University California, Santa Cruz

Younger Lagoon Reserve

Annual Report 2018-2019

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Executive Summary

Over the past year Younger Lagoon Reserve continued to thrive as a living laboratory and outdoor classroom focused on supporting University-level teaching, research and public service while meeting the campus' Coastal Long Range Development Plan (CLRDP) requirements for the protection and enhancement of all natural lands outside of the development areas of the Coastal Science Campus, including native habitat restoration of the 47-acre "Terrace Lands" as outlined in UCSC CLRDP and Coastal Development Permit. Over the past year we continued to increase our support of undergraduate course use. Most formal undergraduate education users were within the Environmental Studies and Ecology and Evolutionary Biology departments. Younger Lagoon Reserve-affiliated internships also supported over 70 undergraduate students who were involved with research, education, and stewardship. The majority of interns were involved in restoration and monitoring activities on the Terrace Lands engaging in a wide range of projects, including working closely with faculty research projects on cost effective methods for native habitat restoration (PI, Karen Holl), evolution of the threespined stickleback (co-PIs Eric Palkovacs and Ben Wasserman), and grassland response to drought (co-PIs Michael Loik and Justin Luong), internship curriculum/handbook materials, small mammal research, invasive species management, and more. Beyond UCSC use, YLR continued to support and increase use by other groups such as the Monterey Bay Aquarium Watsonville Area Teens Conserving Habitats Program, Watsonville Wetlands Watch, Cabrillo College, Santa Cruz Bird Club, local K-12 programs, and other community groups.

Restoration activities in FY 2018-2019 included weed control, planting of approximately 1.5 acres and seed collection. Beyond restoration work we continued to conduct other on-the-ground stewardship activities including trash hauls, removal of illegal camps, fence repair, and public education. This was the eighth year of CLRDP CCC compliance monitoring for Coastal Scrub, and Coastal Prairie areas. YLR is meeting or exceeding restoration targets for nearly all monitored sites and is meeting the restoration goals for Phase 2. FY 2018-2019 represented the ninth full year of implementation of the CLRDP CCC Beach Access Management Plan related activities at Younger Lagoon Reserve. The University's NOID 9 (18-1) summarized the findings of the Beach Access Management Plan to date, and proposed continuation of the Beach Access Management Plan. NOID 9 (18-1) was approved by the CCC in September 2018 with the addition of five special conditions related to increased public access to Younger Lagoon Reserve beach.

In Summary, YLR continued to offer excellent field locations for undergraduate, graduate, and faculty ecological research, support ongoing research and meet all CLRDP related activities and requirements.

Introduction

This report provides an overview of the activities that were conducted at Younger Lagoon Reserve (YLR) during the 2018-2019 fiscal year (July 1, 2018 - June 30, 2019). Younger Lagoon continued to see increases in use and activity in general. Providing an outdoor classroom and living laboratory allows for experiential learning opportunities. These opportunities have profound impacts on students both professionally and personally. This was the ninth year we had fulltime staff on site managing the Reserve. As a direct result, the level of academic and public engagement increased and the Reserve is on target for implementing its obligations required under the Coastal Long Range Development Plan (CLRDP).

Younger Lagoon represents a unique reserve within the UCSC's Natural Reserve portfolio as it has open public access to a portion of the Reserve. Along with the challenges of public access (i.e. impacts to resources, protecting research equipment, protecting endangered and threatened species, implementing regulations, etc.) having public present on-site provides opportunities for outreach and education. During the past year, we continued to implement restoration activities on the Terrace Lands portion of the reserve and, as a direct result, interacted frequently with public users. These interactions have continued to provide opportunities for reserve staff and students to discuss the short and long-term objectives and goals of the restoration work, interpret the flora and fauna of YLR, and discuss ongoing planning and development efforts of the Coastal Science Campus (CSC).

CLRDP Activities

Overview

This year represented the tenth year of CLRDP related activities at Younger Lagoon Reserve. The California Coastal Commission certified the CLRDP for the "Terrace Point" property in 2008. In July of 2008, approximately 47 acres of natural areas of the "Terrace Point" property were incorporated into the University of California Natural Reserve System as part of UCSC's Younger Lagoon Reserve. The inclusion of the 47 acres into YLR, along with continued management of the lagoon portion of YLR, was a requirement of the California Coastal Commission for the UCSC Coastal Science Campus development.

The CLRDP requires that the entire Reserve be protected and used as a living laboratory and outdoor classroom and that the newly incorporated Natural Reserves lands are restored over a 20-year period. Fulfilling the University's mission to support research and teaching, we continue to incorporate research and teaching into all aspects of restoration, monitoring, research and protection throughout YLR. The increased lands and access to restoration and monitoring projects are providing expanded opportunities for undergraduate experiential learning opportunities via class exercises, research opportunities, and internships.

NOIDs 2 (10-1) & NOID 9 (18-1) Beach Access Management Plan

This year represented the eighth full year of Beach Access Management Plan related activities at Younger Lagoon Reserve. In March 2010, the California Coastal Commission (CCC) approved the University of California's Notice of Impending Development for Implementation Measure 3.6.3 of the CLRDP (NOID 2). Implementation Measure 3.6.3 of the CLRDP required that (through controlled visits) the public have access to Younger Lagoon Reserve beach and that a monitoring program be created and implemented to document the condition of native flora and fauna within Younger Lagoon and its adjacent beach. The monitoring plan was to be implemented over a 5-year time period. At the end of the 5-year period (Winter 2015) results were to be compiled and included in a report that summarizes and assesses the effect of controlled beach access on flora and fauna. That report was submitted to the California Coastal Commission in 2016.

The CLRDP requires that University submit a NOID to the CCC that summarizes findings of the Beach Access Management Plan every five years. That NOID (NOID 9) was initially submitted in the Fall of 2016; however, it was withdrawn due to CCC staff workload and was resubmitted in summer of 2017. Although CCC staff recommended approval of NOID 9 as submitted, CCC Commissioners raised questions regarding beach access at the July 2017 meeting, and YLR staff

withdrew NOID 9 prior to the Commissioners vote in order to try and better address these questions. The University resubmitted NOID 9 to the CCC in September 2018.
In September 2018, the Commission approved UCSC's NOID 9 to continue the beach tour program though through 2020 with the addition of five special conditions. These special conditions were at the suggestion of Commission staff, and included 1) requiring that the tours be offered without admission to the Seymour Center), 2) additional tour outreach and advertising, 3) additional tour signage, 4) additional tour monitoring and reporting requirements, and 5) a threat to open the beach to additional public access should the conditions not be met. Condition 5 has the potential to jeopardize not just the research integrity of the reserve, but also the security of the west side of the Marine Lab, including the seawater system and marine mammal research program.

Implementation of the NOID 9 special conditions by the Seymour Center will cost approximately $15,000/year. The campus must submit a new Younger Lagoon Beach Public Access Management Plan NOID in 2020, at which point the Commission could ask for additional public access requirements, which could result in the need for additional funding.

Seymour Marine Discovery Center docent-led tours of the beach continued to be offered 2-4 times a month throughout FY 2018-2019 and biological monitoring of the lagoon and adjacent beach was conducted quarterly in FY 2018-2019. A detailed report on activities under the Beach Access Management Plan is included as Appendix 1. The first NOID 9 Special Conditions Implementation Report is included as Appendix 5.

NOID 3 (10-2) Specific Resource Plan for the Enhancement and Protection of Terrace Lands at Younger Lagoon Reserve

The Resource Management Plan (RMP) within the CLRDP provides a broad outline with general recommendations and specific guidelines for resource protection, enhancement, and management of all areas outside of the mixed-use research and education zones on the CSC site (areas that will remain undeveloped). In addition to resource protection, the CLRDP requires extensive restoration, enhanced public access/education opportunities on site, and extensive monitoring and reporting requirements. The entire project is to be completed over 20 years and, as a condition of inception into the University of California Natural Reserve System, UCSC Campus has committed to providing perpetual funding for the project and continued management of YLR.

The SRP for Phase 1A of restoration (first 7 years) was approved by the CCC in September 2010 (NOID 3, 10-2). Phase 1A projects included Priority 1 weed removal, re-vegetation, baseline monitoring and selection of reference systems. FY 2017-2018 marked the conclusion of the SRP for Phase 1A.

The SRP for Phase 2 of restoration (second 7 years) was submitted to the CCC as part of the 2017-2018 Annual Report.

The SRP for Phase 2 of restoration outlined detailed success criteria for each of the reserve's habitat types (Ruderal, Coyote Brush Grassland-Scrub, and Grassland, Coastal Bluffs, Wetlands, and Wetland Buffers). These criteria set an initial threshold of species richness and cover for specific habitat types throughout the restoration area. These criteria were further refined at the recommendation of the SAC based on results from reference site monitoring of local coastal terrace prairie grassland, seasonal wetland, and coastal scrub sites (See 2009-2010, 2010-2011, 2011-2012, 2012-2013, 2013-2014, 2014-2015, 2015-2016, 2016-2017, and 2017-2018 Annual Reports). FY 2018-2019 marked the eighth year of compliance monitoring for restored Coastal Scrub, and Coastal Prairie areas. A detailed compliance monitoring report is included in Appendix 2.

Restoration of the Terrace Lands continued throughout FY 2018-2019. Activities included weed control, planting, and seed collection.

Restoration Monitoring efforts in 2019-2020

During the 2019-2020 field season, UCSC graduate student Justin Luong and professor Dr. Karen Holl will conduct restoration compliance monitoring at restoration sites 2, 4 and 6 years post planting as per CLRDP requirements, as well as at any sites that have fallen below compliance standards.

NOID 5 (12-2) Public Coastal Access Overlook and Overlook Improvements Project

In August 2012, the California Coastal Commission (CCC) approved the University of California's Notice of Impending Development NOID 5 (12-2) Public Coastal Access Overlook and Overlook Improvements Project. Construction on the Public Coastal Access Overlook and Overlook Improvements Project ("Overlooks Project") began in the winter of 2012/2013 and was completed in the spring of 2013. The project consisted of three new public coastal access overlooks, and improvements to two existing overlooks at UCSC's Marine Science Campus. Several of the overlooks, which are sited at the margins of development zones, therefore are within what is now the Younger Lagoon Reserve: Overlooks C and A are within development zones at the margin of the YLR, while the sites of overlooks D, E and F are within areas incorporated into the YLR as a condition of approval of the CLRDP. The project constructed publicly-accessible overlooks from which to view the ocean coast (Overlook F), Younger Lagoon (Overlook D), a seasonal wetland (W5) (Overlook A), and campus marine mammal pools (Overlook C) for which public access is otherwise limited due to safety hazards or for the protection of marine wildlife and habitats. The facilities include interpretive signs and public amenities such as bicycle parking and benches to enhance public access to, and enjoyment of these restricted and/or sensitive areas.

NOID 6 (13-1) Coastal Biology Building and Associated Greenhouses; Site Improvements Including Road, Infrastructure and Service Yards; Public Access Trails and Interpretative Panels; Wetland Connection in Specific Resource Plan Phase 1B; Sign Program; Parking Program; Lighting Plan.

In August 2013, the California Coastal Commission (CCC) approved the University of California's Notice of Impending Development NOID 6 (13-1) Coastal Biology Building and Associated Greenhouses; Site Improvements Including Road, Infrastructure and Service Yards; Public Access Trails and Interpretative Panels; Wetland Connection in Specific Resource Plan Phase 1B; Sign Program; Parking Program; Lighting Plan. This project included development of a new seawater lab building, three new parking lots along with a parking management program, a research greenhouse complex, and associated site work including storm water treatment and infiltration features. It also consisted of campus utility and circulation improvements to serve both the new lab building and future campus development under the CLRDP. The Project developed a complex of public access and interpretive facilities, including pedestrian access trails, interpretive program shelters, educational signage, and outdoor exhibits. This project initiated campus wide parking, sign, and lighting programs. This project also included mandated wetland restoration and habitat improvements as described in the Specific Resource Plan Phase 1B.

SRP Phase 1B

The Resource Management Plan within the CLRDP requires the reconnection of Upper Terrace wetlands W1 and W2. Wetland W1, on the western margin of the Upper Terrace, is a former agricultural ditch, probably constructed to drain the adjacent agricultural field. It is separated from wetland W2 (located immediately to the east) by a slightly elevated berm that may partially represent spoils left from the ditch construction. The SRP for Phase 1B of restoration detailed Younger Lagoon Reserve's approach for implementing these mandated wetland restoration and habitat improvements.

To reconnect hydrology between W1 and W2, five brush packs (ditch plugs) were installed within W1 in the summer of 2016 and 2017 (See 2016-2017 Annual Report and SRP Phase 1 Summary Report). SRP Phase 1B is now complete. As the hydrology of the site begins to shift to become more favorable to wetland plants, native wetland plants will be installed on the site. All of the brush packs are currently intact and functioning as designed. Although not yet observed, the ditch plugs may create small open water pool habitat and potentially provide new breeding habitat for amphibians.

Domesticated Animals

In 1999, when the University purchased the land for the expanded CSC, a special exception was made in the campus code to allow leashed dogs on the bluff top trail that rings the YLR Terrace Lands. Since that time, the site had become popular with dog owners, many of whom do not obey the leash law. The CLRDP requires that all domesticated animals be eliminated from the campus. Parallel to the start of construction, implementation of the campus "no dog" policy began in May 2015 in conjunction with activities under NOID 6 (13-1), and continued in FY 2018-2019. New trail signage was installed this year to educate the community and the public about the policy change.

Scientific Advisory Committee (SAC) Meetings / Recommendations

A critical component of the CLRDP was the creation of a Specific Restoration Plan (SRP) guided by a Scientific Advisory Committee (SAC). The SAC is comprised of four members: Dr. Karen Holl (SAC chair) Professor and Chair of the Department of Environmental Studies at UCSC; Tim Hyland, Environmental Scientist, State Parks, Santa Cruz District; Bryan Largay, Conservation Director, Land Trust of Santa Cruz County; and Dr. Lisa Stratton, Director of Ecosystem Management, Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara (UCSB). SAC members met with reserve staff on-site and through email/phone consultation in FY 2018-2019. Discussion topics included current and future projects under the CLRDP, restoration, research, and teaching activities at YLR.

Monitoring Recommendations:

Coastal prairie is notoriously difficult to restore and maintain. The 2012 coastal prairie restoration site – which was impacted by construction and drought, has fallen below its success targets. The SAC recommended continuing to monitor this site (and any others that fall below target) once a year rather than every other year, and replanting or changing management regimes if it does not rebound.

Research Recommendations:

SAC members recommend that future research include investigations into methods for seasonal wetland restoration.

Summaries of ongoing research projects undertaken at the direction of the SAC are below.

Efficacy of Exotic Control Strategies for Restoring Coastal Prairie Grasses

Research is needed to evaluate the efficiency of different strategies to control non-native forbs and grasses and reduce competition with planted native species as part of coastal prairie restoration efforts. Holl et al. aimed to test methods that would be suitable in small grassland areas that are surrounding by housing, like Younger Lagoon Reserve. During summer/fall 2010 two senior thesis students and NRS staff set up a factorial experiment comparing several exotic control treatments including one-time (1×) tarping, two-time (2×) tarping, topsoil removal (scraping), herbicide, and a control (no treatment) crossed with applying mulch and not mulching. 2× tarped plots were irrigated in August 2010 and then covered with black plastic for ~2 months to shade out germinated seedlings, whereas both 1× and 2× tarped plots were tarped in the fall a couple of weeks following the first rains. This year Holl et al. collected the ninth year of data, which is reported in Luong (2019). The main results and recommendations are listed below.

- After nine years, mulching had no significant effect and plots that were originally mulched attenuated significant differences found between treatments for native species.
- Herbicide treatments had the highest cover of native grasses and the lowest cover of nonnative forbs whereas scraped plots have the highest cover of native forbs and lowest cover of nonnative grass. Furthermore, even species within the same functional group such as *E. glaucus* and *H. brachyantherum* respond differently to management practices (Fig 3). However, none of these differences were significant compared to the control treatment.
- As plots have a trend of decreasing native cover and increasing invasive cover as time passes from original implementation of management activities, continual maintenance of coastal prairie habitats may be needed to prevent reinvasion by nonnative species.
- Because different functional groups and species respond differentially to different invasive control methods (Fig. 2), it will be important to prescribe management practices based on site specific goals.
- While herbicide, mulch, and tarping reduced weed cover in the first few years, by the ninth year, there was no difference in native or nonnative plant cover between pre-planting weed control treatments and control plots. Results indicate that pre-treatment weed control during restoration has only short-term effects on changing native/nonnative plant cover in Younger Lagoon Reserve's coastal prairie. (Fig 4). Use of targeted hand removal of weeds could potentially change these results. We recommend that limited

resources should focus on additional planting and should be allocated to targeted hand removal to reduce competition as needed, rather than expending resources on extensive pre-planting weed control.

Management Recommendations:
In FY 2018-2019 the SAC discussed the apparent post-construction hydrologic changes to some of the Terrace Lands, and the construction of California Red-Legged Frog (CRLF) Ponds in the upper terrace.

Post-Construction Terrace Lands Hydrologic Changes
CLRDP Implementation Measure 6.1.3 states that the University shall "*Construct, provide, and maintain a public pedestrian and bicycle trail system to facilitate safe and passable public access within, along, and through the Marine Science Campus*."

CLRDP Implementation Measure 7.1.3 states that the University shall "*Develop and manage a drainage system on the Marine Science Campus that maintains pre-development drainage patterns and peak flow rates for up to the 25-year return storm in the post-development drainage system to the maximum extent feasible, provided that accommodating such flows does not require drainage system sizing that exceeds 85th percentile storm event requirements (see Appendix B).*"

A public pedestrian and bicycle trail system was developed on the CSC as part of NOID 6 (13-1). The majority of these trails formalized existing trails, many of which were former dirt farm roads. The informal trails were mostly below surrounding grade (e.g. tire ruts) and conveyed some water off of the Terrace Lands during heavy storm events. Post construction, the trails are now level with the surrounding grade, and they appear to be keeping more water on the Terrace Lands than in the past. Reserve staff have observed new areas of ponding, and the emergence of wetland vegetation in areas that were formerly scrub. However, this past year was wetter than average, and it's possible that these shifts are not due to construction impacts, but rather to inter annual variability in rainfall. The SAC recommends continuing to monitor rainfall, water levels, and make note of vegetation shifts, as these may indicate the need to adjust restoration planting palates.

Upper Terrace CRLF Ponds

CLRDP RMP MM 9 states that the University shall "*Restore, consolidate, expand, and enhance wetlands on the northern part of the site (i.e., north of the Campus access road) to restore historic functional values lost during decades of agricultural use. The restoration program will include integrating the hydrology of Wetlands W1 and W2 to create a consolidated north-south area for wildlife movement to YLR. Hydrological surveys will be conducted by a qualified hydrologist to establish the elevations appropriate for optimizing expected wetland functioning. The area will be graded to provide a natural channel profile and gradient between the culvert at the Union Pacific Railroad tracks and the culvert outlet to Younger Lagoon on the west property line. The area west of the combined W1/W2 hydrologic corridor shall be restored as functioning wetland upland/transitional habitat, as shall buffer areas to the east. Maintain the CRLF potential habitat at the northern end of W-2.*

During the ACoE permitting process for projects impacting wetlands on the Coastal Science Campus (including restoration work in the upper terrace), the US Fish and Wildlife Service (USFWS) was brought in for Section 7 consultation. This discussion included members of the Natural Reserves and Physical Planning and Construction. In April 2014, USFWS approved the University's project as proposed and asked the campus to explore the feasibility of building CRLF pond(s) in the upper terrace as both a benefit to the local population and a demonstration of good faith / collaboration between UCSC and USFWS.

With the support of the reserve, campus agreed to explore the possibility and staffs from both the Resource Conservation District (RCD) and USFWS Coastal Program made a site visit to discuss feasibility and conduct initial studies in the summer and fall of 2014. RCD staff completed a soil evaluation in October 2014 and found groundwater at less than 5' deep at one of the sample points (in sandy soils and in very dry conditions) and believe that CRLF ponds could be engineered on site to hold water for long enough to support breeding. The RCD was ready to move forward with putting together a proposal for designing and building the ponds (this would need to be evaluated by the SAC with our existing RMP obligations in mind - e.g. reconnect wetlands 1 and 2, etc.); however, due to unresolved questions including permitting (e.g. would the RCD's permits work for the site within the permitting requirements and procedures for UC) and potential impacts to future projects, PP&C staff felt there was not enough information to move forward with further RCD planning and/or construction the ponds. Subsequently, PP&C staff engaged additional outside hydrologic and biologic consultants to do a feasibility study in 2016-2017. This study confirmed initial studies by the RCD, and indicated that CRLP Ponds could be engineered on site to hold water for long enough to support breeding. However, the study also warned that factors such as nearby bullfrog and crayfish populations could hinder the success of such ponds.

In 2019, USFWS Coastal Program contacted the University about an opportunity to have a CRLF Frog pond built on-site by the NRCS at little to no expense to the University. Staff representing UCSC Physical Planning, Development, and Operations (PPDO, formerly PP&C), the UCSC NRS, the RCD, and USFWS Coastal Program met in the summer of 2019 to discuss the opportunity further. If permits and approvals can be obtained, the University plans to move forward with plans to build a CRLF pond in the upper terrace in 2020-2021.

The SAC is generally supportive of the idea of CRLF pond(s) in the upper terrace as a way to 1) increase collaboration between UCSC, YLR, and the USFWS, 2) potentially provide opportunities for CRLF teaching, research and outreach on the reserve, and 3) meet habitat restoration and wetland reconnection goals. However, some SAC members have expressed concerns about 1) whether the ponds would function as expected and 2) more broadly, whether or not CRLF ponds are even necessary in our area. The SAC will continue to provide guidance as plans for building a CRLP pond in the upper terrace develop.

SRP Phase 1 Implementation Summary

The SRP for Phase 1A of restoration (first 7 years) was approved by the CCC in September 2010 (NOID 3, 10-2). The SRP for Phase 1B of restoration (upper terrace wetland work) was approved by the CCC in July 2013 (NOID 6, 13-1). Phase 1A projects included Priority 1 weed removal, re-vegetation, baseline monitoring and selection of reference systems. Phase 1B projects included work in wetland areas, including the reconnection of upper terrace wetlands 1 and 2. Both Phase 1A and Phase 1B of restoration are now complete.

Younger Lagoon Reserve successfully implemented Phase 1 of the Specific Resource Plan for the Enhancement and Protection of Terrace Lands at Younger Lagoon Reserve. Nearly all Priority 1 weeds have been eliminated from the Terrace Lands. Over ten acres were planted with native species during Phase 1. Nearly all of those plantings are meeting or exceeding their success criteria targets. Upper terrace wetland reconnection work has been completed. In addition, teaching, research, and public service was incorporated into every aspect of SRP Phase 1 implementation. (See 2009-2010, 2010-2011, 2011-2012, 2012-2013, 2013-2014, 2014-2015, 2015-2016, 2016-2017, and 2017-2018 Annual Reports; and SRP Phase 1 Summary Report).

SRP Phase 2

The SRP for Phase 2 of restoration (second seven years) will follow the same success criterial for each of the reserve's habitat types and will encompass approximately 8.5 acres of restoration in the middle terrace. (See 2017-2018 Annual Report).

Photo Documentation

Photo point locations were established at ten locations within YLR. These locations were chosen to ensure coverage of all major areas on the Terrace. Photos were taken on May 8, 2018. At each photo point we collected the following information:

1. Photo point number
2. Date
3. Name of photographer
4. Bearing
5. Camera and lens size
6. Coordinates
7. Other comments

Photos are included in Appendix 4.

Restoration Activities

Restoration activities continued on the Terrace Lands of YLR and throughout the lagoon portion of the Reserve. Implementation was conducted largely by undergraduate students and community volunteers; thus, utilizing the reserve in a manner consistent with the programmatic objectives (facilitating research, education, and public service) of the University of California Natural Reserves, as well as leveraging funding to increase restoration work (Figure 1). Here we summarize some of the restoration activities that occurred on YLR during the past year.

Figure 1. Volunteers and undergraduate student interns spread mulch in preparation for native planting.

Priority One Weed Removal

Under the SRP, all priority-one weeds (Ice plant, Jubata grass, Monterey cypress, Cape Ivy, Panic veldgrass, Harding grass, French Broom and Monterey Pine) are to be controlled as they are detected throughout the Terrace Lands. Elimination of reproductive individuals is the goal; however, YLR is surrounded by priority-one weed seed sources and it is likely that there will always be a low level of priority-one weeds persisting on the terrace. In FY 2018-2019, reserve staff conducted weed patrols of the entire terrace, continued removing ice plant from the coastal bluffs, removed all Jubata grass re-sprouts from the terrace, removed all French Broom re-sprouts from the terrace, and removed all Cape Ivy re-sprouts from the west arm of the lagoon. In FY 2019-2020, reserve staff will continue weed control projects and patrols. Due to the long-lived seed bank of French Broom, proximity of mature Jubata grass and Panic veldgrass on adjacent properties, and known ability of Cape Ivy fragments to re-sprout, regular patrols and maintenance of these sites will be critical. Removal of new recruit Monterey Pine and Cypress will continue as will targeted removal of current individuals.

Seed Collection and Plant Propagation

In the summer and fall of 2018, reserve staff and student interns collected seeds for restoration growing. These seeds were propagated by the UCSC Teaching Greenhouse in the fall and winter of 2018/2019.

Restoration Planting

In FY 2018-2019, approximately 1.5 acres of upland areas including northern coastal scrub habitats and coastal terrace prairie were planted with native seedlings (Figure 2). The 2018-2019 site was inundated with water during the heavy winter rains – possibly due to a shift in hydrology caused by the new McAllister Way road alignment, making planting challenging; however, the site was successfully planted and is thriving.

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2. 2019 Restoration Site.

Education

Instructional use at Younger Lagoon Reserve continued to increase this year. Courses encompassed a wide variety of disciplines. The increase in course use is a direct result of having fulltime staff on site that are able to actively engage faculty and students through outreach efforts in the classroom as well as providing on-the-ground assistance in teaching activities. The proximity of Younger Lagoon to the campus enables faculty and students to easily use the Reserve for a wide variety of instructional endeavors ranging from Restoration Ecology to Natural History Illustration.

Undergraduate Students – Providing hands-on learning opportunities for future leaders

YLR's proximity to the UCSC Campus and Long Marine Laboratory make it an ideal setting for undergraduate teaching and research (Figure 3). In FY 2018-2019 the reserve hosted classes in Coastal Field Studies, Ecology, Marine Ecology, Freshwater Ecology, Invertebrate Zoology, Plant Physiology, Behavioral Ecology, Molecular Ecology, Plant Ecology, Marine Conservation Biology, Restoration Ecology, Environmental Field Methods, Ecology and Society, Systematic Botany of Flowering Plants, Plant Physiological Ecology, Ecology and Conservation Supercourse, College 8 Service Learning Practicum, Freshwater / Wetland Ecology, Natural History of the UCSC Campus, and Natural History Illustration (Table 1).

Figure 3. Students from *ENVS 162/L - Plant Physiological Ecology/Lab* sort biomass samples collected from Younger Lagoon Reserve.

Internships

In FY2018-2019, YLR staff sponsored over 70 undergraduate interns through the UCSC Environmental Studies Internship Office. The students ranged from entering freshman to graduating seniors and spent between 6 and 15 hours a week working on on-going restoration projects at the reserve. These projects included invasive species removal, re-vegetation with native species, seed collection, and propagation. Student-interns report a deep appreciation for the opportunity to obtain hands-on experience in their field of study (Figure 4).

Figure 4. Undergraduate student interns collect native seeds for restoration plantings.

Table 1. Younger Lagoon Courses

Course Title	**Institution (Department)**	**Instructor's Name**
BIO 11C - Ecology	Cabrillo Community College	Alison Gong
ENVS 189 – Coastal Field Studies	San Jose State University	Rachel Lazzeri-Aerts
BIOE 107 – Ecology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Marm Kilpatrick
BIOE 108 – Marine Ecology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Mark Carr
BIOE 117/L – Systematic Botany of Flowering Plants	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Kathleen Kay
BIOE 122/L - Invertebrate Zoology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Baldo Marinovic
BIOE 135/L – Plant Physiology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Jarmila Pittermann
BIOE 137 – Molecular Ecology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Beth Shapiro
BIOE 140 – Behavioral Ecology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Bruce Lyon
BIOE 145 – Plant Ecology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Ingrid Parker
BIOE 151ABCD/ENVS109ABCD – Ecology and Conservation in Practice Supercourse	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology and Dept. of Environmental Studies)	Don Croll and Gage Dayton
BIOE 165 – Marine Conservation Biology	University of California, Santa Cruz (Dept. of Ecology and Evolutionary Biology)	Don Croll
CLEI 55 - College Eight: Service Learning Practicum	University of California, Santa Cruz (College Eight)	Susan Watrus
ENVS 15 – Natural History of the UCSC Campus	University of California, Santa Cruz (Dept. of Environmental Studies)	Ryan Carl

CLEI 55 - Sustainability Internship	University of California, Santa Cruz (College Eight)	Susan Watrus
ENVS 18 – Natural History Illustration	University of California, Santa Cruz (Dept. of Environmental Studies)	Emily Underwood
ENVS 100 – Ecology and Society	University of California, Santa Cruz (Dept. of Environmental Studies)	Greg Gilbert
ENVS 104A/L - Environmental Field Methods (Summer)	University of California, Santa Cruz (Dept. of Environmental Studies)	Josie Lesage
ENVS 160 - Restoration Ecology	University of California, Santa Cruz (Dept. of Environmental Studies)	Karen Holl
ENVS 162/L - Plant Physiological Ecology/Lab	University of California, Santa Cruz (Dept. of Environmental Studies)	Michael Loik
ENVS 167 - Freshwater / Wetland Ecology	University of California, Santa Cruz (Dept. of Environmental Studies)	Katie L Monsen
ENVS 83 / 183 - Younger Lagoon Reserve Stewardship Interns	University of California, Santa Cruz (Dept. of Environmental Studies)	Vaughan Williams
ENVS 84 / 184 - Younger Lagoon Reserve Stewardship Interns	University of California, Santa Cruz (Dept. of Environmental Studies)	Vaughan Williams

Research

Due in part to its relatively small size and lack of facilities, YLR is unlikely to host many single-site research projects in biology or ecology. However, as one of the few remaining coastal lagoons in California, YLR is well suited to act as one of many research sites in a multi-sited project. Additionally, the close proximity to campus makes it an ideal place for faculty to conduct pilot and our small-scale studies as well as for undergraduate research opportunities.

Last year, research conducted at Younger Lagoon Reserve resulted in the publication of four peer-reviewed articles. A list of those publication is below. The full articles are included as Appendix 6.

Hilton, Timothy W., Loik, Michael E., and Campbell, J. Elliott. Simulating International Drought Experiment field observations using the Community Land Model. United States: N. p., 2019. Web. doi:10.1016/j.agrformet.2018.12.016.

Loik, ME, Lesage, JC, Brown, TM, Hastings, DO. Drought-Net rainfall shelters did not cause nondrought effects on photosynthesis for California central coast plants. Ecohydrology. 2019;e2138. https://doi.org/10.1002/eco.2138

Paccard, A., Wasserman, B. A., Hanson, D. , Astorg, L. , Durston, D. , Kurland, S. , Apgar, T. M., El-Sabaawi, R. W., Palkovacs, E. P., Hendry, A. P. and Barrett, R. D. (2018), Adaptation in temporally variable environments: stickleback armor in periodically breaching bar-built estuaries. J. Evol. Biol., 31: 735-752. doi:10.1111/jeb.13264

Reid, R.E.B., Gifford-Gonzalez, D. and P.L. Koch, 2018, Coyote (Canis latrans) use of marine resources in coastal California: a new behavior relative to their recent ancestors, The Holocene. 10.1177/0959683618788714.

In FY 2018-2019 we approved fifteen research applications. Examples and summaries of new and ongoing research are included below.

Faculty Research Highlight: Evolution of the Threespine Stickleback

Natural selection is important for organisms to adapt to their environment. When environments change, selection may also. Professor Eric Palkovacs and graduate student Ben Wasserman are exploring whether fluctuating selection can maintain genetic diversity, unlike directional selection, which reduces diversity but increases fitness using the threespine stickleback inhabiting Younger Lagoon.

Typically, anadromous populations of threespine stickleback are covered in a continuous row of bony armor plates (20 or more) but freshwater resident populations have few plates (10 or less). This phenotype is known to be determined primarily by which copy of a single gene *Ectodysplasin-A* (*Eda*) the individual has. In the ocean, marine predators select for high plate counts (and *C* alleles), whereas in freshwater it is believed that the energetic cost means that low plate counts (and *L* alleles) are selected for since the strength of selection from predators is less or absent.

In Younger Lagoon and other seasonally closed estuaries in California, stickleback may experience freshwater-style selection for low plate counts during the summer months when the estuary is separated from the ocean and there are no fish predators, but experience marine selection for high plate counts following the estuary breach (Figure 5), when their data show that most individuals are released into the ocean. Palkovacs and Wasserman have collected threespine stickleback from Younger Lagoon every month starting in February of 2014. By counting the plates and determining which copies of the *Eda* gene these individuals have, they can determine how the strength of selection changes over time, and whether both copies of the *Eda* gene can persist in the population over time.

Since their study includes both historic high- and low-rainfall years, they can determine the range of fluctuation over which persistence of allelic diversity is possible. As climate change alters the frequencies of different types of rain years, they might even be able to predict what type of climatic conditions would lead to the loss of genetic diversity.

So far, Palkovacs and Wasserman have tested whether fluctuations in natural selection due to seasonal environmental shifts can function to maintain genetic diversity in a system where stable selection would drive a population to fixation. In threespine stickleback inhabiting intermittently ocean-connected estuaries, they found that traits associated with freshwater and marine residency fluctuate seasonally as predicted. Palkovacs and Wasserman have completed field collections, taken most of the trait measurements, and started the genotypic data collection. They hope to have answers to their questions about the importance of different drivers of interannual variability in future years.

Figure 5. Lagoon breach 2019.

Faculty Research Highlight: International Drought Experiment

Several UC Natural Reserve sites in California are participating in the International Drought Experiment. The experiment is compliant with the *DroughtNet* protocol for comparison to 100 other sites worldwide (drought-net.org). Effects of drought on plant growth and biodiversity are being measured at a number of grassland and shrubland sites along a north-south and coastal-inland gradient in California. At UCSC, professors Michael Loik, Kathleen Kay, and Karen Holl are collaborating with graduate student Justin Luong on this project.

The UCSC Drought Experiment was built with support from the Institute for the Study of Ecological and Evolutionary Climate Impacts (ISEECI) during 2015 at three sites including Younger Lagoon UC Natural Reserve, the UCSC Arboretum, and the UCSC Campus Natural Reserve. The main goal of the experiment is to better understand how long-term drought affects which plant species grow, and by how much, in California coastal prairie. The UCSC Drought Experiment sites span an elevation gradient of about 300 m with changes in rainfall, temperature, and fog. Fog-collectors are co-located with shelters at each site. Initial plot establishment made up the laboratory section activities for ENVS 162/L Plant Physiological Ecology at Younger Lagoon, the Arboretum, and the Campus Natural Reserve during Spring 2015.

Effects of soil water on species composition and productivity will be compared for invaded grassland with 60% rainfall removal, and for ambient, invaded coastal prairie grassland ("control"; no rainfall shelters). At Younger Lagoon, Loik et al. are also conducting experiments with a restoration context by comparing effects of drought on planted native seedlings in comparison to planted native seedlings with 60% rainfall removal. Loik et al. also have water addition plots available for experiments. There are n = 5 plots per treatment. Size = 2 X 2 m, with a 1 m buffer around the 4 m^2 square plot.

Shelter construction commenced in July 2015. Plots were trenched to 50 cm deep and lined with 6 mil plastic to prevent lateral water flow and root encroachment. Shelters were initially constructed of lightweight metal and rainfall is intercepted using clear, v-shaped polycarbonate troughs. In 2017, the shelters were rebuilt using wooden posts. Rainfall interception commenced during the first significant rainfall between 2 -3 November 2015. With *ISEECI* support, Loik et al. began to automatically monitor soil moisture and temperature, as well as air temperature and relative humidity near the ground under the shelters in 2016.

During 2019, the drought experiment activities at Younger Lagoon Reserve (YLR) focused on: 1. Continued measurements and monitoring of plots in accordance with the International Drought Experiment protocol; 2. Continued collection of micrometeorological data from a sensor system set up in a prior year; 3. Continued monitoring of survival and species-specific growth of California native plant seedlings, as well as composition of species cover under drought, control and watering treatments; 4. Measurement of plant functional traits for fourteen native California plant species and nine non-native species; and 5. Measurements of soil hydraulic conductivity and infiltration rates. Undergraduate students assisted with all aspects of this research (Figure 6). A full report on the International Drought Experiment is included in Appendix 3.

Figure 6. Undergraduate students assist with measurements in the rain at the experimental *DroughtNet* shelters.

Public Service

Public service use at Younger Lagoon Reserve continued to increase this year. Public service users encompassed a wide variety of groups. The increase in public service use is a direct result of having fulltime staff on site that are able to actively engage public groups through outreach efforts as well as providing on-the-ground assistance in public service activities. The proximity of Younger Lagoon to the town of Santa Cruz enables members of the public to easily use the Reserve for a wide variety of approved endeavors ranging from birding to K-12 teaching (Figure 7, Table 2, Table 3).

Figure 7. A local *plein air* artist captures the beauty of Younger Lagoon Reserve.

Monterey Bay Aquarium Watsonville Area Teens Conserving Habitats (WATCH) Program
YLR's proximity to the urban center of the city and county of Santa Cruz make it an ideal setting for public service. In FY 2018-2019 the reserve continued its partnership with the Seymour Marine Discovery Center (SMDC) and the Monterey Bay Aquarium Watsonville Area Teens Conserving Habitats (WATCH) program. WATCH is a program offered only at Pajaro Valley, Watsonville and Aptos high schools in Watsonville, California. This year-long program begins in the summer and extends throughout the school year. During the two-week summer component,

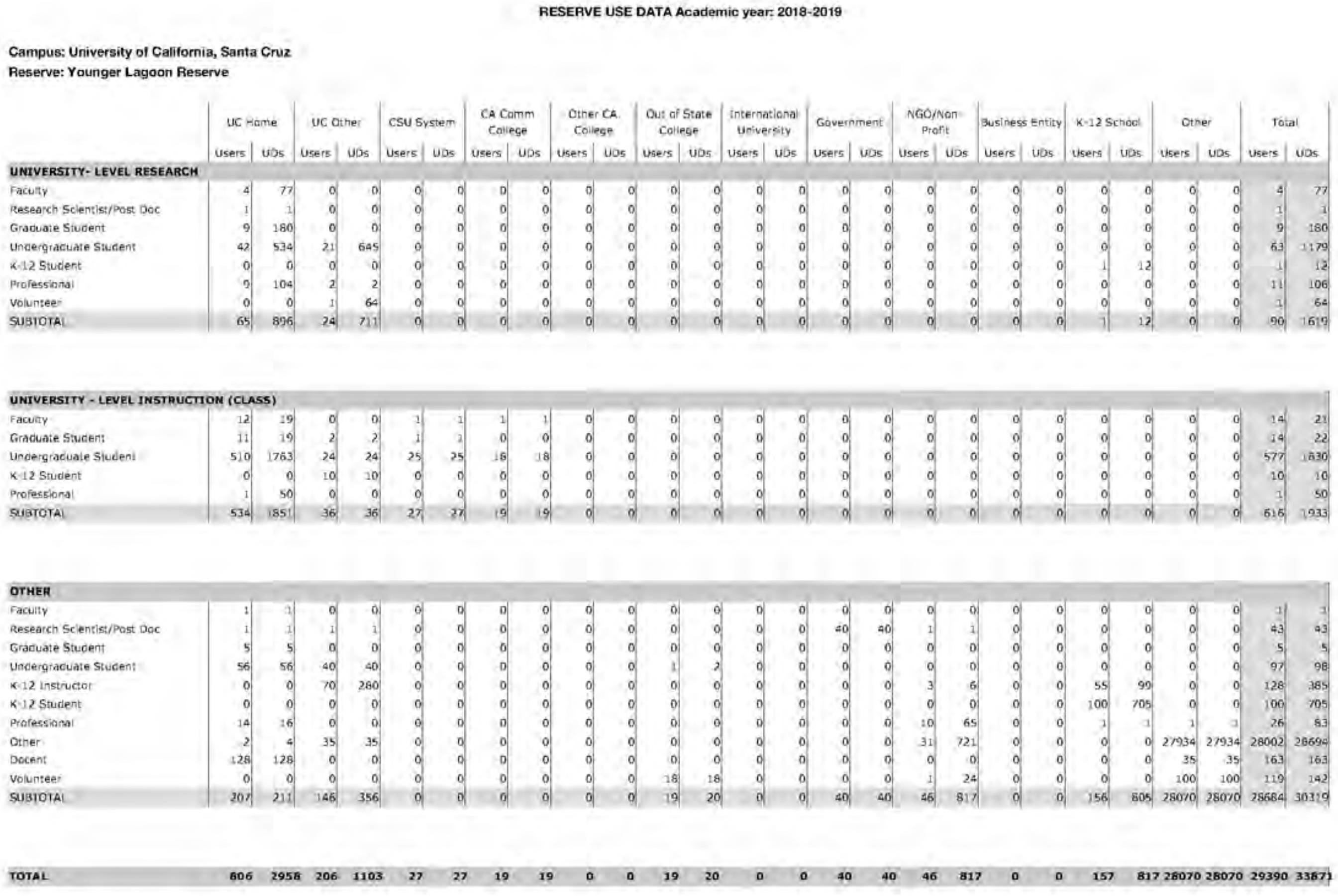
students explore the Pajaro River Watershed and Younger Lagoon Reserve, meet with local scientists and participate in inquiry-based learning. They also learn about environmental issues in their community and participate in local restoration efforts. After the summer, the same students enroll in a WATCH science class at their high school and develop their own field research project based on an environmental topic at either Elkhorn Slough (Pajaro Valley and Watsonville High Schools) or Younger Lagoon Reserve (Aptos High School). Students visit their field sites once a week for ten weeks in the fall to collect data, and work during the winter and spring to analyze, write-up, and present their data (Figure 8). They work with Monterey Bay Aquarium staff and teachers, SMDC staff, YLR staff and undergraduate interns, as well as scientists and educators from the community to complete their projects. Upon completion of the projects, students receive a scholarship and community service hours needed for graduation.

Figure 8. WATCH program staff and participants explore the lagoon and beach.

Reserve Use

The greatest educational user group for YLR in FY 2018-2019 was once again undergraduate education, a breakdown of all user groups is included in Table 2. YLR was used by UC Santa Cruz, UC Berkeley, UC Los Angeles, CSU San Jose, Cal Poly San Luis Obispo, University of Utah, Cabrillo College, Aptos High School, Half Moon Bay High School, Pajaro Valley High School, Watsonville High School, California Academy of Sciences, Monterey Bay Aquarium, Santa Cruz Museum of Natural History, Seymour Marine Discovery Center, Santa Cruz Bird Club, California Naturalist Program, and several local and regional volunteer groups (Table 3).

Table 2. Younger Lagoon Total Use



RESERVE USE DATA Academic year: 2018-2019

Campus: University of California, Santa Cruz
Reserve: Younger Lagoon Reserve

	UC Home		UC Other		CSU System		CA Comm College		Other CA College		Out of State College		International University		Government		NGO/Non-Profit		Business Entity		K-12 School		Other		Total	
	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs
UNIVERSITY- LEVEL RESEARCH																												
Faculty	4	77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	77
Research Scientist/Post Doc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Graduate Student	9	180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	180
Undergraduate Student	42	534	21	645	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	63	1179
K-12 Student	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	0	1	12
Professional	9	104	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	106
Volunteer	0	0	1	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	64
SUBTOTAL	65	896	24	711	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	0	90	1619
UNIVERSITY - LEVEL INSTRUCTION (CLASS)																												
Faculty	12	19	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	21
Graduate Student	11	19	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	22
Undergraduate Student	510	1763	24	24	25	25	18	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	577	1830
K-12 Student	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10
Professional	1	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	50
SUBTOTAL	534	1851	36	36	27	27	19	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	616	1933
OTHER																												
Faculty	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Research Scientist/Post Doc	1	1	1	1	0	0	0	0	0	0	0	0	0	0	40	40	1	1	0	0	0	0	0	0	43	43
Graduate Student	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
Undergraduate Student	56	56	40	40	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	97	98
K-12 Instructor	0	0	70	280	0	0	0	0	0	0	0	0	0	0	0	0	3	6	0	0	55	99	0	0	128	385
K-12 Student	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	705	0	0	100	705
Professional	14	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	65	0	0	1	1	1	1	26	83
Other	2	4	35	35	0	0	0	0	0	0	0	0	0	0	0	0	31	721	0	0	0	0	27934	27934	28002	28694
Docent	128	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	35	163	163
Volunteer	0	0	0	0	0	0	0	0	0	0	18	18	0	0	0	0	1	24	0	0	0	0	100	100	119	142
SUBTOTAL	207	211	146	356	0	0	0	0	0	0	19	20	0	0	40	40	46	817	0	0	156	805	28070	28070	28684	30319
TOTAL	**806**	**2958**	**206**	**1103**	**27**	**27**	**19**	**19**	**0**	**0**	**19**	**20**	**0**	**0**	**40**	**40**	**46**	**817**	**0**	**0**	**157**	**817**	**28070**	**28070**	**29390**	**33871**

*Other includes members of the public who took the SMDC's docent-led tours. All daily tours in FY 2018-2019 visited the Younger Lagoon / Marine Mammal Overlook and received information about the reserve.

