table for all species/category columns, Latitude, Longitude, Quadrat, Site, TideHtMLLWm, and Year

- Made an additional form of the main table (drafted both wide and long format tables) with the following steps:
- Duplicated table 1006607_v1_quadrat-species into a new table 1006607_v1_quadrat-species_longform-draft
- Unpivoted all columns in the longform-draft table except Year, Quadrat, Site, Latitude, Longitude, and TideHtMLLWm; original column names captured into new column Category, cell values moved into new numeric column Quadrat_Square_Count

- Renamed species/category columns in 1006607_v1_quadrat-species by replacing whitespace with underscores, then removed periods from those renamed columns to meet column naming conventions.
- Photo metadata was mising lat,lon so Joined Latitude and Longitude from quadrat_locations into photo_metadata using Quadrat as the join key, keeping all photo_metadata rows (half-outer join)

- Enhanced the photo metadata table by adding the photo filename not just PhotoNumber since file extensions varied and PhotoNumber did not always exactly match the photo name prefix. Achied this with the following steps:
- Split the filename column in quadrat_photo_inventory into PhotoNumber (base name) and filename_ext (extension), preserving the original filename column
- Replaced "IMG_" with "IMG" in the PhotoNumber column of quadrat_photo_inventory
- Joined quadrat_photo_inventory table into photo_metadata table on PhotoNumber column, half-outer mode, pulling in photo_name column

- Updated column metadata (descriptions, standard name IDs, supplied units) for Category, Latitude, Longitude, Quadrat, Quadrat_Square_Count, Site, TideHtMLLWm, and Year on the longform-draft table
- Set column data types on the longform-draft table: Category and Site as string, Latitude/Longitude/Quadrat_Square_Count/TideHtMLLWm as number, Quadrat and Year as integer
- Output files: 1006607_v1_quadrat-species_longform-draft.csv, 1006607_v1_quadrat-species.csv (original wide form table), photo_metadata.csv

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Curation Actions Performed on Metadata
* Standard metadata entry and formatting of provided metadata.
* Note about meaning of blank cells (as opposed to 0 value cells) in the main data table was added to the Data Processing and parameter (column) definitions from information provided by email correspondence.

Known Issues [Potentially Impacting Reuse]
* N/A

Problem Description

To date, data has not been extracted from all photographs. The ability to see organisms attached to the underlying rock is limited where thick growth of kelp obscures the understory. This kelp could not be entirely moved out of the way to see the entire rock level without destructive sampling.

[table of contents | back to top]

Parameters

Parameter	Description	Units
Year	Sample Year	Year
Quadrat	Number identifier	Number
Site	General Site Name	Text
Latitude	Latitude	Decimal degrees N
Longitude	Longitude	Decimal degrees W
TideHtMLLWm	Tide Heigh	Meters above Mean Low Low Water
Category	Category assessed for presence on squares in the quadrat (e.g. 'rock','Hedophyllum sessile', 'Foliose Red Algae',...'Other') See category_taxon_information.csv for more information about each category, including taxonomic names and identifiers for categories that are organisms.	unitless
Quadrat_Square_Count	Count of quadrat squares occupied. A blank value indicates that the category was not assessed. A zero value indicates it was assessed but there was no presence of the category on any squares in the quadrat.	unitless

[table of contents | back to top]

Instruments

Dataset-specific Instrument Name	Panasonic Lumix DMC FZ1000 camera
Generic Instrument Name	Camera
Generic Instrument Description	All types of photographic equipment including stills, video, film and digital systems.

Dataset-specific Instrument Name	Garmin GPSmap 76 GPS unit
Generic Instrument Name	Global Positioning System Receiver
Generic Instrument Description	The Global Positioning System (GPS) is a U.S. space-based radionavigation system that provides reliable positioning, navigation, and timing services to civilian users on a continuous worldwide basis. The U.S. Air Force develops, maintains, and operates the space and control segments of the NAVSTAR GPS transmitter system. Ships use a variety of receivers (e.g. Trimble and Ashtech) to interpret the GPS signal and determine accurate latitude and longitude.