Table 3. Younger Lagoon Group Affiliations

University of California Campus
University of California, Berkeley
University of California, Santa Cruz
University of California, Los Angeles

California State Universities
California Polytechnic State University, San Luis Obispo
California State University, San Jose

California Community College
Cabrillo Community College

Universities outside California
University of Utah

K-12 system
Aptos High School
Half Moon Bay High School
Pajaro Valley High School
Watsonville High School

Non-governmental organizations
Bird School Project
California Academy of Sciences
California Environmental DNA
California Naturalist Program
Monterey Bay Aquarium WATCH Program
Santa Cruz Bird Club
Seymour Marine Discovery Center
Watsonville Wetlands Watch

Governmental Agencies
Army Corps of Engineers

Volunteer Groups
UCSC Wilderness Orientation
Enviroteers

Summary

FY 2018-2019 was a successful year for YLR. The reserve continued to move forward with restoration, initiated new projects, strengthened collaborations, and developed new relationships. The increase in student and course use is a direct result of having superb staff on sight that are actively engaged with students, faculty, and the public. In turn, we are able to achieve our mission of supporting education, research, and public education as well as meet the environmental stewardship obligations the University of California has committed to with the California Coastal Commission and the State of California in general. We look forward to continuing this exciting and important work in FY 2019-2020.

UCSC Natural Reserves Advisory Committee

Charge

The committee provides oversight of on- and off-campus natural reserves of instructional and research interest. It is responsible for developing program vision and policy for the management and use of the UCSC Campus Reserve and of the four UC Natural Reserves System holdings: Año Nuevo Island Reserve, Landels-Hill Big Creek Reserve, Younger Lagoon Reserve and Fort Ord Reserve. The committee coordinates with the systemwide NRS Advisory Committee that advises on policy for all NRS reserves.

In addition to the chair (Faculty Director), membership of the committee is comprised of faculty advisors to each reserve, one faculty representative at large, one non-senate academic appointment, one staff representative, one graduate student and two undergraduate students. The Faculty Director, in consultation with the Dean and the Administrative Director of the UCSC Natural Reserves, appoints the committee. Membership terms begin September 1 unless otherwise specified.

DURATION OF APPOINTMENTS

Faculty Director: 5 years

Faculty Advisors: 3 years

Non-Senate Academic, Staff, and Students: 1 year

Members may be reappointed at the discretion of the Faculty Director in consultation with the Administrative Director.

Hours/Quarter: Chair/NRS Representative-20, Members-10
Reports to: Division of Physical & Biological Sciences Dean

MEMBERSHIPS

Faculty Director of the Natural Reserve System	Don Croll Professor, Ecology & Evolutionary Biology Long Marine Lab, Center for Ocean Health (831) 459-3610 – croll@biology.ucsc.edu
Younger Lagoon Reserve Faculty Advisor	Karen Holl Professor, Environmental Studies Environmental Studies Department (831) 459-3668 – kholl@ucsc.edu

Año Nuevo Reserve Faculty Advisor	Daniel Costa Professor, Ecology & Evolutionary Biology Long Marine Lab, Center for Ocean Health (831) 459-2786 – costa@biology.ucsc.edu
UCSC Campus Reserve Faculty Advisor	Greg Gilbert Professor, Environmental Studies Environmental Studies Department (831) 459-5002 – ggilbert@ucsc.edu
Fort Ord Reserve Faculty Advisor	Laurel Fox Professor, Ecology & Evolutionary Biology Coastal Biology Building (831) 459-2533 – fox@biology.ucsc.edu
Landels-Hill Big Creek Reserve Faculty Advisor	Peter Raimondi Professor, Ecology & Evolutionary Biology Long Marine Lab, Center for Ocean Health (831) 459-5674 – raimondi@biology.ucsc.edu
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Campus Natural Reserve
Natural Sciences II, Rm 465

Joe Miller -- Field Manager
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UCMBEST
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Younger Lagoon Reserve Scientific Advisory Committee (SAC)

Charge

As outlined in the in the CLRDP, restoration, enhancement, and management activities on the Marine Science Campus will be guided by a Scientific Advisory Committee (SAC) that is made up of independent professionals and academicians experienced in and knowledgeable about the habitats of the natural areas on the Marine Science Campus. The SAC shall guide the development of Specific Resource Plans, which shall be consistent with the performance standards set forth in the Resource Management Plan (RMP), and which may be adapted periodically based on findings from ongoing restoration work. The RMP goals and performance standards may be adjusted as directed by the SAC in coordination with the Executive Director to ensure the success of Campus restoration, enhancement, and management efforts. As such, the RMP goals and performance standards are not static requirements per se so much as initial guidelines that may be refined during the SAC process so long as such refinement is consistent with current professional restoration, enhancement, and management goals and standards, and with achieving high quality open space and natural habitat area in perpetuity consistent with this CLRDP. RMP adjustments in this respect may require a CLRDP amendment, unless the Executive Director determines that an amendment is not necessary.

The committee provides guidance for the restoration, enhancement, and management efforts at YLR, and collaborates with YLR staff on the creation and implementation of the Specific Resource Plan as outlined in CLRDP Implementation Measure 3.2.10 (below).

Implementation Measure 3.2.10 – Natural Areas Habitat Management. *Within six (6) months of CLRDP certification, the University in consultation with the Executive Director of the California Coastal Commission shall convene a scientific advisory committee (SAC) to guide the restoration, enhancement, and management of natural areas (i.e., all areas outside defined development zones, except for Younger Lagoon Reserve) on the Marine Science Campus (see Appendix A). Natural areas restoration, enhancement, and management may be completed in up to three phases corresponding to dividing the natural area into thirds (i.e., where Phase 1 accounts for at least one-third of the natural area, Phase 1 plus Phase 2 accounts for at least two thirds, and all of the three phases together account for all of the natural area). All restoration, enhancement, and management activities shall be guided by Specific Resource Plans developed by the University in accordance with the SAC and the criteria contained in the Resource Management Plan (Appendix A) and current professional standards for such plans. The SAC shall be responsible for guiding development of Specific Resource Plans and shall complete its work on the Specific Resource Plan for Phase I restoration and enhancement efforts within four (4) months of convening. The content of Specific Resource Plans shall be consistent with the performance standards set forth in Appendix A, which may be adapted periodically based on findings from ongoing restoration work. The University shall file a Notice of Impending Development for Phase I work within one (1) year of CLRDP certification. All natural areas restoration and enhancement shall be completed within 20 years of CLRDP certification, with* *interim benchmarks that at least one-third of the restoration and enhancement shall be completed within seven years of CLRDP certification and that at least two-thirds shall be completed within 14 years of CLRDP certification.*

The SAC was seated in January 2009. In addition to the chair, membership of the committee is comprised of three independent professionals and academicians experienced in and knowledgeable about the habitats of the natural areas on the Marine Science Campus. Brief bios of the four SAC members are below.

Dr. Karen Holl- Professor, Environmental Studies, University of California at Santa Cruz (UCSC).

Dr. Karen Holl has been on the faculty in the Environmental Studies Department at the University of California, Santa Cruz for nearly 20 years. She has conducted research on restoration ecology in a wide variety of ecosystems, including tropical rain forests, eastern hardwood forests, chaparral, grassland, and riparian systems in California. She has published over 50 journal articles and book chapters on restoring damaged ecosystems and is on the editorial board of the journal Restoration Ecology. She teaches the Restoration Ecology class at UCSC and supervises many of the undergraduate students who work on the UCSC Natural Reserves. She regularly advises numerous public and private agencies along the Central California Coast on land management issues. She recently was selected as an Aldo Leopold Leadership Fellow. Dr. Holl's expertise in restoration ecology, experimental design and data analysis, as well as her affiliation with UCSC and her excellent rapport with University students and staff make her an irreplaceable member of the Scientific Advisory Committee.

Dr. Holl received a Ph.D. in Biology from Virginia Polytechnic Institute and State University, and a Bachelors degree in Biology from Stanford University.

Tim Hyland - Environmental Scientist, State Parks, Santa Cruz District.

Mr. Hyland has worked in the field of wildlands restoration for nearly 20 years. Much of his work has focused on coastal scrub, dune, and wetland restoration at sites throughout the Central Coast, including Wilder Ranch State Park (located approximately one mile west of YLR). He has extensive experience in restoration planning and implementation, vegetation mapping, exotic species control, and native plant propagation. In addition, Mr. Hyland is highly skilled in public education and outreach. His long tenure with California State Parks and direct experience in designing and implementing large-scale restoration projects make him a valuable member of the Scientific Advisory Committee.

Mr. Hyland has a B.A. from California Polytechnic State University, San Luis Obispo.

Bryan Largay – Conservation Director, Land Trust of Santa Cruz County.

Mr. Largay has worked in the fields of hydrology, water quality, and wetlands for fourteen years with a focus on restoration and wildlife habitat. He has conducted wetland restoration, watershed hydrology, and water quality investigations and designed measures to control erosion and treat water quality problems using vegetation. Much of his work has focused on collaborative water quality protection projects with agricultural landowners and growers. He has worked to solve water resource problems with a broad array of individuals, including scientists, planners, engineers, growers, private landowners, and contractors. Prior to joining the staff of The Land Trust of Santa Cruz County, he worked as the Tidal Wetland Project Director at Elkhorn Slough National Estuarine Research Reserve (ESSNER) and participated in the Tidal Wetland Project as a member of the Science Panel and Model Advisory Team. Mr. Largay's experience working on complex, large-scale restoration projects with agricultural neighbors in a non-profit setting make him a very important addition to the Scientific Advisory Committee.

Mr. Largay received an M.S. in Hydrologic Sciences at U.C. Davis, and a Bachelor's degree at Princeton University.

Dr. Lisa Stratton - Director of Ecosystem Management, Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara (UCSB).

Dr. Lisa Stratton has worked in the field of science-based restoration for nearly 20 years. She has extensive experience in restoration planning and implementation in conjunction with campus construction projects. Much of her work at UCSB has focused on involving students and faculty in the Cheadle Center's restoration projects. Dr. Stratton's work at the UCSB has provided her with a rare understanding of some of the unique challenges and opportunities YLR staff face as they undertake the restoration project at YLR. Her combined experience in wildlands restoration and management, scientific research, and working within the University of California system make her a very important member of the Scientific Advisory Committee.

Dr. Stratton received a Ph.D. in Botany and Ecology from the University of Hawai'i, a M.S. in Conservation Biology and Sustainable Development from the University of Wisconsin-Madison, and a Bachelors degree in Comparative Literature from Stanford University

Appendix 1. California Coastal Commission beach monitoring report

Younger Lagoon Reserve

Beach Monitoring Report

2019

***Watsonville Area Teens Conserving Habitats* (WATCH) *Program* Participants at Younger Lagoon**

Elizabeth Howard and Gage Dayton
Younger Lagoon Reserve

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Appendices

Overview and Executive Summary

In March 2010, the California Coastal Commission (Coastal Commission) approved the University of California's Notice of Impending Development Implementation for Implementation Measure 3.6.3 of the CLRDP (NOID 10-1). NOID 10-1 requires that (through supervised visits) the public have access to Younger Lagoon Reserve beach and that a monitoring program be created and implemented to document the condition of native flora and fauna within Younger Lagoon and its beach. The monitoring plan was to be implemented over a 5-year time period. At the end of the 5-year period (Winter 2015) results were to be compiled and included in a report that summarizes and discusses the potential effect of controlled beach access on flora and fauna at Younger Lagoon and submitted as a NOID to the CCC.

The campus began implementing the public access plan and monitoring program in spring 2010, and submitted the report on the results of the monitoring to the Coastal Commission in February of 2016 as part of the Younger Lagoon Reserve Annual Report. The campus submitted NOID 9 (16-2) Public Access to and Within Younger Lagoon Reserve to the Coastal Commission in December 2016. At the request of local coastal staff, the campus withdrew NOID 9 (16-2) resubmitted it as NOID 9 (17-1) in June 2017. The campus presented NOID 9 (17-1) at the July 2017 CCC and although CCC staff found the NOID consistent with the CLRDP, a Commissioner requested the University provide significantly more tours to the beach and that children be allowed for free. The campus withdrew NOID 9 (17-1), made changes to address these requests, and resubmitted it as NOID 9 (18-1) in August 2018.

On September 13, 2018, the Coastal Commission approved UC Santa Cruz's NOID 9 (18-1) as consistent with UCSC's approved Coastal Long Range Development Plan with the addition of five staff-recommended special conditions. These included 1) Free Beach Tours, 2) Beach Tour Outreach Plan, 3) Beach Tour Signs, 4) Beach Tour Availability and Monitoring, and 5) Beach Access Management Plan Duration. Within 30 days of the approval (i.e., by October 13, 2018), UCSC was required to submit a plan for implementation of the special conditions to the Executive Director of the California Coastal Commission. The plan for implementation of the special conditions was submitted to the Executive Director of the California Coastal Commission on October 15, 2018. UCSC received feedback from Coastal Commission staff on the plan, and a revised plan for implementation of the special conditions was submitted to the Executive Director of the California Coastal Commission on December 15, 2018. The revised plan for implementation of the special conditions was approved by the Executive Director on January 30, 2019. Special Condition 4 requires that at least every six months (i.e., by June 30th and December 31st each year), UCSC shall submit two copies of a Beach Tour Monitoring Report for Executive Director review and approval. Although the revised plan for implementation of the special conditions was approved by the Executive Director on January 30, 2019, UCSC began implementing some of the special conditions prior to final approval of the implementation plan. UCSC's initial report on the implementation of these special conditions for the period of January 1, 2019 through June 30, 2019 was submitted on June 28, 2019. Upon review, local Coastal Commission staff requested more detail regarding the implementation of Special Condition 2. UCSC's revised report on the implementation of the special conditions for the period of January 1, 2019 through June 30, 2019 was submitted on September 5, 2019. The report for the period of July 1, 2019 through December 31, 2019 will be submitted by December 31, 2019.

This document serves as both a summary report for activities under NOIDs 2 (10-1) and 9 (18-1) that have taken place since our previous report at the end of fiscal year 2018 and a summary report for the entire 9-year monitoring program. All year's results are included. Data collected indicate that Younger Lagoon Reserve (YLR) supports a wide variety of native flora and fauna, provides habitat for sensitive and threatened species, supports a very unique beach dune community, and is extensively used for research and education. In general, in comparison to the other local beaches surveyed native plant species richness is greatest at YLR and Natural Bridges; however, there is quite a bit of annual variation among the sites. A parameter that we quantified in 2012, and is evident from visual observation and photo documentation, is the presence of dune hummocks and downed woody material at YLR, both of which are almost entirely absent at local beaches due to human use. These features provide habitat for plant species such as the succulent plant dudleya, which grow on downed woody material and dune hummocks at YLR, as well as burrowing owls that use burrows in hummocks and seek shelter beneath downed woody material at YLR. The relatively natural state of YLR beach and dune vegetation is unique among most pocket beaches in Santa Cruz County and likely represents a glimpse into what many of the pocket beaches in the greater Monterey Bay area looked like prior to significant human disturbance. Open access to the beach would likely result in the loss of the unique ecological characteristics of the site and certainly reduce its effectiveness as a research area for scientific study. Controlled beach access through the Seymour Center docent led tours, provides an appropriate level of supervised access that enables people to see and learn about the lagoon habitat while limiting impacts to the system. We recommend that this continue.

Although only required to monitor the YLR beach, YLR staff, faculty, and the Scientific Advisory Committee decided to monitor nearby beaches with varying levels of use (Natural Bridges and Sand Plant Beach) during the first 5-year period in order to examine differences in the flora, fauna and use among the three sites. This effort required hundreds of hours of staff and student time, as well as coordination with State Parks staff. As reported in the 2015 YLR Beach Monitoring Report, beginning in the summer of 2015 and moving forward, YLR staff will continue to monitor YLR as required in IM 3.6.3; however, we will no longer monitor at Natural Bridges State Beach or Sand Plant Beach as the previous 5 years of data collection have provided us with adequate information to assess beach resources.

Introduction

Over 50 years ago, the University of California Natural Reserve System (UCNRS) began to assemble, for scientific study, a system of protected sites that would broadly represent California's rich ecological diversity. Today the UC Natural Reserve System is composed of 41 reserves that encompass approximately 750,000 acres of protected natural land available for university-level instruction, research, and public service. The University of California Natural Reserve System supports research and education through its mission of contributing "*to the understanding and wise management of the Earth and its natural systems by supporting university-level teaching, research, and public service at protected natural areas throughout California*." By creating this system of outdoor classrooms and laboratories and making it available specifically for long-term study and education, the NRS supports a variety of disciplines that require fieldwork in wildland ecosystems. UC Santa Cruz administers four UC Reserves: Younger Lagoon Natural Reserve, Año Nuevo Island Reserve, Landels-Hill Big Creek Reserve, and Fort Ord Natural Reserve.

The objective of the beach monitoring program is to document the presence and distribution of flora and fauna within Younger Lagoon Natural Reserve (YLR) and to evaluate changes in distribution and density over time. Additionally, YLR staff decided to monitor nearby beaches with varying levels of use (Natural Bridges and Sand Plant Beach) in order to examine differences in the flora and fauna among the three sites. Importantly, the data collected in this study provides a quantitative assessment of various attributes (species composition, abundance, etc.) but it is realized that the sites vary significantly from one another and that there is no replication. Thus, although these data comparisons are informative there are significant constraints that make meaningful statistical comparisons between the sites impossible. As such, results shouldn't necessarily be used to create strict prescriptions.

This report is a report for activities under NOIDs 2 (10-1) and 9 (18-1) during Fiscal Year (FY) 2018-2019 (July 1, 2018 – June 30, 2019) which surveyed YLR. In addition, although we are no longer monitoring Natural Bridges and Sand Plant beaches, we have included all year's results from all sites in this report in order to show the entire effort to date. Data for each monitoring objective have been added to previous year's data; thus, the results for this reporting period have been combined with all previous findings. As a result, this report provides a running summary of our findings starting from the inception of the study and running through the end of FY 2018-2019.

Younger Lagoon Access History

History of Public Access to Younger Lagoon Beach

Prior to 1972, Younger Beach was privately owned and closed to the public. The owners (Donald and Marion Younger) actively patrolled for, and removed, trespassers from their property, including the beach. In 1972, the Younger Family donated approximately 40 acres of their property to the University of California for the study and protection of the marine environment. These lands included Younger Lagoon and Beach (approximately 25 acres), and an adjoining parcel of land (approximately 15 acres) which became the site of the original Long Marine Laboratory (LML). At the time of their donation, Donald and Marion Younger intended that the lagoon, beach and surrounding slopes be protected in perpetuity by the University as a bird sanctuary.

In the years between the donation of the property and the start of LML construction (1976), the University leased the future LML site back to farmers who had been farming the property for the Younger family prior to the donation. During those years, the same no trespassing rules for the beach were enforced as they had been when the property was owned by the Younger family.

Once construction of LML began in 1976, the land was no longer under the watch of the farmers, and public pressure on the beach began to increase. Many Santa Cruz locals remember the next several years at Younger Beach fondly as it became a popular nude beach. The increased public access had a noticeable impact on the flora and fauna of the beach, and was not in accordance with the intention of the original donation by the Younger family. By 1978 discussions had begun between the University and the California Coastal Commission regarding the impact of uncontrolled public access to the beach. In 1981, it was decided that the impacts to Younger Beach were significant and the California Coastal Commission, under coastal permit P-1859, closed uncontrolled access to the beach.

After the approval of coastal permit P-1859, the University began to actively patrol the beach for trespass, educate the public about the closure, and use the site for research and education. After YLR was incorporated into the UCNRS in 1986, users were required to fill out applications, or contact NRS staff, for specific research, education, or outreach efforts. As the LML campus grew, a protective berm and fencing were constructed around the perimeter of the lagoon, and informational ‘beach closed’ signs were posted on the cliffs above the beach. Over time, trespass decreased and the reduced public access had a noticeable positive impact on the flora and fauna of the beach.

Public access to YLR beach came to the forefront again during the CLRDP negotiation process (2000-2008). At the time negotiations began, YLR supported a rich composition of plant and animal species despite being surrounded by agricultural and urban development. Reserve staff were concerned that any increase in public access could threaten the already heavily impacted habitat. At the time of CLRDP certification (2010), all parties agreed to the Beach Access Management Plan outlined in NOID 10-1. Under the Beach Access Management Plan, the YLR beach remains closed to unsupervised public access and the reserve is implementing a management and monitoring plan that includes docent-guided tours.

Because of the importance of maintaining a natural and pristine environment (Figure 1) and protecting scientific studies and equipment, uncontrolled access to YLR is not allowed. Uncontrolled use of YLR is likely to have a negative impact on native coastal flora and fauna that inhabit the reserve, hamper research endeavors, and impact the area for future scientific and educational endeavors. Rather than an open public access policy, users are required to fill out applications, or contact NRS staff, for specific research, education, or outreach efforts. In 2010 YLR began hosting docent-guided tours that are offered by the Seymour Marine Discovery Center (Seymour Center).

Beach Access Tours

From 2010 - 2017, docent-led beach tours were offered twice monthly through the Seymour Marine Discovery Center (Seymour Center). Starting in January 2018, tours are offered twice a month during the slower fall and winter months (October-February), and four times a month during the busier spring and summer months (March-September), for a total of 38 tours per year. From 2010-2018, these tours were offered free with admission to the Seymour Center, Starting in 2019, these tours are now offered for free. In addition, all of the docent led daily tours run by the Seymour Center (approximately 1,500 tours annually) include an informational stop about YLR that includes visual access to the beach.

The extent of the beach access area varies depending on tidal conditions and the location of plants, as foot traffic is only permitted seaward of the dune vegetation. Thus, the exact access area may vary slightly from the areas depicted in Figure 2 below and Figure 3.11 of the CLRDP. The trail provides an interpretive experience for visitors that begins with a narrative history of the UC Natural Reserve System (UCNRS), an overview of the lagoon, a walk through a restored coastal scrub habitat with opportunities to view the rear dune, and ends on the beach. Tours are led by Seymour Center docents trained in the natural history and ecology of YLR and provide detailed information about flora, fauna, geology, and the UCNRS. Tour curriculum, which was first presented to the Seymour Center docents during the regular winter docent-training program in 2010, focuses on the unique ecology of the YLR beach.

In addition to the docent-guided beach tours, visual access to the lagoon and back dune is provided to the public via Overlook E along McAllister Way. Overlook E is open to the public from dawn to dusk. Visual access to the Younger Lagoon beach and information about Younger Lagoon Reserve is also provided to all visitors taking the Seymour Center's docent-guided Reserved and Daily Tours via the Overlook C. Last year, nearly 25,000 visitors took these tours.

Public Education and Outreach Programming on the Coastal Science Campus

Seymour Marine Discovery Center

The free docent guided beach tours are part of broader public education and outreach programming on the Coastal Science Campus offered through the Seymour Center. Every year, nearly 70,000 people visit the Seymour Center, and nearly 15,000 visitors take docent-guided tours. The Seymour Center provides marine science education to hundreds of classes, comprised of thousands of students, teachers, and adult chaperones from across the country. Many of the classes served come from schools classified as Title 1—schools with high numbers of students from low-income families. Scholarships are made available to Title 1 schools, making it possible for students to participate who would not otherwise have the opportunity to experience a marine research center. Teachers often incorporate the Seymour Center into their weeklong marine science field study courses.

Every year, dozens of children ages 7-14, enroll in weeklong summer science sessions known as Ocean Explorers. Students actively learn about and participate in marine research at the Seymour Center and Long Marine Laboratory, where participants work alongside marine mammal researchers and trainers. Participants gain experience with the scientific process, focusing on honing their observation and questioning skills. Ocean Explorers also investigate the coastal environment at field sites around Monterey Bay, including rivers and watersheds, sandy beaches, rocky intertidal areas, and kelp forests by kayak. Young participants generally come from Santa Cruz, Santa Clara, and San Mateo Counties. Full and partial scholarships are extended to low-income participants.

While part of UC Santa Cruz, the Seymour Center must raise its ~$1.5 million budget annually (including all operating costs, salaries, and benefits) from earned revenue, private donors and grants. Earned revenue—admissions, program fees, facility rentals, and the Ocean Discovery Shop—makes up approximately half of its general operating requirements.

The Seymour Center actively promotes its activities with press releases and calendar listings throughout the region. Every year, traditional print ads are placed in newspaper and magazines. The Seymour Center's activities are also often covered in the local newspaper, the Santa Cruz Sentinel. Public radio ads run throughout the year on the NPR-affiliate, KAZU.

Coupons for discounted admissions are available in various formats. The most highly used program is through the many Bay Area municipal libraries. Called Discover and Go, hundreds of families from across the region utilize these discount coupons. The Seymour Center continued to connect with the public through Facebook, Twitter, Instagram, Pinterest, Flickr, and bi-monthly e-blasts.

Watsonville Area Teens Conserving Habitat (WATCH)

Last year, the Seymour Center, Younger Lagoon Reserve and the Monterey Bay Aquarium again partnered to support high school students in the Watsonville Area Teens Conserving Habitats (WATCH) program. WATCH students from Aptos High School design and carry out field-based research projects in Younger Lagoon Reserve on topics including endangered fish, aquatic invertebrates, and birds. These students make repeated visits to the Reserve throughout the year. Find out more at: https://www.montereybayaquarium.org/education/teen-programs/watsonville-area-teens-conserving-habitats-watch

Community Bioblitz

Last year, Younger Lagoon Reserve and the California Academy of Sciences again partnered to host an annual Younger Lagoon Reserve Bioblitz. A bioblitz is a community event that brings together a wide variety of people – citizen scientists - to rapidly inventory the living organisms found in a particular place. The Younger Lagoon Reserve Bioblitz is held during the spring, and is open to members of the public. Participants explored the lagoon and beach areas as part of this event. A link to the page advertising this community event can be found here: https://www.inaturalist.org/projects/younger-lagoon-reserve-bioblitz-2019

Volunteer Stewardship Days

Last year, Younger Lagoon Reserve hosted numerous volunteer stewardship days. These events are advertised on social media and open to the public. Volunteer stewardship days provide members of the public with the opportunity to learn about the reserve and its unique habitats, wildlife, research, restoration, and teaching programs while giving back.

Figure 1. Burrowing owl on the beach at Younger Lagoon.

Study Areas

Flora, fauna, and human use were monitored at Natural Bridges State Park, Younger Lagoon Reserve, and Little Wilder/Sand Plant Beach from 2010-2015 (Figure 2). These three sites have similar characteristics (all have beach and lagoon habitat), are within close proximity to one another, and experience varying levels of human use. Although site characteristics are similar in many ways, they are also different in many ways, and these differences likely influence species composition. Three of the primary differences among the sites are human use levels, composition of adjacent upland habitat, and the overall size of the beach and wetland areas. Starting in FY 2015-2016 and moving forward, only Younger Lagoon Reserve has been and will continue to be monitored.

Younger Lagoon Reserve

Younger Lagoon Reserve is located in Santa Cruz County, approximately 4.5 miles from the main UC Santa Cruz campus; adjacent to the UC Santa Cruz Long Marine Laboratory. One of the few relatively undisturbed wetlands remaining on the California Central Coast, Younger Lagoon Reserve encompasses a remnant Y-shaped lagoon on the open coast just north of Monterey Bay. For most of the year, the lagoon is cut off from the ocean by a sand barrier. During the winter and spring months, the sand barrier at the mouth of Younger Lagoon breaches briefly connecting the lagoon to the ocean. The lagoon system provides protected habitat for 100 resident and migratory bird species. Approximately 25 species of water and land birds breed at the reserve, while more than 60 migratory bird species overwinter or stop to rest and feed. Opossums, weasels, brush rabbits, ground squirrels, deer mice, coyote, bobcat, woodrat, raccoon, and skunk are known to occupy the lagoon; gray and red foxes as well as mountain lion have also been sighted. Several species or reptiles and amphibians, including the California Red-legged Frog, also are found in the Reserve. Reserve habitats include salt and freshwater marsh, backdune pickleweed areas, steep bluffs with dense coastal scrub, pocket sand beach, grassland, and dense willow thickets.

Sand Plant Beach ("Little Wilder")

Sand Plant Beach is located in Santa Cruz County, approximately 1.5 miles west of YLR adjacent to Wilder Ranch State Park. Sand Plant Beach is approximately 23 acres and includes a pocket beach, dunes, cliffs and lagoon. It is open to the public for recreational use from dawn until dusk, 365 days a year; however, requires a hike to get to it and thus experiences less human use than many of the more accessible beaches in Santa Cruz. The surrounding Wilder Ranch State Park covers approximately 7,000 acres and allows human, bike and equestrian access. Much of the interior lagoon/upland habitat has been modified for agricultural production and/or ranching over the past century. Today most of the vegetation that persists inland of the lagoon is dominated by freshwater emergent vegetation and willow thickets. Major wetland restoration projects have increased native flora and fauna in the area (Friends of Santa Cruz State Parks, 2010).

Natural Bridges Lagoon

Natural Bridges Lagoon is located in Santa Cruz County, approximately 0.5 miles east of YLR on the urban edge of the city of Santa Cruz CA in Natural Bridges State Park. Natural Bridges Lagoon, beach, and State Park encompasses approximately 63 acres and includes a wide pocket beach, lagoon, cliffs, and diverse upland habitat (scrub, grass, iceplant, willow thicket, live oak, eucalyptus, and cypress). The park is world-renowned for its yearly migration of monarch butterflies and famous natural bridge. Natural Bridges State Park allows human access as well as dogs that are on leash and remain on paved roads and in parking lots (Friends of Santa Cruz State Parks, 2010). The beach is a popular destination at all times of the year; however, it is especially popular in the spring, summer, and fall months.

Figure 2. Study Areas.

Methods

User Data

User data from tours conducted by the Seymour Center, as well as research and education use of YLR, were recorded and maintained by Seymour Center and YLR Staff. User data from educational programs and fee collection are recorded and maintained by California State Parks staff for Natural Bridges State Parks. No user data was available for Sand Plant Beach.

Human Beach Use

We used remote cameras to quantify human use quarterly througout the study peroiod. Cameras were placed along the eastern edge of Sand Plant Beach and Natural Bridges Beach from FY 2010-2011 – FY 2014-2015 and at the western edge of Younger Lagoon from FY 2010-2011 – present with each separate quarterly sampling events each consisting of two days. Cameras were set to automatically take photos at 15 minute intervals. Number of people were quantified for 15 minute intervals during the day (camera times varied across sampling periods due to day length and postion; however, were standardized within each sampling period). The total survey area varied between sites and among individual sampling efforts due the placement of the camera and available habitat for human users at the time of the survey (i.e. often less beach area surveyed at Sand Plant Beach compared to Younger Lagoon and Natural Bridges). In order to control for area, specific regions of photos were chosen and number of individuals within each region were counted; thus, the number of people counted per unit area and time was standardized. We used the largest survey area during each sampling period to standardize use within each specific region of the beach during each sampling effort. Thus, if a particular site had more or less habitat monitored, the number of individuals was standardized across sites making comparisons comparable.

Photo Documentation of Younger Lagoon Natural Reserve

Photo point locations were established at four locations within YLR (Figure 3). These locations were chosen to ensure coverage of all major areas of the beach. Photos were taken once during the reporting period. At each photo point we collected photo point number, date, name of photographer, bearing, and camera and lens size.

Tidewater Goby Surveys

Tidewater goby surveys were conducted quarterly throughout the study period. Surveys were conducted using a 4.5 ft x 9 ft beach seine with 1/8 inch mesh. The objectives of the surveys were to document tidewater goby presence and evidence of breeding activity (determined by the presence of multiple size/age classes). All fish were identified to species and counted. When individuals exceeded ~50 per seine haul, counts were estimated. Sampling was conducted with the goal of surveying the various habitats within each site (e.g. sand, sedge, willow, pickleweed, deep, shallow, etc.); thus, different numbers of seine hauls were conducted at each site. Species richness was compared among sites.

Figure 3. Locations of monitoring points, plots, and regions for YLR beach. Monitoring areas varied between sampling efforts depending upon the high water mark, vegetation patterns, and water levels.

Species Composition and Coverage of Beach Dune Vegetation

Dune vegetation from the lowest (nearest to the mean high tide line) occurring terrestrial plant to 10 meters inland into the strand vegetation was surveyed quarterly throughout the study period. The exact location and extent of the area surveyed each time varied depending upon the location of the "lowest" plant detected during each sampling effort. At each location we established a 50-m east-west transect across the dune vegetation and measured the distance from the estimated mean high tide line to the "lowest" plant on the beach. Herbaceous species composition was measured by visual estimation of absolute cover for each species in ten 0.25 m^2 quadrats along the transect. Quadrats were placed every 5 m on alternating sides of the transect starting at a randomly selected point between 1 and 5 meters (a total of 10 quadrats per transect). A clear plastic card with squares representing 1, 5, and 10% of the sampling frame was used to help guide visual cover estimations. Species cover (native and exotic), bare ground, and litter were estimated at 5% intervals. Litter was specifically defined as residue from previous year's growth while any senescent material that was recognizable as growth from earlier in the current growing season was counted as cover for that species. After all cover estimates had been made, we conducted surveys within 2 m of either side of the transect (a 4 × 50 m belt). In the belt transects, individual plants were recorded as either seedlings or greater than 1 year old. Presence of flowers and seeds was also noted.

Non-avian Vertebrate Monitoring

Tracks

Vertebrate tracks were measured using raked sand plots at each site quarterly throughout the study period. Tracking stations were placed throughout the beach area in constriction zones where vegetation was absent. The objective of these surveys was simply to detect what species use the beach habitat. As such, size of plot varied from approximately depending upon the amount of available open sandy area at each location. Track stations were raked each evening and checked for tracks in the morning. Stations remained open for two days during each monitoring bout. Tracks were identified to species when possible. Species composition was summarized; however, abundance was not quantified due to the fact that most often tracks cannot be used to identify individual animals (e.g. a single individual could walk across the plot multiple times).

Small Mammals

Sherman live traps were placed for two nights every quarter of the study period - a total of 30 traps were placed used (60 trap nights per sampling bout). Traps were set at dusk and collected at dawn. Each trap was baited with rolled oats and piece of synthetic bedding material was placed in each trap to ensure animals did not get too cold. Individuals were identified to species, marked with a unique ear tag, and released at the site of capture.

Invertebrate Monitoring

Terrestrial invertebrates on beach habitat were monitored by placing 12 oz plastic containers (pit fall traps) at each tracking station (one at each corner of the plot) during tracking efforts. Traps were buried to the lip of the container and checked each morning and all individuals were collected, identified, and counted.

Avian Monitoring

We conducted ocular surveys of birds on the beach, lagoon, and cliff habitats quarterly throughout the study period. Survey locations were selected along one edge of the beach on the cliff. At Sand Plant Beach the entire beach area, fore portion of the lagoon, and western cliff were surveyed from the eastern edge of the lagoon (FY 2010-2011 – FY 2014-2015). At YLR the entire beach area, fore portion of the lagoon, and western cliff were surveyed from the eastern edge of the lagoon and the top and western face of the rock stack that is located at the beach/ocean edge was surveyed (FY 2010-2011 – present). At Natural Bridges surveys were conducted from the eastern edge of the beach on the cliff adjacent to De Anza Mobile Home Park or from the beach to the west; fore lagoon and approximately the western ¼ of the beach area (including beach/ocean interface) was included in the survey area (FY 2010-2011 – FY 2014-2015). Survey areas were chosen with the goal of surveying approximately the same area and types of habitat. Counts were recorded quarterly throughout the study. Surveys were conducted in the dawn or dusk hours within approximately 2 hours of sunrise or sunset and of one another. Data from the two days during each sampling effort were combined and individuals were identified and counted.

Results

User Data

Younger Lagoon Reserve

There were a wide variety of public and non-profit research and educational groups that used Younger Lagoon (Table 1). The greatest user group for YLR was undergraduate education, a breakdown of all user groups is included in Table 2. The greatest user group was “other” which consists primarily of public tour groups attending daily tours at the Seymour Center. Those users were provided an overlook of the beach, interpretive information via docent led tours, and opportunities to read interpretive material presented on signs about the reserve; however, did not access the beach. During the 18-19 fiscal year a total of 222 participants went on the free Seymour Center docent led Younger Lagoon beach tours, an increase of more than 10% over the previous year. Since the start of the Seymour Center docent led beach access tours, 203 tours have gone out and more than 1,038 visitors have participated. The beach access tours are part of a broad offering of public outreach and education programming on the Coastal Science Campus managed by the Seymour Center, including K-12 school visits to the Seymour Center, the Ocean Explorers Summer Camp, Bay Area Libraries Discover and Go Program, as well as print, web, social media, and radio campaigns.

Despite ongoing staff efforts towards public outreach and education, some unauthorized uses of Younger Lagoon Reserve, including trespass and vandalism occurred in FY 2018-2019. Thus far, no significant damage to ecologically sensitive habitat areas, research sites, research equipment, or facilities has occurred. Reserve staff will continue their public outreach and education efforts, and continue to partner with UCSC campus police to ensure the security of the reserve and protect sensitive resources and ongoing research.

Table 1. Younger Lagoon user affiliations.

University of California Campus
University of California, Berkeley
University of California, Santa Cruz
University of California, Los Angeles

California State Universities
California Polytechnic State University, San Luis Obispo
California State University, San Jose

California Community College
Cabrillo Community College

Universities outside California
University of Utah

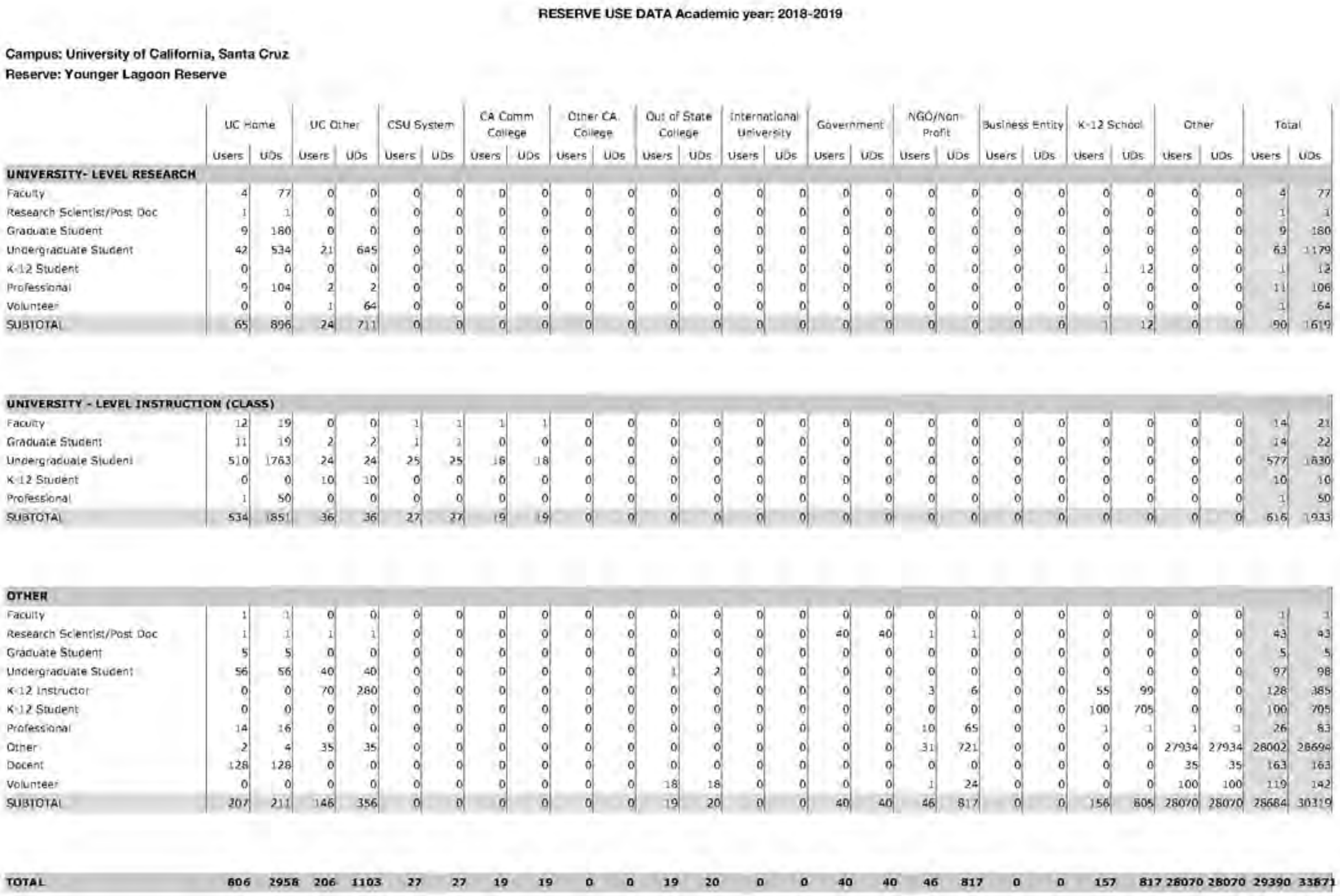
K-12 system
Aptos High School
Half Moon Bay High School
Pajaro Valley High School
Watsonville High School

Non-governmental organizations
Bird School Project
California Academy of Sciences
California Environmental DNA
California Naturalist Program
Monterey Bay Aquarium WATCH Program
Santa Cruz Bird Club
Seymour Marine Discovery Center
Watsonville Wetlands Watch

Governmental Agencies
Army Corps of Engineers

Volunteer Groups
UCSC Wilderness Orientation
Enviroteers

Table 2. Younger Lagoon Total Use.



RESERVE USE DATA Academic year: 2018-2019

Campus: University of California, Santa Cruz
Reserve: Younger Lagoon Reserve

	UC Home		UC Other		CSU System		CA Comm College		Other CA College		Out of State College		International University		Government		NGO/Non-Profit		Business Entity		K-12 School		Other		Total	
	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs	Users	UDs
UNIVERSITY- LEVEL RESEARCH																										
Faculty	4	77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	77
Research Scientist/Post Doc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Graduate Student	9	180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	180
Undergraduate Student	42	534	21	645	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	63	1179
K-12 Student	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	0	1	12
Professional	9	104	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	106
Volunteer	0	0	1	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	64
SUBTOTAL	65	896	24	711	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	0	90	1619
UNIVERSITY - LEVEL INSTRUCTION (CLASS)																										
Faculty	12	19	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	21
Graduate Student	11	19	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	22
Undergraduate Student	510	1763	24	24	25	25	18	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	577	1830
K-12 Student	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10
Professional	1	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	50
SUBTOTAL	534	1851	36	36	27	27	19	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	616	1933
OTHER																										
Faculty	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Research Scientist/Post Doc	1	1	1	1	0	0	0	0	0	0	0	0	0	0	40	40	1	1	0	0	0	0	0	0	43	43
Graduate Student	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
Undergraduate Student	56	56	40	40	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	97	98
K-12 Instructor	0	0	70	280	0	0	0	0	0	0	0	0	0	0	0	0	3	6	0	0	55	99	0	0	128	385
K-12 Student	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	705	0	0	100	705
Professional	14	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	65	0	0	1	1	1	1	26	83
Other	2	4	35	35	0	0	0	0	0	0	0	0	0	0	0	0	31	721	0	0	0	0	27934	27934	28002	28694
Docent	128	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	35	163	163
Volunteer	0	0	0	0	0	0	0	0	0	0	18	18	0	0	0	0	1	24	0	0	0	0	100	100	119	142
SUBTOTAL	207	211	146	356	0	0	0	0	0	0	19	20	0	0	40	40	46	817	0	0	156	805	28070	28070	28684	30319
TOTAL	**806**	**2958**	**206**	**1103**	**27**	**27**	**19**	**19**	**0**	**0**	**19**	**20**	**0**	**0**	**40**	**40**	**46**	**817**	**0**	**0**	**157**	**817**	**28070**	**28070**	**29390**	**33871**

*Other includes members of the public who took the SMDC's docent-led tours. All daily tours in FY 2018-2019 visited the Younger Lagoon / Marine Mammal Overlook and received information about the reserve.

Sand Plant Beach (Little Wilder)

Sand Plant Beach is located adjacent to Wilder State Park and is frequented by Wilder State Park visitors along a coastal bluff trail. Because of the size of Wilder Ranch State Park (over 7,000 acres, with over 35 miles of trails) and its multiple points of access, it is unknown exactly how many people visit Sand Plant Beach each year. However, even though it requires a hike it is one of the more popular beaches along this section of Wilder Ranch as there is relatively easy access along the coastal bluff trail. We surveyed Sand Plant Beach from FY10-11 – FY14-15.

Natural Bridges Lagoon

We did not obtain user data for Natural Reserves during the survey period; however, more than 925,000 people are estimated to have visited Natural Bridges State Park in 2005 (Santa Cruz State Parks 2010). The proportion of those visitors that use the beach and lagoon habitat is unknown. It is likely that the number of visitors remains in this range from year to year. We surveyed Natural Bridges Lagoon from FY10-11 – FY14-15.

Human Use During Survey Efforts

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Number of users at YLR beach during the survey efforts varied among beach as well as between sampling dates. However, the pattern of total use and the number of people per photo (15 minute interval standardized for area surveyed) was consistent across sampling periods (Table 3). Examples of photos captured during a typical monitoring session in 2010 are included as Figure 4.

Table 3. Number of people observed in photo human use monitoring.

Site	Month	[1]Total # of people	[1]Ave # of People / 15 minute
Natural Bridges	May, 2010	313	3.13
Sand Plant	May, 2010	92	1.21
Younger Lagoon	May, 2010	2	0.28
Natural Bridges	August, 2010	224	2.69
Sand Plant	August, 2010	15	0.17
Younger Lagoon	August, 2010	0	0
Natural Bridges	November, 2010	207	2.07
Sand Plant	November, 2010	7	0.17
Younger Lagoon	November, 2010	1	0.02
Natural Bridges	February, 2011	185	2.64
Sand Plant	February, 2011	10	0.25
Younger Lagoon	February, 2011	2	0.06

Site	Month	[1]Total # of people	[1]Ave # of People / 15 minute
Natural Bridges	May, 2011	236	2.8
Sand Plant	May, 2011	13	0.38
Younger Lagoon	May, 2011	5	0.18
Natural Bridges	July, 2011	795	2.44
Sand Plant	July, 2011	7	0.25
Younger Lagoon	July, 2011	0	0
Natural Bridges	December, 2011	49	0.63
Sand Plant	December, 2011	39	1.16
Younger Lagoon	December, 2011	0	0
Natural Bridges	April, 2012	442	6.93
Sand Plant	April, 2012	120	2.05
Younger Lagoon	April, 2012	0	0
Natural Bridges	May, 2012	624	2.67
Sand Plant	May, 2012	14	0.19
Younger Lagoon	May, 2012	0	0
Natural Bridges	October, 2012	210	4.84
Sand Plant	October, 2012	83	1.06
Younger Lagoon	October, 2012	3	0.04
Natural Bridges	January, 2013	100	4.90
Sand Plant	January, 2013	24	0.81
Younger Lagoon	January, 2013	9	0.11
Natural Bridges	May, 2013	615	19.81
Sand Plant	May, 2013	21	0.52
Younger Lagoon	May, 2013	0	0
Natural Bridges	July, 2013	560	25.42
Sand Plant	July, 2013	29	0.96
Younger Lagoon	July, 2013	5	0.06
Natural Bridges	November, 2013	3.44	13.04
Sand Plant	November, 2013	6	0.19
Younger Lagoon	November, 2013	12	0.15
Natural Bridges	February, 2014	71	6.37
Sand Plant	February, 2014	6	0.20
Younger Lagoon	February, 2014	1	0.01

Site	Month	[1]Total # of people	[1]Ave # of People / 15 minute
Natural Bridges	June, 2014	1723	21.01
Sand Plant	June, 2014	239	2.92
Younger Lagoon	June, 2014	2	0.02
Natural Bridges	August, 2014	852	23.68
Sand Plant	August, 2014	227	2.52
Younger Lagoon	August, 2014	2	0.02
Natural Bridges	November, 2014	2131	21.69
Sand Plant	November, 2014	146	1.78
Younger Lagoon	November, 2014	2	0.02
Natural Bridges	January, 2015	1889	23.04
Sand Plant	January, 2015	225	2.75
Younger Lagoon	January, 2015	11	0.13
Natural Bridges	April, 2015	699	7.13
Sand Plant	April, 2015	-	-
Younger Lagoon	April, 2015	0	0
Younger Lagoon	July, 2015	6	0.02
Younger Lagoon	October, 2015	0	0
Younger Lagoon	February, 2016	0	0
Younger Lagoon	May, 2016	1	0.02
Younger Lagoon	July, 2016	0	0
Younger Lagoon	November, 2016	0	0
Younger Lagoon	February, 2017	0	0
Younger Lagoon	April, 2017	0	0
Younger Lagoon	August, 2017	19	0.16
Younger Lagoon	October, 2017	6	0.05
Younger Lagoon	February, 2018	0	0
Younger Lagoon	May, 2018	27	0.22
Younger Lagoon	July, 2018	11	0.09
Younger Lagoon	November, 2018	14	0.15
Younger Lagoon	February, 2019	62	0.65
Younger Lagoon	May, 2019	0	0

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[1] Standardized by area surveyed.

Figure 4. Photos captured by remote camera during the Spring 2010 monitoring effort. Top to bottom: Sand Plant Beach, Natural Bridges, and Younger Lagoon.

Photo Documentation of YLR

Photos were taken one time during each reporting period. Photos for this year's report are included as Appendix 1.

Tidewater Goby Surveys

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Evidence of breeding (multiple size classes) continued to be observed at YLR during the reporting period (Table 4).

Table 4. Fish species encountered during sampling efforts.

	Tidewater Goby	**Stickleback**	**Sculpin**	**Mosquito Fish**	**Halibut**	**CRLF[1]**	**Bluegill**
April 9, 2010							
Little Wilder	X	X					
Younger Lagoon	X	X					
Natural Bridges	X	X	X				
August 13, 2010							
Little Wilder	X	X					
Younger Lagoon	X	X					
Natural Bridges	X	X	X	X			
November 18, 2010							
Little Wilder	X	X					
Younger Lagoon	X						
Natural Bridges	X	X	X	X			
February 23, 2011							
Little Wilder	X	X					
Younger Lagoon	X						
Natural Bridges	X	X	X	X			
May 12, 2011							
Little Wilder	X	X					
Younger Lagoon	X	X	X		X		
Natural Bridges	X	X	X				
August 8, 2011							
Little Wilder	X	X					
Younger Lagoon	X	X					
Natural Bridges	X	X					
December 12, 2011							
Little Wilder	X	X					
Younger Lagoon	X						
Natural Bridges	X	X					
March 8, 2012							
Little Wilder	X	X					
Younger Lagoon	X						
Natural Bridges	X	X					
May 15, 2012							
Little Wilder	X	X					
Younger Lagoon	X	X					
Natural Bridges	X	X	X				
August 29, 2012							
Little Wilder	X	X				X	

Younger Lagoon	X	X		X
Natural Bridges	X	X		
October 23, 2012				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X	X		
February 2, 2013				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X	X		
May 6, 2013				
Little Wilder	X	X		X
Younger Lagoon	X	X		X
Natural Bridges	X	X		
July 16, 2013				
Little Wilder	X	X		X
Younger Lagoon	X	X		
Natural Bridges	X	X	X	
November 14, 2013				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges				
February 21, 2014				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X			
May 2, 2014				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X			
August 11, 2014				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X	X		
November 25, 2014				
Little Wilder	X	X		
Younger Lagoon	X	X		
Natural Bridges	X	X		
January 26, 2015				
Little Wilder	X	X		
Younger Lagoon	X	X		

Natural Bridges	X		
April 13, 2015			
Little Wilder	X	X	
Younger Lagoon	X	X	
Natural Bridges	X	X	X
July 8, 2015			
Younger Lagoon	X	X	
November 4, 2015			
Younger Lagoon	X	X	
February 9, 2016			
Younger Lagoon	X	X	
May 13, 2016			
Younger Lagoon	X	X	
July 20, 2016			
Younger Lagoon	X	X	
November 17, 2016			
Younger Lagoon	X	X	
March 1, 2017			
Younger Lagoon			
May 3, 2017			
Younger Lagoon	X	X	
August 9, 2017			
Younger Lagoon	X	X	
November 9, 2017			
Younger Lagoon	X	X	
February 9, 2018			
Younger Lagoon	X	X	
May 2, 2018			
Younger Lagoon	X	X	
July 16, 2018			
Younger Lagoon	X	X	
November 18, 2018			
Younger Lagoon	X		
February 21, 2019			
Younger Lagoon			

May 14, 2019							
Younger Lagoon	X	X				X	
No. of sites	3	3	2	2	1	2	1

[1] CRLF = California Red-legged Frog (*Rana draytonii*). Tadpoles have been observed at Little Wilder. Tadpoles, juveniles, young of year, and adults have been observed at YLR and Little Wilder.

Species Composition and Coverage of Beach Dune Vegetation

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Evidence of reproduction (flowers, seeds, and seedlings) of native and non-native vegetation has been detected at all three sites. Distance from mean high tide to the lowest plant on the beach was consistently greatest at Natural Bridges and lowest at Sand Plant Beach and Younger Lagoon (Table 5). Plant cover was generally higher at Sand Plant and Younger Lagoon (as exhibited by proportion of bare ground) but varied across sampling efforts (Figure 5).

Native plant species richness was consistently greatest at Younger Lagoon; however, it varied across sampling periods (Figure 6). Mean proportion of non-native species was greatest at Natural Bridges (69%) and least at Younger Lagoon (33%) (Table 6).

Table 5. Distance (m) from mean high tide to the lowest plant on the beach.

Site	**Spring, 10**	**Summer, 10**	**Fall, 10**	**Winter, 11**	**Spring, 11**	**Summer, 11**	**Fall, 11**	**Winter, 12**	**Spring, 12**
Younger Lagoon	56	51	20	42	55	49	26	30	28
Sand Plant Beach	33	34	56	56	40	51	29	31	38
Natural Bridges	128	130	141	146	146	138	155	160	123

Site	**Summer, 12**	**Fall, 12**	**Winter, 13**	**Spring, 13**	**Summer, 13**	**Fall, 13**	**Winter, 14**	**Spring, 14**
Younger Lagoon	47	20	30	36	37.3	32.1	26.4	36.5
Sand Plant Beach	35	38	31	41	48.1	49.9	45.6	24.2
Natural Bridges	91	75	100	72	88.9	107.3	87.4	83.2

Site	**Summer, 14**	**Fall, 14**	**Winter, 15**	**Spring, 15**	**Summer, 15**	**Fall, 15**	**Winter, 16**	**Spring, 16**
Younger Lagoon	21.4	10	26.4	19.5	19.3	20.5	31.4	42.8
Sand Plant Beach	27.5	31	24.5	29.2				
Natural Bridges	74.3	89.4	71	75.8				

Site	**Summer, 16**	**Fall, 16**	**Winter, 17**	**Spring, 17**	**Summer, 17**	**Fall, 17**	**Winter, 18**	**Spring, 18**
Younger Lagoon	36.6	46.3	19.5	37.3	22.3	39.3	32	29

Site	**Summer, 18**	**Fall, 18**	**Winter, 19**	**Spring, 19**
Younger Lagoon	28	22	23	24.7

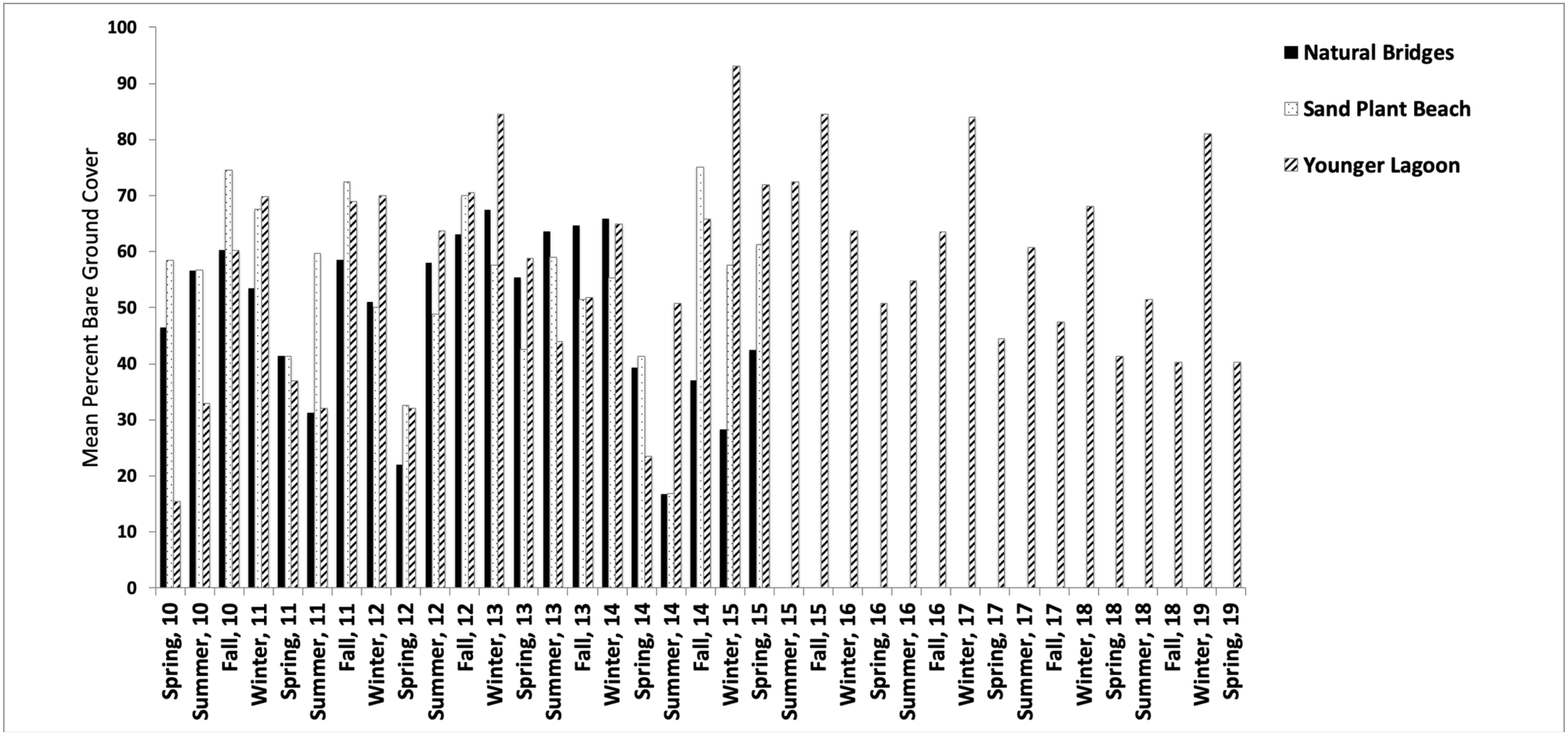


Figure 5. Mean percent bare ground encountered at each site.

Table 6. Number and proportion of native and non-native plant species encountered during surveys. Mean is calculated across all samples.

Site	Spring, 10	Summer, 10	Fall, 10	Winter, 11	Spring, 11	Summer, 11	Fall, 11	Winter, 12	Spring, 12
Natural Bridges									
Native	7 (41%)	8 (44%)	9 (60%)	8 (44%)	9 (43%)	6 (67%)	8 (62%)	9 (47%)	11 (48%)
Non-native	10 (59%)	10 (56%)	5 (40%)	10 (66%)	12 (57%)	9 (33%)	5 (38%)	10 (53%)	12 (52%)
Total	17	18	14	18	21	15	13	19	23
Younger Lagoon									
Native	11 (85%)	11 (85%)	11 (85%)	11 (73%)	12 (80%)	13 (81%)	9 (82%)	6 (50%)	6 (43%)
Non-native	2 (15%)	2 (15%)	2 (15%)	4 (27%)	3 (20%)	3 (19%)	2 (18%)	6 (50%)	8 (57%)
Total	13	13	13	15	15	16	11	12	14
Sand Plant Beach									
Native	7 (88%)	7 (63%)	7 (70%)	8 (80%)	7 (88%)	7 (88%)	9 (82%)	3 (33%)	4 (40%)
Non-native	1 (12%)	2 (37%)	3 (30%)	2 (20%)	1 (12%)	1 (12%)	2 (18%)	6 (67%)	6 (60%)
Total	8	9	10	10	8	8	11	9	10

Site	Summer, 12	Fall, 12	Winter, 13	Spring, 13	Summer, 13	Fall, 13	Winter, 14	Spring, 14
Natural Bridges								
Native	5 (35%)	10 (59%)	7 (88%)	9 (56%)	7 (37%)	6 (35%)	6 (43%)	10 (50%)
Non-native	9 (65%)	7 (41%)	8 (12%)	6 (44%)	12 (63%)	11 (65%)	8 (57%)	10 (50%)
Total	14	17	15	16	19	17	14	20
Younger Lagoon								
Native	12 (67%)	7 (88%)	9 (69%)	12 (75%)	13 (72%)	14 (74%)	10 (83%)	12 (67%)
Non-native	6 (33%)	1 (12%)	4 (31%)	4 (25%)	5 (28%)	5 (26%)	2 (17%)	6 (33%)
Total	18	8	13	16	18	19	12	18
Sand Plant Beach								
Native	2 (40%)	3 (50%)	4 (100%)	4 (67%)	6 (100%)	6 (100%)	5 (100%)	5 (83%)
Non-native	3 (60%)	3 (50%)	0 (0%)	2 (33%)	0 (0%)	0 (0%)	0 (0%)	1 (17%)

Total	5	6	4	6	6	6	5	6

Site	Summer, 14	Fall, 14	Winter, 15	Spring, 15	Summer, 15	Fall, 15	Winter, 16	Spring 16
Natural Bridges								
Native	5 (42%)	5 (45%)	4 (33%)	5 (31%)				
Non-native	7 (58%)	6 (55%)	8 (67%)	11 (69%)				
Total	12	11	12	16				
Younger Lagoon								
Native	9 (69%)	5 (62%	10 (67%)	10 (67%)	11 (73%)	2 (67%)	5 (100%)	10 (83%)
Non-native	4 (31%)	3 (38%)	5 (33%)	5 (33%)	4 (27%)	1 (33%)	0 (0%)	2 (17%)
Total	13	8	15	15	15	3	5	12
Sand Plant Beach								
Native	4 (50%)	4 (40%)	5 (50%)	4 (33%)				
Non-native	4 (50%)	6 (60%)	5 (50%	8 (67%)				
Total	8	10	10	12				

Site	Summer, 16	Fall, 16	Winter, 17	Spring, 17	Summer, 17	Fall, 17	Winter, 18	Spring, 18
Younger Lagoon								
Native	10 (83%)	8 (57%)	3 (60%)	13 (68%)	12 (70%)	13 (76%)	12 (70%)	9 (82%)
Non-native	2 (17%)	6 (43%)	2 (40%)	6 (32%)	5 (30%)	4 (24%)	5 (30%)	2 (18%)
Total	12	14	5	19	17	17	17	11

Site	Summer, 18	Fall, 18	Winter, 19	Spring, 19
Younger Lagoon				
Native	9 (82%)	8 (57%)	8 (57%)	9 (67%)
Non-native	2 (18%)	2 (43%)	2 (43%)	3 (33%)
Total	11	10	10	12

Site	Proportion of native and non-native species across all sample periods
Natural Bridges	

Native	**47%**
Non-native	**53%**
Total	
Younger Lagoon	
Native	**74%**
Non-native	**26%**
Total	
Sand Plant Beach	
Native	**68%**
Non-native	**31%**
Total	

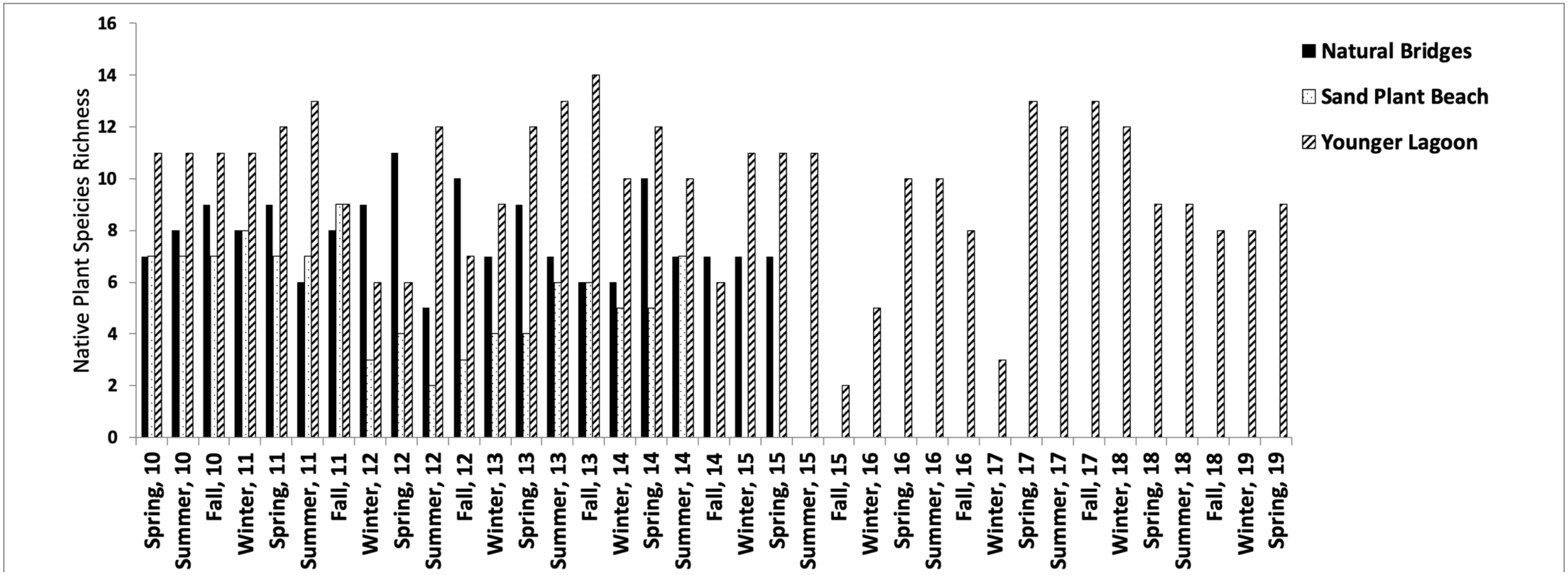


Figure 6. Number of native plant species encountered at each site.

Track Plate Monitoring

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Native species richness of mammals detected in raked sand plots was across all three sites (n = 8). Ground squirrel were not detected at Natural Bridges and opossum have not been detected in our track surveys at Sand Plant Beach or Younger Lagoon Reserve (Table 7). It is likely that ground squirrels occur at Natural Bridges and opossum are likely using upland habitat at Sand Plant Beach and Younger Lagoon Reserve; however, they were not detected in our survey efforts. Dogs and bicycles were detected at Natural Bridges and Sand Plant Beach and vehicles were detected at Natural Bridges (Table 7). Frequency of detection and species richness for each species is summarized in Table 8.

Table 7. Summary of track plate sampling effort at each site.

	Rodent^1	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**
May 1-2, 2010													
Little Wilder	X			X	X	X			X	X			X
Younger Lagoon	X	X		X	X								X
Natural Bridges	X	X		X	X				X	X	X	X	X
August 11-12, 2010													
Little Wilder		X		X	X							X	X
Younger Lagoon	X	X	X	X		X							
Natural Bridges	X	X	X									X	X
November 17-18, 2010													
Little Wilder	X		X	X					X				X
Younger Lagoon	X	X											X
Natural Bridges	X	X		X							X	X	X
February 8 -9, 2011													
Little Wilder	X			X	X				X	X			X
Younger Lagoon	X	X			X				X				
Natural Bridges		X		X					X		X		X
May 3 - 4, 2011													
Little Wilder	X		X	X									

	Rodent[1]	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**
Younger Lagoon		X	X	X	X				X				
Natural Bridges		X			X				X			X	X
July 22 - 23, 2011													
Little Wilder	X	X			X				X				X
Younger Lagoon	X	X	X	X	X								
Natural Bridges	X	X	X		X							X	X
March 8 - 9, 2012													
Little Wilder	X								X				X
Younger Lagoon				X					X				
Natural Bridges							X				X	X	X
May 15 - 16, 2012													
Little Wilder	X		X	X									X
Younger Lagoon	X	X		X					X				
Natural Bridges	X			X				X				X	X
August 16 - 17, 2012													
Little Wilder	X	X	X	X	X		X		X				X
Younger Lagoon	X	X		X		X	X						
Natural Bridges	X	X	X	X	X		X				X	X	X
October 22 - 23, 2012													
Little Wilder	X						X		X				X
Younger Lagoon		X		X					X				X
Natural Bridges			X		X		X				X		X
January 16 -17, 2013													
Little Wilder	X			X					X				X
Younger Lagoon	X	X		X					X				X
Natural Bridges		X		X	X				X			X	X
May 15 - 16, 2013													
Little Wilder	X			X	X								X
Younger Lagoon	X	X		X					X				X
Natural Bridges	X	X			X							X	X

	Rodent[1]	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**
July 18 - 19, 2013													
Little Wilder	X	X		X					X			X	X
Younger Lagoon	X	X		X					X				
Natural Bridges		X		X	X						X	X	X
October 21- 22, 2013													
Little Wilder		X		X									
Younger Lagoon		X		X					X				X
Natural Bridges	X	X			X				X		X	X	X
February10-11, 2014													
Little Wilder	X	X		X									X
Younger Lagoon									X				X
Natural Bridges		X			X						X		X
April 27-28, 2014													
Little Wilder		X		X					X				X
Younger Lagoon		X							X				
Natural Bridges		X		X	X						X	X	X
July 30-31, 2014													
Little Wilder		X		X					X				X
Younger Lagoon		X		X					X				
Natural Bridges		X			X		X		X		X	X	X
November 4-5, 2014													
Little Wilder				X					X			X	X
Younger Lagoon		X		X					X				
Natural Bridges		X					X				X		X
January 26-27, 2015													
Little Wilder	X								X				X
Younger Lagoon	X	X		X			X						X
Natural Bridges	X				X		X		X		X	X	X
April 14-15, 2015													

	Rodent[1]	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**
Little Wilder	X	X							X				X
Younger Lagoon	X	X		X					X				
Natural Bridges	X				X		X		X		X	X	X
July 8-9, 2015													
Younger Lagoon	X			X	X								
									X				X
October 29-30, 2015													
Younger Lagoon		X		X									
February 2-3, 2016													
Younger Lagoon		X							X				
May3-4, 2016													
Younger Lagoon		X							X				
July 12-13, 2016													
Younger Lagoon		X		X									
November 9-10, 2016													
Younger Lagoon		X		X					X				
March 1-2, 2017													
Younger Lagoon	X	X		X									
April 25-26, 2017													
Younger Lagoon		X					X		X				X
August 2-3, 2017													
Younger Lagoon					X				X				
October 25-26, 2017													
Younger Lagoon		X					X		X	X			X
February 7-8, 2018													
Younger Lagoon	X			X	X								X

	Rodent[1]	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**
May 1-2, 2018													
Younger Lagoon	X								X				
July 12-13, 2018													
Younger Lagoon	X			X					X				X
November 7-8, 2018													
Younger Lagoon	X	X					X		X				X
February 20-21, 2019													
Younger Lagoon	X	X							X				
May 15-16, 2019													
Younger Lagoon	X			X					X				X
	3	3	3	3	3	2	3	1	3	3	1	2	3

[1] Unidentified small rodent.

Table 8. Frequency of occurrence, and native species richness, of animals and human use types through spring 2019 track plate sampling efforts. Actual detections are included parenthetically.

Site	**Rodent**	**Raccoon**	**Cottontail**	**Bobcat**	**Skunk**	**Squirrel**	**Deer**	**Opossum**	**Coyote**	**Bicycle**	**Vehicle**	**Dog**	**Human**	**[1]Native sp. Richness**
Little Wilder	(15) 71%	(10) 48%	(4) 19%	(15) 71%	(6) 29%	(1) 6%	(2) 10%	0%	(15) 71%	(2) 10%	0%	(3) 14%	(19) 91%	8
Younger Lagoon	(21) 60%	(23) 65%	(2) 6%	(25) 71%	(9) 25%	(2) 6%	(5) 14%	0%	(26) 74%	(1) 3%	0%	0%	(15) 43%	8
Natural Bridges	(9) 43%	(15) 71%	(4) 19%	(9) 43%	(13) 62%	0%	(8) 38%	(1) 5%	(9) 43%	(1) 5%	(14) 67%	(16) 76%	(21) 100%	8

[1] Bicycle, vehicle, dog, and human excluded.

Small Mammal Trapping

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. A total of 281 individual small mammals representing four species have been captured during small mammal trapping efforts (Table 9).

Table 9. Summary of Sherman trapping efforts

Site	Pema[1]	Mica[1]	Reme[1]	Rara[1,2]	**TOTAL**
April 24 -25, 2010					
Little Wilder	8	5			**13**
Younger Lagoon	2				**2**
Natural Bridges			3		**3**
August 11-12, 2010					
Little Wilder	5	4			**9**
Younger Lagoon			1		**1**
Natural Bridges					**0**
November 15-16, 2010					
Little Wilder	5	1			**6**
Younger Lagoon				1	**1**
Natural Bridges		3	1		**4**
February 15-16, 2011					
Little Wilder	5				**5**
Younger Lagoon	6	5	0		**11**
Natural Bridges			2		**2**
April 29-30, 2011					
Little Wilder	4				**4**
Younger Lagoon	1				**1**
Natural Bridges					**0**
August 8-9, 2011					
Little Wilder	6	2			**8**
Younger Lagoon	3		3		**6**
Natural Bridges		1	5		**6**

Site	Pema[1]	Mica[1]	Reme[1]	Rara[1,2]	**TOTAL**
March 30, 2012					
Little Wilder	6				**6**
Younger Lagoon	1		1		**2**
Natural Bridges		5	2		**7**
May 15-16, 2012					
Little Wilder	4	1			**5**
Younger Lagoon	3				**3**
Natural Bridges		5			**5**
August 25-26, 2012					
Little Wilder	4				**4**
Younger Lagoon	3				**3**
Natural Bridges		4	2		**6**
November 5-6, 2013					
Little Wilder	2		1		**3**
Younger Lagoon	3				**3**
Natural Bridges		3	1		**4**
January 13-14, 2013					
Little Wilder	2		4		**6**
Younger Lagoon	2				**2**
Natural Bridges		2	1		**3**
May 1-2, 2013					
Little Wilder	1		1		**2**
Younger Lagoon	3		2		**5**
Natural Bridges		5			**5**
July 16-17, 2013					
Little Wilder	3		1		**4**
Younger Lagoon	1				**1**
Natural Bridges			1		**1**
October 22-23, 2013					
Little Wilder	5	1		1	**7**
Younger Lagoon	1				**1**

Site	Pema[1]	Mica[1]	Reme[1]	Rara[1,2]	**TOTAL**
Natural Bridges		1	2		**3**
February 12-13, 2014					
Little Wilder	2	1	1		**4**
Younger Lagoon	1		1		**2**
Natural Bridges		2			**2**
April 28-29, 2014					
Little Wilder	4	1			**5**
Younger Lagoon	3		1		**4**
Natural Bridges	1				**1**
July 30-31, 2014					
Little Wilder	1	1			**2**
Younger Lagoon	2				**2**
Natural Bridges	1		1		**2**
November 4-5, 2014					
Little Wilder	3	1			**4**
Younger Lagoon	4				**4**
Natural Bridges	2	1	3		**6**
January 26-27, 2015					
Little Wilder	3		1		**4**
Younger Lagoon	4		5		**9**
Natural Bridges			3		**3**
April 14-15, 2015					
Little Wilder	2		3		**5**
Younger Lagoon	3				**3**
Natural Bridges					**0**
July 8-9, 2015					
Younger Lagoon	7		1		**8**

October 29-30, 2015				
Younger Lagoon	2	6		**8**
February 2-3, 2016				
Younger Lagoon		6		**6**
May 3-4, 2016				
Younger Lagoon		3	1	**4**
July 12-13, 2016				
Younger Lagoon		4		**4**
November 9-10, 2016				
Younger Lagoon	2	1		**3**
March 1-2, 2017				
Younger Lagoon	2	1		**3**
April 25-26, 2017				
Younger Lagoon		1		**1**
August 2-3, 2017				
Younger Lagoon				**0**
October 25-26, 2017				

Site	Pema[1]	Mica[1]	Reme[1]	Rara[1,2]	**TOTAL**
Younger Lagoon	1	1	2		**4**
February 8-9, 2018					
Younger Lagoon	2				**2**
May 1-2, 2018					
Younger Lagoon	1		2		**3**
July 12-13, 2018					
Younger Lagoon	6				**6**
November 7-8, 2018					
Younger Lagoon	7		2		**8**
February 20-21, 2019					
Younger Lagoon	5		2	1	**8**
May 14-15, 2019					
Younger Lagoon	4				**4**
TOTAL	**164**	**56**	**84**	**4**	**309**

[1] Pema = *Peromyscus maniculatus*; Mica = *Microtus californicus*; Rema = *Reithrodontomys megalotis*; Rara = *Rattus norvegicus.* [2] Escaped before positive ID; however, suspected to be Norway Rat.

Invertebrate Monitoring

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Over all, Younger Lagoon consistently had the greatest number of individuals captured; however, patterns of species richness varied among sampling sessions (Figures 7-8). This may have been at least partially due to trapping methodology and disturbance as raccoons and perhaps coyote disturbed sample cups during some of the sampling efforts. Individuals were identified as distinct taxa; however, at the time of the writing of this report they have not been taxonomically keyed out.

Avian Surveys

Although we are no longer monitoring Natural Bridges and Sand Plant beaches, we continue include results in order to have standalone reports that include all data going forward. Avian species varied among sites and sampling dates (Table 10); however, number of species and abundance were consistently greatest at Natural Bridges and Younger Lagoon.

Figure 7. Species richness of invertebrates across all beaches

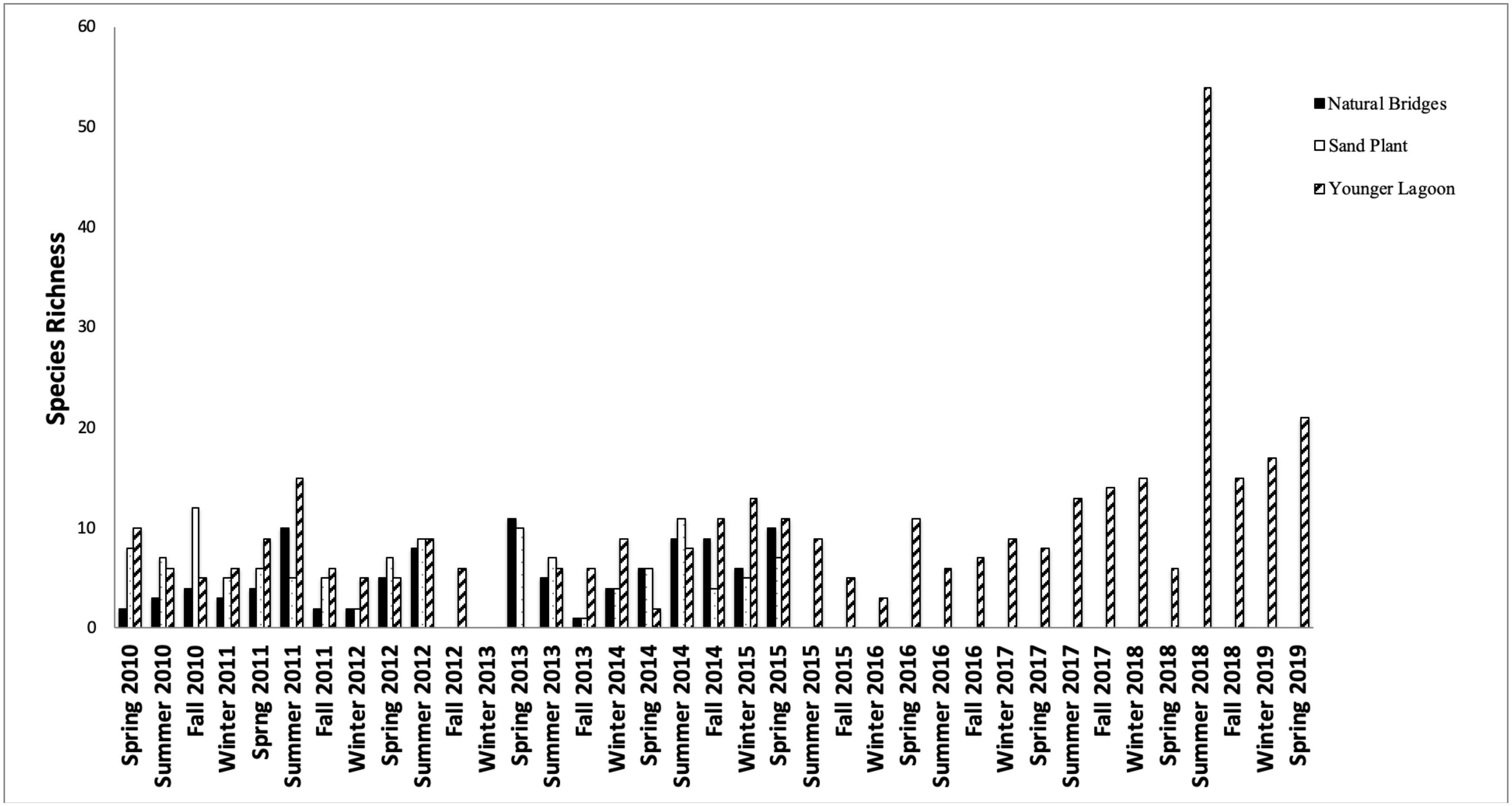


Figure 8. Total abundance of invertebrates at Natural Bridges, Sand Plant Beach, and Younger Lagoon beaches.

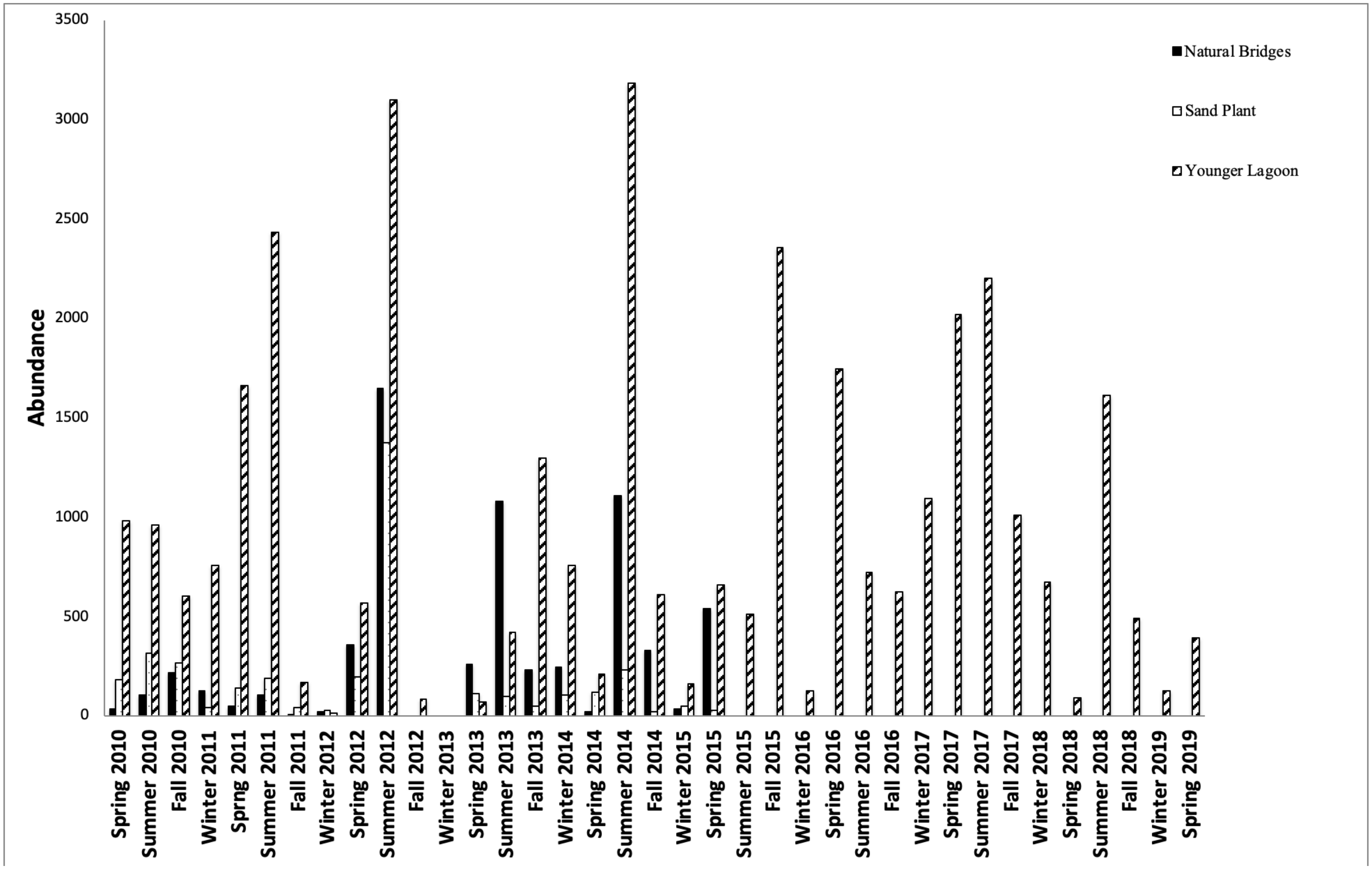
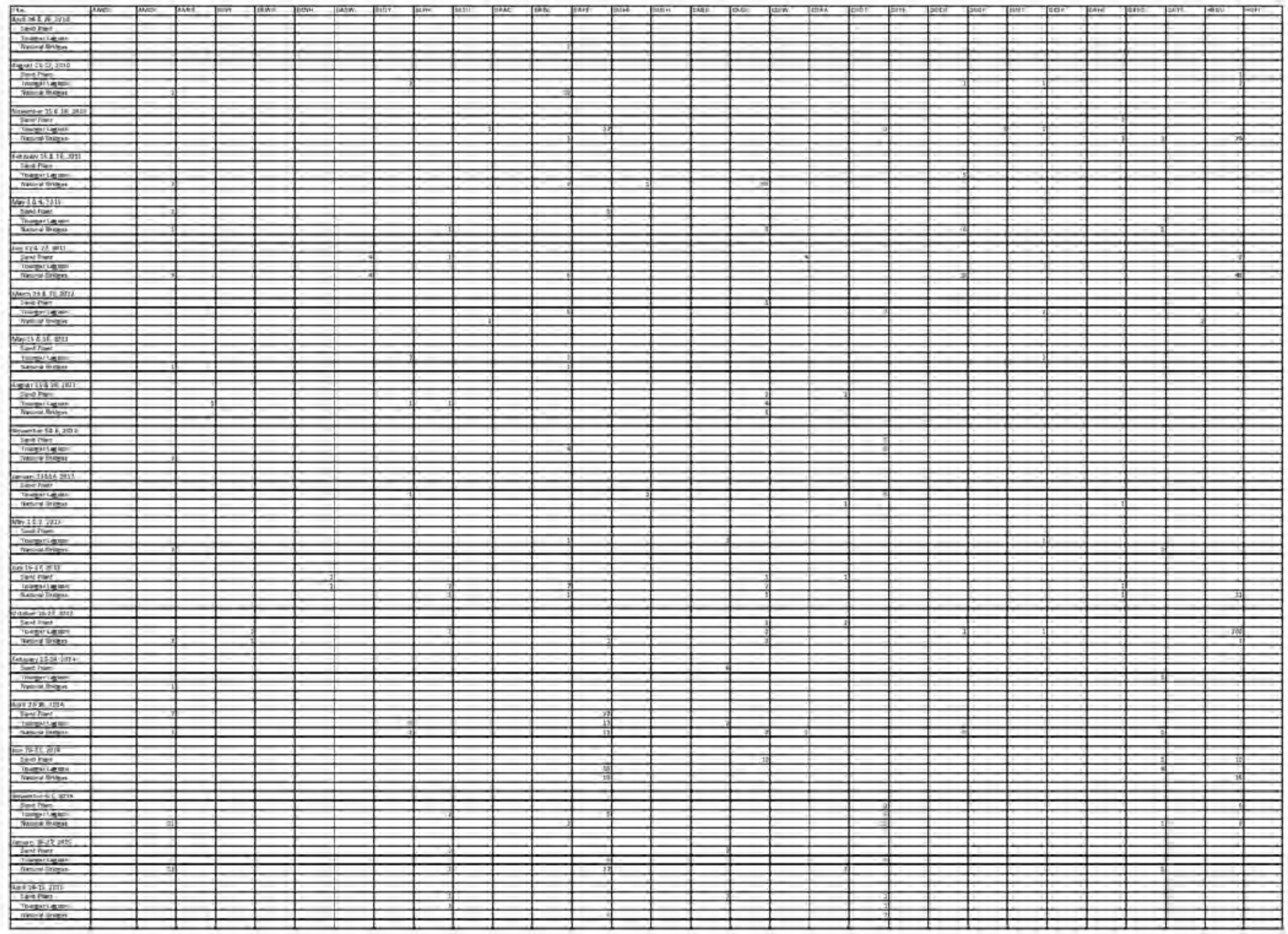
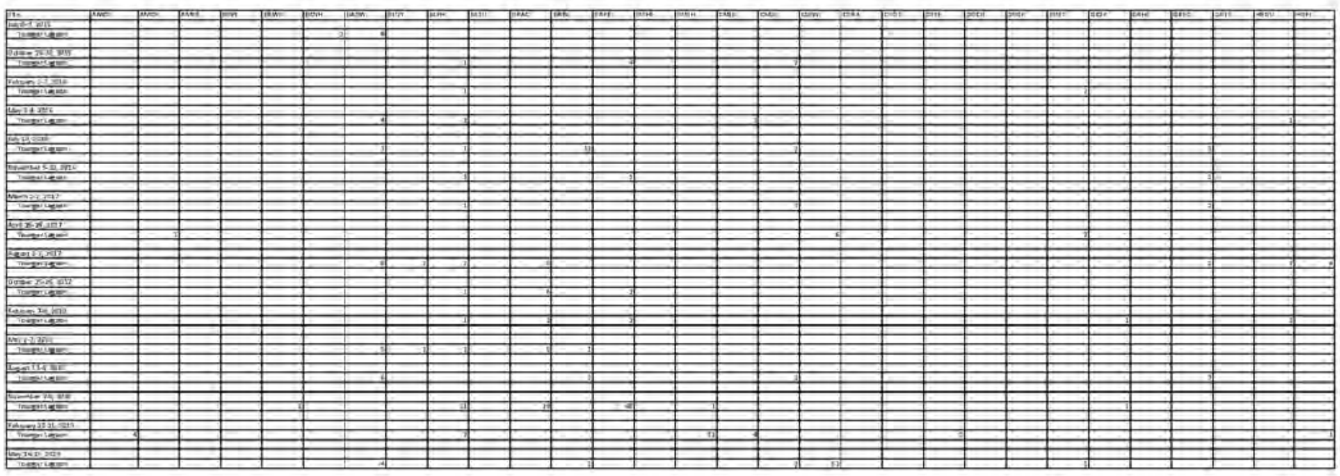
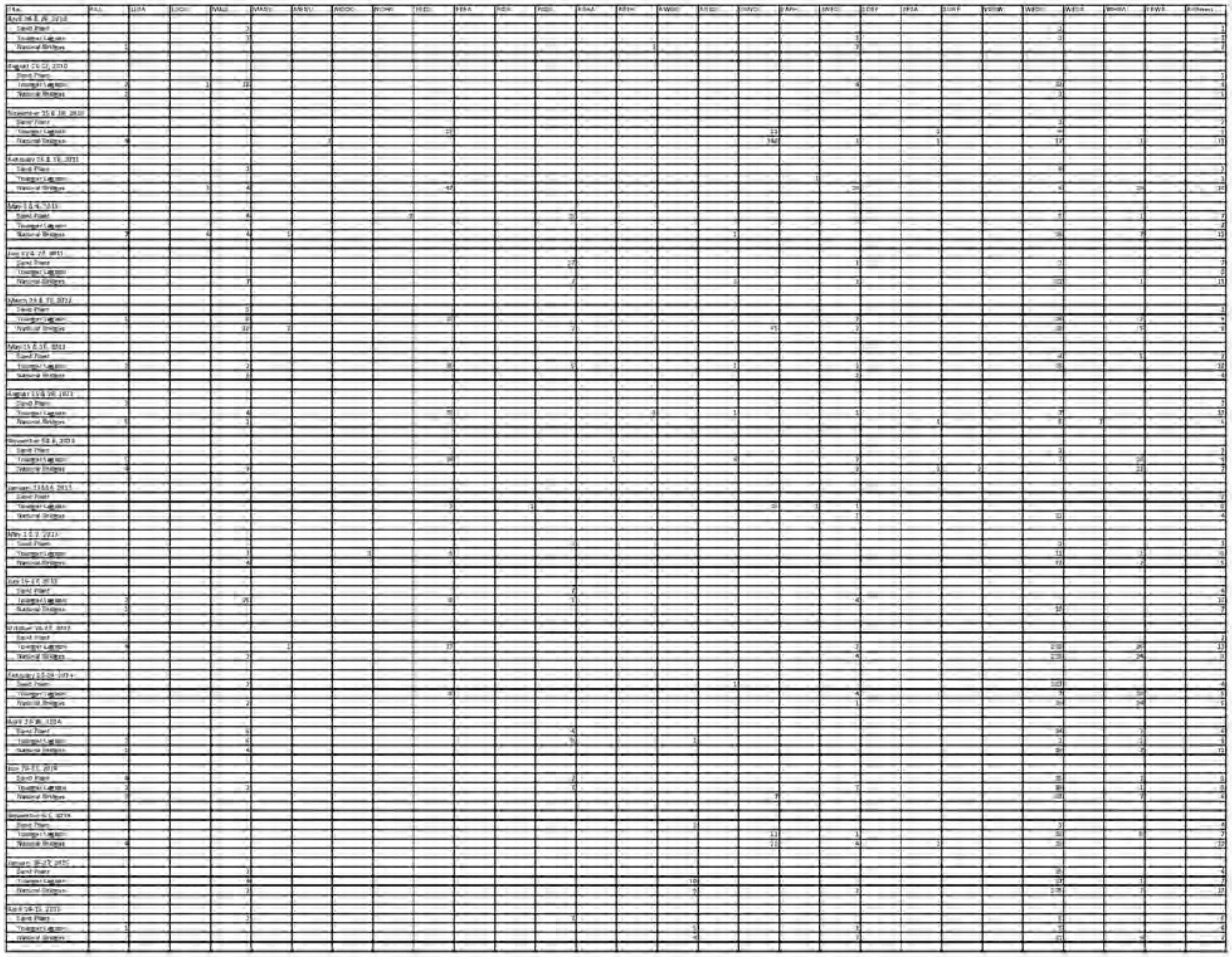
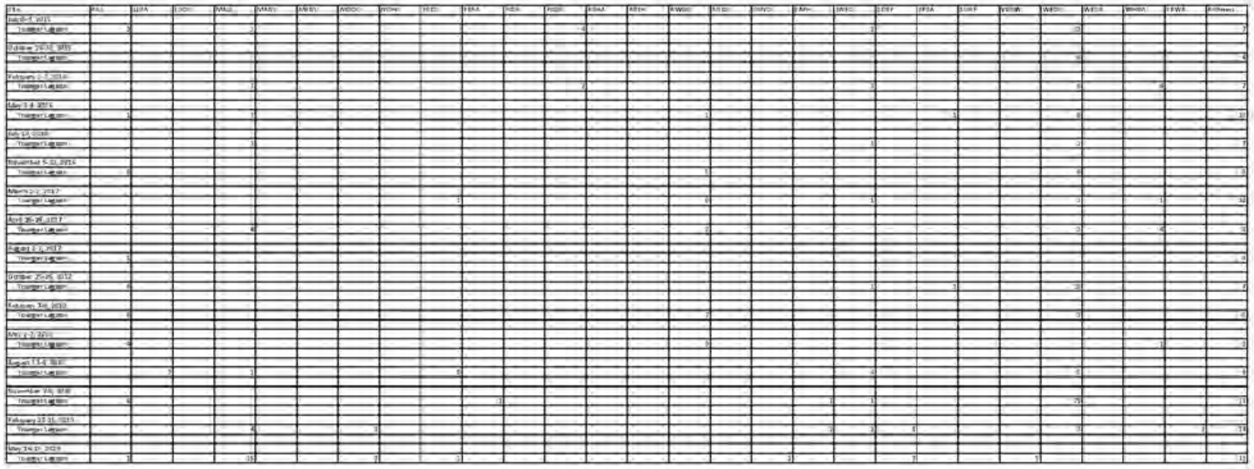


Table 10. Summary of bird surveys at Sand Plant Beach, Younger Lagoon, and Natural Bridges beaches.