Dataset-specific Instrument Name	Dewalt DW074KD self-leveling laser level
Generic Instrument Name	Levels and staffs
Generic Instrument Description	Optical instruments and graduated poles used in surveying to determine the elevation of a location relative to a datum level.

[table of contents | back to top]

Project Information

Eco-Evolutionary Response to the Scale of Temporal Environmental Fluctuation (Eco Evolutionary Response)

Coverage: Salish Sea, Washington, USA

NSF Award Abstract:
Cyclical variations in environmental conditions, like tides or seasons, comprise a common theme in nature. Living organisms must cope with repetitive arrivals of unfavorable conditions for survival. Therefore species around the world are under evolutionary pressure to schedule their "life cycles" or "life histories" to fit the environmental cycle regimes within which they reside. Recent climate change has shifted historical cyclical patterns in many ecosystems, such as season length, resulting in mismatches between life histories and the ideal environmental conditions of plants and animals, to the detriment of population persistence and ecological stability. Adaptive evolution offers a mechanism that may buffer these mismatches. Accumulating evidence of shifts in life history schedules from around the world shows us that much remains to be done to understand how life histories are "fit" to environmental cycles, and to changes in cycles, despite their everyday familiarity. Testing theoretical ideas with data and experiments is essential. Marine coastal habitats are subject to conspicuous cycles occurring at multiple time scales, such as diel, tidal, lunar, seasonal, and multi-annual fluctuations. Populations of the intertidal crustacean Tigriopus californicus occupy rocky shore across the entire eastern Pacific coastline in upper tidepools that are periodically wave-swept at high tide at varying intervals. This project develops mathematical models to uncover fundamental rules of life history variation and adaptation in regularly varying environments, and tests hypotheses across Tigriopus californicus populations experiencing varying tidal disturbances using efficient and highly replicated field collections and manipulative experiments in the lab. Beyond producing broadly applicable theory and abundant open-access data, the investigators engage with local Makah Tribe students near field sites for sampling and natural history studies to enhance STEM education in an underserved rural community. Furthermore, the project expands the nation's scientific capacity by training undergraduate and graduate students in experimental design, theoretical modelling in population ecology and life history evolution, and data analysis.

How natural populations persist in variable environments has been a long-standing question in ecology and evolution. In particular, cyclical variability is common in nature, and many species show predictable life history strategies that follow cycles in nature (e.g. phenology). However, a general conceptual framework is lacking for how adaptation to cycles occurs and how the scaling of life histories to fluctuations buffers changes in the environment. Marine environments fluctuate predictably across a range of temporal scales, such as tidal and

seasonal, and provide unique opportunities to study population persistence and evolution in cyclical environments. A general mathematical framework is developed that explores life history optimization in the context of cyclically varying environments. The marine intertidal copepod Tigriopus californcus is ideal for testing model predictions and motivating extensions. Many isolated populations can be sampled entirely in the field, and the short timescale of tide cycles, short generation times, and ease of frequent sampling will provide a dense dataset of eco-evolutionary patterns in response to natural disturbance regimes. Pilot studies have established experimental populations in the laboratory, and have proven that Tigriopus californcus is amenable to careful manipulations of simulated disturbance frequency (both cyclical and stochastic) that seamlessly translate to the model framework. The combination of modelling, field parameterization, and experimental investigation of life histories in cyclical and stochastic environments is a novel and holistic approach to the question of life history diversity within an environment. Finally, a general understanding of evolutionary mechanisms in cyclical environments can improve predictions of the fate of populations when natural cycles are perturbed, which is expected across many ecosystems due to climate change.

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.

Effects of Demography and Genetics on Extinction in Small Populations: Experiments with an Exploited Kelp (Experiments with an Exploited Kelp)

Coverage: Tatoosh Island, Washington, United States of America, and the surrounding shores of Cape Flattery, Washington, United States of America

NSF Award Abstract:
The process of species extinction represents both a basic ecological and societal concern. Despite interest in extinction processes, there is little empirical information on mechanisms leading to extinction, particularly in marine systems, because extinction events involve small population sizes and are infrequent. Small population size is thought to increase the risk of extinction through several different mechanisms. Ecological mechanisms include increased variation in population growth rates due to chance events (demographic stochasticity), and positive density dependence (i.e., reduced population growth at low density). Genetic mechanisms include loss of favorable alleles due to chance events (genetic drift) and inbreeding depression.