Site	AMCR	AMPE	BBPL	BCNH	BASW	BLOY	BLPH	BLTU	BRAC	BRBL	BRPE	BUHE	CAGO	CAGU	CLSW	CORA	COOT	DOCO	DUSP	EUST	GCSP	GRHE	GREG	GRTE	HEGU	HOFI
Sand Plant														10									1		10	
Younger Lagoon											18												4			
Natural Bridges											18														15	
November 4-5, 2014																										
Sand Plant																	2								6	
Younger Lagoon							2				5						6									
Natural Bridges	11									2							10						1		9	
January 26-27, 2015																										
Sand Plant							2						2													
Younger Lagoon											6						9									
Natural Bridges	12						1				27					3							1			
April 14-15, 2015																										
Sand Plant							1						2				1									
Younger Lagoon							2										1									
Natural Bridges											6						7									
July 8-9, 2015																										
Younger Lagoon				2	4																					
October 29-30, 2015																										
Younger Lagoon							1				4			2												
February 2-3, 2016																										
Younger Lagoon							1													2						
May 3-4, 2016																										
Younger Lagoon					4		2						2												1	
July 12, 2016																										
Younger Lagoon					3		1			12				2									1			
November 9-10, 2016																										
Younger Lagoon							2				1												1			
March 1-2, 2017																										
Younger Lagoon							1							3									1			
April 25-26, 2017																										
Younger Lagoon	1														6					2						
August 2-3, 2017																										
Younger Lagoon					8	2	2		8														1		2	6
October 25-26, 2017																										
Younger Lagoon							1		6		2															
February 7-8, 2018																										
Younger Lagoon							1		2		2										1				3	
May 2-3, 2018																										
Younger Lagoon					5	2	2		5	1																

Site	KILL	LOCU	MALL	MAGO	MEGU	MODO	NOHA	PECO	PIGR	PIGU	REHA	REPH	RWBB	RODO	SAND	SAPH	SNEG	SPSA	SURF	WEGU	WESA	WHIM	Richness
April 24 & 26, 2010																							
Sand Plant			2																	2			1
Younger Lagoon			3														2			2			3
Natural Bridges	1											2					2						2
August 11-12, 2010																							
Sand Plant																							1
Younger Lagoon	2	1	10														4			32			9
Natural Bridges	1																			3			5
November 15 & 16, 2010																							
Sand Plant																				1			2
Younger Lagoon								15							11			1		4			9
Natural Bridges	4				2										140		1	1		17		1	11
February 15 & 16, 2011																							
Sand Plant			2																	6			2
Younger Lagoon																1							2
Natural Bridges		3	4					47									18			6		19	10
May 3 & 4, 2011																							
Sand Plant			4				2			35										5		1	7
Younger Lagoon																							0
Natural Bridges	7	4	4	1										1						16		7	12
July 22 & 23, 2011																							
Sand Plant										17							1			1			7
Younger Lagoon																							0
Natural Bridges			7							3				2			2			81		1	11
March 29 & 30, 2012																							
Sand Plant			5																				2
Younger Lagoon	1		8					13									2			16		2	9
Natural Bridges			10	3						2					65		2			10		5	9
May 15 & 16, 2012																							
Sand Plant																				4		5	2
Younger Lagoon	3		2					25		5				1			2			15			10
Natural Bridges			6														2						4
August 25 & 26, 2012																							
Sand Plant	3																						3
Younger Lagoon			4					35				8		1			1			7			10
Natural Bridges	5		1															1		5	1		6
November 5& 6, 2012																							
Sand Plant																				1			2
Younger Lagoon	5							14			1			4			2			3		10	9
Natural Bridges	4		9														2	1	2			12	7
January 13&14, 2013																							
Sand Plant																							0
Younger Lagoon								3	1						38	1	1						8
Natural Bridges																	1			11			4
May 1 & 2, 2013																							
Sand Plant										8										2			2
Younger Lagoon			3			2		9												11		2	8
Natural Bridges			4																	23		2	5
July 16-17, 2013																							
Sand Plant										7													4
Younger Lagoon	2		25					8		1							4						10
Natural Bridges	1																			10			7
October 22-23, 2013																							
Sand Plant																							2
Younger Lagoon	4			1				33									3			150		26	13
Natural Bridges			2														4			110		24	8
February 13-14, 2014																							
Sand Plant			2											1						103			4
Younger Lagoon								8									4			7		10	5
Natural Bridges			2														1			19		24	5
April 27-28, 2014																							
Sand Plant			6							4										24		2	6
Younger Lagoon	3		6							8			1							2		2	9
Natural Bridges	1		4																	18		7	11
July 30-31, 2014																							

Site	KILL	LOCU	MALL	MAGO	MEGU	MODO	NOHA	PECO	PIGR	PIGU	REHA	REPH	RWBB	RODO	SAND	SAPH	SNEG	SPSA	SURF	WEGU	WESA	WHIM	Richness
Sand Plant	4									3										25		2	8
Younger Lagoon	2		2							3							3			28		1	8
Natural Bridges	3														7					80		7	6
November 4-5, 2014																							
Sand Plant													2							3			4
Younger Lagoon															11		1			10		8	7
Natural Bridges	4														20		4	1		18			10
January 26-27, 2015																							
Sand Plant			2																	25			4
Younger Lagoon			4										10							27		1	7
Natural Bridges			2										9				2			175		3	10
April 14-15, 2015																							
Sand Plant			2							3										5			6
Younger Lagoon	1												5				2			5			6
Natural Bridges													4				3			21		9	7
July 8-9, 2015																							
Younger Lagoon	2		2							4							2			31			7
October 29-30, 2015																							
Younger Lagoon																				6			4
February 2-3, 2016																							
Younger Lagoon			3							2							3			9		4	7
May 3-4, 2016																							
Younger Lagoon	1		3										1					1		8			10
July 12, 2016																							
Younger Lagoon			3														1			2			7
November 9-10, 2016																							
Younger Lagoon	6												5							6			8
March 1-2, 2017																							
Younger Lagoon								1					6				1			2		1	10
April 25-26, 2017																							
Younger Lagoon			4										2							2		4	8
August 2-3, 2017																							
Younger Lagoon	1																						8
October 25-26, 2017																							
Younger Lagoon	6																1	1		10			7
February 7-8, 2018																							
Younger Lagoon	6												7							3			8
May 2-3, 2018																							
Younger Lagoon	4												9									2	8

Discussion

Data collected indicate that Younger Lagoon Reserve (YLR) supports a wide variety of native flora and fauna, provides habitat for sensitive and threatened species, supports a very unique beach dune community, and is extensively used for research and education.

A parameter that we have mapped, and is evident from visual observation and photo documentation, is the presence of dune hummocks and downed woody material at YLR, both of which are almost entirely absent at Sand Plant Beach and Natural Bridges (Figure 9). It is likely that the hummocks and woody material are absent at Natural Bridges and Little Wilder due to human trampling, collection, and burning. These features provide habitat for plant species such as the succulent plant dudleya, which grow on downed woody material and dune hummocks at YLR, as well as burrowing owls that use burrows in hummocks and seek shelter beneath downed woody material at YLR.

Although Younger Lagoon does experience human use, the intensity and number of users is small. Additionally, users of the YLR beach are educated about the reserve, unique natural features, and are not allowed to collect woody material or trample dune vegetation. The relatively natural state of YLR beach and dune vegetation is unique among the three sites and most pocket beaches in Santa Cruz County and likely represents a glimpse into what many of the pocket beaches in the greater Monterey Bay area looked like prior to significant human disturbance.

Open access to the beach would likely result in the loss of the unique ecological characteristics of the site and certainly reduce its effectiveness as a research area for scientific study. Controlled beach access through the free Seymour Center docent led tours, provides an appropriate level of supervised access that enables people to see and learn about the lagoon habitat while limiting impacts to the system. We recommend that this continue.

Figure 9. Younger Lagoon dune map. Survey data and resulting elevation model output shows topographic features on Younger Lagoon Beach.

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Appendix 1. Younger Lagoon Photos.

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Beach Photopoint #4. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

Appendix 2. Compliance monitoring report

Compliance Monitoring Report for Coastal Prairie and Coastal Scrub Restoration Sites at Younger Lagoon Reserve – Spring 2019

Justin C. Luong

Introduction

In keeping with the goals of the restoration plans for theYounger Lagoon Reserve Terrace Lands prepared for the California Coastal Commission (UCNRS 2010, UCNRS 2018), reserve employees, interns, and volunteers have continued to perform native plant community restoration activities. This report presents the results of the 2019 monitoring data for 2011, 2012, 2013 and 2015 coastal prairie habitat plantings along with 2013, 2015 and 2017 coastal scrub plantings. Monitoring efforts begin two years post-planting. If a site meets restoration targets, monitoring is then conducted every other year for the first six years post-planting, and then every five years after that. If a site doed not meet restoration targets, the site is monitored annually until it reaches restoration targets (UCNRS 2018). The 2012 coastal prairie habitat was monitored this year (normally monitored in even years) because it did not meet compliance standards in 2018.

Methods

Planting

Seeds for the coastal prairie planting projects were collected from local reference sites in coastal regions of Santa Cruz and San Mateo Counties. The seeds were grown in Ray Leach stubby (SC7) conetainers^{TM} for several weeks in the UC Santa Cruz greenhouses before being planted at the site. Site preparation prior to planting typically involved the hand removal of large weeds (such as *Carpobrotus edulis*) and/or the application of herbicide and tarping to reduce weed cover. Subsequently, a heavy layer of wood chip mulch (~10-15 cm) was applied to all restoration sites prior to planting to suppress weed emergence. Teams of volunteers, interns, and staff planted the native plugs primarily between December and February using dibblers. Sites received supplemental irrigation during the first year following planting to help improve establishment. After the first year, there was no supplemental irrigation. Follow up management included hand removal and targeted herbicide application for emerging weeds during the first 18 – 24 months following planting. All sites were mowed twice annually in the years following planting. Fall mowing was intended to reduce thatch, and spring mowing was intended to reduce seed set from nonnative species prior to native perennial species began to reproductively develop.

Sampling

To measure cover in coastal prairie habitats, a 0.25 × 1-m quadrat was placed on alternating sides of a 50-m transect tape every 5 m, for a total of ten quadrats per 50-m transect. For each transect, the quadrat was randomly placed between 1 and 5 m as the starting point. In some areas, 50-m transects did not fit the shape of the restoration area, so transects were split and divided into sections to better fit the site. Cover was measured using a modified Braun-Blanquet class system within each quadrat, with increases in 5% intervals, starting with 0-5%. The midpoint each cover class was used for data analysis (e.g. 2.5%, 7.5%, etc.). Richness was measured using a 2-m belt transect on either side of the 50-m transect tape to visually detect any native species not measured in the cover quadrat sampling. To measure cover in scrub habitats, the area of each species and bare ground under the length of the transect was measured. Percent cover was determined from the length covered by an individual divided by the total length of the transect. Shrub cover may exceed 100% if multiple species are overlapping on the transect. In some areas, herbaceous cover and scrub were mixed, and both shrub measurements and herbaceous cover quadrats were quantified for these transects.

The 2012 coastal prairie planting area was measured using three transects of 35, 45, and 45 m, for a total of 25 quadrats (Figure 1, 3). The 2013 coastal prairie was measured using one transect of 50 m, for a total of 10 quadrats (Figure 1, 3). The 2015 coastal prairie area was measured using two transects of 50 m each for a total of 20. The 2013 predominantly scrub plantings were measured using transects of 31.3 m, with no herbaceous cover quadrat measurements (Figure 1, 3). The 2015 scrub plantings were measured using three transects of 16.2, 31.5, and 43.5 m, with 4 herbaceous quadrant measurements (Figure 1, 3). For analysis these measurements were separated into prairie-identified habitats and scrub-identified habitats, consistent with previous years. The 2017 scrub plantings were measured using four transects of 19.1, 23.8, 27.9 and 37.4 m with no herbaceous cover quadrat measurements. For each planted area, cover was averaged across transects/quadrats. Richness for each planted area is a count of all unique taxa found across transects/quadrats for restored habitat type by year (Table 1).

All sites are expected to meet the targets laid out for the California Coastal Commission (UCNRS 2010, UCNRS 2018). The 2011, 2012 and 2013 plantings are expected to meet six-year targets, the 2015 sites should meet four-year targets, and the 2017 sites should meet two-year targets. Targets for all habitat types and year-post-planting are available in Appendix 1.

Results

Native species cover targets were met and surpassed in all but the 2012 coastal prairie sites (Table 1). The 2012 coastal prairie had a native cover of 10.2 ± 3.2%, which does not meet the requirement of ≥ 25% native cover. The 2011 and 2013 coastal prairie sites had observed cover values of 25.4 ± 3.9% and 33.5 % (one transect), respectively, surpassing their post-year-six target of ≥ 25%. The 2015 coastal prairie sites had an average native species cover of 24.6 ± 5.6, exceeding the ≥ 15% native cover target. In the 2013, 2015 and 2017 coastal scrub sites, native cover goals were also met. Only one transect was completed at the 2013 scrub site with native scrub cover at 117%, therefore there is no standard error, but it meets the cover goal of ≥ 40%. In the 2015 and 2017 sites native cover was 82.9 ± 5.2% and 103.6 ± 14.7%, respectively, exceeding the shrub cover goals of ≥ 25% and ≥ 10%. Within these scrub areas, herbaceous cover were also above targets (Table 1).

Native species richness measurements were also at or above defined target levels for all planted areas (Table 2). The 2012 coastal prairie, which did not meet species richness targets in 2018, now exceeds target goals. The 2011 coastal prairie area had an average native species richness of 12.7 ± 0.7 species with a total of 23 native species observed across all transects which meets monitoring targets. Transects in the 2012 coastal prairie area had an average native species richness of 6.3 ± 0.9 species, with a total of 12 species in all transects which meets the requirement of ≥ 8 species. The 2013 and 2015 coastal prairie sites had observed richness values of 15 (one transect) and an average of 12 ± 2 species, and a total of 15 and 20 native species respectively, surpassing their ≥ 8 and ≥ 6 species richness targets. The 2013, 2015 and 2017 coastal scrub areas met their ≥ 8 native species in 2013 and ≥ 6 native species in 2015 and 2017. The scrub areas had 11 (one transect), an average of 11.7 ± 0.3, an average of 13.8 ± 0.8 native species per transect, and a total of 11, 19 and 24 native species respectively for 2013, 2015 and 2017.

All planted areas showed evidence of recruitment for multiple native species.

Discussion

Nearly all restoration areas at Younger Lagoon Reserve met or exceeded the restoration targets laid out for the California Coastal Commission for their respective habitats (UCNRS 2010, UCNRS 2018). The 2011, 2013, and 2015 coastal prairie areas, and the 2013, 2015 and 2017 coastal prairie and scrub areas all appear to successfully have restored native species cover and richness. Only the 2012 coastal prairie area did not meet its restoration targets for native cover. The 2012 coastal prairie site did not meet the target goal for species richness or native cover in 2017 or 2018 (Lesage, 2017, Lesage, 2018). However, the 2012 coastal prairie area is now meeting species richness goals.

The 2012 coastal prairie plantings had a native cover of 10.2 ± 3.2% (target ≥ 25%), and species richness of 12 species (target ≥ 8 species). Low cover values indicate that follow-up invasive plant control and native replanting will be necessary for this location. These transects were dominated by non-native forb species, primarily *Medicago polymorpha*, in 2018. These transects are now dominated by non-native grass species, indicating management may have been successful in decreasing non-native forb cover. In 2015, native cover was 31.2 ± 4.1% (target ≥ 25%), and species richness of 6.3 ± 1.2 species (target ≥ 8 species) (Lesage, 2015), which decreased to 17.0 ± 5.1% in 2018 and now to 10.2%, demonstrating the difficulty of maintaining native cover and richness at coastal prairie restoration sites without ongoing intensive invasive species maintenance.

A comparison of monitoring data from 2017 and 2019 shows interesting trends in the coastal prairie and coastal scrub plantings (Lesage 2017). In previous years, the 2011 and 2013 coastal prairie data were lumped together due to a record keeping error. Ongoing and future monitoring and analysis will differentiate these areas (**Fig.** 1). In 2017, the combined 2011 and 2013 coastal prairie plantings had an average native cover of 18.7 ± 3.5%, which is below the target of ≥ 25% native cover. This year, the 2011 coastal prairie had an average of 25.4 ± 3.9% native cover per transect and the 2013 coastal prairie had an average of 33.5 ± 10.7% native cover per transect, both of which exceed the target of ≥ 25% native cover. In 2017 the 2011/2013 coastal prairie habitat had an average species richness of 9.8 ± 0.8 species per transect with a total of 17 unique species (Lesage, 2017), whereas the 2011 site now has an average of 12.7 ± 0.7 species with a total of 23 unique species and the 2013 site now has 15 unique species (one transect). This increase in native cover and species richness within the 2011 and 2013 coastal prairie indicate that ongoing management practices are sufficient for maintaining those specific areas. In 2017, the 2015 coastal prairie had an average native cover of 31.8 ± 5.1%, a species richness of 14.0 ± 5 species per transect and a total of 22 unique species in the area. This year, native cover in the 2015 coastal prairie declined to an average of 24.6 ± 5.6%, and a an average species richness of 12 ± 2 per transect with a total of 20 unique species.

For coastal scrub plantings only the 2015 plantings can be compared with previous monitoring efforts because this is the first year 2013 and 2017 scrub planting areas have been monitored. The 2013 scrub planting should have been monitored in past years; however, this small area was overlooked in 2015 and 2017, possibly due to construction impacts near the site, which is adjacent to a trail that was under construction during those years. In 2017, the 2015 scrub plantings achieved a native cover of 56.2 ± 9.6% which increased in 2019 to a native cover of 82.9 ± 5.2%. In 2017, species richness for 2015 scrub planting was on average 9 species per transect with a total of 21 unique species. In 2019 average species richness per transect increased to 11.7 ± 0.3 species per transect, but total species richness in the area decreased from 21 to 19.

Overall, these findings suggest that coastal prairie habitat may be difficult to maintain into the future without more intensive management, whereas restored coastal scrub sites will not require as intensive methods.

Management Recommendations

Generally, the restoration efforts at Younger Lagoon Reserve are meeting their target goals. Management strategies, such as irrigation during the first year, hand-weeding of sites, and seasonal mowing are maintaining native cover and richness in restored coastal prairie and coastal scrub areas. Only the 2012 coastal prairie planting did not meet its target for native cover. Because the 2012 coastal prairie did not meet its native cover goal, it is recommended that Younger Lagoon staff provide that area more intensive weed control. Additional planting of rhizomatous species such as *Achellia millefolium* or *Sidalcea malviflora* may aid in reaching native cover goals, especially as native cover continues to decline each year.

Additional weed control and supplemental plantings are also recommended for the 2011, 2014, 2015 coastal prairie sites in order to prevent them from falling below compliance standards. Although the 2011 coastal prairie site has rebounded and is now exceeding compliance standards, if more intensive actions or adaptive management actions are not taken, this site may once again fall below compliance during the 2021 monitoring effort. A decline in native species richness and cover was observed in the 2014 coastal prairie sites in 2018 (Lesage, 2018), and in the 2015 coastal prairie sites this year. It is recommended that Younger Lagoon Reserve supplement seasonal mowing in these areas with more intensive, targeted hand removal near species most at risk from being loss from competition with non-native species. Planting in these areas could also increase chances that these areas will exceed compliance in future years. The observed increase in both native cover and species richness in the 2011 and 2013 coastal prairie habitats in 2019 compared to 2017 indicates that coastal prairie restoration is feasible with additional management.

As all scrub planting areas are exceeding target goals, no further management recommendations for scrub sites are needed.

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Tables and Figures

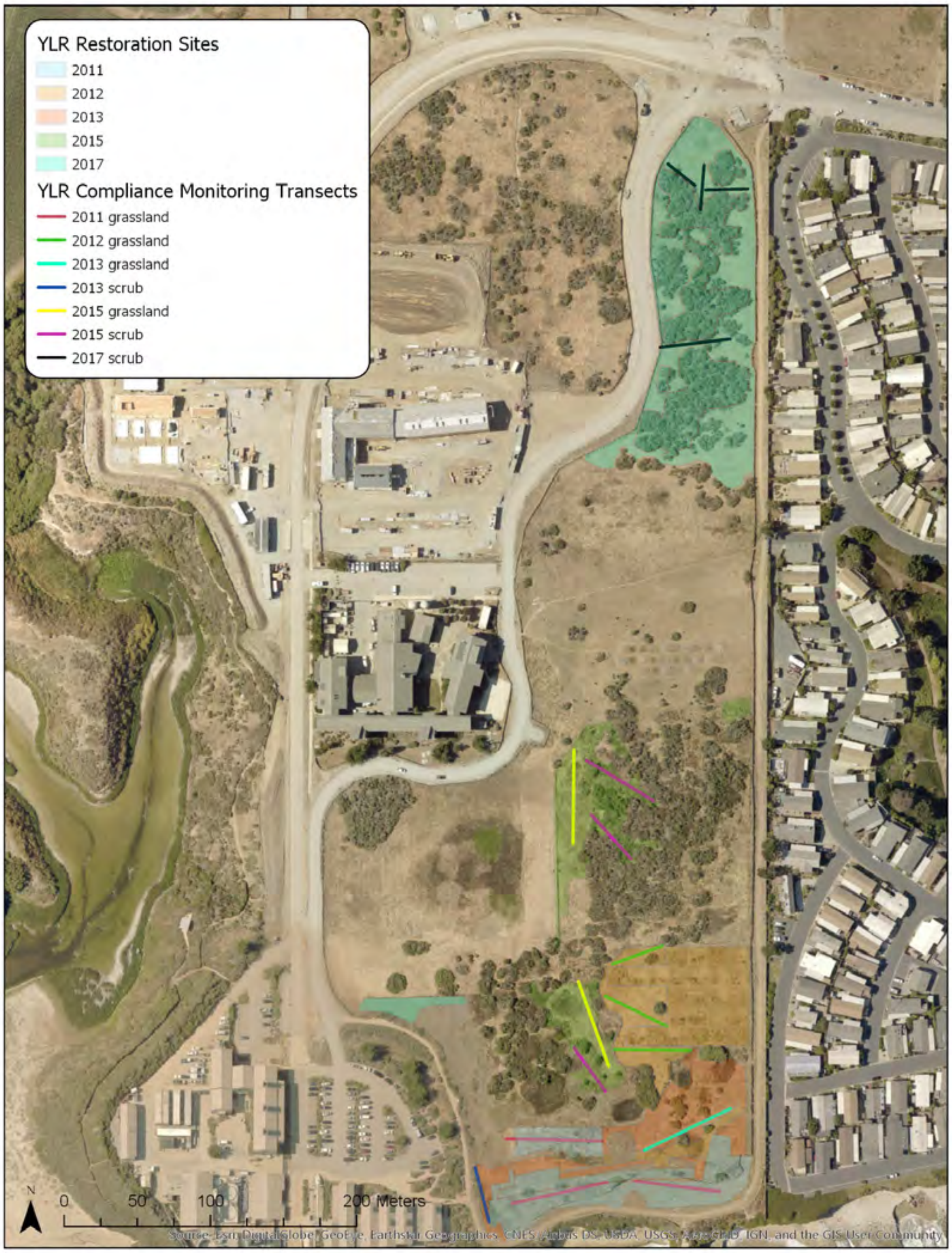

Figure 1. Overview map of locations for compliance monitoring in 2019 which includes the coastal scrub and prairie transects and planting areas. Note that some transects were split to fit the sites or to address changes in vegetation type.

Figure 2. Map of locations for northern area in compliance monitoring in 2019 which includes the 2017 coastal scrub transects and planting areas (black lines in teal shaded area). Note that some transects were split to fit the sites or to address changes in vegetation type.

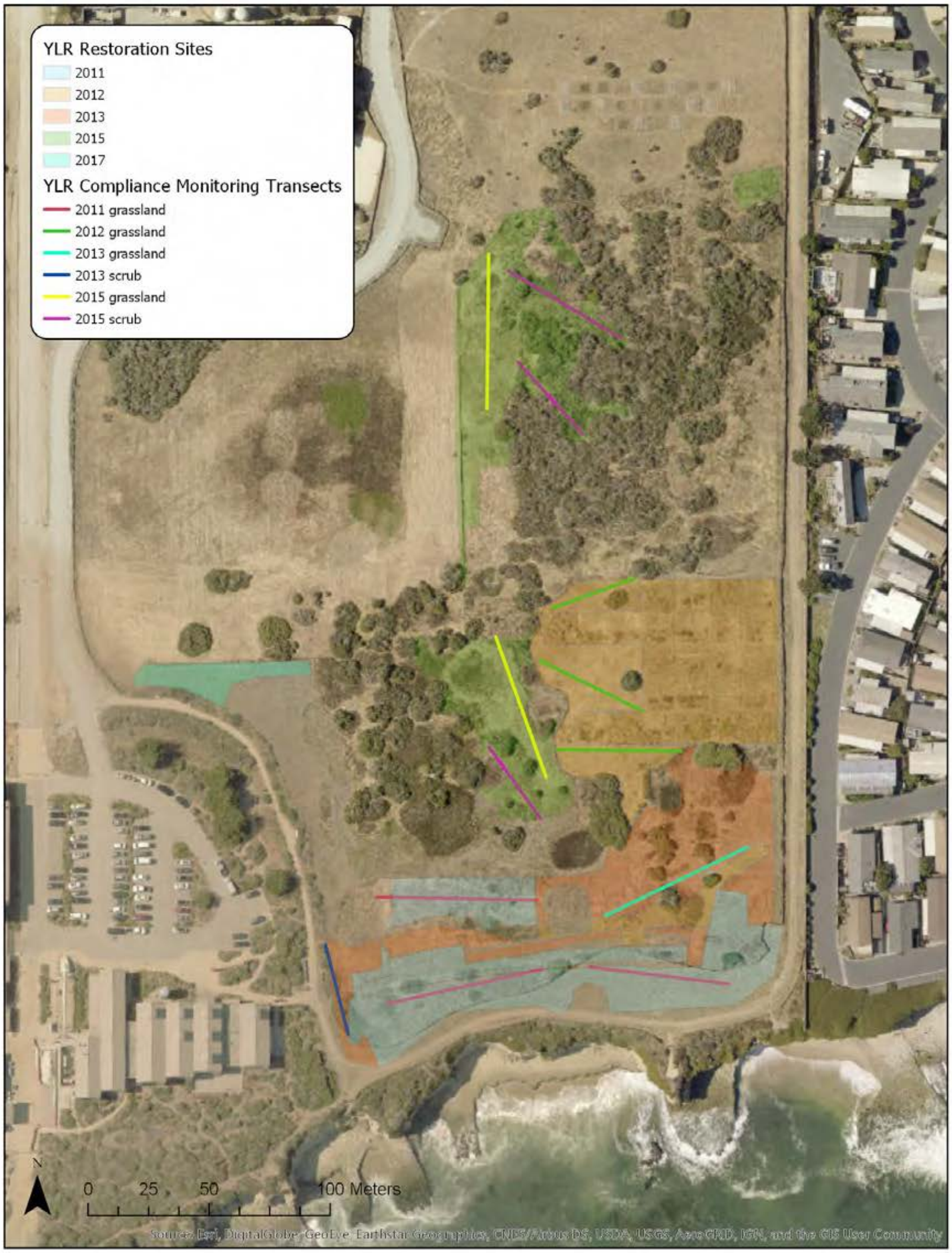

Figure 3. Map of locations for southern area in compliance monitoring in 2019 which includes the 2013, 2015 and 2017 coastal scrub and 2011, 2012, 2013 and 2015 prairie transects and planting areas.

Table 1. Table of native species cover and richness targets and observed values (± SE) in the 2011, 2013, and 2015 coastal prairie, 2013, 2015 and 2017 coastal scrub restoration areas at Younger Lagoon Reserve. *Quadrats were not taken for herbaceous cover for 2017 shrubs, as there were not interstitial prairie habitats.⊛Standard error for 2013 scrub is not provided because there is only one transect for analysis.

Restoration Area	Observed Native Cover (%)	Target Native Cover (%)	Average Native Richness (species/transect)	Observed Native Richness (species/habitat)	Target Native Richness (species/habitat)
2011 Coastal Prairie	25.4 ± 3.9	≥ 25	12.7 ± 0.7	23	≥ 8
2012 Coastal Prairie	10.2 ± 3.2	≥ 25	6.3 ± 0.9	12	≥ 8
2013 Coastal Prairie	33.5 ± 10.7	≥ 25	15	15	≥ 8
2015 Coastal Prairie	24.6 ± 5.6	≥ 15	12 ± 2	20	≥ 6
2013 Coastal Scrub					
Shrub Cover	117⊛	≥ 40	11	11	≥ 8
Herb Cover	NA*	≥ 25	NA*		
2015 Coastal Scrub					
Shrub Cover	82.9 ± 5.2	≥ 25	11.7 ± 0.3	19	≥ 6
Herb Cover	28.75 ± 11.6	≥ 15	2 ± 0.7		
2017 Coastal Scrub					
Shrub Cover	103.6 ± 14.7	≥ 10	13.8 ± 0.8	24	≥ 6
Herb Cover	NA*	≥ 5	NA*		

Table 2. Table of the native species observed in the 2011, 2012, 2013 and 2015 coastal prairie, 2013, 2015 and 2017 coastal scrub restoration areas at Younger Lagoon Reserve. Chart shows species found in at least one transect for each site. Growth forms abbreviated (AF=Annual Forb, PF=Perennial Forb, PG=Perennial Grass, PGRM=Perennial Graminoid, AGRM = Annual Gramminoid, S=Shrub, T=Tree).

Scientific Name	**Common name**	**Growth Form**	**2011 Coastal Prairie**	**2012 Coastal Prairie**	**2013 Coastal Prairie**	**2015 Coastal Prairie**	**2013 Scrub**	**2015 Scrub**	**2017 Scrub**
Cardamine oligosperma	western bittercress	AF	X		X	X	X	X	
Erigeron canadensis	Canadian horseweed	AF	X	X	X	X	X		
Epilobium brachycarpum	willowweed	AF			X				
Epilobium cilatum	Willow herb	AF	X			X		X	
Pseudognaphalium sp.	Cudweed	AF	X						
Achillea millefolium	Yarrow	PF	X	X	X	X	X	X	X
Baccharis glutinosa	marsh Baccharis	PF	X		X	X	X	X	X
Chlorogalum pomeridianum	Soaproot	PF	X			X		X	X
Clinopodium douglasii	yerba buena	PF							X
Eschscholzia californica	California poppy	PF							
Fragaria chiloensis	beach strawberry	PF						X	X
Grindelia stricta	Gumweed	PF	X						X
Horkelia californica	California horkelia	PF						X	X
Marah fabacea	California man-root	PF							X
Oenthera elata	Hooker's primrose	PF					X		
Prunella vulgaris	Selfheal	PF							
Ranunculus californica	California buttercup	PF	X						
Sanicula crassicaulis	Pacific sanicle	PF		X					
Scrophularia californica	California bee plant	PF			X	X		X	X
Sidalcea malviflora	checker-bloom	PF							

***Table 2**, continued*

Scientific Name	**Common name**	**Growth Form**	**2011 Coastal Prairie**	**2012 Coastal Prairie**	**2013 Coastal Prairie**	**2015 Coastal Prairie**	**2013 Scrub**	**2015 Scrub**	**2017 Scrub**
Sisyrinchium bellum	western blue-eyed grass	PF	X						X
Symphyotrichum chilense	Pacific aster	PF	X	X	X	X	X	X	X
Aesculus californica	California Buckeye	T							X
Frangula californica	Coffee berry	T/S						X	X
Bromus carinatus	California brome	PG			X	X			
Danthonia californica	California oatgrass	PG	X						
Deschampsia cespitosa	Tufted hair grass	PG	X						
Elymus glaucus	blue wild rye	PG	X	X	X	X	X	X	
Elymus triticoides	creeping wild rye	PG	X	X	X	X		X	
Festca rubra	Red fescue	PG				X			
Hordeum brachyantherum	meadow barley	PG	X	X	X	X		X	
Stipa pulchra	purple needle grass	PG	X	X		X			
Carex hartfordii	Monterey sedge	PGRM				X			X
Juncus mexicanus	Mexican rush	PGRM				X		X	X
Juncus patens	spreading rush	PGRM	X	X	X				
Juncus occidentalis	Western rush	AGRM			X				
Artemisia californica	California sagebrush	S		X		X	X	X	X
Baccharis pilularis	coyote brush	S		X	X	X	X	X	X
Ericameria ericoides	Mock heather	S							X
Eriophyllum staechadifolium	Seaside golden yarrow	S	X	X	X	X	X	X	X
Lupinus arboreus	Bush lupine	S	X						
Mimulus aurantiacus	sticky monkey flower	S					X	X	X

Ribes sanguineum	flowering currant	S							
Rosa californica	California wild rose	S							X
Rubus ursinus	pacific blackberry	S	X			X		X	X
Toxicodendron diversilobum	Poison Oak	S							X
Observed Native Species Richness:			23	12	15	20	11	19	24
Target Native Species Richness:			≥ 8	≥ 8	≥ 8	≥ 6	≥ 8	≥ 6	≥ 6

Table 3. Rainfall for Santa Cruz for rainfall years starting with the 2011-2012 rain year. Rainfall years are measured from October to September of the following year. Data from the California Department of Water Resources.

Rainfall Year	**Total Precipitation**
100 Year Average	75.8 cm
2011-2012	52.6 cm
2012-2013	45.8 cm
2013-2014	36.6 cm
2014-2015	55.1 cm
2015-2016	82.7 cm
2016-2017	129.7 cm
2017-2018	49.7cm
2018-2019	92.3 cm

Appendix 1 – Relevant Compliance Monitoring Standards for YLR Restoration Efforts

Excerpted from: *UCSC Natural Reserves Staff and the Younger Lagoon Reserve Scientific Advisory Committee (UCNRS). 2010. Enhancement and Protection of Terrace Lands at Younger Lagoon Reserve. Plan prepared for the California Coastal Commission.*

Grassland / Coastal Prairie

Performance Standard: 8 native plant species appropriate for habitat established in planted areas to comprise 25% cover.

Years Post Planting	Goal
2 years after planting	6 or more native plant species established comprising > 5% cover and evidence of natural recruitment present
4 years after planting	6 or more native plant species established comprising > 15% cover and evidence of natural recruitment present
6 years after planting and every 5 years after that	8 or more native plant species established comprising > 25% cover and evidence of natural recruitment present

Scrub

Performance Standard: 8 native plant species appropriate for habitat established in planted areas to comprise 40% cover.

Years Post Planting	Goal
2 years after planting	6 or more native plant species established comprising > 10% cover and evidence of natural recruitment present
4 years after planting	6 or more native plant species established comprising > 25% cover and evidence of natural recruitment present
6 years after planting and every 5 years after that	8 or more native plant species established comprising >40 % cover and evidence of natural recruitment present

Appendix 3. Student reports

2019 Annual Report – Drought-Net Activities at Younger Lagoon UC Natural Reserve

Justin Luong, Michael Loik Environmental Studies, UC Santa Cruz

During 2019, the drought experiment activities at Younger Lagoon Reserve (YLR) focused on: 1. Continued measurements and monitoring of plots in accordance with the International Drought Experiment protocol; 2. Continued collection of micrometeorological data from a sensor system set up in a prior year; 3. Continued monitoring of survival and species-specific growth of California native plant seedlings, as well as composition of species cover under drought, control and watering treatments; 4. Measurement of plant functional traits for fourteen native California plant species and nine non-native species; and 5. Measurements of soil hydraulic conductivity and infiltration rates. Highlights for each are summarized below.

1. Measurements and monitoring of plots in accordance with the International Drought Experiment protocol

In 2019, we measured aboveground net primary productivity (ANPP) and plant diversity of IDE drought shelter and control plots at YLR, as well as at the UCSC Arboretum and UCSC Campus Reserve lands at Twin Gates. These data represent year four of the IDE treatment. Our early analyses suggest a "reverse shelter" effect at YLR for winter 2017, for which plants under shelters grew more than plants in control plots. We have not yet processed results for plant diversity. Data from 2015 – 2018 are now being analyzed as part of the IDE cross-site study.

2. Continued monitoring of the micrometeorological conditions on control and drought plots.

We continue monitoring air and soil temperature (two depths), soil moisture (two depths), photosynthetically active radiation, solar radiation, relative humidity, and fog interception at 30 minute frequency. We monitor conditions below rain interception shelters as well as on open control plots. Some of these data were used for the first manuscripts from the drought project at YLR (Loik et al. 2019). We also have sensors on plots with planted native seedlings under rain-out shelters and control (open) plots. Four additional water soil moisture sensors were installed in fall 2018 in planted plots.

Loik M. E., Lesage J. C., Brown T. M., and **D. O. Hastings**. 2019. Drought-Net rainfall shelters did not cause non-drought effects on photosynthesis for California central coast plants. Ecohydrology https://doi.org/10.1002/eco.2138

3. Continued monitoring of survival and growth of California native plant seedlings under drought , control and watering treatments

This work was started by Prof. Kathleen Kay (Ecology and Evolution Biology at UC Santa Cruz) in 2016 and 2017. Work was then continued by Justin Luong, a PhD student in Environmental Studies at UC Santa Cruz in 2018 and 2019. Seedling survival and species-specific growth measurements have been conducted annually. In addition, Justin began measurements of aerial cover for all surviving native California seedlings, and monitoring of the composition of plant species cover recorded within all 15 plots planted with native California seedlings. Species such as *Ericameria* *ericoides*, *Lupinus nanus* and *L. variicolor* were replanted to provide sufficient replication for trait analysis (detailed below). Four undergraduate interns and one high school student assisted with this work in 2019.

4. Measurements of plant functional traits and community assemblages

In order to better understand the effects of drought on the establishment of native California plants, we tested for effects of the drought shelters on the California native plant seedlings within the restoration drought experiment (described in section 3) at YLR, started in 2016. Focal species include: *Stipa pulchra*, *Bromus carinatus* (Poaceae), *Sidalcea malviflora* (Malvaceae), *Mimulus aurantiacus* (Scrophulariaceae), *Artemisia californica*, *Achillea millefolium* (Asteraceae), *Eschscholzia californica* (Papaveraceae), and *Sisyrinchium bellum* (Iridaceae). Justin also collected from replanted species that did not have sufficient replication the previous year: *Ericameria ericoides* (Asteraceae), *Lupinus nanus* (Fabaceae) and *L. variicolor* (Fabaceae). Justin also replanted *Hosackia gracilis* for the same purpose with seeds collected by Groundswell Ecology, however the species was misidentified when collected. It was actually *Lotus corniculatus,* a non-native species. All planted *L. corniculatus* individuals were hand removed from all plots.

Justin collected leaf samples in order to measure drought specific functional traits, including Specific Leaf Area (leaf area ÷ oven dried weight), leaf thickness, major vein length per unit area, leaf carbon:nitrogen (C:N) ratios and $\delta^{13}C$ to determine Water Use Efficiency. Justin hypothesize that the planted seedlings that have survived to 2018 will have functional traits that confer drought tolerance, such as lower SLA , higher thickness, higher vein length per unit area (VLA), and higher WUE [measured via $\delta^{13}C$]. All data from 2019 are still being processed. This work was completed with the assistance of nine undergraduates and four high school students. Funds for the work completed by three of the high school students were provided by the UC Santa Cruz Science Internship Program (SIP).

Results

All results presented below are from 2018 data unless otherwise stated. Data collected in 2019 haves not been fully analyzed. Kaplan-Meier survival estimates are the same as the previous year. Hazard-Cox analysis which includes functional traits and main treatment effects on the planted community are analyses not previously reported on.

In 2018, Kaplan-Meier survival estimates showed that 4 out of 12 native plant species selected for restoration showed significant differences across treatments in survivorship from 2016-2018. *Sidalcea malviflora*, *Ericameria ericoides*, and *Stipa pulchra* exhibited significant differences in survivorship between treatments ($p < 0.05$), while *Eschscholzia californica* experienced marginal differences between treatments ($p = 0.09$; **Fig.** 1). For *E. ericoides,* differences primarily occurred during the first two years, while in the third year, treatment effects converged resulting in high death throughout.

Cox proportional hazard models found that both the shelter and water treatments significantly decreased the hazard risk of 12 planted native species when examined at the community level ($p < 0.05$; **Fig**. 3). Furthermore, we found at the community level, native species with more resource acquisitive traits such as high growth rate, large size and high major vein length per unit area (VLA) experienced higher hazard risk ($p < 0.05$). Native species with greater cumulative phylogenetic distance (CPD) experienced a decrease in hazard risk ($p <0.05$; **Fig.** 3). The larger the value of CPD the less related an individual is to its neighboring plant community. When looking only at the drought treatment we find that functional traits such as growth rate and VLA still significantly increase hazard risk ($p < 0.05$), but greater CPD does not decrease hazard risk. For the control treatment the functional traits are no longer significant predictors of hazard and CPD becomes the dominant factor, where greater CPD decreases hazard risk ($p < 0.01$).

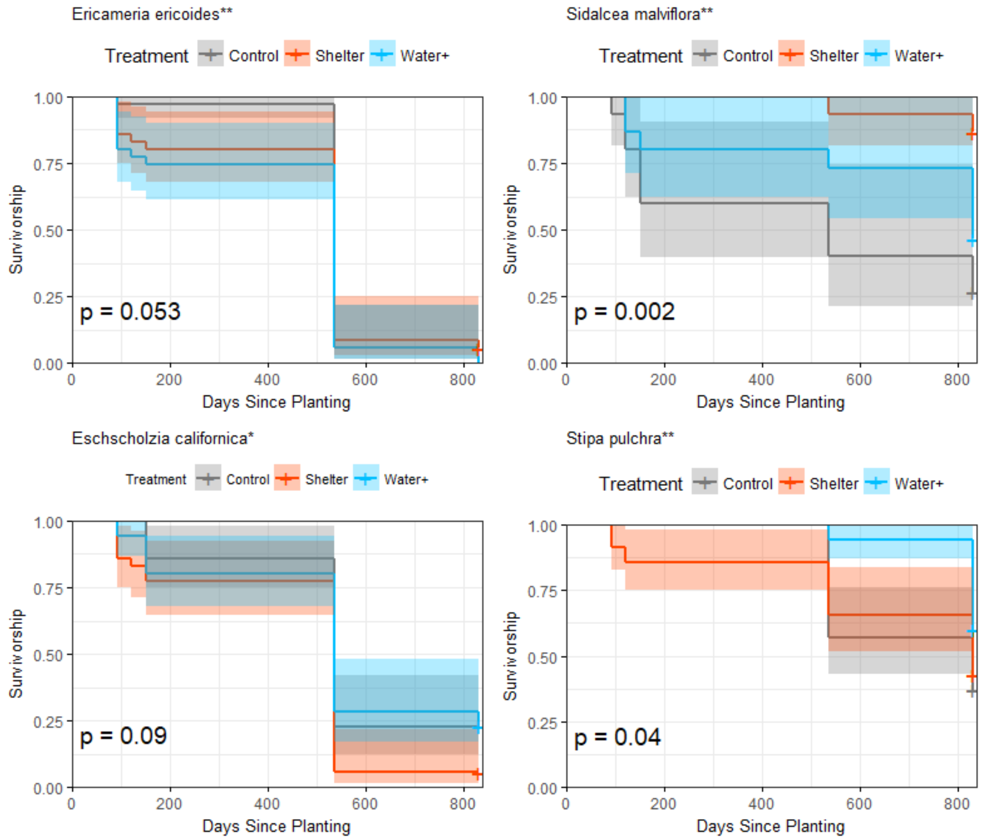

Fig. 1 Kaplan Meier Survival Curves for species that were found to have significant differences in survivorship by treatment type. Differences between treatments were determined through a non-parametric log-rank test. Pairwise differences between treatments were determined using a Cox Proportional Hazard Model.

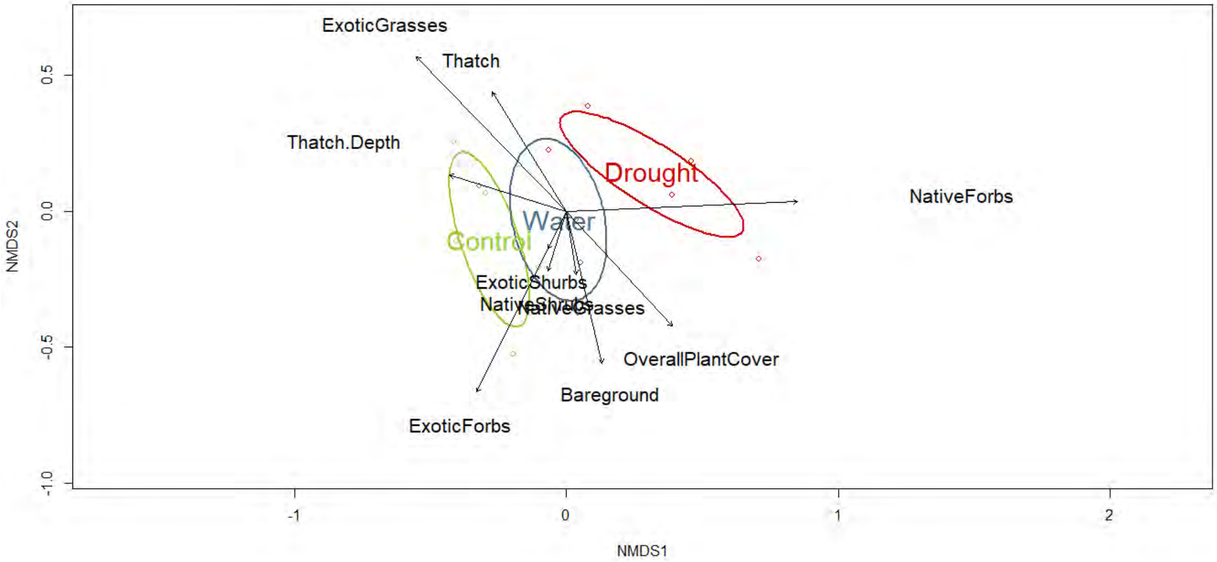

Fig. 2 Plot compares the vegetative community based on presence and total cover using Bray-Curtis dissimilarity indices. Vegetative communities of different treatment types are seen to clearly separate, with slight overlap in control and water treatments. Although multiple factors were significant, we found that exotic grass and forb cover play the strongest role in distinguishing these communities. Colored dots represent respective treatment types, where text could not be displayed due to overlapping text.

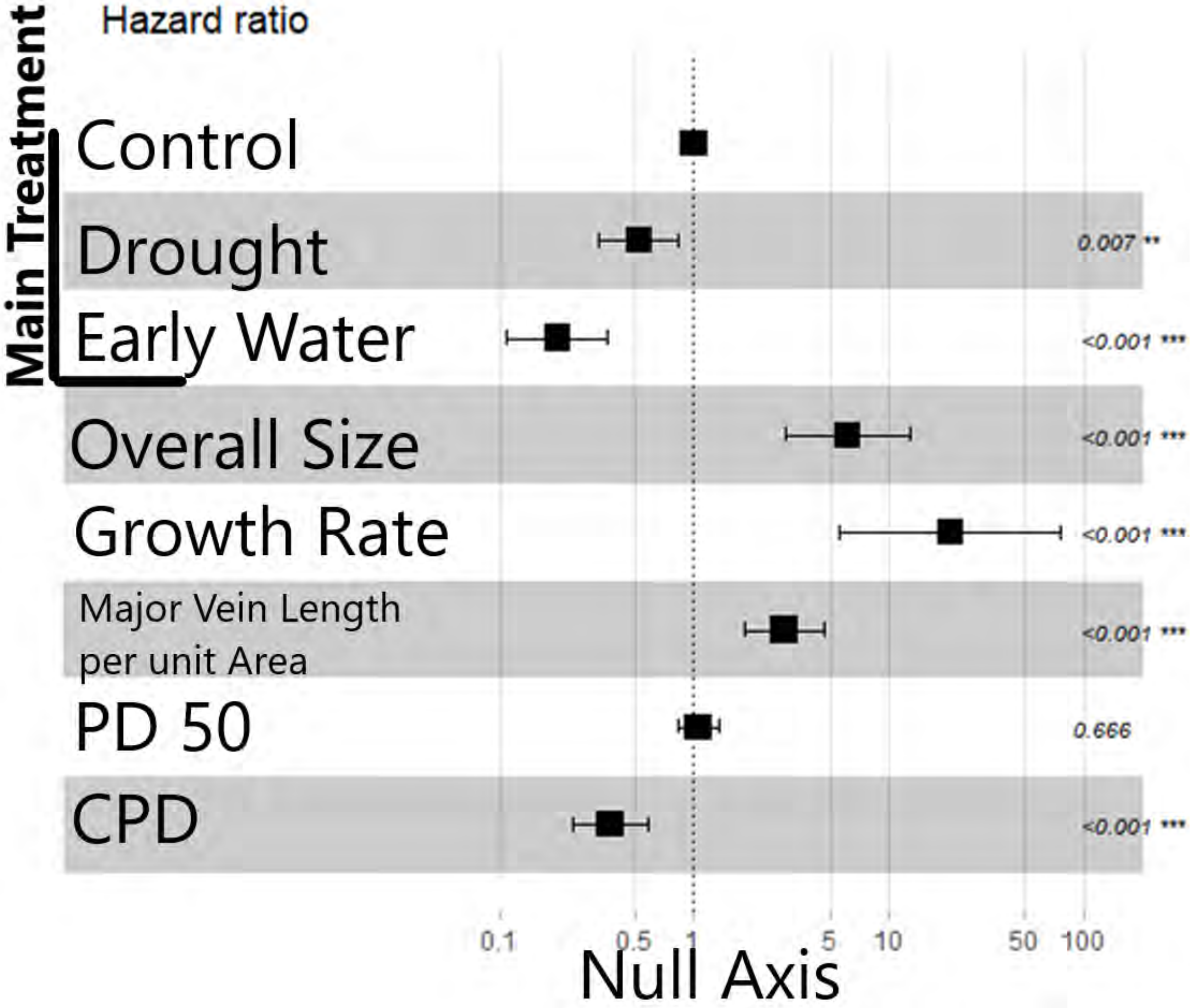

Fig. 3 Hazard-Cox Proportional Forest Plot shows the hazard potential for native species related to main treatment effects, functional traits and phylogenetic relationships. Note, specific leaf area was correlated with growth rate and major vein length per unit area and was not included in this analysis to reduce colinearity. It is assumed that it will follow a similar trend to values it is correlated to. Leaf thickness was correlated to VLA and cumulative phylogenetic distance which made its pattern undetectable. The null axis represents a point where there is no effect on hazard risk by treatment or trait. If the point falls to the right of the axis it indicates significantly higher hazard risk. If the point falls to the left of the axis it represents a significant decrease in hazard risk. The hazard ratio on the x-axis is the multiplier of risk (e.g. at five, 5× the hazard risk, at 0.5, 0.5× the hazard risk or half the risk).

Justin found that the shelter treatment lowered the overall cover of one native species, *Eschscholzia californica*, compared to the water and control treatments in 2018. But, there were no differences between water and control treatments. Conversely, there was higher cover in the shelter treatments for *Achillea millefolium* and *Stipa pulchra.* In 2018, *A. millefolium* also had a significantly greater spread in shelter treatments (80.93 cm) compared to control (60.61 cm) and water treatments (63.82 cm). No significant differences were found when analyzing species-specific growth parameters (such as rhizome spread in *A. millefolium*) from 2016-2018.

Justin found that the shelter treatment altered plant community composition in the plots (**Fig**. 2). In particular, we found that native grass cover, bare ground cover, exotic grass cover, thatch cover, thatch depth, exotic forb cover, native forb cover and native shrub cover were significantly different between treatments (PERMANOVA; $p < 0.05$) although weak, exotic grass and forb cover had the strongest correlations (PERMANOVA; $r^2 = 0.154$ and 0.142 respectively). In 2019, we found that the plant community composition in the plots had a similar pattern, still indicating that the drought significantly altered plant communities (**Fig.** 4).

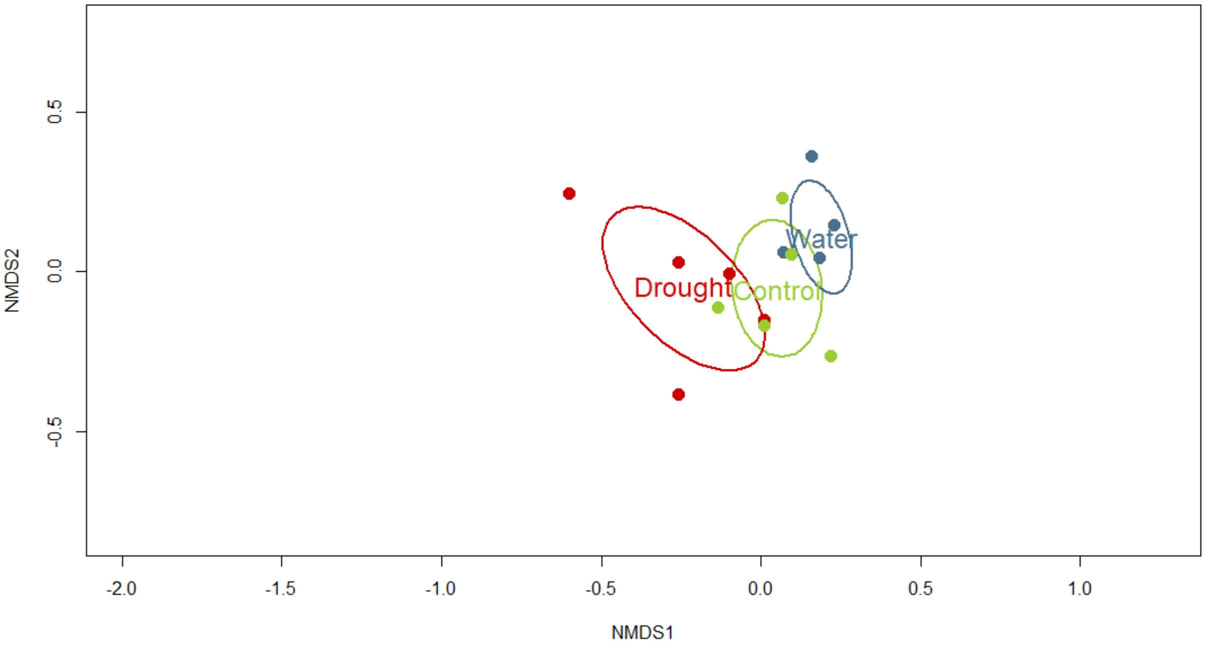

Fig. 4 Plot compares the vegetative community based on presence and total cover using Bray-Curtis dissimilarity indices. Vegetative communities of different treatment types are seen to separate, with slight overlap in treatments. Patterns are consistent with 2018 findings which indicate that drought will modify plant communities. Colored dots represent respective treatment types, where text could not be displayed due to overlapping text.

Discussion

Thus far, our results show that the majority of the twelve native plant species selected for restoration likely are adapted to drought, as the majority of species show no significant differences in species-specific growth, cover or survival. However, there are exceptions; for example, *E. californica* was shown to have lower cover in shelter treatments. Conversely, *S. malviflora* had higher survivorship under the shelter treatment, further indicating their potential drought resistance. Interestingly, *S. pulchra* was found to have greater survival when given water for establishment in the first year of planting. *A. millefolium* and *S. pulchra* both had greater cover in shelter plots. Additionally, *A. millefolium* had a greater lateral spreading distance in shelter treatments. At a community level, results indicate that these plants make a drought resistant community with lower drought hazard risk compared to ambient conditions.

Results suggest that watering in the first year to increase establishment could be beneficial for some native species such as *S. pulchra* on an individual level, but irrelevant to the survival of the other species we tested. At the community level, early watering was found to decrease the overall hazard risk indicating that early, targeted irrigation can improve native plant establishment. Combined with the community composition results, we hypothesize that native species with greater growth in shelter plots are experiencing competitive release. In fact, shelter plots were found to have less exotic grasses and exotic forbs. Shelter plots also had less thatch, which could have potentially affected young plant growth. Additionally, when treatments are separated, we find that functional traits are more important to hazard risk during drought whereas cumulative phylogenetic distance, a proxy for competition, is not important. This trend reverses in the control plots indicating that competition is less important to survival during drought and important in non-drought situations, which further indicates competitive release. However, controlled experiments are needed to determine whether differences are caused by release from direct competition for water, or due to alterations in local nutrient cycling based on varying thatch depth and cover. We are currently conducting functional trait analyses to further illuminate the importance between different drought adaptations.. If there is no correlation between drought functional traits and survival or growth, differences would likely be due to competitive release.

5. Measurements of hydraulic conductivity and infiltration

In 2019, we measured the hydraulic conductivity and the soil water infiltration rate for all 25 plots. Information about plot hydrology may prove to be covariates in determining differences between plant communities, and in future studies concerned with water and nutrient cycling. This work was completed with the assistance of three undergraduate interns.

6. Glasshouse Experiments on Competitive Release

This work, conducted by undergraduate Emma Clabby tests the hypothesis that native species are experiencing competitive release within drought-induced plots. As Justin found that native species have greater survival in drought plots, Justin and Emma have collected seeds from 6 native species used in the experiment and the 5 most dominant invasive species. These six native species are *Mimulus aurantiacus*, *Stipa pulchra*, *Bromus carinatus*, *Eschscholzia californica*, *Lupinus nanus* and *Sidalcea malviflora*. The non-native species consist of *Festuca bromoides*, *Carduus pycnocephalus*, *Geranium dissectum*, *Medicago polymorpha* and *Rapahanus sativus*. Native species will be grown in a factorial design with a drought and competition treatment. Results from this experiment will illuminate whether or not native species are experiencing competitive release from dominant invasive species when experiencing extreme drought. This work is supported by the Keeley Coastal Scholars provided through the Physical Sciences and Biology Dean's Office.

Personnel

We thank YLR Staff: Elizabeth Howard, Vaughan Williams, Kyla Roessler and the numerous interns at Younger Lagoon for supporting this work as well as ENVS graduate student Josephine Lesage. We thank undergraduates from Dr. Michael Loik's Plant Physiology class for assisting with field collection in spring 2019. We thank the Science Internship Program for providing funds to allow high school students to assist with this work. We thank support provided by the Keeley Coastal Scholar's award for the glasshouse competition experiment.

References

Loik M. E., Lesage J. C., Brown T. M., and **D. O. Hastings**. 2019. Drought-Net rainfall shelters did not cause non-drought effects on photosynthesis for California central coast plants. Ecohydrology https://doi.org/10.1002/eco.2138

Appendix 4. Photo monitoring

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #2. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

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YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

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YLR Beach Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Beach Photopoint #4. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Terrace Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

YLR Terrace Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

YLR Terrace Photopoint #1. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

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YLR Terrace Photopoint #3. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)


YLR Terrace Photopoint #4. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)


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YLR Terrace Photopoint #5. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

YLR Terrace Photopoint #5. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

YLR Terrace Photopoint #5. May 20, 2019. Photographer: Kyla Roessler. Apple iPad Pro (10.5)

YLR Terrace Photopoint #5. June 6, 2019. Photographer: Kyla Roessler. Camera: Apple iPhone 8

YLR Terrace Photopoint #5. June 6, 2019. Photographer: Kyla Roessler. Camera: Apple iPhone 8

YLR Terrace Photopoint #5. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Terrace Photopoint #6. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Terrace Photopoint #6. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


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YLR Terrace Photopoint #6. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Terrace Photopoint #7. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Terrace Photopoint #7. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


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YLR Terrace Photopoint #9. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

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YLR Terrace Photopoint #9. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)


YLR Terrace Photopoint #10. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Terrace Photopoint #10. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

YLR Terrace Photopoint #10. May 20, 2019. Photographer: Kyla Roessler. Camera: Apple iPad Pro (10.5)

Appendix 5. NOID 9 (18-1) special conditions implementation reports

UC Santa Cruz NOID 9 (18-1)

Revised Special Conditions Implementation Report 1

January 1, 2019 – June 30, 2019

Burrowing owl on the Younger Lagoon Reserve Beach Dunes

UC Santa Cruz NOID 9 (18-1)

Revised Special Conditions Implementation Report 1

Overview

UC Santa Cruz's Coastal Long Range Development Plan (CLRDP) Implementation Measure (IM) 3.6.3 requires that the public have supervised access to Younger Lagoon Reserve beach through docent-led visits, and that a monitoring program be created to document the condition of native flora and fauna within Younger Lagoon and its beach over a five-year period. IM 3.6.3 also requires that the campus prepare a report at the end of the five-year period which presents the results of the monitoring and a discussion of the potential effect of supervised beach access on flora and fauna at Younger Lagoon. At the end of each five-year period, the University must submit a NOID to the Coastal Commission to implement a beach access plan for the next five years.

In March 2010, the California Coastal Commission (Coastal Commission) approved the University of California's first NOID for Implementation Measure 3.6.3 (NOID 2 (10-1)). The campus began implementing the public access plan and monitoring program in spring 2010, and submitted the report on the results of the monitoring to the Coastal Commission in February of 2016 as part of the Younger Lagoon Annual Report.

The campus submitted NOID 9 (16-2) *Public Access to and Within Younger Lagoon Reserve* to the Coastal Commission in December 2016. At the request of local Coastal Commission staff, the campus withdrew NOID 9 (16-2) resubmitted it as NOID 9 (17-1) in June 2017. The campus presented NOID 9 (17-1) at the July 2017 Coastal Commission meeting. Although Coastal Commission staff found the NOID consistent with the CLRDP, a Commissioner requested the University consider providing significantly more tours to the beach and allow children to attend free of charge. The campus withdrew NOID 9 (17-1), worked with Coastal Staff on language for the resubmission, made changes to address Commissioner and Staff requests, and resubmitted it as NOID 9 (18-1) in August 2018.

On September 13, 2018, the California Coastal Commission approved UC Santa Cruz's NOID 9 (18-1) as consistent with UCSC's approved Coastal Long Range Development Plan with the addition of five staff-recommended special conditions. These included 1) Free Beach Tours, 2) Beach Tour Outreach Plan, 3) Beach Tour Signs, 4) Beach Tour Availability and Monitoring, and 5) Beach Access Management Plan Duration. Within 30 days of the approval (i.e., by October 13, 2018), UCSC was required to submit a plan for implementation of the special conditions to the Executive Director of the California Coastal Commission. The plan for implementation of the special conditions was submitted to the Executive Director of the California Coastal Commission on October 15, 2018. UCSC received feedback from Coastal Commission staff on the plan, and a revised plan for implementation of the special conditions was submitted to the Executive Director of the California Coastal Commission on December 15, 2018. The revised plan for implementation of the special conditions was approved by the Executive Director on January 30, 2019. Special Condition 4 requires that at least every six months (i.e., by June 30th and December 31st each year), UCSC shall submit two copies of a Beach Tour Monitoring Report for Executive Director review and approval. Although the revised plan for implementation of the special conditions was approved by the Executive Director on January 30, 2019, UCSC began implementing some of the special conditions prior to final approval of the implementation plan. UCSC's initial report on the implementation of these special conditions for the period of January 1, 2019 through June 30, 2019 was submitted on June 28, 2019. Upon review, local Coastal Commission staff requested more detail regarding the implementation of Special Condition 2. UCSC's revised report on the implementation of the special conditions for the period of January 1, 2019 through June 30, 2019 is detailed in this report. The report for the period of July 1, 2019 through December 31, 2019 will be submitted by December 31, 2019.

Background

More than fifty years ago, the University of California Natural Reserve System began to assemble, for scientific study, a system of protected sites that would broadly represent California's rich ecological diversity. Today the UC Natural Reserve System is composed of 41 reserves that encompass approximately 750,000 acres of protected natural land available for university-level instruction, research, and outreach. The University of California Natural Reserve System supports research and education through its mission of contributing *"to the understanding and wise management of the Earth and its natural systems by supporting university-level teaching, research, and public service at protected natural areas throughout California."* By creating this system of outdoor classrooms and living laboratories, and making it available specifically for long-term study and education, the NRS supports a variety of disciplines that require fieldwork in wildland ecosystems. UC Santa Cruz administers four UC Natural Reserves: Younger Lagoon Reserve, Año Nuevo Island Reserve, Landels-Hill Big Creek Reserve, and Fort Ord Natural Reserve as well as a 400-acre campus reserve.

History of Public Access to Younger Lagoon Beach

This summary provides a coarse overview of the major events that affected beach access at Younger Lagoon. Prior to 1972, Younger Beach was privately owned and closed to the public. The owners (Donald and Marion Younger) actively patrolled for, and removed, trespassers from their property, including the beach. In 1972, the Younger Family donated approximately 40 acres of their property to the University of California for the study and protection of the marine and coastal environment. These lands included Younger Lagoon and Beach (approximately 25 acres), and an adjoining parcel of land (approximately 15 acres) which became the site of the original Long Marine Laboratory. At the time of their donation, Donald and Marion Younger intended that the lagoon, beach and surrounding slopes be protected in perpetuity by the University as a bird sanctuary, and the original coastal permit for the site (P-1859) deemed that the "lagoon will be managed and preserved as a natural area for waterfowl and terrestrial birds and animals".

In the years between the donation of the property and the start of Long Marine Laboratory construction (1976), the University leased the future Long Marine Laboratory site back to farmers who had been farming the property for the Younger family prior to the donation. During those years, the same no-trespassing rules for the beach were enforced as when the property was owned by the Younger family.

Once construction of Long Marine Laboratory began in 1976, the land was no longer under the watch of the farmers, and public pressure on the beach began to increase. Many Santa Cruz locals remember the next several years at Younger Beach fondly as it became a popular nude beach. The increased public access had a noticeable impact on the flora and fauna of the beach, and was not in accordance with the intention of the original donation by the Younger family. By 1978 discussions had begun between the University and the California Coastal Commission regarding the impact of uncontrolled public access to the beach. In 1981, it was decided that the impacts to Younger Beach were significant and the California Coastal Commission, under coastal permit P-1859, closed uncontrolled access to the beach.

After the approval of the 1981 coastal permit P-1859, the University began actively to patrol the beach for trespass and to educate the public about the closure. After Younger Lagoon Reserve was incorporated into the UC Natural Reserve System in 1986, users were required to fill out applications or contact Natural Reserve staff for specific research, education, or outreach efforts. As the Long Marine Laboratory campus grew, a protective berm and fencing were constructed around the perimeter of the lagoon, and informational 'beach closed' signs were posted on the cliffs above the beach. Over time, trespass decreased and the reduced public access had a noticeable positive impact on flora fauna as well as beach/dune habitat. (See 2009-2010, 2010-2011, 2011-2012, 2012-2013, 2013-2014, 2014-2015, 2016-2017, and 2017-2018 Annual Reports).

Public access to Younger Lagoon Reserve beach came to the forefront again during the CLRDP negotiation process (2000-2008). At the time negotiations began, Younger Lagoon Reserve supported a rich composition of plant and animal species despite being surrounded by agricultural and urban development. Reserve staff were concerned that any increase in public access could threaten the already heavily impacted habitat and impact ongoing and future research efforts. After CLRDP certification (2009), Beach Access Management Plans were implemented as outlined in UC Santa Cruz's NOID 2 (10-1) and NOID 9 (18-2). Under the current Beach Access Management Plans, the Younger Lagoon Reserve beach remains closed to unsupervised public access and the reserve has implemented a management and monitoring plan that is consistent with other UC Reserves and includes public access through free docent-guided beach tours. Although infrequent, unauthorized uses including trespass and vandalism of the Younger Lagoon Reserve beach continue and put research equipment and sensitive resources at risk. Reserve staff will continue to work hard to protect sensitive resources and maintain the Younger Lagoon Reserve beach as an important outdoor classroom and living laboratory.

Members of the public entering Younger Lagoon Reserve are required to adhere to the UC Natural Reserve System Reserve Use guidelines. Because beach tours are limited to groups with trained docents. No additional signage or fences on the beach have been required. The beach access trail consists of a simple dirt/mulch path that was in place prior to the approval of NOID 2 (10-1). The trail is maintained by clipping overgrown vegetation and maintaining the earthen path and timber steps as needed.

Special Condition 1.

FREE BEACH TOURS

All beach tours shall be offered for free, and UCSC shall not require that beach tour users pay any separate admission fee to any other facility in order to take the beach tour. This condition shall not be construed as affecting existing already allowed admission fees for UCSC's Seymour Marine Discovery Center. Beach tour signups may be provided online (e.g., at UCSC Marine Science Campus and Seymour Marine Discovery Center websites) but shall at a minimum be made available by phone and at the Seymour Marine Discovery Center front desk. UCSC shall also identify and implement a mechanism for tracking the number of tour requests that are denied due to lack of tour availability or because tours are fully booked. All UCSC materials referencing the beach at Younger Lagoon and/or beach tours shall be required to be modified as necessary to clearly identify that access to the beach is available for free via beach tours. Within 30 days of this approval (i.e., by October 13, 2018), UCSC shall provide evidence to the Executive Director identifying the manner in which (1) free beach tour signups are made available, (2) tour request denials are quantified and recorded, and (3) UCSC materials have been modified to reflect that beach access is available for free via beach tours, all consistent with this condition.

Implementation Report

All beach tours are now offered for free (without admission fee). Beach tour sign-ups are available by phone and at the Seymour Marine Discovery Center (Seymour Center) public admissions counter. Seymour Center staff track any tour requests that are denied due to lack of tour availability or because tours are fully booked as part of their ongoing monitoring of all visitor programs. Seymour Center staff record the number of participants that were denied, the number of participants that were wait listed, as well as the date of the request and the date of the tour being requested (see Appendix 1). The Younger Lagoon Reserve and the Seymour Marine Discovery Center websites have been modified to clearly identify that access to the beach is available for free via beach tours.

https://youngerlagoonreserve.ucsc.edu/about-us/index.html
https://youngerlagoonreserve.ucsc.edu/research-teaching-public-service/visit/public-tours.html
https://seymourcenter.ucsc.edu/visit/behind-the-scenes-tours/

Special Condition 2.

BEACH TOUR OUTREACH PLAN

Within 30 days of this approval (i.e., by October 13, 2018), UCSC shall submit two copies of an Outreach Plan for Executive Director review and approval, where such Plan shall identify all measures and venues to be used to advertise and increase awareness of the free beach tours (e.g., UCSC Marine Science Campus and Seymour Marine Discovery Center websites, press releases, calendar listings with UCSC Events and local media (e.g., Good Times newspaper), ads on radio (e.g., public radio station KAZU), print ads, social media (including Facebook, Twitter, and Instagram), etc.). The Plan shall identify the language to be used in describing the free beach tours (where said language shall be required to be consistent with the terms and conditions of this approval), and shall provide a schedule for each type of outreach, with the goal being to reach as many potential free beach tour audiences as possible, including audiences that might not normally be reached through traditional and local means (e.g., inland communities). UCSC shall implement the approved Outreach Plan as directed by the Executive Director.

Implementation Report

Outreach was conducted according to the following plan during the reporting period:

Venue	Language	Schedule	Notes
Seymour Center Website	Younger Lagoon Reserve tours are free and open to the public. Space is limited to 14 participants. Call **831-459-3800**.	Permanent webpage: https://seymourcenter.ucsc.edu/visit/behind-the-scenes-tours/	Website updated April 14, 2019
YLR Website	Younger Lagoon Reserve tours are free and open to the public. Space is limited to 14 participants. Call **831-459-3800**.	Permanent webpages: https://youngerlagoonreserve.ucsc.edu/research-teaching-public-service/visit/public-tours.html	Websites updated April 14, 2019
Seymour Center Social Media o Facebook o Twitter o Instagram	Younger Lagoon Reserve tours are free and open to the public. Space is limited to 14 participants. Call **831-459-3800**.	Facebook—Monthly Twitter, Instagram ---Once a quarter	Recurring event posted on April 10, 2019 to Seymour Center Facebook for each tour date in 2019. Each tour date remains posted until the tour passes. As of July 1, 2019, the post had

			reached 621 people and received 39 responses. Link: https://www.facebook.com/events/569400223466408/ Free beach tours posted to Seymour Center Instagram on May 11, 2019. As of July 1, 2019, the post had received 63 likes. Link:https://www.instagram.com/p/BxVWf8HDqAD
YLR Social Media o Facebook o Instagram	Younger Lagoon Reserve tours are free and open to the public. Space is limited to 14 participants. Call **831-459-3800**.	Once a quarter	Free beach tours posted to YLR Facebook on May 3, 2019. As of July 1, the Facebook post had received 3 likes and 3 shares. Link: https://www.facebook.com/youngerlagoonreserve/photos/a.674854832580620/2390061137726639/?type=3&theater Free beach tours posted to YLR Instagram On May 6, 2019, Younger Lagoon Reserve staff posted the beach tours to Instagram. As of July 1, the Instagram post received 53 likes. Link: https://www.instagram.com/p/BxIfvgPAh4R/
Calendar Listings o UCSC Events o Good Times Newspaper (Santa Cruz) o KAZU public radio (Santa Cruz) o Register Pajaronian Newspaper (Watsonville)	Younger Lagoon Reserve tours are free and open to the public. Space is limited to 14 participants. Call **831-459-3800**. For Spanish language outlets: Las visitas guiadas a la reserva de la	Submitted monthly (calendar listings appear at the discretion of the media outlet.) Submitted monthly (calendar listings appear at the	**UCSC Events** Submitted for the entire 2019 year in December 2018, revised text submitted in April 2019. Posted for the entire calendar year. Link:https://calendar.ucsc.edu/event/seymour_center_younger_lagoon#.XVSEiJPYqCQ

o The Californian Newspaper (Salinas) o La Network Campesina Radio 107.9 (Salinas)	laguna Younger son gratuitas y están abiertas al público. El espacio está limitado a 14 participantes. Llame al **831-459-3800**.	discretion of the media outlet.)	**Good Times Newspaper (Santa Cruz)** Submitted for the entire 2019 year in December 2018, revised text submitted in April 2019. Posted for the entire calendar year. Link:https://www.santacruz.com/events/younger-lagoon-reserve-tours-at-seymour-marine-discovery-center-aug-15th-2019-10-30am-2 Posting revised July 2019 to correct typo reference to beach tours. Link:https://www.santacruz.com/events/younger-lagoon-reserve-tours-at-seymour-marine-discovery-center-sep-8th-2019-10-30am-2 **KAZU public radio (Santa Cruz)** Submitted for the entire 2019 year in April 2019. Posted for the remainder of the calendar year. Link:https://www.kazu.org/community-calendar/event/471794#stream/0 **Register Pajaronian Newspaper (Watsonville)** Submitted for the entire 2019 year in April 2019. No known postings as of July 1, 2019. **The Californian Newspaper (Salinas)** Submitted for the entire 2019 year in April 2019.

			Posted in English and Spanish for the remainder of the calendar year. Link: http://events.thecalifornian.com/santacruz/events/younger-lagoon-reserve-tour-/E0-001-129064520-4 **La Network Campesina Radio 107.9 (Salinas)** Submitted for the entire 2019 year in April 2019. No known postings as of July 1, 2019.

Additional Public Education Opportunities on the Coastal Science Campus

Seymour Marine Discovery Center

The free docent guided beach tours are part of broader public education and outreach programming on the Coastal Science Campus offered through the Seymour Center. Every year, nearly 70,000 people visit the Seymour Center, and over 17,000 visitors take docent-guided tours. The Seymour Center provides marine science education to hundreds of classes, comprised of thousands of students, teachers, and adult chaperones from across the country. Many of the classes served come from schools classified as Title 1—schools with high numbers of students from low-income families. Scholarships are made available to Title 1 schools, making it possible for students to participate who would not otherwise have the opportunity to experience a marine research center. Teachers often incorporate the Seymour Center into their weeklong marine science field study courses, and every year, nearly 10,000 students visit the Seymour Center through the Seymour Center's school groups program.

Every year, dozens of children ages 7-14, enroll in weeklong summer science sessions known as Ocean Explorers. Students actively learn about and participate in marine research at the Seymour Center and Long Marine Laboratory, where participants work alongside marine mammal researchers and trainers. Participants gain experience with the scientific process, focusing on honing their observation and questioning skills. Ocean Explorers also investigate the coastal environment at field sites around Monterey Bay, including rivers and watersheds, sandy beaches, rocky intertidal areas, and kelp forests by kayak. Young participants generally come from Santa Cruz, Santa Clara, and San Mateo Counties. Full and partial scholarships are extended to low-income participants.

While part of UC Santa Cruz, the Seymour Center must raise its ~$1.5 million budget annually (including all operating costs, salaries, and benefits) from earned revenue, private donors and grants. Earned revenue—admissions, program fees, facility rentals, and the Ocean Discovery Shop—makes up approximately half of its general operating requirements.

Watsonville Area Teens Conserving Habitat (WATCH)

Over the last five years, the Seymour Center, Younger Lagoon Reserve and the Monterey Bay Aquarium have partnered every year to support high school students in the Watsonville Area Teens Conserving Habitats (WATCH) program. WATCH students from Aptos High School design and carry out field-based research projects in Younger Lagoon Reserve on topics including endangered fish, aquatic invertebrates, and birds. These students make repeated visits to the Reserve throughout the year. Find out more at: https://www.montereybayaquarium.org/education/teen-programs/watsonville-area-teens-conserving-habitats-watch

Community Bioblitz

Over the last four years, Younger Lagoon Reserve and the California Academy of Sciences have partnered to host an annual Younger Lagoon Reserve Bioblitz. A bioblitz is a community event that brings together a wide variety of people – citizen scientists - to rapidly inventory the living organisms found in a particular place. The Younger Lagoon Reserve Bioblitz is held during the spring, and is open to members of the public. Participants explored the lagoon and beach areas as part of this event. A link to the page advertising this community event can be found here: https://www.inaturalist.org/projects/younger-lagoon-reserve-bioblitz-2019

Volunteer Stewardship Days

Every year, Younger Lagoon Reserve hosts numerous volunteer stewardship days. These events are advertised on social media and open to the public. Volunteer stewardship days provide members of the public with the opportunity to learn about the reserve and its unique habitats, wildlife, research, restoration, and teaching programs while giving back.

Special Condition 3.

BEACH TOUR SIGNS

Within 30 days of this approval (i.e., by October 13, 2018), UCSC shall submit two copies of a Beach Tour Sign Plan for Executive Director review and approval, where such Plan shall provide for installation of signage outside of the Seymour Marine Discovery Center and inside at its front desk, at Campus overlooks, and at other appropriate public access locations on the Marine Science Campus that describe free beach tour availability, including "day of" signs for each day beach tours are offered to ensure maximum notice is provided. All such signs shall be sited and designed to be visually compatible with the area, shall be consistent with the Campus sign program (and CLRDP sign requirements), and shall provide clear information in a way that minimizes public view impacts. UCSC shall implement the approved Beach Tour Sign Plan as directed by the Executive Director.

Implementation Report

UCSC's Beach Tour Sign Plan was reviewed and approved as part of the NOID 9 Special Conditions Implementation Plan on January 30, 2019. Per the approved sign plan, information on the free beach tours is currently displayed "day of" on a large sign in the front window of the Seymour Center and at the public admissions counter. The Seymour Center is in the process of purchasing and installing a large colorful monitor to replace the "day of" sign in the front window. Admissions counter signage includes the brown and white footprints on wave logo, and the following language "Free Younger Lagoon Reserve Beach Tours Today" (see Figures 1 and 3). Signage has been added to the information kiosk outside of the Seymour Center and to Overlooks A-F. Overlooks, admissions counter, and kiosk signage include the brown and white footprints on wave logo, and include the following language "Free Younger Lagoon Reserve Beach Tours, Call (831) 459-3800" (see Figures 2 and 4).

Figure 1. “Day of” sign design.

Figure 2. Overlooks and kiosk sign design.

Figure 3. “Day of” sign displayed at the Seymour Center front admissions desk.

Figure 3. “Day of” sign displayed at the Seymour Center front entrance window.

Figure 4. Representative overlook sign installation (Overlook C).

Additional Public Access and Signage on the Coastal Science Campus

Public Trails, Overlooks, Signage

UC Santa Cruz CLRDP Policy 6.1 requires that maximum public access to the coastal resources of the Coastal Science Campus and the adjacent shoreline and coastal area be provided consistent with public safety, fragile coastal resources, implementation of the educational and research missions of the Campus, and security of sensitive facilities and research activities on the site. Since the approval of the CLRDP, numerous public access improvements have been implemented on the campus, including public ADA accessible multi-use trails that connect with the adjacent De Anza Mobile Home Park public access gate and beach (NOID 6 (13-1)), public benches (NOID 5 (12-1)), and NOID 6 (13-1)), public overlooks (NOID 5 (12-1) and NOID 6 (13-1)), interpretive signage (NOID 5 (12-1)) and NOID 6 (13-1)), and signage advertising the free beach tours (NOID 9 (18-1)) (Figure5).

Visual access to the lagoon and back dune is provided to the public via Overlook E (Figure 6). Overlook E is open to the public and includes interpretative signage that provides information on the free beach tour. Visual access to the Younger Lagoon beach, information about Younger Lagoon Reserve, bilingual interpretative signage, and signage that provides information on the free beach tour is provided to all visitors taking the Seymour Center's docent-guided Reserved and Daily Tours and all K-12 visitors participating in the Seymour Center's School Groups Programs at Overlook C (Figure 7). Last year, nearly 25,000 visitors participated in these programs. Visual access to the lagoon and back dune, bilingual interpretative signage, and signage that provides information on the free beach tour is provided to all visitors taking the free beach tour and other approved reserve user groups, including K-12 visitors at Overlook D (Figure 8).

<ins>Figure 5</ins>. UC Santa Cruz Coastal Science Campus Public Access Improvements. This photo shows improvements along the Bluff Trail that are representative of improvements throughout the campus, including public ADA accessible multi-use trails, public benches, public overlooks, bilingual interpretive signage (English and Spanish), and signage advertising the free beach tour. The overlook in this photo, Overlook F, is open to the public and provides visual access to the coast.

Figure 6. The view from Overlook E located along McAllister Way. Overlook E is open to the public and includes interpretative signage that provides information on the free beach tour.

Figure 7. The view from Overlook C. Overlook C is accessible through docent-guided tours and includes bilingual interpretative signage and signage that provides information on the free beach tour. Approximately 25,000 people visit Overlook C annually as part of the Seymour Center's docent guided tour and school groups programs.

Figure 8. Overlook D. Overlook D is accessible through docent-guided tours and to other approved users, including k-12 groups. Overlook D includes bilingual interpretative signage and information on the free beach tour.

Special Condition 4.

BEACH TOUR AVAILABILITY

Beach Tour Availability and Monitoring. UCSC shall offer at least four beach tours per month (of which at least one per month is a weekday tour and at least two per month are weekend tours) from March 1st through September 30th each year, and shall provide at least two beach tours per month (of which at least one per month is a weekday tour and at least one per month is a weekend tour) otherwise (a minimum of 38 total beach tours per year). UCSC may limit the number of beach tour participants to 14 persons per tour, but this number may be exceeded per tour on a case by case basis, and beach tours shall not require any minimum number of participants to be provided (i.e., if at least one person signs up, the tour shall be provided). UCSC shall document the date/time and number of participants for each beach tour, as well as the number of tour requests that are denied due to lack of tour availability or because tours are fully booked (see also ***Condition 1****).*

At least every six months (i.e., by June 30th and December 31st each year), UCSC shall submit two copies of a Beach Tour Monitoring Report for Executive Director review and approval, where the Report shall at a minimum provide information regarding compliance with these conditions of approval, including a section identifying UCSC's activities under the approved Beach Tour Outreach Plan (see ***Condition 2****), as well as the required information described in the previous paragraph. Each such Monitoring Report shall include a section that identifies recommendations about whether user data suggests that beach tours should be increased in terms of frequency of tours and/or number of tour attendees, or otherwise modified to better respond to user demand, including the potential to offer a more limited beach area tour (e.g., designed to allow participants to access just the sandy beach area itself in a shorter amount of time) as a means of offsetting demand. UCSC shall implement any Executive Director-approved recommendations from each Beach Tour Monitoring Report.*

Implementation Report

Free beach tours are offered at least four times per month (of which at least one per month is a weekday tour and at least two per month are weekend tours) from March 1st through September 30th, and at least two times per month (of which at least one per month is a weekday tour and at least one per month is a weekend tour) otherwise (a minimum of 38 total beach tours per year). During the time period covered by this report, free beach tours were offered twice a month in January and

February, and four times per month in March, April, May, and June. A total of 20 free beach tours were offered in the first six months of this calendar year (See Appendix 1). Beach tour participants were limited to 14 persons per tour on all but one tour. In that instance, the number of beach tour participants was increased to 16 persons (the maximum number the docent felt comfortable leading), and another two persons were denied a beach tour and instead offered a Seymour Center daily tour, which included vistas of the lagoon and beach. Beach tours do not require any minimum number of participants to be provided (i.e., if at least one person signs up, the tour will be provided). UCSC has documented the date/time and number of participants for each beach tour, as well as the number of tour requests that are denied due to lack of tour availability or because tours are fully booked (see also Condition 1, and Appendix 1).