This project will experimentally disentangle the effects of different mechanisms associated with small population size in a commercially-harvested marine kelp, the sea palm Postelsia palmaeformis. To test effects of genetic variation, experimental populations will be established from either a single founder, multiple founders from the same population, or multiple founders from different source populations. The genetic treatment will be combined with a density manipulation (large and small populations) to test for ecological effects of population size. Experimental populations will be monitored for times to extinction, and the underlying processes will be studied in detail by marking individual plants and measuring survival, fecundity, and growth rates. These data will be incorporated into a population model to determine the relative sensitivity of population growth to different effects of small population size and to different life stages. Concurrent monitoring of genetic structure of the experimental populations using AFLP fingerprinting techniques will provide an independent measurement of genetic dynamics and effects on population performance, and will validate basic assumptions of the study. The study will increase our understanding of the effects of small population size on extinction risk, help to characterize the life cycle of marine kelps, and provide important information for developing effective conservation and remediation strategies for exploited marine species.

Field Parameterization and Experimental Tests of the Neutral Theory of Biodiversity (Neutral Theory of Biodiversity)

Coverage: Tatoosh Island, Washington, United States of America

NSF Award Abstract:
A persistent challenge for ecology is to connect a mechanistic understanding of population dynamics with the generation of large-scale aggregate patterns of community structure, such as species-abundance and

species-area relationships. Hubbell's Neutral Theory of Biodiversity has shown promise in its ability to do this in both marine and non-marine systems. If the theory is correct, then a radical shift is needed in the perspective of how communities are organized, with minimal role for species differences (niche variation) and an emphasis on metacommunity dynamics, dispersal/recruitment control, and the interplay of speciation and extinction dynamics. Past evaluations of the theory have depended on asking whether the neutral theory can fit aggregate patterns, such as species-abundance distributions. This approach is relatively weak, involving tuning of two critical model parameters. This project will provide a strong test of the theory in a rocky intertidal community by reformulating the theory to make it more empirically accessible, extending a dataset on the transition dynamics of space use, parameterizing the model with this dataset, and then using several species deletion experiments to provide an independent test of the theory. The experimental approach will also relax several key assumptions of the neutral theory, including no recruitment limitation or variation and differences in species and their interactions, and explore the consequences of these assumptions. Aside from providing a strong test of an important synthetic theory, the research will expand knowledge of metacommunity dynamics, which are particularly relevant for understanding marine systems with oceanic transport, and will provide empirical information on the consequences of chronic species deletion in nearshore environments. Broader Impacts. This project will train undergraduate, graduate, and post-Ph.D. scientists at the interface of quantitative and field-based ecology, will involve interaction with tribal natural resource managers, and will facilitate access to a unique long-term multi-species dataset for probing transition-based approaches to environmental science that may provide some predictive insight into the consequences of biodiversity loss.

LTREB: Ecological Dynamics in an Experimentally-Tractable Natural Ecosystems (LTREB Ecological Dynamics)

Coverage: Tatoosh Island, Washington, United States of America

NSF Award Abstract for DEB-0919420:

This award is funded under the American Recovery and Reinvestment Act of 2009 (Public Law 111-5).

A core challenge for ecologists is to develop frameworks to predict how complex natural communities and ecosystems will respond to environmental impacts such as species extinction and global change. Because ecological interactions are comprised of complex networks, meeting this challenge requires an integration of mathematical frameworks with empirical data. In this project, the investigator will extend several long-term multi-species data sets for marine rocky intertidal organisms and environmental conditions, and use these data to estimate species interaction strengths in dynamic, multi-species models. These results will then be used to test for general patterns of interaction strength and to generate predictions for different potential environmental impacts. Long-term species manipulation experiments in this intertidal habitat will be used to validate predictions generated by multi-species models.

Results of this study will significantly enhance the ability to address an urgent societal need - the prediction of natural ecosystem responses to global change, including climate change. In the process, the study will increase collaboration and data sharing among university researchers and governmental management agencies (Tribal and NOAA National Marine Sanctuary staff), provide advanced training for Ph. D. students, and facilitate research experience for undergraduate in ecological science. Data associated with the project will be publicly available through the University of Chicago, the Knowledge Network for Biocomplexity, and through the Ecological Society of America's Ecological Archives.