At least every six months (i.e., by June 30th and December 31st each year), UCSC will submit two copies of a Beach Tour Monitoring Report for Executive Director review and approval, where the Report will at a minimum provide information regarding compliance with these conditions of approval, including a section identifying UCSC's activities under the approved Beach Tour Outreach Plan (see Condition 2), as well as the required information described in the previous paragraph and Condition 4 above. The first such report was submitted by June 30, 2019, the revised report (this report) will be completed by August 31, 2019.

UCSC offered 20 free beach tours (103 participants) during the first six months of 2019 (January 1, 2019 – June 30, 2019) (see Appendix 1). All but one of these tours had at least one participant. One tour did not go out due to lack of sign-ups. Ten of the tours that went out included walk-in / "day-of" participants. Only one tour was overbooked. In that case, the tour group size was increased to 16, and the remaining two interested participants were denied a beach tour and instead offered a Seymour Center daily tour, which included vistas of the lagoon and beach.

In comparison, UCSC offered 20 beach tours (95 participants) during the first six months of 2018 (January 1, 2018 – June 30, 2018) (see Appendix 2). Two tours did not go out due to lack of sign-ups, and one tour was canceled due to weather. Four of the tours that went out included walk-in / "day-of" participants. No tours were overbooked during the first six months of 2018.

Although not required by the special conditions, in addition to tracking user data, UCSC also collected data on the biological impacts of the tours. Beginning on April 14, 2019, Younger Lagoon Reserve staff accompanied tours, and documented impacts to avian wildlife on the beach. Staff observed birds flushing from the wet sandy beach, beach dunes, coastal stack, and lagoon in response to every tour (see Appendix 3).

Recommendations

Although only in place for a few months, the beach tours as specified by UCSC’s NOID 9 special conditions appear to be meeting user demand. The number of tour participants served increased approximately 10% compared to the same time period during the previous year. Over the last six months, only two participants were denied a tour, and these participants were accommodated on another Seymour Center tour that offered vistas of the lagoon and beach later that day. The documented biological impacts to avian wildlife described above, along with ongoing quarterly beach monitoring efforts indicate that open access to the beach would result in the loss of the unique ecological characteristics of the site, reduce its effectiveness as a research area for scientific study, and likely have a negative impact on sensitive and protected species (See 2009-2010, 2010-2011, 2011-2012, 2012-2013, 2013-2014, 2014-2015, 2015-2016, 2016-2017, and 2017-2018 Annual Reports). We recommend continuing the tours as outlined in the special conditions for the next six months.

Special Condition 5.

BEACH ACCESS MANAGEMENT PLAN DURATION

This approval for UCSC's public beach access management plan at Younger Lagoon Beach shall be effective through December 31, 2020. UCSC shall submit a complete NOID, consistent with all CLRDP requirements, to implement its next public beach access management plan at Younger Lagoon Beach (for the period from January 1, 2021 to December 31, 2025) no later than July 1, 2020. Such complete NOID shall at a minimum summarize the results of the Beach Tour Monitoring Reports (see Condition 4), and shall identify the manner in which UCSC's proposed management plan responds to such data, including with respect to opportunities to increase public access to the beach area (when considered in light of potential impacts to UCSC research and coastal resources). If such complete NOID has not been submitted by July 1,2020, then UCSC shall allow supervised (via beach and trail monitors only) general public access to Younger Lagoon Beach during daylight hours (i.e., one hour-before sunrise to one hour after sunset) until such NOID has been submitted.

Implementation Report

UCSC will submit a complete NOID, consistent with all CLRDP requirements, to implement its next public beach access management plan at Younger Lagoon Beach (for the period from January 1, 2021 to December 31, 2025) no later than July 1, 2020.

Appendix 1. Tour Data January 1, 2019 – June 30, 2019

Tour Date	Day	Participants	Walk in	Reservation	No Show	Denial / Wait list
1/3/19	Thursday	2	2	0	0	0
1/13/19	Sunday	7	0	7	0	0
2/7/19	Thursday	3	0	3	0	0
2/10/19	Sunday	6	1	5	0	0
3/3/19	Sunday	10	3	7	0	0
3/719	Thursday	3	0	4	1	0
3/1019	Sunday	9	6	3	0	0
3/2119	Thursday	3	0	4	1	0
4/4/19	Thursday	10	6	4	0	0
4/7/19	Sunday	9	4	5	0	0
4/14/19	Sunday	9	2	11	4	0
4/18/19	Thursday	5	1	5	1	0
5/2/19	Thursday	1	0	1	0	0
5/5/19*	Sunday	0	0	0	0	0
5/12/19	Sunday	2	0	2	0	0
5/16/19	Thursday	1	0	1	0	0
6/2/19	Sunday	3	0	3	0	0
6/6/19	Thursday	1	1	0	0	0
6/9/19	Sunday	16	4	14	0	2**
6/20/19	Thursday	3	1	2	0	0

*5/5/19 - No tour; no participants

**Denial due to overdemand; participants accommodated on a Seymour Center daily tour, which included vistas of the lagoon and beach, later that day.

Appendix 2. Tour Data January 1, 2018 – June 30, 2018

Tour Date	Day	Participants	Walk in	Reservation	No Show
1/4/18	Thursday	3	1	2	0
1/14/18	Sunday	3	0	3	0
2/1/18	Thursday	6	0	6	0
2/11/18	Sunday	2	1	1	0
3/1/18*	Thursday	1	0	1	0
3/4/18	Sunday	2	0	2	0
3/11/18	Sunday	6	1	5	0
3/15/18	Thursday	2	2	0	0
4/5/18	Thursday	11	0	11	0
4/8/18	Sunday	2	0	2	0
4/19/18	Thursday	8	0	8	0
4/22/18	Sunday	2	0	3	1
5/3/18	Thursday	11	0	11	0
5/6/18	Sunday	7	0	7	0
5/13/18	Sunday	2	0	2	0
5/17/18**	Thursday	0	0	0	0
6/3/18	Sunday	0	0	0	0
6/7/18	Thursday	10	0	11	1
6/10/18	Sunday	7	0	7	0
6/21/18	Thursday	10	0	13	3

*3/1/18 – Canceled due to weather

**5/17/18 – Canceled; no sign-ups

***6/3/18 – Canceled; no sign-ups

Appendix 3. Avian Wildlife Impact Data, April 14, 2019 – June 30, 2019

Tour Date	Day	Species Present	Species Flushed
4/14/19	Sunday	AMCO, BLOY, BRAC, CCGO, GREG, MALL, SNEG, WEGU	BLOY, CCGO, MALL
4/18/19	Thursday	BLOY, BRAC, MALL, SNEG, SOSP, WEGU	BLOY, MALL, SNEG
5/2/19	Thursday	CCGO, BRBL, GREG, KILL, MALL, RSHA, WEGU	BRBL, CAGO, GREG, MALL, WEGU
5/5/19*	Sunday	No tour	No tour
5/12/19	Sunday	MALL, NOMO RNPH, WEGU, WESA	WESA
5/16/19	Thursday	BLPH, BRAC, GREG, KILL, MALL, RNPH, WEGU	MALL
6/2/19	Sunday	BARS, BLPH, MALL, PIGU, WEGU, WESA	BLPH, MALL WESA
6/6/19	Thursday	AMRO, BARS, BLPH, BRAC, BRBL, CAGO, CLSW, GREG, MALL, PECO, PIGU, WEGU	CAGO, GREG, PIGU, WEGU
6/9/19	Sunday	BARS, BLPH, BRAC, KILL, PIGU, RWBL, SOSP, WEGU	BARS, BLPH, PIGU, RWBB
6/20/19	Thursday	AMCR, BARS, BLPH, BRAC, PIGU, WEGU	BLPH, PIGU, WEGU

*5/5/19 - No tour; no participants

AMCO – American coot, **AMCR** – American crow, **AMRO** – American robin, **BARS** – Barn swallow, **BLOY** – Black oystercatcher, **BLPH** – Black phoebe, **BRAC** – Brand's cormorant, **BRBL** – Brewer's blackbird, **CCGO** – Canada goose, **GREG** – Great egret, **MALL** – Mallard, **NOMO** – Northern mockingbird, **PECO** – Pelagic cormorant, **PIGU** – Pigeon guillemot, **RNPH** – Red-necked phalarope, **RSHA** – Red-shouldered hawk, **RWBL** – Red-winged blackbird, **SNEG** – Snowy Egret, **SOSP** – Song sparrow , **WEGU** – Western gull

Appendix 6. Publications

Simulating International Drought Experiment field observations using the Community Land Model

Article *in* Agricultural and Forest Meteorology · January 2019

3 authors:


Timothy Hilton
University of California, Santa Cruz
26 PUBLICATIONS **434** CITATIONS
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Michael E Loik
University of California, Santa Cruz
103 PUBLICATIONS **4,693** CITATIONS
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John Campbell
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Agricultural and Forest Meteorology 266–267 (2019) 173–183

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Simulating International Drought Experiment field observations using the Community Land Model

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ABSTRACT

Anthropogenic climate change will alter regional hydrologic cycles around the world, in part by increasing the frequency or duration of droughts in some areas. The International Drought Experiment (IDE) is investigating the impact of severe drought on terrestrial vegetation by experimentally reducing precipitation at dozens of sites. Here we implement the IDE precipitation reduction protocol using the Community Land Model (CLM). Though many model results suggest that carbon fertilization will outpace drought-caused reduction of terrestrial carbon uptake, uncertainty is large. We therefore configure CLM to consider carbon cycling impacts of reduced moisture availability without intertwining the effects of carbon fertilization or phenological changes. California hosts a number of IDE sites and a wide range of topography, climate, and biomes. CMIP5 predictions suggest 21st century California will experience droughts in excess of the 1000-year climatological record for both frequency and magnitude. CLM suggests that some regions, including much of Northern California, may experience a steeper decline in gross primary productivity (GPP) during 21st century severe droughts than during 20th century severe droughts. Vegetation in Northern California experiences virtually all of this GPP reduction during the dry season, with little wet season GPP reduction even during severe drought. Southern California vegetation experiences soil moisture GPP limitation at virtually all times, increasing substantially with drought severity. Southern California should experience a more pronounced shift in GPP seasonality and decline in magnitude relative to Northern California during droughts. Some parts of every vegetated continent see changes to drought response and seasonality similar to Southern California. Our CLM results provide drought impacts that forthcoming IDE field observations may test, can help to spatially upscale site-based IDE observations of drought impact, and provide CLM's prediction of reduced precipitation impacts per unit leaf area index.

1. Introduction

Anthropogenic climate change is already profoundly altering local, regional and global circulation, and will affect weather and climate in the 21st century relative to 20th century norms (IPCC, 2013). Implications include critical alteration of regional hydrologic cycles relative to the 20th century (Collins et al., 2013; Trenberth et al., 2014; Dai, 2012; Prudhomme et al., 2014). Indeed, recent analyses suggest it is not out of the question that such changes are underway and detectable (Dai, 2012; Prein et al., 2016). The Coupled Model Intercomparison Project Phase 5 (CMIP5) ensemble of tens of general circulation models consistently predict drier soil conditions around the Mediterranean, parts of South America, southern Africa, and the Southwest USA. These drier soils are forced by changes in precipitation supply, as well as evaporative demand due to higher air temperatures (Collins et al., 2013).

Effects of drought may include changes in ecological succession (Clark et al., 2016; Fauset et al., 2012), widespread plant mortality (Anderegg et al., 2016; McDowell et al., 2015), and physiological changes within plants that affect gross photosynthetic productivity (GPP) and carbon cycling (Hogg et al., 2008; Zhao and Running, 2010; McDowell et al., 2015). Carbon dioxide (CO_2) fertilization is likely to at least partially offset drought-driven GPP decline (Swann et al., 2016) for at least some regions of the world and all CMIP5 models consistently predict increased future global GPP, although considerable uncertainty exists surrounding the magnitude and spatial behavior of that increase (Friedlingstein et al., 2014; Reichstein et al., 2013; Schimel et al., 2015; Liu et al., 2016). This uncertainty, the potential of disturbances such as

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droughts to limit or offset carbon fertilization-driven increase in the terrestrial CO_2 sink (Reichstein et al., 2013), and the IDE occurring now (in present, not future, CO_2 levels) make it useful to study drought impacts in isolation of carbon fertilization.

Field studies or remote sensing provide indispensable knowledge but are poorly suited to the problem of separating drought-driven carbon cycle changes from changes driven by carbon fertilization. Single-site field studies of fundamental relationships between precipitation and ecology provide crucial mechanistic linkages between soil water availability and plant, community and ecosystem responses, but they are limited to relatively small spatial areas and short time scales (Ogle et al., 2015). Distributed experiments can help identify emergent properties and unifying principles across larger spatial scales (Knapp et al., 2017). Upscaling such experiments to landscape-scale is difficult because land surface heterogeneity causes many drought impacts to be highly localized (Reed and Loik, 2016; Assal et al., 2016). Remote sensing methods offer a far greater spatial perspective, but it is challenging to separate long-term structural ecosystem changes from phenological changes forced by interannual climate variability (Assal et al., 2016).

In contrast to field observations and remote sensing, ecosystem models provide a framework to scale site-based observations and interpret remote sensing data from a process-based perspective (Schaefer et al., 2012; Hilton et al., 2014). Here we present a set of land surface model experiments using the Community Land Model (CLM) (Oleson et al., 2010) version 4.0, using forcings (described in detail in Section 2) consistent with the International Drought Experiment (IDE). The IDE (http://www.drought-net.org) is a research coordination network to quantify sensitivity of biodiversity and above-ground productivity to drought for terrestrial ecosystems around the world. The goal of our experiments was to identify emergent properties across time and space, and to help generate hypotheses by which the IDE site-level experiments may test CLM. Many published studies have examined CLM's performance in reproducing observations and have identified important biases, and we do not seek here to extend these studies. We examine instead the differences between CLM simulations driven by “standard” atmospheric data and simulations driven by the IDE forcings. This differencing approach should allow the known CLM biases to cancel one another, while preserving the effects of meteorological drought. We focused on California IDE sites to help interpret future IDE observations, and to help upscale IDE results to regional or global scales.

California IDE sites have tremendous biological diversity that is driven in part by climatic differences across the state. Yet biological diversity and productivity are constrained by several factors: California receives most of its annual precipitation in the winter months, interannual variability in precipitation is quite high, the amount of precipitation is generally higher for Northern compared to Southern California, there are substantial coast-to-inland gradients of temperature and precipitation, and drought is enhanced statewide by increasingly warmer atmospheric temperatures. Regional analyses of the Southwest USA suggest that the hydrologic cycle of the next 100 years is likely to change significantly relative to the 20th century (Cook et al., 2015; Wuebbles et al., 2014; Seager et al., 2013, 2007; Seager and Vecchi, 2010). The CMIP5 ensemble predicts an increase in winter (January, February, March) precipitation for the northern half of California, and decreased precipitation there during all other seasons and in the southern half of the state in all seasons (Seager et al., 2013). However the predicted Northern California winter precipitation increase is counterbalanced by increased temperatures from radiatively forced warming, causing concurrent increased evaporation in excess of precipitation gains. Thus, the CMIP5 ensemble strongly trend toward significantly less moisture available to plants throughout California during the 21st century relative to CMIP5 simulations spanning the years 1850–2000 (Seager et al., 2013; Cook et al., 2015) (though the models are not unanimous (Cheng et al., 2016) and uncertainty is nontrivial (Mankin et al., 2017)). These projected 21st century droughts are also more severe than any historical droughts in the North American Drought Atlas (NADA) 1000-year paleoclimate reconstruction from tree ring data (Cook et al., 2015). Observed precipitation from 1980 to 2010 suggests that the 21st century drying trend predicted for California by the CMIP5 model ensemble is underway (Prein et al., 2016). Furthermore, the observed drying is driven by decreased frequency of precipitation-causing weather patterns – a change in the base state of the climate – and not decreased intensity of individual precipitation events, which would be more attributable to natural variability (Prein et al., 2016).

The past several years in California have exhibited many of these predicted changes, with the state experiencing a drought not seen for 700–1200 years (Robeson, 2015; Griffin and Anchukaitis, 2014) during 2012–2015. The drought was immediately followed by the third-highest October to April precipitation total since 1895 (NOAA National Centers for Environmental Information, 2017), restoring by May 2017 statewide snowpack and reservoir levels to 180% and 110%, respectively, of their 1979–2015 averages (up from 2% and 65%, respectively, in May 2015) (Cal. Dept. of Water Resources, 2017).

The precipitation we used to drive our model results simulates the IDE precipitation reduction protocol and spans the wide range of extreme hydrological swings that California has recently experienced. In light of this and the hydrological changes predicted for California and the Southwest USA, we identify slope changes in the photosynthetic productivity (gross primary productivity, GPP) response to precipitation. We analyze these changes in our simulations for eight field stations on a North-South spatial transect across California and then apply them globally.

2. Materials and methods

The IDE protocol prescribes a universal rainfall interception methodology for all sites, consisting of adjacent experimental and control plots. At each site the annual proportion of precipitation allowed to reach the ground is determined from 100-year records of annual precipitation – roughly creating the one-year-in-one hundred-years drought. We focus on eight California locations (Fig. 1, Table 1) to examine our CLM results: five University of California Natural Reserve System (UCNRS) sites (Younger Lagoon Reserve, McLaughlin Reserve, Sedgwick Reserve, Box Springs Reserve, Sierra Nevada Aquatic Research Laboratory (SNARL)), as well as Loma Ridge Global Change Experiment, Sierra Foothill Research Extension Center, and Carrizo Plain. We also examine three heavily studied more easterly sites in North America (Table 1) to provide context for the California sites.

We used the Community Earth System Model (CESM) (CESM Software Engineering Group (CSEG), 2013) to generate scenarios of GPP for 1-in-100 year extreme droughts corresponding to the IDE. CESM is a coupled global climate model developed to address research questions about the interactions of Earth's atmosphere, oceans, cryosphere, and biogeochemical systems. CLM is the land surface component of the CESM.

Version 4.0 of CLM (Oleson et al., 2010) may be run with or without prognostic carbon and nitrogen pool simulations and may be run coupled or uncoupled from an atmospheric model (Lawrence et al., 2011). When uncoupled from the atmosphere, a prescribed and static “data atmosphere” drives land surface processes. In this offline mode, land surface processes are affected by the atmosphere, but the atmosphere is unaffected by land surface processes. When run without prognostic carbon and nitrogen pools, observations from the satellite-borne Moderate Resolution Imaging Spectroradiometer (MODIS) are used to prescribe seasonal leaf area indices, stem area indices, and vegetation height (Lawrence et al., 2011). This CLM configuration is conventionally (and hereafter) referred to as CLM4SP (version 4.0, Satellite Phenology).

We conducted two 15 model-year CLM4SP simulations: a control run and an experimental run. Both runs used a horizontal resolution of

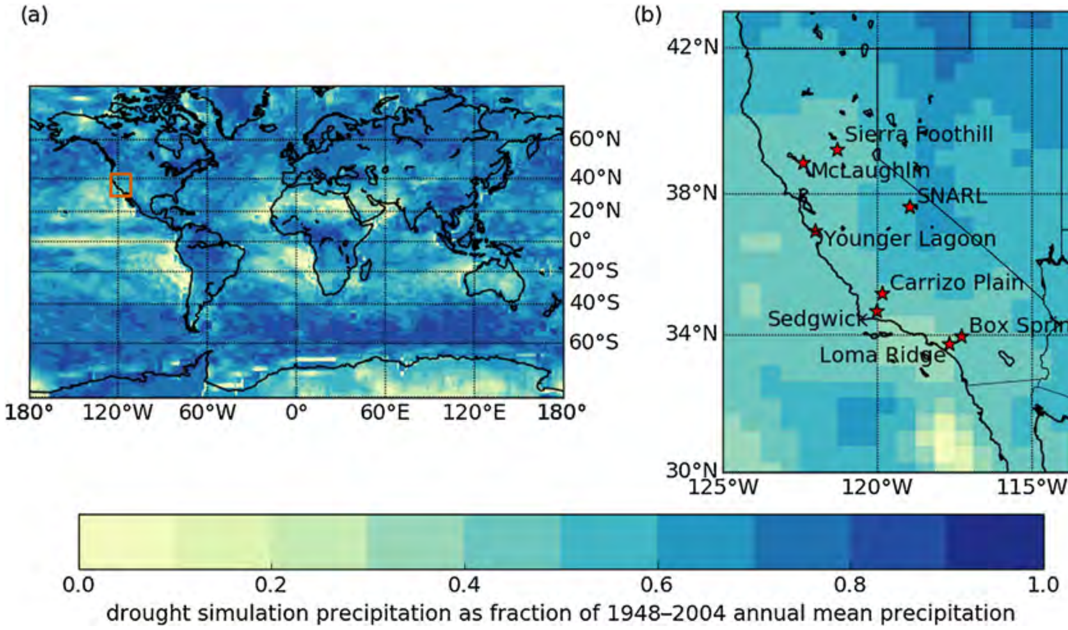

Fig. 1. International Drought Experiment (IDE) per-gridcell precipitation reduction. Panel (a): global precipitation reduction as a fraction of the 1948–2004 annual mean total precipitation. Panel (b): as panel (a), but zoomed to the California, USA analysis area (shown in the orange box in panel (a)). Precipitation reduction fractions are calculated as ((1st percentile)/(50th percentile)) of the 1948–2004 (Qian et al., 2006) annual total precipitation (see Section 2). Red stars on the panel (b) denote the California analysis sites described in Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Locations used for model evaluation (see also Fig. 1b).

	Latitude	Longitude	Reference
Site (California, USA)			
Younger Lagoon Reserve	36.97° N	122.03° W	Reed et al. (2011)
McLaughlin Reserve	38.87° N	122.43° W	http://nrs.ucdavis.edu/McL/
Sedgwick Reserve	34.70° N	120.02° W	http://sedgwick.nrs.ucsb.edu/
Box Springs Reserve	33.98° N	117.30° W	http://www.ucnrs.org/
Loma Ridge Global Change Experiment	33.73° N	117.70° W	Nelson et al. (2015)
Sierra Foothill Research Extension Center	39.25° N	121.28° W	Millikin and Bledsoe (1999)
Carrizo Plains National Monument	35.19° N	119.86°	Buck-Diaz and Evens (2011)
Sierra Nevada Aquatic Research Laboratory (SNARL)	37.61° N	118.83° W	Reed and Loik (2016)
Site (Central/East USA)			
Harvard Forest	42.54° N	72.17 ° W	Urbanski et al. (2007)
WLEF	45.95° N	90.27° W	Davis et al. (2003)
ARM Southern Great Plains	36.61° N	97.49° W	Fischer et al. (2007)

0.47 by 0.63 degrees and were driven by a “data atmosphere” (compset I_2000). The two runs differed only in the magnitudes of precipitation events.

CLM-simulated carbon fluxes have been compared extensively to eddy covariance observations both globally and regionally (e.g. Stöckli et al., 2008; Lawrence et al., 2011; Bonan et al., 2011) as well as locally (e.g. Levis et al., 2012; Hudiburg et al., 2013; Raczka et al., 2016; Duarte et al., 2017). We do not seek to extend here these crucial evaluations of CLM performance, but rather focus our attention on regional characteristics of the drought–control run differences in CLM simulations. This approach provides a framework for using forthcoming IDE observations to help evaluate model performance. It also mitigates the impact of known CLM biases, described in above references, as they should largely cancel out when CLM fluxes are subtracted from one another.

We used the satellite phenology formulation of CLM4 for several reasons. First, this separates the GPP impacts of reduced precipitation from the greenness-increasing GPP impacts of CO_2 fertilization (Mankin et al., 2017). CLM4SP reports how CLM4 predicts drought should impact GPP per unit LAI. This per-unit-LAI result is useful both for examining a piece of future GPP responses to drought as well as interpreting IDE field observations in the present day, before the onset of late 21st century emissions-driven carbon fertilization. Though the prognostic carbon and nitrogen cycle formulations of CLM4 provide more parameters and simulate more processes, it does not necessarily follow that these simulations are more accurate. For example, two recent studies considered CLM simulations of LAI at two different evergreen needleleaf (ENF) sites in the Western USA, and demonstrated that in the absence of site-specific parameter estimations, CLM4.5 underestimated ENF LAI in Washington, USA (Duarte et al., 2017) and overestimated ENF LAI in Colorado, USA (Raczka et al., 2016). Our global simulation necessarily uses global (that is, non-site-specific) parameters. Using CLM4SP forces the model with realistic LAI and avoids the uncertainties of prognostic LAI.

We drove the control simulation with the “standard” forcing data for CLM4SP offline mode (section 17 of Oleson et al., 2010), which uses precipitation, solar radiation, temperature, wind, humidity, and pressure for the years 1972–2004 from Qian et al. (2006). The forcing data are on a global 2.0 by 2.0 degree grid at 6-hourly (precipitation, solar radiation) or 3-hourly (temperature, wind, humidity, pressure)

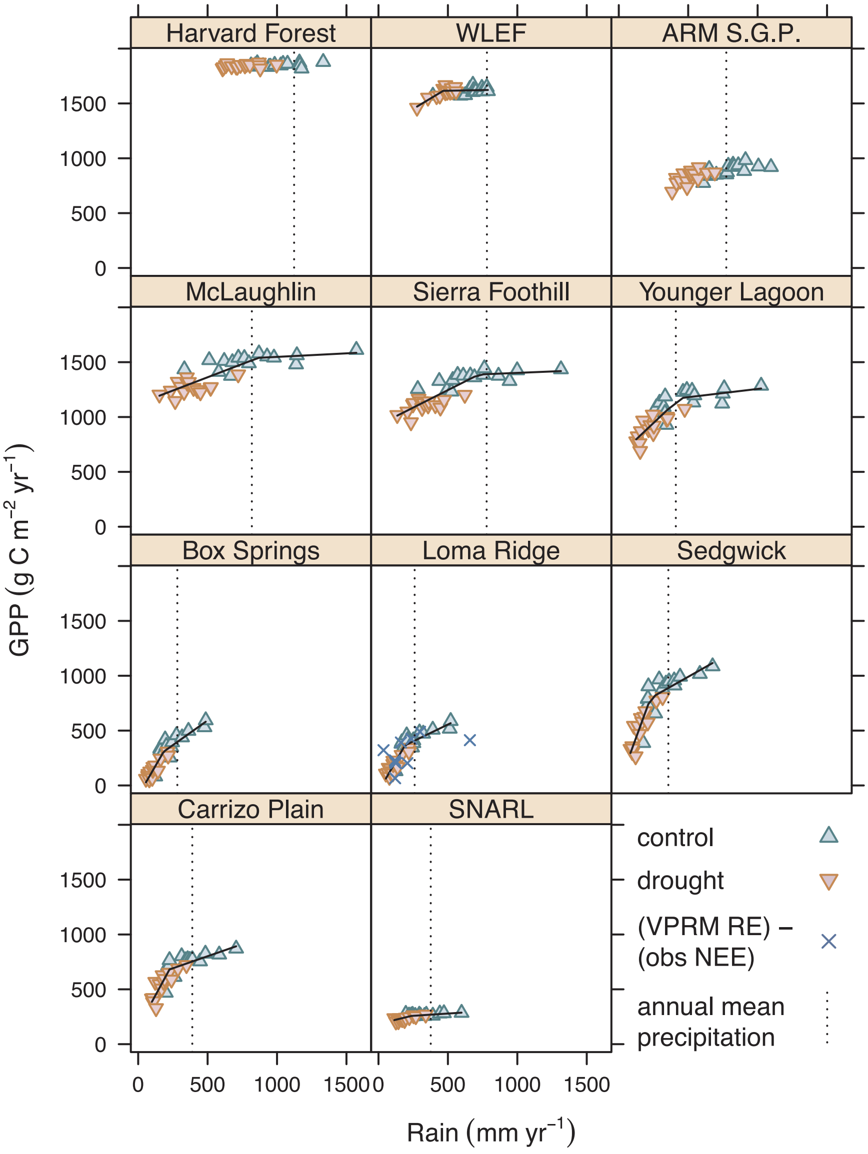

Fig. 2. Site-level empirical slope fits for modeled GPP–precipitation curves. Site locations are in Table 1 and Fig. 1b. AIC (Akaike, 1976) chose the two-slope fit (black lines) over a one-slope linear fit at all California sites demonstrating that CLM-simulated California GPP decreases more per unit decline in precipitation in drier conditions than in wetter conditions. Absence of a black line indicates that a one-slope linear best fit the data. Blue "X" markers on the Loma Ridge panel show GPP estimated by subtracting eddy covariance net ecosystem exchange (NEE) observations from Vegetation Photosynthesis and Respiration Model (VPRM) respiration (RE) as described in Section 2. Loma Ridge is the only one of the California sites that collects eddy covariance observations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

temporal resolution.

Our experimental simulation is forced by precipitation we derived from the Qian et al. (2006) precipitation by reducing the magnitudes of all precipitation events according to the IDE experimental protocol. We calculated annual total precipitation within each grid cell for all years in the Qian et al. (2006) dataset (1948–2004), and within each grid cell calculated the 1st and 50th percentile of these annual precipitation totals. The 1st percentile approximates the one-in-one-hundred-year drought, while the 50th percentile approximates the 20th century long-term average precipitation. We calculated a reduction fraction for each grid cell as (1st percentile) divided by (50th percentile). We then multiplied each grid cell's 6-hourly precipitation time series by this grid cell reduction fraction to create a forcing dataset for the experimental run. The experimental run used unaltered (Qian et al., 2006) solar radiation, temperature, wind, humidity, and pressure to be consistent with the IDE protocol.

We conducted a 50 model-year CLM4SP spinup run (Kluzek, 2013) using the 1972–2004 Qian et al. (2006) atmospheric forcing data. CLM4SP recycles the atmospheric driver data automatically, so the 50 model-year spinup was forced by 1972–2004 data followed by 1972–1990 data. We ran the experimental and control runs as "hybrid" CLM4SP runs (Kluzek, 2013) initialized with the final model state of the spinup run.

We tested two models of the precipitation–GPP relationship. A simple linear regression describes a GPP–precipitation relationship with a single unchanging slope. Watts and Bacon (1974) presented a hyperbola that fits "two-regime straight-line data": data characterized by two straight lines on either side of a join point. The Watts and Bacon (1974) hyperbola, defined by five parameters, is a two-slope curve with arbitrary join point and slopes. Within every CLM grid cell we calculated linear fits using lm() from the R language and platform for statistical computing (R Core Team, 2017), and we estimated the Watts and Bacon (1974) slopes and join point using the DEoptim package in R (Ardia and Mullen, 2009). We used AIC (Akaike, 1976) to determine whether the one-slope linear or two-slope hyperbolic model best fit the CLM precipitation–GPP data. AIC provides a quantitative method to balance goodness of fit against parsimony when fitting a model to data.

Loma Ridge Global Change Experiment (Table 1) has made eddy covariance net ecosystem exchange (NEE) observations since 2007. Hilton et al. (2013) optimized site-specific parameter values for the Vegetation Photosynthesis Respiration Model (VPRM, Mahadevan et al., 2008) to these observations. We estimated Loma Ridge GPP independently from CLM by adding VPRM ecosystem respiration to eddy covariance-observed NEE. Loma Ridge is the only one of our eight California sites (Table 1) with co-located eddy covariance flux observations. As noted above, CLM has been compared extensively with

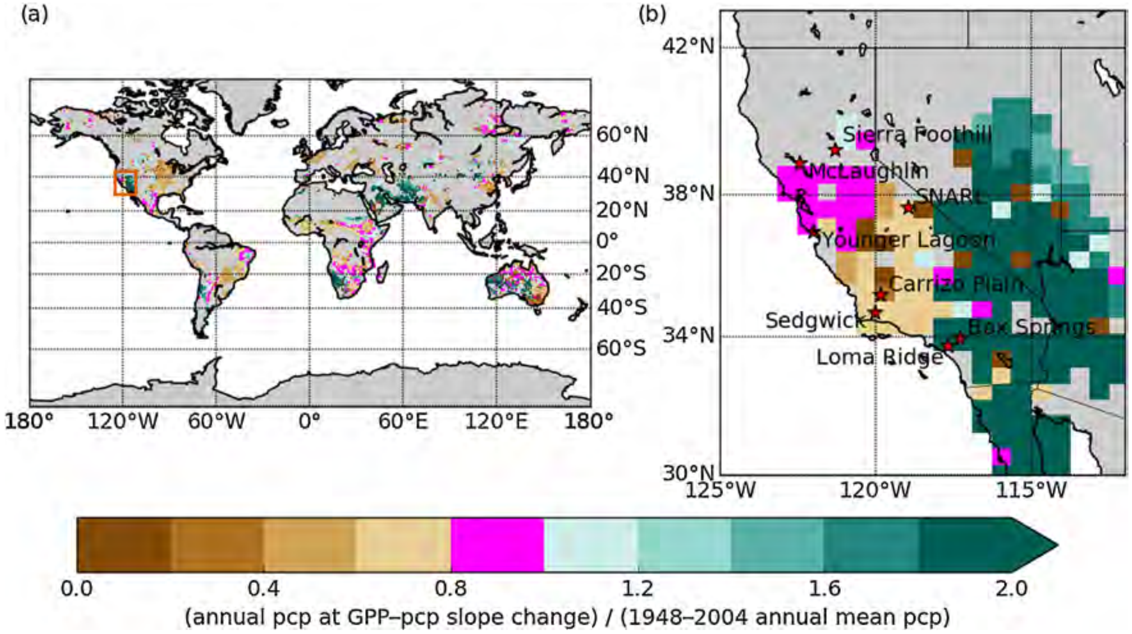

Fig. 3. Long-term mean annual precipitation (pcp) (Qian et al., 2006) versus the empirically fit transition point in the modeled GPP–pcp relationship. At colored points AIC (Akaike, 1976) preferred the two-regime straight-line fit (black lines) over a linear fit. At uncolored points GPP–pcp did not show a significant slope transition. Points in magenta show a ratio between 0.8 and 1.0, indicating that the long-term mean pcp is slightly wetter than the GPP-pcp inflection point. This suggests that a small decrease in pcp at these locations could produce a larger decline in GPP than previous behavior might indicate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

eddy covariance flux observations, and we do not seek to extend these important analyses here. We do consider the Loma Ridge GPP estimates a useful reality check that CLM's simulations are plausible and useful for our purposes, and therefore report these observations along with CLM results.

3. Results

3.1. GPP–Precipitation slope transitions

Fig. 2 compares annual total GPP against annual total rainfall for the 15-year CLM control run and 15-year CLM drought run across the UCNRS sites. We quantitatively compared two descriptions of the GPP–precipitation curves in Fig. 2 (see Section 2). AIC chose the two–slope regime over the linear fit for all eight California sites (Fig. 1b). The overlaid black curves in Fig. 2 show these two-slope fits. The slope transition point occurs at 500–750 mm annual precipitation for the three wetter northerly sites (McLaughlin, Sierra Foothill, and Younger Lagoon), but at 250–300 mm annual precipitation for the drier southerly sites (Box Springs, Loma Ridge, and Sedgwick). The larger difference between mean annual precipitation and the slope transition point indicates the drier sites are resilient to larger precipitation reductions.

Fig. 3 generalizes Fig. 2 in space by showing the ratio of precipitation at the point of slope transition (see Section 2) to observed annual mean precipitation (calculated from 1948 to 2004 observations). Land grid cells plotted in gray are locations where AIC concluded a single-slope linear fit best fit the simulated GPP–precipitation relationship. Grid cells plotted in brown, green, or magenta are locations where AIC chose the two-slope GPP–precipitation curve as the best fit for the simulations. Grid cells plotted in shades of brown are locations where long-term mean precipitation is wetter than the slope transition point; that is, a drought could result in a switch to a different GPP–precipitation slope. Magenta grid cells are locations where the 1948 to 2004 mean observed precipitation is between 100% and 125% of the slope transition points. Long-term mean precipitation positions these points closer than others to entering a new GPP–precipitation slope as a result of a drought. In other words, a small decrease in precipitation at these locations could produce a larger decline in GPP than previous behavior might indicate. Much of Northern California, sizable portions of sub-Saharan Africa and Australia, and parts of the Amazon basin and Siberia are in this category.

3.2. Drought-induced annual cycle changes

Fig. 4 shows the modeled annual mean cycle for GPP at daily resolution for several sites in the coterminous USA.

The relatively mesic sites Harvard Forest (Massachusetts, USA) and WLEF (Wisconsin, USA) exhibit little decline in GPP even during one-in-100-year drought simulations. Moving from the relatively wet and humid eastern North America sites toward the more arid west, ARM S. Great Plains (Oklahoma, USA) exhibits a summer and autumn decline in GPP in the drought relative to the control runs. Northern California sites Sierra Foothill, McLaughlin, and Younger Lagoon show lower peak GPP magnitude, an earlier peak in the annual cycle, and annual total GPP reduction of 15% to 20% for drought relative to control simulations. These effects become even more pronounced at Southern California sites Box Springs, Loma Ridge, Sedgwick, and Carrizo Plain, with GPP reduction approaching 50% relative to control simulations.

Fig. 5 shows the annual cycle for transpiration beta factor (β_t) at daily resolution. β_t is an attenuation factor ranging from 0.0 to 1.0 employed within CLM that reduces simulated GPP according to soil moisture stress (Oleson et al., 2010). During the drought simulations the Southern California sites often experience near total reduction of GPP because of soil water stress, with β_t near zero at Box Springs and Loma Ridge for several months of the year during drought simulations. For the control simulations (driven by 1972–1987 observed precipitation), the β_t 95% confidence interval at these sites never dips below 0.10. This indicates that complete downregulation of GPP never occurred in the control simulations, even though their driving precipitation included the severe drought of 1976–1977 (Cal. Dept. of Water Resources, 1983).

Fig. 6, Fig. 7, and Fig. 8 generalize these analyses to the mean annual cycle decline in maximum GPP magnitude, percent decline, and

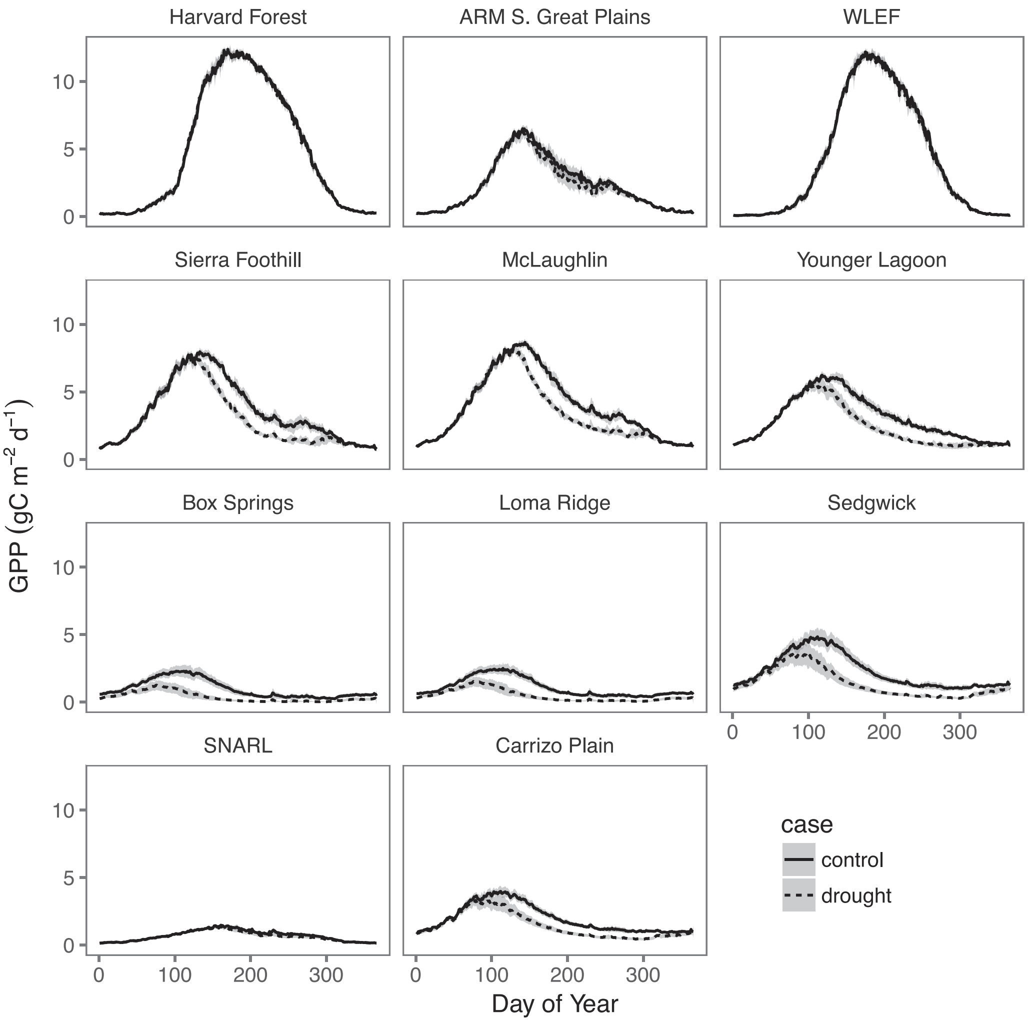

Fig. 4. Mean annual cycle (solid and dashed lines) and 95% confidence intervals (gray envelopes) in CLM GPP at selected U.S. analysis sites (site locations in Fig. 1b and Table 1). The means are calculated over the 15-year simulations (see Section 2).

shift in the day of year of annual maximum GPP, respectively, for each CLM grid cell. Virtually every location shows some decline in annual maximum GPP during severe drought, with the southwestern USA, much of sub-Saharan Africa, Eastern Brazil, and Australia showing the largest GPP declines in excess of 40% (Figs. 6 and 7). These same regions, with the addition of western South America, show a pronounced shift in the timing of the annual cycle (Fig. 8), with the annual maximum GPP occurring several weeks to more than a month earlier in the growing season for the drought scenario.

4. Discussion

GPP–climate feedback uncertainties are responsible for much of the overall spread in global climate predictions (Friedlingstein et al., 2014; Ciais et al., 2013), and a substantial portion of these feedback uncertainties originate in the effects of water availability on GPP (Lei et al., 2014). A change in the slope of GPP versus precipitation identifies a precipitation amount at which the GPP response to a given precipitation change enters a different phase. Examining the CLM precipitation–GPP curves (Figs. 2 and 3) for a discrete change in slope tests the hypothesis that plants in more arid and drought-prone areas (e.g. Southern California) should display a greater resilience to severe drought conditions than plants in more temperate hydrologic climes (e.g. Northern California). The six sites where a two-slope regime best fit the GPP–pcp data (Fig. 2) show a steeper drop in GPP per unit precipitation decrease at low precipitation levels than at higher levels. This demonstrates that GPP sensitivity to drought increases with increasing drought severity, but also that GPP rebounds more quickly from a severe drought than from a milder drought per unit of precipitation increase.

All of the eight sites examined in California exhibited a significant slope change in the GPP–precipitation curve. This occurred between 500 and 750 mm annual precipitation for Northern California, and around 300 mm annual precipitation for Southern California. This demonstrates a steeper decline in GPP per unit precipitation reduction at drier sites, but also a more responsive increase per unit precipitation following a return to wetter conditions.

A large section of Northern California – and many other areas around the world – featured mean 1948–2004 annual precipitation values between 100 and 125 percent of the GPP–precipitation slope change (magenta areas in Fig. 3). This suggests that these locations may see a more drastic decline in GPP during drought conditions than past observations might suggest, at least under the conditions used in the present study. Also, although Northern California typically sees more precipitation and photosynthetic productivity relative to Southern California, Northern California also appears to have a reduced margin between 20th century norms and the transition point to steeper GPP reduction per unit precipitation decrease (Fig. 3, right panel).