NSF Award Abstract for Continuing Award DEB-1556874:

A central goal for ecology is to document if and how the environment is changing, to determine the causes of these changes, and to predict what the consequences of these changes will be to ecological systems. This is a challenge because of the complex network of connections among the living organisms and the non-living parts of ecosystems. Mathematical models are essential tools to keep track of these ecological interactions and to predict how they will respond to environmental changes. However, models need to be linked to data from nature. Two major challenges in developing predictive models of environmental change are 1) collecting sufficient data on how interactions among a complete set of species and environmental factors change over time, and (2) rigorously testing model predictions with experiments. This study will combine a quarter-century long series of data on 100+ species and relevant environmental variables in the rocky shoreline of Tatoosh Island in Washington state, with a long-term field experiment that mimics the extinction of a key species, the California mussel. The long term data will be applied to several different modeling approaches and predictions

from these models will subsequently be tested with the long-term field experiment. The research will identify the most promising modeling approaches for making ecological prediction, and make them available to ecosystem managers and policy makers interested in the consequences of environmental impacts such as species extinction and global change. The comprehensive data series also will be made available to other scientists to be used as a platform for additional studies. This project will also engage undergraduate students in field research, data management, mathematical modeling, and in communicating with the public, managers, and policy makers. Furthermore, because the challenge of understanding networks of species interactions is shared with other scientific disciplines that deal with complex networks, project results will be of general value in other disciplines.

The researcher will conduct annual surveys of replicated permanent plots for plants and animals on the shoreline in two ways: 1) by documenting the species identities under 2,600 fixed points over a 5-year period and generating annual transition probabilities among species, and 2) by generating abundance estimates in permanent 60 x 60 cm census plots. Fifteen experimental plots will be maintained by selectively removing individuals of Mytilus californianus when they appear, leaving all other species undisturbed. Environmental data will be collected every 30 minutes using a submersible data logger and a land-based weather station. Water chemistry, including critical nutrients, will be monitored. These data will be analyzed in several ways, including 1) parameterizing transition-based models (Markov chain models, spatially-explicit cellular automata) with environmental dependencies, 2) parameterizing multi-species population dynamic models from plot counts, 3) applying multi-spatial cross-convergent mapping and testing whether it accurately detects key species known to have strong causal effects from independent experiments, 4) applying neural network models and testing their predictions about the consequences of species extinction, and 5) testing whether there is a relationship between the variability of a species' abundance through time and its importance to the ecosystem as assessed by independent experiments. The community modeling projects enabled by the rich long term data sets have a strong potential to advance our understanding of mechanisms underlying community dynamics and their response to environmental change.

[table of contents | back to top]

Program Information

Long Term Research in Environmental Biology (LTREB)

Website: https://www.nsf.gov/funding/opportunities/ltreb-long-term-research-environmental-biology

Long Term Research in Environmental Biology (LTREB)

Supports research for a period of 10 years or longer to generate an extended time series of data with a focus on evolutionary biology, ecology and ecosystem science.

Synopsis
The Long Term Research in Environmental Biology (LTREB) Program supports the generation of extended time series of data to address important questions in evolutionary biology, ecology, and ecosystem science. Research areas include, but are not limited to, the effects of natural selection or other evolutionary processes on populations, communities, or ecosystems; the effects of interspecific interactions that vary over time and space; population or community dynamics for organisms that have extended life spans and long turnover times; feedbacks between ecological and evolutionary processes; pools of materials such as nutrients in soils that turn over at intermediate to longer time scales; and external forcing functions such as climatic cycles that operate over long return intervals.

[table of contents | back to top]

Funding

Funding Source	Award
NSF Division of Ocean Sciences (NSF OCE)	OCE-0928232
NSF Division of Ocean Sciences (NSF OCE)	OCE-1851489
NSF Division of Environmental Biology (NSF DEB)	DEB-0919420
NSF Division of Environmental Biology (NSF DEB)	DEB-1556874
NSF Division of Ocean Sciences (NSF OCE)	OCE-2329475

[table of contents | back to top]