Transpiration beta factor (β_t) parameterizes the effect of drought stress on GPP, and does not attempt to describe plant hydraulic stress mechanistically. This is a known shortcoming of CLM version 4.5 (Trugman et al., 2018), and β_t has been replaced with a mechanistic

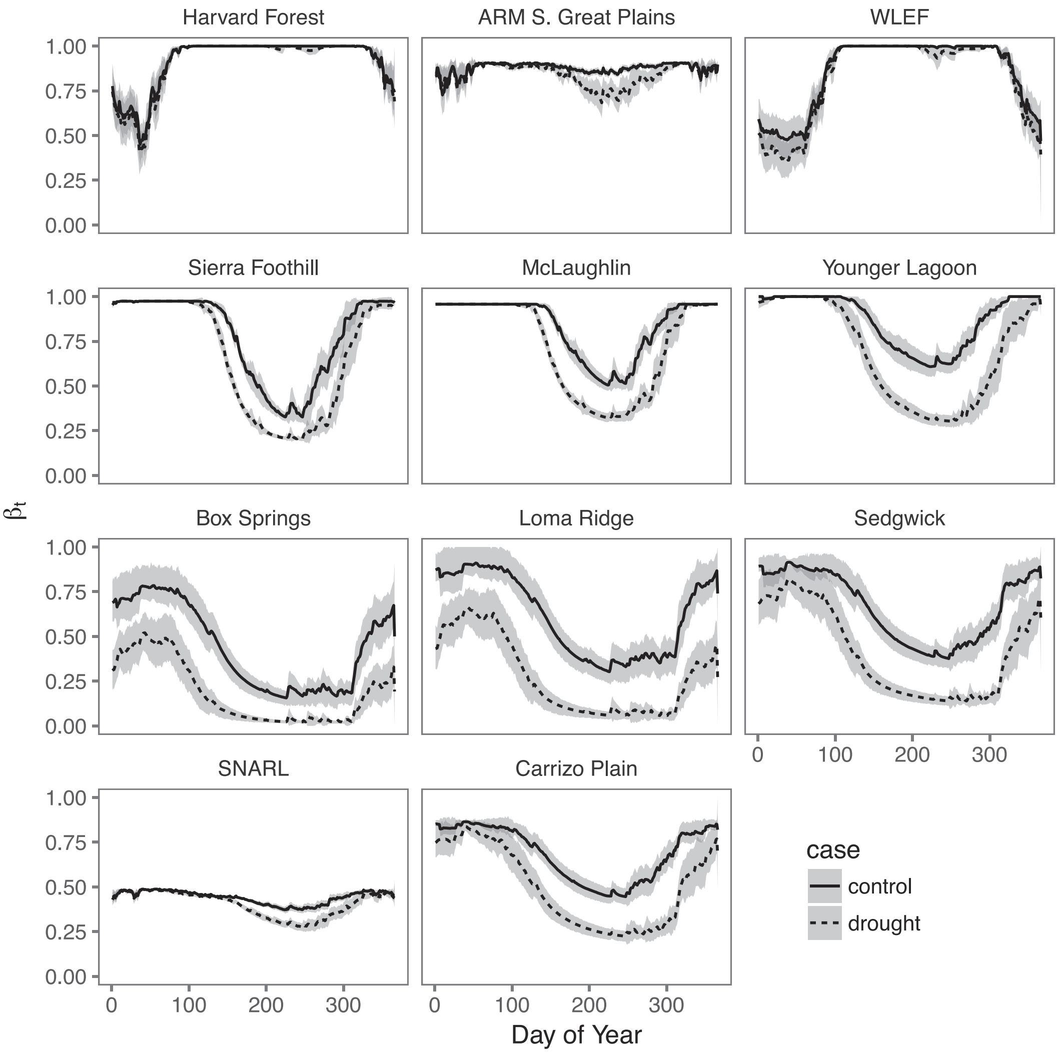

Fig. 5. Mean annual cycle (solid and dashed lines) and 95% confidence intervals (gray envelopes) in CLM transpiration beta factor (β_t) parameter at selected U.S. analysis sites (site locations in Fig. 1b and Table 1). Within CLM (β_t) varies between 0.0 and 1.0 to attenuate photosynthesis (Oleson et al., 2010) in response to soil water shortage.

description of hydraulic stress in CLM version 5.0 (Lawrence et al., 2018). CLM 5.0 was not yet released when our work was performed. Despite this non-mechanistic treatment of hydraulic stress in CLM4SP, the difference in β_t from our control run to our drought-forced run exhibits regional coherence in both Northern and Southern California, and is consistent across sites in those regions. This suggests that CLM sees differences in hydraulic stress response to severe drought between these regions.

The CLM-diagnosed transpiration beta factor suggests that vegetation in Northern California does not experience wet season limitation of GPP from low soil moisture, even during many years of consecutive severe drought. Severe drought extends the dry season period of soil moisture constraints on GPP to earlier in the spring and later into the autumn relative to non-drought conditions. Indeed, timing of soil moisture availability may be more important than precipitation amount for GPP in California grasslands (Xu and Baldocchi, 2004). Similarly, the timing of the onset of the dry season is key for productivity of Mediterranean forest ecosystems (Maselli et al., 2014).

Southern California sites face GPP limitation from low soil moisture at virtually all times, and may see near complete reduction of GPP owing to soil moisture stress during severe drought. This condition never arose during control simulations driven by observed late 20th century climate.

Our results suggest that vegetation processes related to GPP may be impacted differently by a 1-in-100 year drought in Northern versus Southern California, with Southern California's annual GPP experiencing a relatively larger magnitude reduction and a more pronounced change in its seasonal cycle timing. Sizable parts of sub-Saharan Africa, Australia, and the Amazon responded to drought similarly to Southern California.

The results reported here are not meant to comprehensively forecast future ecosystem responses to severe drought, but rather to provide context for interpreting field experiments and remote sensing products. The four following caveats should guide interpretation of the results reported here. First, CLM grid cells are essentially independent of one another, with inter-gridcell transport of above- and below-ground water, energy, and mass handled by other components of CESM that are beyond the scope of this study and therefore were not activated. The results we report simulate the response of each CLM grid cell to a severe drought independent of interactions with other gridcells except as prescribed by the static atmospheric driver data.

Second, our CLM4SP simulations examine the plant response to severe drought while holding leaf area index (LAI) constant. This is a useful accompaniment to remote sensing drought impact measures because drought-driven phenology changes can be difficult to disentangle from longer-term changes in an ecosystem (Assal et al., 2016). Moreover, CLM prognostic LAI is known to over-estimate LAI at some sites while under-estimating at similar sites in the absence of site-

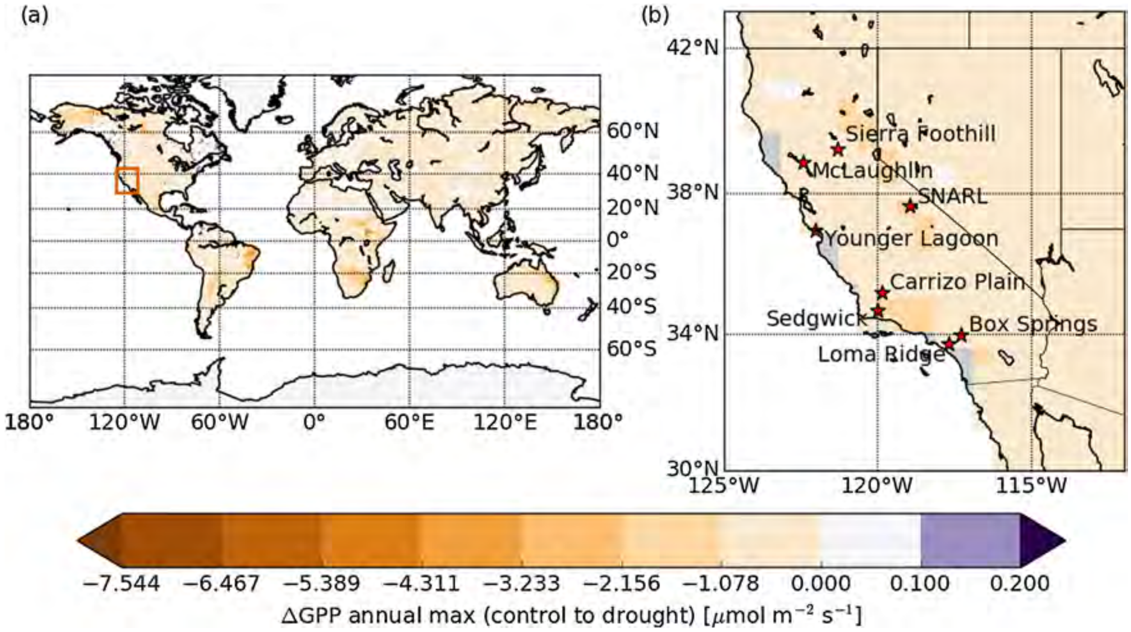

Fig. 6. Absolute decline in mean annual maximum CLM GPP, CLM control runs to CLM drought runs (drought minus control). Grey land areas denote areas masked to water on the CLM 0.47 by 0.63 degree grid. (For interpretation of colors in this figure legend, the reader is referred to the web version of this article.)

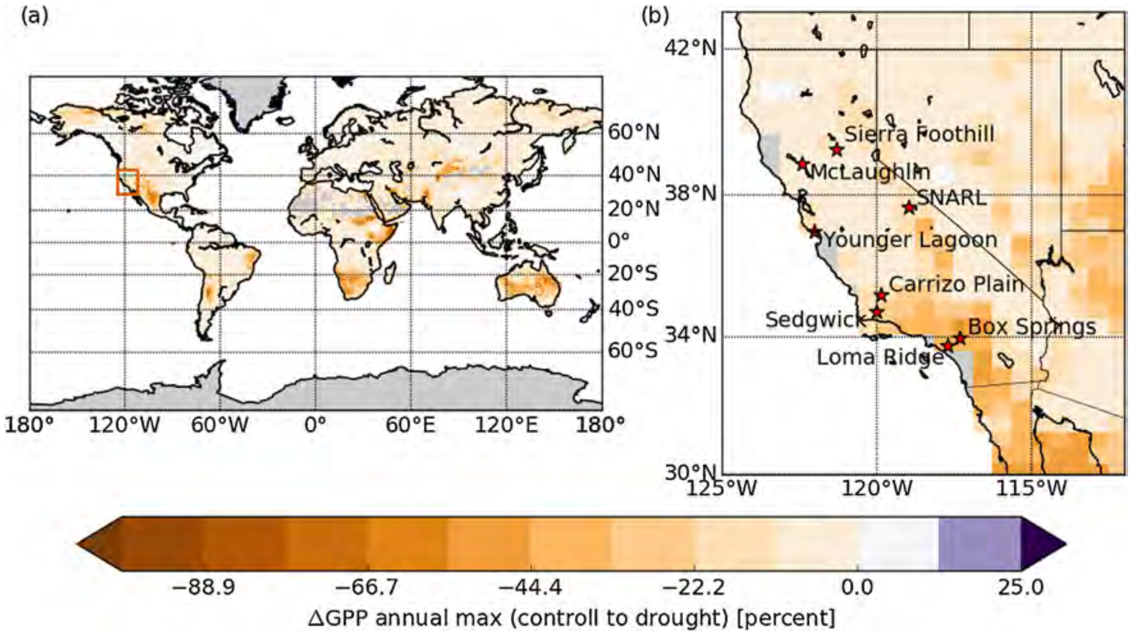

Fig. 7. Percent decline in mean annual maximum CLM GPP, CLM control runs to CLM drought runs. Grey land areas denote areas masked to water on the CLM 0.47 by 0.63 degree grid. (For interpretation of colors in this figure legend, the reader is referred to the web version of this article.)

specific parameterization (Duarte et al., 2017; Raczka et al., 2016). Leaf area changes are a primary response to drought (Wellstein et al., 2017); this is one of reasons that our results are not a comprehensive prediction of drought response. They are instead a measure of CLM's expectation of drought impacts *per unit LAI*.

Third, all CLM runs in the present study were driven by observed atmospheric CO_2 concentrations from the year 2000 (compset I_2000). This choice simulates the ambient CO_2 conditions prescribed by the IDE experimental protocol so that the CLM results can aid interpretation of IDE results and IDE results may inform future CLM work. Constructing model runs this way isolates them from the carbon dioxide fertilization effects that many models predict will accompany future drought realizations.

Fourth, by its nature the IDE cannot – and our model experiment therefore does not – simulate increased atmospheric demand for water due to warmer temperatures and drought-driven lower humidity. This is another reason that our results are more useful for interpreting upcoming field experiments than comprehensively forecasting future real-world conditions. The regional coherence of GPP–precipitation slope changes (Fig. 3) can, however, provide guidance for extrapolating IDE observations in space. For example, Fig. 3b identifies a subset of Northern California that could be more likely to experience GPP reduction from reduced precipitation in excess of what a 20th century observed GPP–precipitation regression would predict. Were IDE observations to confirm this, the spatial extent of the affected region might not be entirely obvious from purely remote-sensing based land

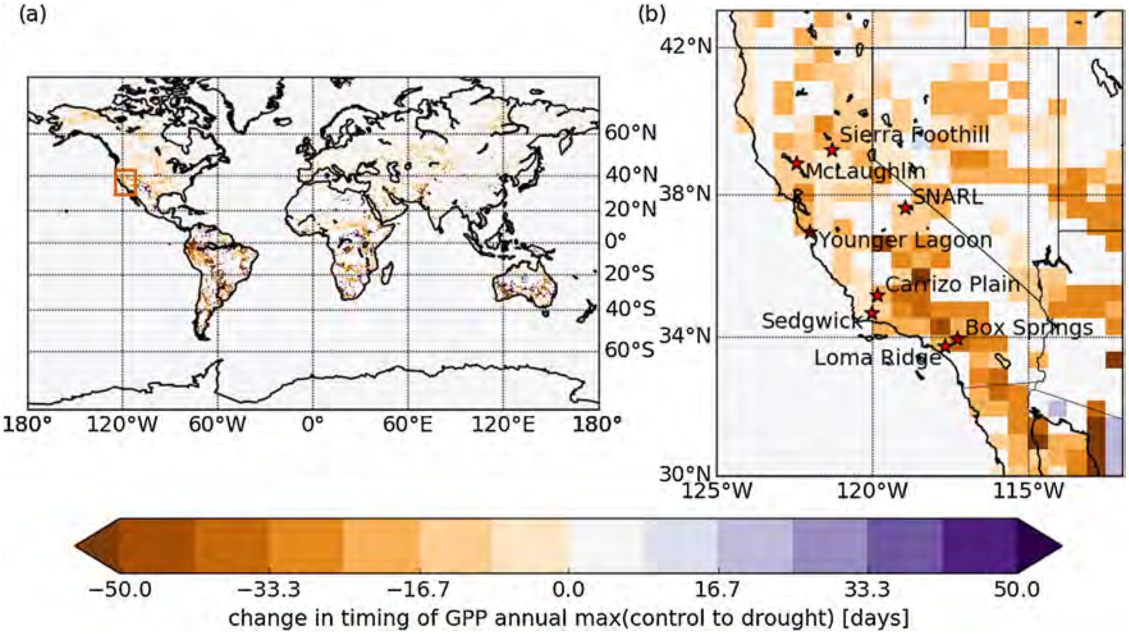

Fig. 8. Shift in day of year of mean annual maximum CLM GPP, CLM control runs to CLM drought runs. (For interpretation of colors in this figure legend, the reader is referred to the web version of this article.)

surface classifications such as plant functional types.

Future work could more thoroughly investigate the ability of CLM in our configuration to produce GPP estimations that match flux observation-informed GPP estimates at more field sites. This work, beyond the scope of the present study, could support or discourage interpreting our results to predict future real-world conditions.

In any interpretation, our results demonstrate the highly regional nature of ecosystem drought responses. Key sectors in California and worldwide – water management and agricultural production – as well as land management for biodiversity, wildland fire risk, and forest health, should plan for regionally-specific sensitivity to extreme drought.

Code availability

Source code and documentation for all components of the CESM version 1.2 is available from http://www.cesm.ucar.edu/models/cesm1.2/ (accessed 18 November 2018).

Supporting code for analyses described here is archived at https://github.com/Timothy-W-Hilton/CLM_IDE_analyses.

Competing interests

None.

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RESEARCH ARTICLE

WILEY

Drought-Net rainfall shelters did not cause nondrought effects on photosynthesis for California central coast plants

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Abstract

Rainfall interception shelters are frequently used to study the ecological consequences of drought. One common shelter design employs V-shaped plastic troughs spaced on a supporting frame to intercept rainfall. Shading, reflection, and infrared radiation may alter the radiative environment under shelters in ways independent of their intended effect on soil moisture. We measured microclimate and several photosynthetic variables for watered, potted plants under rain-out shelters and in open-air, unsheltered plots. We tested whether the shelter infrastructure altered aboveground micrometeorology and photosynthesis for watered, potted plants of native Californian species: *Elymus glaucus*, *Eriogonum latifolium*, *Mimulus aurantiacus*, and *Morella californica*. We quantified the effects on photosynthesis in terms of light harvesting by photosystem II (PSII) and leaf-level gas exchange on open-air and shelter plots, the quantum yield of PSII for darkened leaves, dark respiration, and nocturnal stomatal conductance. The rain-out shelter reduced daily integrated photosynthetically active radiation by 20%. Air temperature, leaf temperature, and leaf-to-air vapour pressure difference were not different under shelters compared with controls during the day. Likewise, there were no effects of shelters on net CO_2 assimilation, stomatal conductance to water vapour (g_s), internal leaf (CO_2), or electron transport rate through PSII during the daytime. At night, T^{air} was 0.6°C higher under shelters, but there were no effects on dark respiration or stomatal conductance. Despite some differences in micrometeorology under rain-out shelters compared with open-air plots, there were little or no aboveground nondrought effects of the shelters on leaf-level photosynthesis for watered, potted plants of these California native plant species.

KEYWORDS

Elymus, *Eriogonum*, *Mimulus*, *Morella*, rain-out, stomatal conductance

1 | INTRODUCTION

Understanding and predicting drought effects resulting from climate change are important because of their widespread impacts on ecological, agricultural, and societal well-being (Dai, 2011; Marshall et al., 2008; Penuelas et al., 2013; Trnka et al., 2018). Particularly in arid and semiarid systems, drought is the climate change driver that is likely to have the biggest impact on terrestrial ecosystem structure and functions, including enhanced mortality for certain plant populations (Martinez-Vilalta & Lloret, 2016). Drought can also lead to modified responses to disturbances (Loehman et al., 2018), altered species distributions (Aubin et al., 2016), long-term changes in community structure (Hoover, Knapp, & Smith, 2014; LaForgia, Spasojevic, Case, Latimer, & Harrison, 2018; Ochoa-Hueso et al., 2018; Phillips et al., 2018), widespread changes in ecosystem function (Tredennick, Kleinhesselink, Taylor, & Adler, 2018), and shifts in ecotone boundaries (Greenville et al., 2018).

It is difficult to fully understand the ecological consequences of drought without manipulative experiments because observations are complicated by temporal correlates with weather, topography, and soils. Whereas numerous studies have provided extensive information about site-specific responses of plants and ecosystems to changes in precipitation patterns, synthesis of experimental results can be confounded by differences in methodological approaches. For example, manipulative experiments often differ in magnitude, sign, and even direction of precipitation change (Weltzin et al., 2003). Nevertheless, syntheses of results from multiple experiments have resulted in important insights about ecological responses to precipitation (Huxman et al., 2004; Ogle et al., 2012; Ogle et al., 2015). Coordinated distributed experiments can help address the issue of idiosyncratic designs across experiments by promoting the use of uniform manipulations, measurements, and analytical approaches (Knapp et al., 2017).

The Drought-Net coordinated distributed experiment (https://drought-net.colostate.edu/) established the International Drought Experiment (IDE), a network-level distributed experiment that was designed and coordinated *a priori*, with common research protocols, measurements, and methodologies (Knapp et al., 2017). The main goal of the network is to assess potential mechanisms underlying ecosystem sensitivity to drought by comparing responses across many global locations and ecosystem types. A secondary goal is to encourage diverse participation by institutions and countries worldwide. The IDE protocol aims to keep initial infrastructure costs low to promote such accessibility and participation.

In order to assess the key features of precipitation for design of the network protocol, Drought-Net analysed precipitation from over 1,600 locations for 100 years and showed that wet years usually have multiple large precipitation events by comparison with average or drought years, whereas arid regions typically have more days between precipitation events (Knapp et al., 2015). The IDE protocol uses rainfall interception shelters (Yahdjian & Sala, 2002) to impose a reduction in precipitation to a level consistent with a 1-in-100 year extreme drought. This design utilizes the natural frequency of precipitation events but retains site-specific precipitation magnitude and seasonal timing; this is critical because precipitation amount varies widely across global biomes (Knapp et al., 2017). The IDE uses clear plastic V-shaped troughs to intercept rain and to divert the water off plots. Although proper control plots would include full infrastructure (by which rain would drop onto plots from inverted V-shaped troughs), funding constraints often preclude such controls. This means that control plots are often left open to the bulk air and lack the possible infrastructure effects, such as shortwave radiation reflection, shading of leaves, and longwave (infrared) radiation emission that may produce nondrought effects on photosynthesis and productivity in treatment plots.

This study was conducted to test for aboveground nondrought effects of the Drought-Net IDE protocol rain-out shelters on the microclimate, photosynthesis, and respiration of well-watered, potted plants by comparison with plants in nonsheltered plots open to the sky. We conducted this study during the summer in a California coastal prairie grassland in which much of the extant vegetation had undergone seasonal drying and senescence. Leaf-level photosynthetic physiology was compared for California native plant species (a grass, forb, subshrub, and shrub) after 6 days and 3 weeks exposure to conditions on open-air plots or under rain-out shelters built according to the Drought-Net protocol for the IDE. We tested the following hypotheses regarding unintended rain-out shelter effects: (a) photosynthetically active radiation (*PAR*; 400–700 nm) would be lower during the daytime under rain-out shelters by comparison with conditions on open plots, due to shading or reflection of shortwave radiation by the rain-out shelter infrastructure; (b) air temperatures would be warmer under the shelters at night, due to longwave emission from the rain-out shelter infrastructure; (c) there would be lower daytime photosystem II (PSII) electron transport, stomatal conductance to water vapour, and photosynthetic CO_2 assimilation for well-watered, potted plants under rain-out shelters compared with those on open plots; (d) there would be higher night-time respiration and nocturnal stomatal conductance and lower efficiency of PSII at night for plants under rain-out shelters compared with open plots; and (e) after 3-week exposure to conditions under rain-out shelters or in open plots, well-watered, potted plants would exhibit functional differences in PSII.

2 | MATERIALS AND METHODS

2.1 | Plant material

Experimental plants (*Elymus glaucus*, *E. triticoides* [Poaceae] Buckley; *Eriogonum latifolium* [Polygonaceae] Sm.; *Mimulus aurantiacus* [Phrymaceae] Curtis [Jeps.]; and *Morella californica* [Myricaceae] Wilbur) were grown outdoors under partial shade at the Plant Growth Facility on the UC Santa Cruz campus (36° 59′ 53.5596″ N, 122° 3′ 42.804″ W). Plants were started from locally collected seed inside a glasshouse with a mean daily temperature of 17°C (highs were approximately 10° above ambient and lows were near ambient temperature). After 8 weeks, the seedlings were moved outdoors and were grown in 15 cm-dia (3.79 l) pots in Premier Pro Mix HP inoculated with mycorrhizae. Individuals of *M. californica* were 2 years old at the time of experiments and were kept under the same conditions as the seedlings once they were moved outdoors. The other species were grown for another 8 weeks before being placed under rain-out shelters or in open-air "control" plots. Plants were watered daily to the flow-through point to prevent soil drying.

2.2 | Drought shelters

Drought (or rain-out) shelters were built in summer 2015 at Younger Lagoon Reserve at the UCSC Coastal Science Campus near Santa Cruz, California, USA (36° 57′ 6.8724″ N, 122° 3′ 47.592″ W, elev = 15 masl). Each shelter covers 4 × 4 m; research plots occupy the central 2 × 2 m with a 1-m buffer along each edge under the shelter. The spacing between adjacent shelters is a minimum of 3 m.

The drought treatment is created by diverting 60% of ambient precipitation from plots using overhead rainfall interception shelters (Yahdjian & Sala, 2002). Precipitation is intercepted by polycarbonate plastic panels bent into a V-shaped trough, held over research plots on a support frame. The support frame is made of 1.9 cm outside diameter electrical tubing conduit. There are three parallel, horizontal bars at 60, 100, and 150 cm height above the ground, one each on the east and west edges of the plot, and one in the middle. Each horizontal bar was supported by three vertical posts. This design produces a "wedge-shaped" shelter (Figure S1) with an upper and lower edge above the plant canopy. Based on a wind rose for this site, shelters were oriented to WNW (275°) so that the downward slope of the troughs faced into the prevailing coastal winds, which can be quite strong at times. Although this orientation deviates from the Drought-Net protocol, it was necessary because of strong winds. And the tallest sides of our shelters point east and south to maximize *PAR* interception. Troughs were spaced on the frames to create 60% rainfall interception, corresponding to the first percentile extreme drought for this region. The troughs sit above the plant canopy and slope downward and empty into gutters on the lower end. The gutters empty into flexible drain pipes that channel water away from the plots. The surrounding edges of the 4 × 4 m plots were trenched and lined with a 6-mil plastic to a depth of 50 cm prior to the construction of the overhead shelter infrastructure.

2.3 | Micrometeorological conditions

Air temperature ($T_{50}{}^{A}$), relative humidity (*RH*), and *PAR* (400–700 nm) were monitored at 50 cm height above the ground on one rain-out shelter and one open-air plot every minute, and average values were recorded every 10 min on Campbell Scientific Model 200× data loggers. Air temperature and relative humidity were measured using Vaisala Humitter HMP50 sensors in static radiation shelters at 50 cm above the soil surface, which was about 25 cm below the polycarbonate troughs of the shelter. We used a Li-Cor Model 190S quantum sensor to detect *PAR* at 50 cm above the soil surface. Additional air and leaf temperatures were obtained from the photosynthesis measurements described below.

2.4 | Photosynthesis measurements

We placed well-watered and fertilized plants in 20 cm diameter black pots directly on the soil surface under n = 5 shelters and n = 5 open plots in August 2016. Plants were watered every 2 to 3 days thereafter. There was no shading from neighbouring plants because the vegetation under the shelters had undergone seasonal senescence. Plants were momentarily moved from under shelters for watering, so that drained water did not enter shelter plot soils. Five days after placing the potted plants under the shelters or on open plots, we measured air temperature adjacent to the leaf (T^{air}), leaf temperature (T^{leaf}), leaf-level stomatal conductance to water vapour (g_s), and net CO_2 assimilation (A) using two cross-calibrated Li-Cor LI-6400-XT portable photosynthesis systems. The following night, we measured leaf temperature, dark respiration, and tested for any nocturnal stomatal conductance. We also used a chlorophyll fluorometer with the LI-6400 to measure the apparent quantum efficiency of PSII in the dark-adapted state for leaves of the five species on open and shelter plots. Last, we tested for changes in chloroplast-level photosynthetic processes after 3-week deployment under rain-out shelters or on open-air plots based on the photosynthetic light dose-response model ("A-Q curves"). These comparisons tested the potential for slower structural and functional responses within PSII under the rain-out shelters and on open-air plots.

Photosynthetic gas exchange responses to the micrometeorological conditions under the rain-out shelters were compared with those for open-air "control" plots. We chose to monitor these processes because decreased photosynthesis due to the nondrought effects of the shelter infrastructure might shift the carbon balance from net gain (via photosynthesis) towards net loss (via respiration) and result in reduced growth and survival. We compared photosynthesis for plants under rain-out shelters and open-air plots using instantaneous or "spot" measurements. We measured photosynthetic gas exchange of leaves with two cross-calibrated, open-mode portable photosynthesis systems (LI-6400XT, Li-Cor Inc., Lincoln, NE, USA) and assessed light harvesting by PSII with integrated leaf chamber fluorometers (LCF, Model LI-6400-40).

For all photosynthetic measurements, individual leaves were enclosed in the leaf cuvette using the 2-cm^2 area of the LCF. The flow rate was set to 500 μmol s^{-1}, the block temperature was maintained at 25°C, *PAR* (400–700 nm) was kept at a light-saturating 1,500 μmol m^{-2} s^{-1} (generated by red and blue LEDs in the LCF), and the leaf-to-air vapour pressure difference (VPD^L) was maintained between 1.2 and 1.8 kPa using the desiccant adjustment. Leaf temperatures were recorded with a copper-constantan thermocouple pressed to the abaxial surface of the leaf within the cuvette. Photosynthetic measurements were recorded when all stability criteria were met when the coefficient of variation for A and g_s combined was <0.5%, which generally required no longer than 4 min. Leaves were exposed to ambient irradiation for at least 2 hr before measurements of electron transport rate (*ETR*) in PSII. Steady-state conditions were confirmed in preliminary experiments.

Photosynthetic (A) responses to light (Q) were measured at an ambient CO_2 concentration of 400 μmol mol^{-1} for 12 light levels between 1,500 and 0 μmol m^{-2} s^{-1}. Photosynthesis (A, g_s, C_i, and *ETR*) and microclimate adjacent to leaves (T^{air}, T^{leaf}, and VPD^L) were measured at *PAR* of 1,500, 1,000, 750, 500, 350, 200, 100, 50, 20, 10, and 0 μmol m^{-2} s^{-1}. Plants were allowed to acclimate to light intensity changes for 4 to 5 min before measurements were recorded. For measurements of chlorophyll *a* fluorescence from PSII (i.e., daytime *ETR* and night-time F_V/F_M), we used an integrated LI-6200-40 fluorometer. Leaves were exposed to ambient *PAR* (e.g., for *ETR*) or dark-adapted between 01:00 and 04:00 hr for full reduction of PSII before F_V/F_M measurements (Logan, Adams, & Demmig-Adams, 2007; Maxwell & Johnson, 2000). We used a rectangular saturating flash of 0.8-s duration, an intensity of 8, a modulation of 20 kHz, and the filter was set at 50. The measurement was conducted with the intensity at 5, the filter at 1, the gain was 10, and the modulation was 20 kHz.

Daytime photosynthetic measurements were made between 08:00 and 14:00 hr local time, and night-time measurements were made between 01:00 and 05:00 hr.

2.5 | Data analysis

Initial statistical analyses of the micrometeorological and physiological data revealed unequal variances, so we used nonparametric comparisons of variables measured under rain-out shelters and on open-air plots. We used unpaired, two-sample Mann–Whitney *U* tests to examine the likelihood that values of each micrometeorological or physiological parameter from different treatments were drawn from the same distribution. Analyses were conducted in R Statistical Environment version 3.5.1 (R Core Team (2018). We initially compared five species, but in most cases, we show data for four of the five species because (a) two of the species are grasses from the same genus (*Elymus*) with very similar responses to one another, and (b) A-Q curves did not fully iterate to a solution for two of the species due to low photosynthetic rates.

The photosynthetic dose-response to light (the A-Q light response curve) was modelled as a nonrectangular hyperbola per Marshall and Biscoe (1980):

$$A_n = \frac{\Phi PAR + A_{\max} - \sqrt{(\,\Phi PAR + A_{\max})^2 - 4\ \theta\ \Phi PARA_{\max}}}{2\theta} - R_d, \quad (1)$$

where A_n is net assimilation rate (μmol CO_2 m^{-2} s^{-1}), Φ is the initial quantum yield (mol CO_2 mol photons^{-1}), *PAR* is the photosynthetic photon flux density (μmol photons m^{-2} s^{-1}), $A_{\max}$ is the maximum photosynthetic rate (μmol CO_2 m^{-2} s^{-1}), θ is a dimensionless curvature parameter, and R_d is daytime respiration (μmol CO_2 m^{-2} s^{-1}). The parameters were estimated using non-linear least squares regression in R 3.5.1 (R Core Team, 2018) with code from (Heberling, Brouwer, & Kalisz, 2017).

3 | RESULTS

3.1 | Microclimate under rain-out shelters

Microclimatic conditions under the rain-out shelters were generally similar to those on open-air plots with some exceptions (Figure 1). Instantaneous levels of *PAR* (400–700 nm) were up to 70% higher on open-air compared with rain-out shelter plots, though this only occurred for a few minutes during the day when the infrastructure caused temporary shading on the *PAR* sensor at 50 cm above the ground. Integrated over the daytime, shelter shade reduced *PAR* by 20%. Air temperature ($T_{50}{}^{A}$) and water vapour pressure deficit ($VPD_{50}{}^{L}$) at 50 cm were not significantly different over the course of 24 h, though $T_{50}{}^{A}$ under the rain-out shelter was higher for ~1 hr than $T_{50}{}^{A}$ on open-air plots during the middle of the day (Figure 1). A similar pattern was observed for $VPD_{50}{}^{L}$, which was lower under shelters than in the open for about 2 hr. Air temperature at 50 cm height was ~0.6° higher under shelters versus in the open plots at night (Table 1).

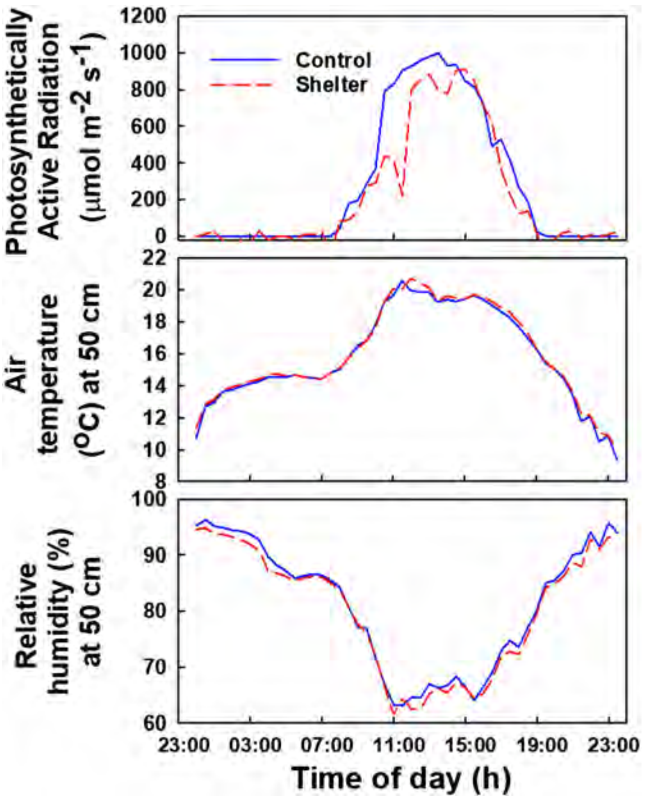

FIGURE 1 Diel micrometeorological conditions in open-air "control" plots and under rain-out shelters. (a) Photosynthetically active radiation (400–700 nm). (b) Air temperature at 50 cm height above the ground, adjacent to study leaves. (c) Relative humidity at 50 cm height above the ground, adjacent to study leaves. Data are shown for conditions in an open-air control plot (blue) and under a rain-out shelter (red) in August 2016

3.2 | Daytime photosynthesis

Compared across species, net leaf-level CO_2 assimilation (*A*) on open plots varied from 7.33 (0.74; mean [*SE*], *n* = 5) μmol m^{-2} s^{-1} for the woody shrub species *M. californica* to 21.5 (1.74) μmol m^{-2} s^{-1} for the perennial bunchgrass *Elymus glaucus* (Figure 2). Stomatal conductance to water vapour (g_s) similarly increased from the woody shrub to grass species. Leaf internal CO_2 concentration (C_i) was lower for *M. californica* compared with the other species and was the only daytime physiological response variable to be significantly different for plants under rain-out shelters compared with those on open-air plots. Likewise, the rate of electron transport through PSII (*ETR*) for *M. californica* was about one third that for the herbaceous perennial *E. latifolium*.

TABLE 1 Daytime micrometeorological conditions adjacent to leaves in open-air, control plots ("open"), and under rain-out shelters ("shelter")

Species	Treatment	VPD_{50}^{L} (kPa)	T_{50}^{A} (°C)	T_{50}^{L} (°C)
Elymus glaucus	Open	1.07 (0.14)	22.7 (1.2)	23.3 (1.4)
	Shelter	0.99 (0.12)	22.0 (1.1)	22.4 (1.4)
Eriogonum latifolium	Open	0.94 (0.10)	22.6 (1.0)	22.9 (1.2)
	Shelter	1.06 (0.12)	23.0 (1.2)	23.4 (1.4)
Mimulus aurantiacus	Open	1.04 (0.12)	22.5 (1.1)	23.1 (1.3)
	Shelter	1.16 (0.17)	23.2 (1.3)	23.7 (1.6)
Morella californica	Open	1.10 (0.13)	22.5 (0.6)	23.6 (1.0)
	Shelter	1.20 (0.11)	22.6 (1.0)	23.7 (1.2)

Note. Data are leaf-to-air vapour pressure deficit (VPD_{50}^{L}, kPa), air temperature (T_{50}^{A}, °C), leaf temperature (T_{50}^{L}, °C) at a height of 50 cm above the ground under rain-out shelters, and open-air "control" plots. Data are means and standard errors for n = 5 plants (except n = 4 for *E. glaucus* on shelter plots).

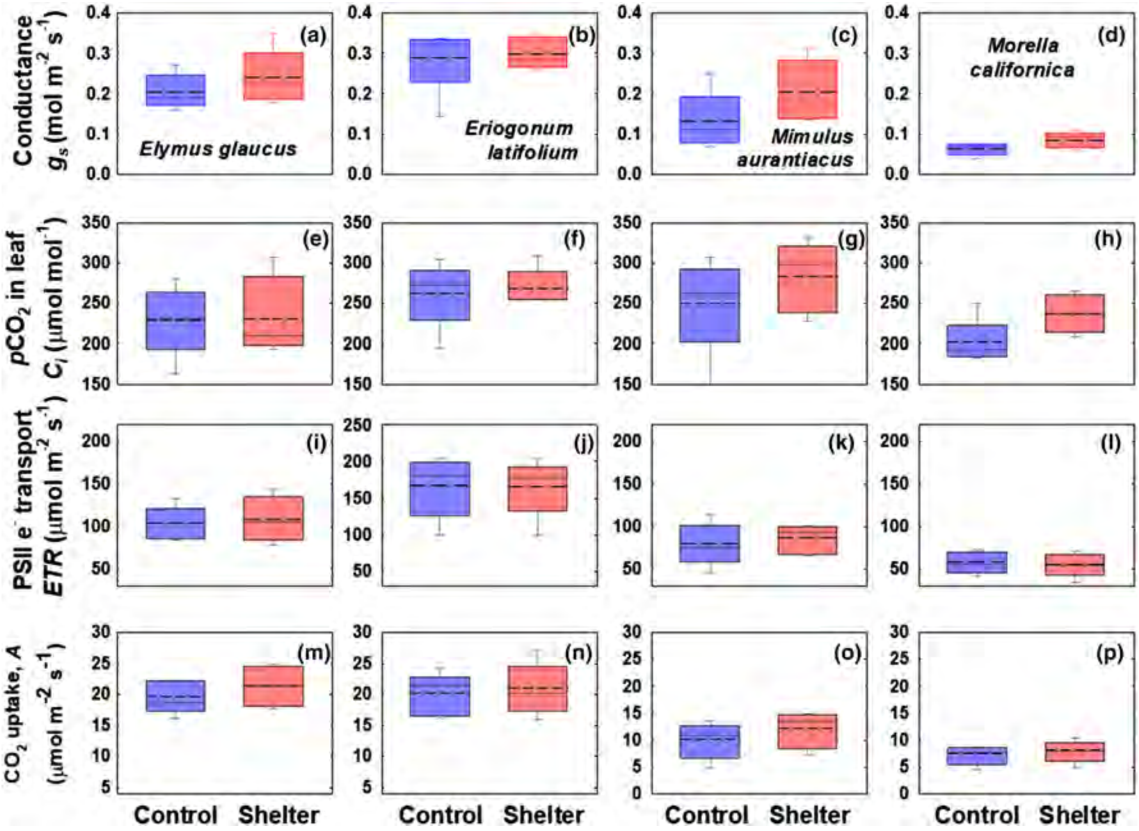

FIGURE 2 Leaf-level steady-state photosynthesis for *Elymus glaucus* (a, e, i, m), *Eriogonum latifolium* (b, f, j, n), *Mimulus aurantiacus* (c, g, k, o), and *Morella californica* (d, h, l, p) in open-air "control" plots (blue) and under rain-out shelters (red). Leaf-level photosynthetic processes were quantified as stomatal conductance to water vapour (g_s, panels a–d), leaf internal CO$_2$ concentration (C_i, panels e–h), electron transport through photosystem II (*ETR*, panels i–l), and instantaneous CO$_2$ assimilation (*A*; panels m–p). Data are mean (dashed line), median (solid line), standard error (box), and standard deviation (whiskers) for n = 5 measurements per species and treatment

There were no differences in air temperature near the canopy (T^{air}) or leaf temperature (T^{leaf}) nor leaf-to-air vapour pressure deficit (VPD^{L}) during the daytime on open compared with rain-out shelter plots (Table 1). There were few significant differences between plants under rain-out shelters compared with those on open plots in terms of net photosynthesis, stomatal conductance, internal CO$_2$ concentration, or electron transport rate in PSII (Table 1; Figure 2).

3.3 | Night-time physiology

Air temperature during the night near the leaves (T_n^{air}) of *M. californica* was significantly higher under rain-out shelters (Table 2). Leaf temperatures at night were somewhat higher under rain-out shelters compared with open plots for all species, but not significantly so.

TABLE 2 Night-time micrometeorological conditions adjacent to leaves and instantaneous steady-state leaf-level photosynthetic physiology in open-air, control plots ("open"), and under rain-out shelters ("shelter")

Species	Treatment	T^{air} (°C)	T^{leaf} (°C)	R_d (μmol m^{-2} s^{-1})	C_i (μmol mol^{-1})	g_s^n (μmol m^{-2} s^{-1})	F_V/F_M (unitless)
Elymus glaucus	Open	15.1 (0.1)	14.2 (0.1)	−2.92 (0.50)	417 (6)	0.249 (0.049)	0.780 (0.004)
	Shelter	16.2 (0.1)	15.4 (0.1)	−1.43 (0.10)	419 (11)	0.129 (0.044)	0.797 (0.006)
Eriogonum latifolium	Open	15.1 (0.2)	13.4 (0.4)	−1.16 (0.27)	400 (1)	0.661 (0.230)	0.798 (0.003)
	Shelter	15.9 (0.0)	14.9 (0.0)	−1.87 (0.15)	430 (6)	0.091 (0.022)	0.826 (0.002)
M. aurantiacus	Open	15.1 (0.1)	13.7 (0.1)	−0.81 (0.24)	400 (3)	0.411 (0.129)	0.763 (0.015)
	Shelter	15.3 (0.4)	13.9 (0.6)	−1.55 (0.46)	405 (3)	1.868 (1.313)	0.778 (0.010)
Morella californica	Open	**15.2 (0.3)**	14.3 (0.4)	−2.09 (0.97)	426 (14)	0.195 (0.131)	0.653 (0.011)
	Shelter	**16.7 (0.6)**	15.8 (0.6)	−0.73 (0.18)	424 (16)	0.084 (0.050)	0.565 (0.071)

Note. Data include air temperature (T^{air}), leaf temperature adjacent to leaves (T^{leaf}), net respiratory CO_2 flux (R_d), nocturnal stomatal conductance to water vapour (g_s^n), and apparent quantum efficiency of photosystem II for dark-adapted leaves (F_V/F_M). Data are means and standard errors for $n = 5$ plants (except $n = 4$ for *E. glaucus* on shelter plots). Bold indicates significant differences between values at the $P < .05$ level as determined by Mann–Whitney *U* tests.

The apparent quantum yield of PSII for dark-adapted leaves (F_V/F_M) measured between 01:00 and 05:00 hr was above 0.700 for all species except *M. californica* (Table 2). Dark respiration (R_d) varied from −0.73 (0.18) μmol m^{-2} s^{-1} for *M. californica* under shelters to −2.92 (0.50) μmol m^{-2} s^{-1} for *E. glaucus* on open plots. There were no clear trends between nocturnal (g_s^n) and diurnal stomatal conductance (g_s) when comparing species or between rain-out shelter and open-air plots. There were no significant differences for any of the photosynthetic traits for plants under rain-out shelters compared with open-air plots.

3.4 | A-Q after 3 weeks

Three weeks after the start of experiments, we tested the potential for slower structure–function responses of PSII to the micrometeorological conditions under the drought shelter by using the A-Q dose-response model. On the basis of plant survival and A-Q curve convergence, we focused on *E. triticoides*, *M. aurantiacus*, and *M. californica*. Mean values for light-saturated photosynthesis (A_{max}), dark respiration (R_d), and quantum yield (Φ) for *E. triticoides* and *M. aurantiacus* underneath the rain-out shelters were not significantly different than for plants on open-air plots, based on Student's *t* tests (Figure S2). Sample sizes precluded *t* test comparisons for *M. californica*.

4 | DISCUSSION

We found minimal differences between microclimatic conditions on open-air plots and under shelters, particularly for air temperature adjacent to leaves (T_{50}^{A}) and relative humidity. Using the original design upon which our rain-out shelters are based, Yahdjian and Sala (2002) found similar reductions in instantaneous *PAR* of 10% to 20%, depending on the amount of incoming *PAR*. Their maximal daytime air temperatures were between 5° cooler to 2° warmer than ambient, and daily minimal temperatures were within 2° of ambient. This is a greater diel variation between rain-out shelter and ambient than what we observed under our rain-out shelters compared with open-air plots. Many other studies have tested for aboveground effects of rain-out shelters. For example, continuous rain-out roofs in Arizona, USA, resulted in minimal effects on wind speed, air temperature, or relative humidity at plant height (English, Weltzin, Fravolini, Thomas, & Williams, 2005). For a grassland drought study in Germany, shelters reduced *PAR* by 10% and had little effect on air temperature under shelters compared with open-air controls (Signarbieux & Feller, 2012). Large interception troughs in New Mexico, USA, affected near-surface air temperatures by up to 4°, and an air temperature effect was found in relation to distance from the troughs (Pangle et al., 2012). In some cases, effects of rain-out shelters on air temperature were smaller than our night-time increase of ~0.6 K (Kundel et al., 2018; Vogel et al., 2013), whereas other studies found a larger effect on temperature (Power et al., 2016). Overhead rain-out shelters almost always reduce instantaneous *PAR* (Power et al., 2016). Our shelters caused a reduction in mean integrated daily *PAR* by about 20%, lower than the reduction of *PAR* in southeast Australia (Power et al., 2016), but similar in proportion to reductions in midday shortwave or net radiation in Germany (Kreyling et al., 2017). We found no differences in PSII function revealed by the A-Q analysis after plants were under shelters or on open-air plots for 3 weeks. Notably, the 20% reduction in daily integrated *PAR* under shelters results in almost no effect on net leaf-level CO_2 assimilation. Other studies have shown important feedbacks on microclimatic conditions under rain-out shelters driven by seasonal weather patterns and vegetation type (Carlyle, Fraser, & Turkington, 2011; Kreyling et al., 2017). We note that our measurements were conducted under relatively calm, clear conditions in coastal California, USA, and results may be different in other locations. Moreover, we do not know about the effects of the rain-out shelters on wind speed or summertime coastal fog deposition in our plots. Our rain-out shelters allow quite a bit of light into plots from the sides, especially from the southern edge which is the side with the tallest vertical supports. We did not test the effect of the polycarbonate on UV or other light quality parameters, but this could be important depending on the availability of plastic. Polycarbonate absorbs UV effectively (Loik et al., 2017), which could influence plant growth (Tevini & Teramura, 1989). We also did not detect much of a penumbral effect of light transmission through the polycarbonate edge on variation in *PAR* as the sun's angle changes. These potential effects warrant further examination. Nevertheless, we conclude that there are minimal differences in air temperature and relative humidity on open-air plots compared with under shelters in our system.

Almost none of the leaf-level photosynthetic traits were significantly affected by rain-out shelter conditions after 6 days (daytime A, g_s, ETR, and night-time g_s^n or F_V/F_M) or 3 weeks (as photosynthesis-light response curve variables Φ, R_d, or A_{max}) of treatment for the four species. In fact, the only physiological measurement that was marginally significantly different (P = .056) on open-air plots versus under rain-out shelters was leaf internal $p\mathrm{CO}_2$ (C_i) for *M. californica*. Because the plants were well-watered and fertilized in pots, their physiology should have been de-coupled from the drought shelter effects on soil water content, and any differences should be due to aboveground micrometeorological conditions associated with the shelters. Responses to drought shelters may be related to functional group type, as forbs and legumes exposed to drought did not have significant changes in stomatal conductance and net CO_2 uptake, whereas grasses had reduced gas exchange under drought shelters at certain elevations in Germany (Bollig & Feller, 2014; Signarbieux & Feller, 2012). Leaf- and canopy-level responses of photosynthesis to soil moisture under drought shelters may not be symmetrical to increased precipitation effects, resulting in different resource use efficiencies (Zhang et al., 2017). And ambient weather patterns can affect the physiological responses of plants to conditions under drought shelters. In this regard, leaf water potential, stomatal conductance, and quantum efficiency can differ under shelters on warm compared with cool days, yet there were no aboveground effects of drought shelters on photosynthetic physiology for a phytometer experiment in Germany (Kreyling et al., 2017).

We utilized species from different families that are common in central coastal California and represent different life forms and combinations of traits: a grass species *Elymus glaucus*, a long-lived perennial herbaceous forb *E. latifolium*, a semiwoody subshrub *M. aurantiacus*, and the woody shrub *M. californica*. Little is known of the photosynthetic physiology of these species, although there appear to be trade-offs between resource acquisition and drought for *E. glaucus* (Balachowski & Volaire, 2018). Some life history trade-offs might appear minor but cause important interactions with drought (Shriver, 2017). Moreover, we used potted, watered, fertilized plants, so they were presumably not affected by competition for light, water, or nutrients as would be plants rooted in the soil of plots. For plants with roots in the ground, competition may complicate responses to the different physical effects (shading, reflection, and infrared radiation emission) of the rain-out shelter infrastructure (Concilio, Nippert, Ehrenfeucht, Cherwin, & Seastedt, 2016). For example, some studies have found interactions of disturbance or trophic relationships (Gill et al., 2018) or soil invertebrates (Johnson, Staley, McLeod, & Hartley, 2011) with drought. Additionally, soil microbial communities may be affected by changes in soil temperature in addition to moisture under rain-out shelters (Cable et al., 2011; Ochoa-Hueso et al., 2018), but we used sterilized soil so this may not be an issue for our potted plants.

When it comes to *in situ* drought experiments, it may be possible in some habitats or locations to use rain-out shelters to reduce precipitation with minimal unintended, nondrought micrometeorological effects on photosynthesis. However, full control infrastructure (i.e., inverted experimental controls and open-air infrastructure controls) should be used where possible because some other factors that we have not considered (e.g., raindrop size) might be importantly affected by control structures. We recommend that investigators test for nondrought effects on micrometeorology and photosynthetic physiology as part of *in situ* precipitation manipulation experiments, especially if open-air plots are used as controls. We conclude that the lack of major differences found for air temperature and relative humidity on open-air plots and under shelters means the shelter design (Yahdjian & Sala, 2002) employed by the coordinated distributed experiment network Drought-Net can be used to manipulate rainfall with minimal unintended effects on aboveground conditions.

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AUTHOR CONTRIBUTIONS

M. L. and J. L. conceived the ideas and designed the methodology. T. B. and M. L. constructed the rain-out shelters. M. L. and J. L. collected the data. M. L., J. L., and D. H. analysed the data. M. L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the University of California's Dash Data Repository.

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SUPPORTING INFORMATION

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Adaptation in temporally variable environments: stickleback armor in periodically breaching bar-built estuaries

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Abstract

The evolutionary consequences of temporal variation in selection remain hotly debated. We explored these consequences by studying threespine stickleback in a set of bar-built estuaries along the central California coast. In most years, heavy rains induce water flow strong enough to break through isolating sand bars, connecting streams to the ocean. New sand bars typically re-form within a few weeks or months, thereby re-isolating populations within the estuaries. These breaching events cause severe and often extremely rapid changes in abiotic and biotic conditions, including shifts in predator abundance. We investigated whether this strong temporal environmental variation can maintain within-population variation while eroding adaptive divergence among populations that would be caused by spatial variation in selection. We used neutral genetic markers to explore population structure and then analysed how stickleback armor traits, the associated genes *Eda* and *Pitx1* and elemental composition (%P) varies within and among populations. Despite strong gene flow, we detected evidence for divergence in stickleback defensive traits and *Eda* genotypes associated with predation regime. However, this among-population variation was lower than that observed among other stickleback populations exposed to divergent predator regimes. In addition, within-population variation was very high as compared to populations from environmentally stable locations. Elemental composition was strongly associated with armor traits, *Eda* genotype and the presence of predators, thus suggesting that spatiotemporal variation in armor traits generates corresponding variation in elemental phenotypes. We conclude that gene flow, and especially temporal environmental variation, can maintain high levels of within-population variation while reducing, but not eliminating, among-population variation driven by spatial environmental variation.

Introduction

Spatial variation in selection is known to shape spatial variation in adaptive traits (Endler, 1986; Schluter, 2000; Hendry, 2017); less certain is the role of temporal variation. In fact, different meta-analyses of selection gradients have come to opposite conclusions about the prevalence and importance of temporal variation in selection (Siepielski *et al.*, 2009; Morrissey & Hadfield, 2012). Indeed, although the strength and direction of selection have been shown to greatly vary across time (Reimchen & Nosil, 2002; Hunt *et al.*, 2008; Siepielski

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et al., 2009), others found that it was not necessarily the case (Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Morrissey & Hadfield, 2012). Consequently, the effect of temporal variation in selection on phenotypic and genetic divergence remains unclear. Similarly, theoretical models evaluating the evolutionary importance of temporal environmental stochasticity come to variable conclusions that depend on the specific parameters used to calculate fitness at different time points (Coulson & Tuljapurkar, 2008; Chevin *et al.*, 2010; Chevin, 2013; Saether & Engen, 2015). Despite these variable attempts at generalization, many specific instances are known where the direction and magnitude of selection vary through time in correspondence with environmental conditions (Hairston & Dillon, 1990; Grant & Grant, 2002; Reimchen & Nosil, 2002; Mustonen & Lässig, 2007; Sletvold & Grindeland, 2007; Simons, 2009). Indeed, it has been recently argued that temporal variation in environmental conditions can explain an important amount of the temporal variation in selection coefficients analysed across studies (Siepielski *et al.*, 2017). Thus, temporal variation in selection is sometimes strong, but just how important this variation is for evolution remains much debated.

What might be the consequences of temporal variation for evolutionary processes? First, temporal environmental variation dictates that current conditions are not necessarily reflective of past selection and, hence, populations might not appear particularly well adapted to the specific conditions at any given time (Michel *et al.*, 2014). Second, and for the same reason, temporally variable environments might not allow (or favour) strong adaptive divergence across space even if spatial environmental variation is strong at any given time (Bell, 2010). Third, because the particular alleles favoured by selection vary through time, temporal environmental variation can sometimes maintain adaptive genetic variation within populations (Ellner & Hairston, 1994; Sasaki & Ellner, 1997). Fourth, because phenotypic plasticity can sometimes allow a given genotype to quickly adjust its phenotype to fluctuating conditions, it might be favoured over genetic adaptation in temporally fluctuating environments (Chevin & Lande, 2010). Finally, temporal variation can favour bet-hedging strategies, where individuals adopt strategies that reduce long-term variance in fitness even at the expense of short-term mean fitness (Childs *et al.*, 2010). In short, the potential consequences of temporal variation in environments and selection are many – highlighting the need for focused empirical studies in natural ecosystems.

Some of the above theoretical expectations have been confirmed in empirical studies. For instance, stable environments can harbour low genetic variation (Kellermann *et al.*, 2006, 2009), low phenotypic plasticity (Lind & Johansson, 2007; Lind *et al.*, 2010; Baythavong, 2011) and low bet hedging (Simons, 2009). However, the importance of temporal environmental variation in shaping genetic and phenotypic variation within and among populations that experience spatial environmental variation remains uncertain. Some studies have found that spatial differences in adaptive traits are generally maintained through time, suggesting that temporal variation does not overwhelm spatial variation (Mojica *et al.*, 2012; Morrissey & Hadfield, 2012; Gotanda & Hendry, 2014). However, these studies often examine populations known *a priori* to consistently differ in adaptive traits, so one might not expect a strong role for temporal variation (Hendry, 2017). What is needed, then, are studies examining within- and among-population trait variation in systems subject to strong spatial environmental variation but also strong temporal environmental variation.

Stickleback predator defence in bar-built estuaries

We suggest that the evolutionary consequences of temporal environmental variation might be profitably assessed using estuarine threespine stickleback (*Gasterosteus aculeatus*) known to experience extreme seasonal fluctuations. These populations inhabit 'bar-built' estuaries along the central coast of California, USA, which are characterized by fluctuations in ocean connectivity driven by seasonal rainfall patterns. Rainfall connects estuaries to the ocean in times of sufficiently high stream flow (Allen *et al.*, 2006), typically during the winter and/or spring months when heavy rains induce flows strong enough to breach the sand bar and thus connect the estuary to the ocean (Fig. 1b, Fig. S1; Behrens & Bombardelli, 2009; Behrens *et al.*, 2013; Rich & Keller, 2013). Once the high flows stop, a sand bar forms at the mouth of the estuary due to wave action and the deposition of new sand from the stream, forming a brackish-to-freshwater lagoon (Bradley & Griggs, 1976). Owing to these geophysical properties, a given bar-built estuary can greatly and rapidly vary in environmental conditions over the course of a single year, as well as across years. These properties also lead to frequent and dramatic shifts in biotic conditions, including the presence vs. absence of various stickleback fish predators (Becker & Reining, 2008; Frechette *et al.*, 2016).

To consider the evolutionary consequences of this environmental variation associated with bar-built estuaries, we focus on stickleback armor traits, including spines, body shape and lateral plates, all of which differ strongly between marine and freshwater environments, especially in relation to spatial variation in predators (Hoogland *et al.*, 1956; Reimchen, 1980, 1992, 1994, 1995; Reimchen & Nosil, 2002; Marchinko, 2009). Stickleback armor traits are also known for their strong genetic basis (Peichel *et al.*, 2001; Colosimo *et al.*, 2004; Jones *et al.*, 2012). In addition, these traits are expected to have ecological effects on their environment through

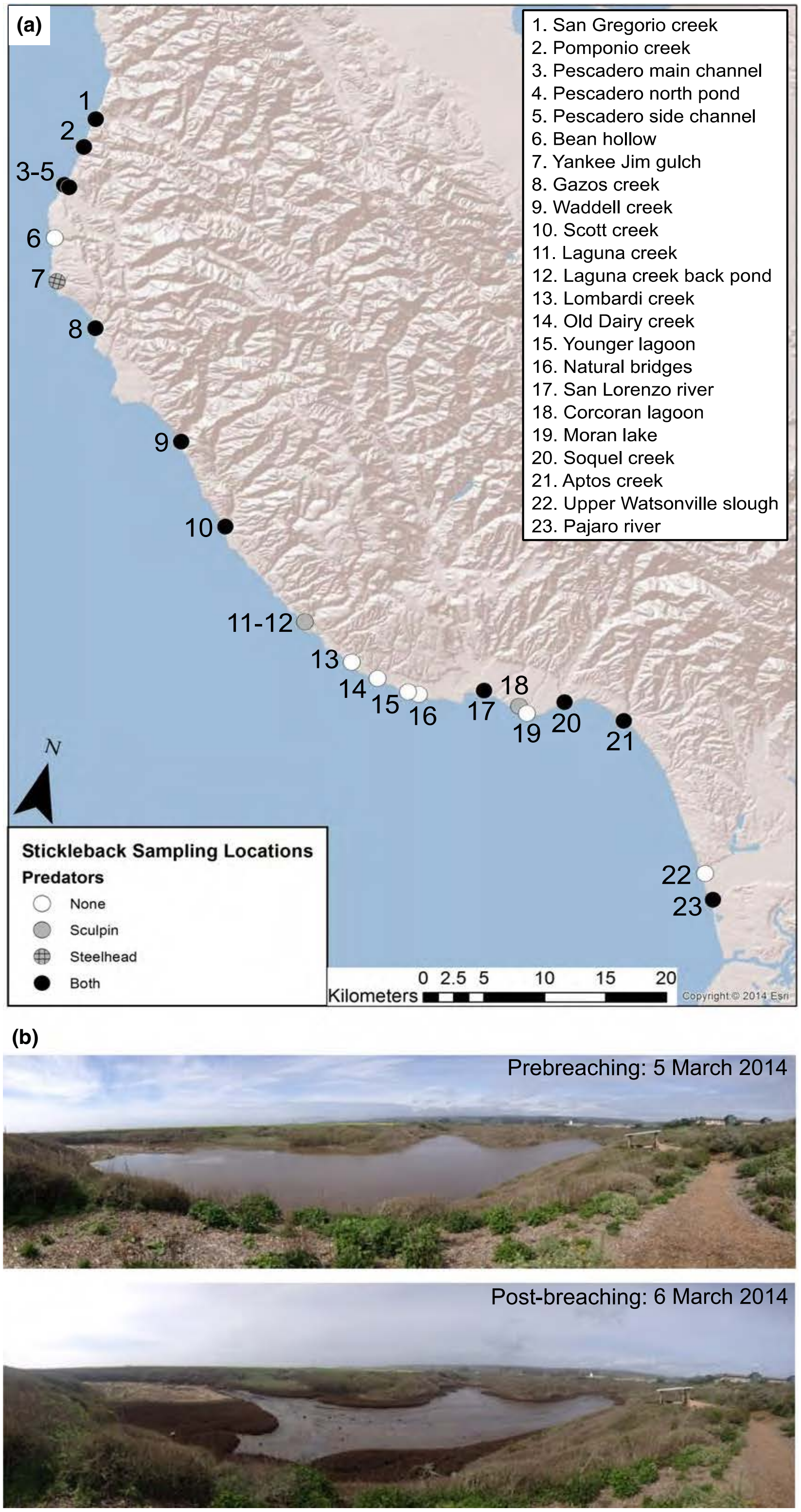

Fig. 1 Map of study sites (a) and photographs of a breaching event in Younger lagoon (b). Coloured markers indicate the presence of known stickleback predators.

their influence on nutrient dynamics (El-Sabaawi *et al.*, 2016), thus allowing us to consider the potential consequences of temporal variation not only for evolution but also eco-evolutionary dynamics (Hendry, 2017). For instance, variation in fish elemental composition can indicate specific changes in individual behaviour (e.g. foraging) that influence zooplankton community structure (El-Sabaawi *et al.*, 2016; Durston & El-Sabaawi, 2017). We structured our analysis around four key questions:

1 *Is gene flow sufficiently restricted to enable adaptive divergence among the estuary populations?* We investigate this question by assessing variation in neutral genetic markers that can inform the extent and nature of gene flow among stickleback populations in the different estuaries.
2 *Do stickleback in the different estuaries differ in armor traits, and are these differences associated with spatial variation in predators?* Because the genetic basis of several stickleback armor traits is well known (e.g. *Eda* for lateral plates and *Pitx1* for pelvic structures), we examined variation in both the traits and marker alleles associated with *Eda* and *Pitx1*.
3 *Do estuary stickleback have particularly high levels of (presumed) adaptive variation, as would be expected in their temporally variable environments?* This within-population variation could also be maintained by high among-population gene flow, thus linking to our first question above.
4 *How does an important ecological effect trait, elemental composition (phosphorus content, %P), vary in relation to phenotypes (armor), genotypes (Eda) and predation regime?* Such variation would indicate the potential for genetically based spatiotemporal variation in traits to impact nutrient dynamics, thus generating potential eco-evolutionary links.

Materials and methods

Field collections

Between April and August 2014, after most estuaries were closed for the summer (i.e. the sand bar separating the estuary from the ocean was in place), we collected threespine stickleback from 23 coastal estuary sites along a 90 km stretch of the central cost of California from San Gregorio State Beach in San Mateo County to the Pajaro River in Santa Cruz County (Table S1, Fig. 1a). Using a combination of minnow traps and beach seines, we collected 30 stickleback of length > 30 mm per site and immediately killed them with an overdose of tricaine methanosulphonate (MS-222). The fish were then placed on ice until they could be stored in a freezer before further processing. At each site, we also visually recorded from seine net catches the presence of known stickleback predators: steelhead trout (*Oncorhynchus mykiss*) and sculpin species (*Cottus asper* and *Leptocottus armatus*). Importantly, predator abundance in bar-built estuaries fluctuates with the frequency of breaching events (Becker & Reining, 2008). We also calculated watershed area for each creek using ArcGIS v. 10.2. Watershed area is a reliable proxy for stream flow, with larger watersheds tending to sustain greater flows and therefore spending longer periods of time with the estuary mouth open (Elwany *et al.*, 1998; Mohamoud & Parmar, 2006). In the laboratory, the collected stickleback were placed in 10% formalin (VWR, Radnor, PA, USA) after the right pectoral fin was removed and stored in 95% ethanol for genetic analyses. Stickleback specimens were then stained using alizarin red dye. To do so, they were first soaked in water for 24 h, then in a solution of alizarin red and 0.5% KOH for 24 h, followed by a second soak in water for 24 h to remove excess dye. Fish were then stored in 40% isopropyl alcohol until further processing.

Population genetics

DNA was extracted from stickleback fin clip tissue using a phenol–chloroform-based protocol. Briefly, tissues were left overnight in tissue digestion buffer and proteinase K at 55 °C, followed by phenol–chloroform and ethanol washes to isolate the DNA. Nine microsatellite markers were amplified on 10–59 individuals per population (Table S1). Two of these markers, stn381 and stn82, are linked to genes *Eda* and *Pitx1*, respectively (Shapiro *et al.*, 2004; Colosimo *et al.*, 2005), and the other seven unlinked loci were chosen for their putative neutrality (stn30, stn173, stn196, stn174, stn185, stn70 and stn199; Peichel *et al.*, 2001). Stn381 is a diagnostic in/del marker for *Eda*, with 'low' and 'complete' alleles that have been shown to be associated with plate count variation (Colosimo *et al.*, 2004). In contrast, although regulatory mutations at *Pitx1* are associated with pelvic spine reduction allelic variation at stn82, a nonintergenic marker, is not directly associated with pelvic spine length (Shapiro *et al.*, 2004; Chan *et al.*, 2010). Nevertheless, stn82 remains a useful marker to test for the effect of selection on *Pitx1* (Mäkinen *et al.*, 2008). Polymerase chain reactions (PCRs) were prepared using the Type-it Microsatellite PCR kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's protocol. All PCRs were carried out on an Eppendorf™ Mastercycler™ Pro with cycling conditions standardized for all loci: denaturation at 95 °C for 5 min and 28 cycles at 95 °C for 30 s, 60 °C 90 s, 72 °C 30 s and then cooled at 4 °C. The resulting products were sequenced using a ABI 3730XL sequencer at Génome Québec (Montréal, Canada) with a 5-min denaturation step at 95 °C before injection. Peak call analysis was performed using Geneious version 8.8.1 (Biomatters Ltd., Auckland, New Zealand) using the Microsatellite Analysis External Plugin version 1.4.0. To compare the focal estuary populations to a pure marine type, we amplified the same loci on 30 fish from a pure marine population collected from Bodega Bay (Sonoma County, CA, USA).

Using GENEPOP version 4.5.1 (Rousset, 2008), we first tested each neutral locus (those not linked to *Eda* and *Pitx1*) for departures from Hardy–Weinberg equilibrium and for potential linkage between loci after

Bonferroni correction ($\alpha = 0.05$, $K = 601$). A *G*-test (Goudet *et al.*, 1996) performed with the R package *adegenet* (Jombart, 2008) with 99 simulations showed that no F values were greater than expected by chance (simulated $P < 0.01$). With the same R package, we then calculated Nei's pairwise F_{ST} estimates (Nei, 1973).

We explored population structure through several complementary analyses. (i) We performed a correspondence analysis (CA) based on allele frequencies at the seven neutral markers, replacing missing values by the mean of the allele frequency of each locus (similar results were obtained using PCA). (ii) We used STRUCTURE version 2.3.4 (Pritchard *et al.*, 2000) with the admixture model with 10 000 repetitions for burn-in and 200 000 for run length over 10 iterations for $K = 1–24$. We determined the most likely value of *K* by taking the averaged log-likelihoods across the 24 runs and applying the ΔK method (Evanno *et al.*, 2005). (iii) We performed an analysis of molecular variance (AMOVA; Excoffier *et al.*, 1992) on all estuary populations (i.e. excluding Bodega Bay) with the R package *poppr* version 2.2.0 (Kamvar *et al.*, 2014), testing significance by randomly permuting the sample matrices over 500 iterations. (iv) Based on allele frequencies at the seven neutral markers, we calculated – between all population pairs – Edward's genetic distance (Edwards, 1971), which assumes that allele frequencies differ because of drift. These distances were used to compute a hierarchical clustering analysis and build a genetic tree. (5) We tested for isolation by distance between estuary populations (i.e. excluding Bodega Bay) by first computing a matrix of geographic distances based on latitudinal and longitudinal coordinates. We then used a Mantel test (Mantel, 1967) with 999 permutations comparing pairwise Edward's distance to pairwise geographic distance.

Although the assumption that California estuaries represent potential hybrid zones between marine and upstream freshwater population has been historically rejected (Bell, 1976, 1979a, b; Bell, 1981, 1982; Baumgartner & Bell, 1984; Baumgartner, 1986, 1992, 1994; Bell & Richkind, 2015), we used our genetic data to confirm this interpretation for our contemporary samples. Within each population, we selected fish homozygote at the 'complete' *Eda* allele and tested whether those fish were more likely to be assigned to the neutral marine genetic cluster of Bodega Bay. For this inference, we used STRUCTURE version 2.3.4 (Pritchard *et al.*, 2000) with the admixture model with 10 000 repetitions for burn-in and 200 000 for run length over 10 iterations for $K = 1–19$ (five populations did not have any fish homozygote 'complete' at *Eda*). We determined the most likely value of *K* by taking the averaged log-likelihoods across the 19 runs and applying the ΔK method (Evanno *et al.*, 2005). As described above, we considered whether (as would be expected for hybrid zones) our populations were out of Hardy–Weinberg equilibrium at neutral loci. If fish with the homozygote 'complete' at *Eda* do not cluster with the Bodega Bay neutral marine population cluster, and if our populations are in Hardy–Weinberg equilibrium at neutral markers, then our estuaries are – as historically inferred – not hybrid zones.

Divergence associated with predator regimes

To test whether *Eda* and *Pitx1* have experienced divergent selection among estuaries, we used an F_{ST}-outlier detection method implemented in LOSITAN version 1.44 (Antao *et al.*, 2008). Lositan is an allele frequency-based method that identifies outliers from the joint distribution of F_{ST} and expected heterozygosity, using coalescent simulations to determine the F_{ST} null distributions and assuming an island model. In this analysis, the distribution of F_{ST} is characterized by estimating the quantiles of the distribution and defining a window in which 95% of the data points are expected to lie (Beaumont & Nichols, 1996). Based on the simulated distribution, it is possible to calculate *P*-values for loci of interest. Loci with a high F_{ST} value are putatively under directional selection (*P*-value > 0.975), whereas loci with a low F_{ST} value are putatively under balancing selection (*P*-value < 0.025). We used the infinite alleles model with 50 000 simulations, a 95% confidence interval and a false discovery rate of 0.1. Finally, we tested for associations between particular *Eda* alleles and predator regime by regressing the 'complete' allele frequency (*Eda* C allele), which is strongly associated with high plate counts (Colosimo *et al.*, 2005), in a given population against the environmental predictors of watershed area, presence of steelhead and presence of sculpin.

Univariate morphometrics

We first took ventral and left lateral photographs of all stained fish with a Canon EOS Rebel *X3i* digital camera fitted with a 50-mm lens under standardized light conditions with a millimetre ruler in the image for scale. Small pins were inserted into the fish to help indicate anatomical points for placing digital landmarks (e.g. Kaeuffer *et al.*, 2012). We then blotted the fish dry and measured mass to the nearest hundredth of a gram on an electronic balance. We next used digital callipers to measure, to the nearest hundredth of a millimetre: standard length from the tip of the upper jaw to the end of the vertebral column on the caudal peduncle, the lengths of the first and second dorsal spine and the length of the left pelvic spine. We also counted lateral plates on each side of the fish under a dissecting microscope, not including any keel plates at the end of the caudal peduncle (Bell, 1981). Finally, we dissected all fish and inspected the gonads to visually identify sex.

Morphological analyses were performed on up to 30 individuals per population of standard length > 30 mm

(Table S1). All spine length measurements were standardized to a common body size following the allometric approach: $M_S = M_o(L_S/L_o)^b$, where M_S is the standardized spine length measurement, M_o is the unstandardized spine length measurement, L_S is the overall mean body length of all fish, and L_o is the body length of the individual (Lleonart *et al.*, 2000). The exponent *b* was calculated as the common within-group slope from a linear mixed-effects model regressing $\log_{10}(M_o)$ on $\log_{10}(L_o)$ with population as the random factor (Reist, 1986; Hendry & Taylor, 2004).

We used linear mixed-effects models to find the best set of predictors for the length of each size-corrected spine using the R package nlme (Pinheiro *et al.*, 2016). We included a random intercept term for population and fixed terms for watershed area, presence of steelhead and presence of sculpin. As the larger predatory fishes tended to be found in estuaries with larger watersheds (and therefore more upstream habitat), we tested for multicollinearity of predictors by examining variance inflation factors (VIFs). All VIFs were within acceptable limits: VIF < 3 (Zuur *et al.*, 2009). Log-transformed plate counts were analysed in a separate model with the same structure as above.

Geometric morphometrics

We placed 18 homologous landmarks on the lateral photographs using tpsDig software (Rohlf, 2006; Fig. S2; Table S1). Immature fish and fish with large internal parasites were discarded from the analysis. The 18 landmarks were then superimposed using the generalized Procrustes analysis of *geomorph* (Adams & Otarolla-Castillo, 2013), yielding 36 Procrustes residuals representing shape differences among individuals after removing effects of (isometric) scale, rotation and translation. A Procrustes ANOVA (Goodall, 1991; Adams & Otarolla-Castillo, 2013) using body shape as the response variable and sex as the predictor variable revealed a significant effect of sex ($F = 62.14$, $P < 0.01$). To correct for this effect, residuals from this Procrustes ANOVA were added to the mean consensus shape of all individuals. This sexual dimorphism-free shape dataset was used for further analysis.

We performed a multivariate analysis of variance (MANOVA) using Wilks' lambda (λ) as the test statistic. The PCs derived from the 36 Procrustes residuals were allometrically adjusted for centroid size and body depth using the common within-group slope approach described above (Reist, 1986; Lleonart *et al.*, 2000; Rolshausen *et al.*, 2015). The PCs were then used as the dependent variables with presence of steelhead, presence of sculpin and population as fixed explanatory variables. We performed a canonical variates analysis (CVA) using fish facing different predator regimes as separate factors (Webster & Sheets, 2010). This method allows for the identification of different patterns of shape among populations by providing an ordination of the population in morphological space (Leinonen *et al.*, 2006). Thus, the canonical vector (or divergence vector) extracted from this analysis maximizes the morphometric variance for a specific factor (here predator presence/absence). We used the mean individual scores from this divergence vector for each population to visualize body shape differences along this factor.

Elemental composition

Whole fish elemental composition was analysed for 10 fish from each of 15 populations, except for Gazos Creek ($N = 9$) and Younger Lagoon ($N = 20$; Table S1). These fish were different individuals from those analysed above because the two analysis procedures were incompatible on the same fish. Individuals analysed for elemental composition came from estuaries where the two predator types (steelhead and sculpin) were either both present or both absent. We quantified the following phenotypes for each of these fish: standard length, head length (cm), body depth (cm), pelvis length (combined length of anterior and posterior processes, in cm) and lateral plate count (left side). For these traits, we then applied the allometric standardizations as described above (Reist, 1986; Hendry & Taylor, 2004).

Digestive and reproductive tissues were discarded prior to elemental analysis (El-Sabaawi *et al.*, 2012). Stickleback specimens were freeze-dried for 72 h using a LABCONCO 77545-00-J (Kansas City, MO, USA). Dry mass was then recorded and relative condition calculated based on the length–mass relationship (Froese, 2006). Phosphorus content (%P) was determined as the mean of three 9–11 mg subsamples of the ground body tissue. These samples were ashed at 500 °C for 2 h and digested with 1N HCl at 105 °C for 2 h before assay with a Mandel UVmini-1240 spectrophotometer using an acid molybdate method (Murphy and Riley 1962). The mean coefficient of variance was < 3% between fish replicates, and extraction efficiency was > 95% for bonemeal (NIST 1486) and spinach (NIST 1570a) standards.

Two different statistical inferences were explored. First, to test whether lateral plates or *Eda* genotypes predict elemental composition, we created two GLMMs. The first GLMM used only size-corrected phenotypic traits as main effects (standard length, pelvis length, head length, body depth, condition and lateral plate count), whereas the second replaced lateral plate count with *Eda* genotype. All models included population as a random effect, and collinearity was again (as above) within acceptable limits. We then used an AICc-based model search conducted in the MuMIn package to select the best model from each global model (Grueber *et al.*, 2011; Bartoń, 2016). Second, we used GLM to test whether the presence of predatory fish (fixed factor) is associated with stickleback %P, with condition as the only other predictor.

Comparing within- and among-population variation to other stickleback systems

We first verified whether our estuary populations would display greater levels of within than among-population variation. For each trait, we calculated the proportion of the total variation attributable to within vs. between-population variation in our system using a nested ANOVA with trait as the dependent variable and individuals nested in populations as the predictor variable. Within- and among-population variance explained (η^2) was calculated by dividing the sum of squares of each fixed term (individual nested in population and population, respectively) by the total sum of squares. We tested for differences in percentage of variance explained across traits using a two-sided *t* test.

To test whether strong temporal environmental fluctuations would lead to high levels of trait variation, we compared levels of within-population variation in our estuaries to within-population variation from stickleback populations that experience comparatively lower temporal environmental variation. We are not asserting here that populations from these other systems are completely temporally stable, but that they are typically less variable than those in bar-built estuaries subject to dramatic and rapid breaching events, which can lead to extreme changes in abiotic and biotic conditions over a period of hours (Fig. 1b, Fig. S1). Using Tukey's honest significance tests, we compared our within-population standard deviation values with equivalent within-population values from temporally stable lakes, streams and marine environments reported in the literature (Table S7; Whitlock & Schluter, 2009).

Finally, we tested whether environmental variation would lead to relatively lower between-population differences by comparing levels of among-population variation in plate counts in our system to among-population variation from relatively temporally stable stickleback populations experiencing divergent predator regimes (Table S8). To calculate among-population variation, we computed ANOVAs in each system separately with mean population plate counts as dependent variable and populations as predictor. Among-population variation was calculated by dividing the population term sum of squares by the total number of populations in each system, respectively.

Results

Population genetics

No indication of linkage disequilibrium was found between our microsatellite markers (Fisher's exact test, average $\chi^2 = 29.37$, average d.f. = 43.33 and average *P* between pairwise testing = 0.83), as was expected based on their positions on separate linkage groups (Peichel *et al.*, 2001). The markers also showed no within-population departures from Hardy–Weinberg equilibrium after Bonferroni correction.

Correspondence analysis did not reveal obvious discontinuous structuring of the estuary populations (Fig. S3) – apart from our reference marine population, which was a clear outlier (results for the other estuary populations did not change when excluding the marine population). However, STRUCTURE revealed two somewhat distinct groups with the ΔK method identifying two clusters as most likely (Fig. 2 and Table S2 for F_{ST}-based measures of pairwise genetic differentiation). At one end of the spectrum was the marine population composed almost entirely of genotypes from that cluster. At the other end of the spectrum were Lombardi Creek, Old Dairy Creek and Younger Lagoon composed mostly of genotypes from the other cluster. These later three populations were geographically close to each other and had smaller watershed areas as compared to the other estuary populations (mean of 3.4 ± 3 km^2 and 414.9 ± 1015 km^2, respectively). Smaller watersheds tend to have lower stream flows and therefore spend shorter periods of time with the estuary mouth open, suggesting that these populations will be less often connected to the ocean, thus explaining their partial genetic isolation from other populations. Their geographic proximity also means that they are likely to breach at similar times and then exchange migrants with each other, thus explaining their genetic similarity to each other. The other populations contained a variable mixture of alleles from the two clusters. AMOVA revealed *Phi* (*Ø*) statistics below 0.2 (Table S3), confirming low population differentiation that was nevertheless significant (Table S4, Fig. S4). The hierarchical clustering tree showed again that the marine population from Bodega Bay was distinct from the estuary populations, with the estuaries appearing to branch mostly based on geographic proximity (Fig. S5). The Mantel test performed on the estuary populations alone (excluding the marine population) revealed low but significant isolation by distance (Fig. S6 simulated $P = 0.02$).

As noted above, our neutral markers showed no signs of deviations from Hardy–Weinberg equilibrium. Further, when considering only fish homozygote 'complete' at *Eda*, STRUCTURE revealed two distinct groups with the ΔK method identifying two clusters as most likely: one representing the genetic cluster of Bodega Bay and the other representing our estuaries (Fig. S7). Both outcomes support historical analyses in inferring that stickleback in bar-built estuaries are coherent populations, as opposed to hybrid zones.

Divergence associated with predator regimes

LOSITAN revealed that *Eda* was putatively under directional selection ($H_{\mathrm{e}} = 0.88$, $F_{\mathrm{ST}} = 0.12$, $P_{Simul.\ Fst\ <\ sample\ Fst} = 0.97$), whereas *Pitx1* was putatively under balancing selection ($H_{\mathrm{e}} = 0.45$, $F_{\mathrm{ST}} = 0.25$, $P_{Simul.\ Fst\ <\ sample\ Fst} < 0.02$). Stickleback in estuaries with sculpin showed a higher frequency of the C allele at *Eda* than did

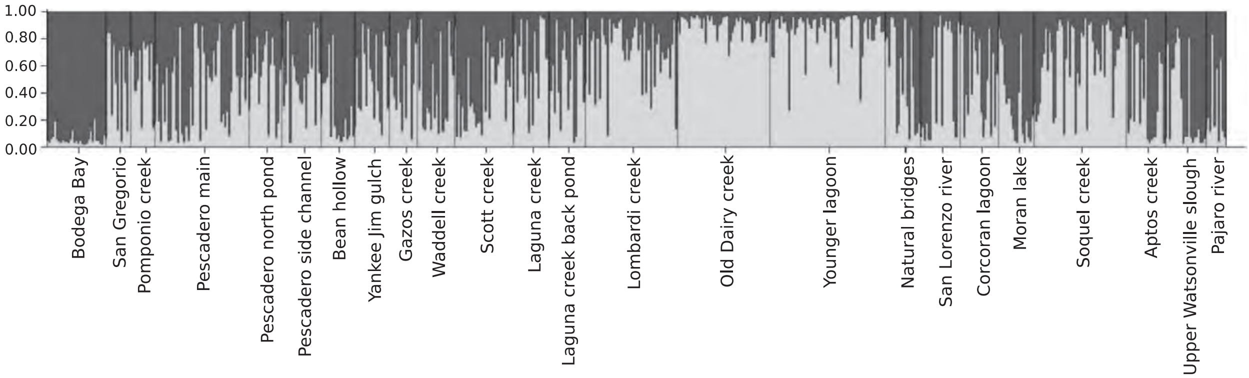

Fig. 2 Individual assignment to population structure inferred by STRUCTURE. Each bar represents an individual. The *y*-axis represents the probability of classification to a cluster.

stickleback in estuaries without sculpin (mean across populations: 0.46 vs. 0.18; Table 1, Fig. 3).

Univariate morphometrics

Mixed models with population as a random effect significantly improved the fit of linear models for spine length and plate count as measured by a likelihood ratio test (Table S5). None of our fixed predictors (presence of sculpin, presence of steelhead and watershed size) for the length of the first dorsal spine were significant (Table 1). However, stickleback had somewhat longer second dorsal and pelvic spines, as well as more lateral plates, in estuaries with sculpin than in estuaries without sculpin (Table 1, Fig. 3).

Table 1 Results of mixed-models analysis testing the effect of the presence of sculpin, steelhead and watershed size.

Response	Predictor	Coef.	SE	*T*-value	*P*-value
First spine length	Sculpin	0.41	0.26	1.59	0.121
	Steelhead	−0.11	0.26	−0.42	0.656
	Watershed size	0.01	0.01	1.12	0.281
Second spine length	Sculpin	0.45	0.22	2.07	0.052
	Steelhead	−0.13	0.22	−0.59	0.543
	Watershed size	0.01	0.01	0.77	0.439
Pelvic spine length	Sculpin	0.58	0.32	1.82	0.081
	Steelhead	−0.21	0.33	−0.62	0.535
	Watershed size	−0.01	0.01	−0.95	0.419
Log plate count	Sculpin	0.73	0.23	3.14	**0.005**
	Steelhead	−0.22	0.24	−0.89	0.382
	Watershed size	−0.01	0.01	−1.45	0.165
C allele frequency	Sculpin	0.43	0.16	2.75	**0.013**
	Steelhead	−0.15	0.16	−0.93	0.363
	Watershed size	−0.01	0.01	−0.94	0.359

Coefficient (Coef.), standard error (SE) *T* and *P*-values are reported. d.f. were 19 for all variables. Intercepts and random effects are not shown. $P \leq 0.05$ are in bold.

Geometric morphometrics

The first two axes explained 49% of the total shape variation (33% for PC1 and 16% for PC2), with both axes mainly related to body depth. In particular, stickleback scoring negatively were shallower bodied whereas fish scoring positively were deeper bodied, in the posterior part of the body (PC1) or the anterior part of the body (PC2) (Fig. S8). MANOVA on all 36 PCs revealed a significant influence of population ($\lambda = 0.01$, d.f. = 22, $F = 2.61$ and $P < 0.01$), sculpin ($\lambda = 0.71$, d.f. = 1, $F = 4.99$ and $P < 0.01$) and steelhead ($\lambda = 0.83$, d.f. = 1, $F = 2.37$ and $P < 0.01$). Testing the effect of presence vs. absence of each predator type alone yielded a similar outcome ($\lambda = 0.74$, d.f. = 1, $F = 4.31$ and $P < 0.01$). Overall, stickleback tend to be shallower bodied in the presence than absence of predatory fishes (Fig. 4), although most estuaries showed a great diversity of body shapes, with individuals scoring positively and negatively.

Elemental composition

Phosphorus content ranged from 2.8% to 6.9% among the collected stickleback. In the best phenotypic model (using plate number rather than *Eda* genotype), five main effects explained over one-third of the total variation ($R^2_{\text{Marg.}} = 0.35$) and, when combined with population as a random effect, explained double that ($R^2_{\text{Cond.}} = 0.72$). Of these factors, condition had the largest effect on %P ($P < 0.001$), with high condition fish showing reduced phosphorus content (Table S6). Standard length, head length and lateral plate count were also significant predictors of %P ($P < 0.001$) and had similar effect sizes ($\eta^2 = 0.35$–0.50, Table S6). In each case, %P was positively correlated with trait values (Fig. S9). The best genotypic model (using *Eda* genotype rather than plate number) showed similar relationships and explanatory power (Table S6, Fig. 5a). In this case, six main effects explained 0.42% of the variation and, when combined with population as a random effect explained 0.77%. Again, condition had the

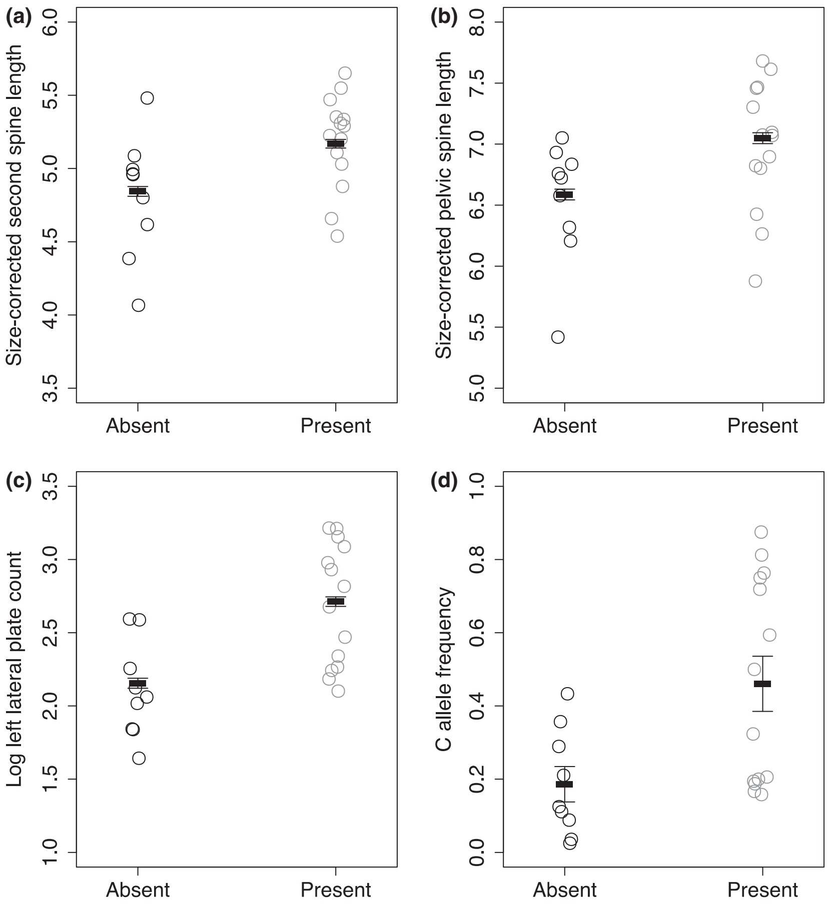

Fig. 3 Armor morphology in the presence or absence of sculpin. (a) Size-corrected first dorsal spine length. (b) Size-corrected pelvic spine length. (c) Log left lateral plate count. (d) *Eda* complete allele frequency. Each circle depicts the mean value of a particular estuary population in the absence (black) or presence (grey) of sculpin. Bars represent the overall mean value (± SE) in the presence of absence of sculpin.

largest effect ($\eta^2 = -1.11$) with *Eda* genotype having the second largest effect ($\eta^2 = -0.68$ for LL vs CC genotypes). Predation and condition influenced %P differences among populations ($\eta^2 = 0.24$, $P < 0.001$), predation having a greater effect than condition ($\eta^2 = 0.24$ vs 0.15). Across the 15 populations, those in estuaries with predators were 20% higher in %P (5.1% vs 4.2%; Fig. 5b).

Within- and among-population variation

In our study system, the proportion of variance explained (η^2) was significantly greater within than among populations for all traits, except %P ($t = -2.72$, d.f. = 12, $P < 0.01$, Fig. S10). Within-population variation in plate count, *Eda* complete allelic count, and shape was significantly greater in our Santa Cruz estuaries than in presumed more stable environments documented in the literature, except in lakes for the *Eda* complete allelic count (Table 2, Fig. 6a–c). Among-population variation in plate counts was lower in Santa Cruz populations than in other systems, including systems with populations exposed to divergent predator regimes (Haida Gwaii and Vancouver Island, Table 3, Fig. 6d; Reimchen *et al.*, 2013; Miller *et al.*, 2015). Note that, as compared to our bar-built system, the other systems used in this comparative analysis face much lower gene flow. For instance, the lakes in Québec and on Vancouver Island are completely geographically isolated from each other, ensuring no gene flow between populations (Lacasse & Aubin-Horth, 2012; Miller *et al.*, 2015). For Alaska, most of the populations reported in Table 3 are also geographically isolated, except for those present in the Matanuska-Susitna valley, which nevertheless have a mean F_{ST} much greater (0.111: Bell & Orti, 1994; Aguirre, 2009; W.E. Aguirre, 2010 unpublished data) than in our system (0.003). The same is true from populations from North Uist in Scotland (mean F_{ST} of 0.199).

Discussion

We considered potential consequences of the extreme temporal environmental variation present in bar-built estuaries for within- and among-population variation in stickleback armor traits and their potential ecological effects. We first describe our main results and then discuss the nuances and implications in more detail. First, stickleback gene flow was high among many of the estuaries, but not so high as to entirely prevent divergence in armor traits in response to different predation

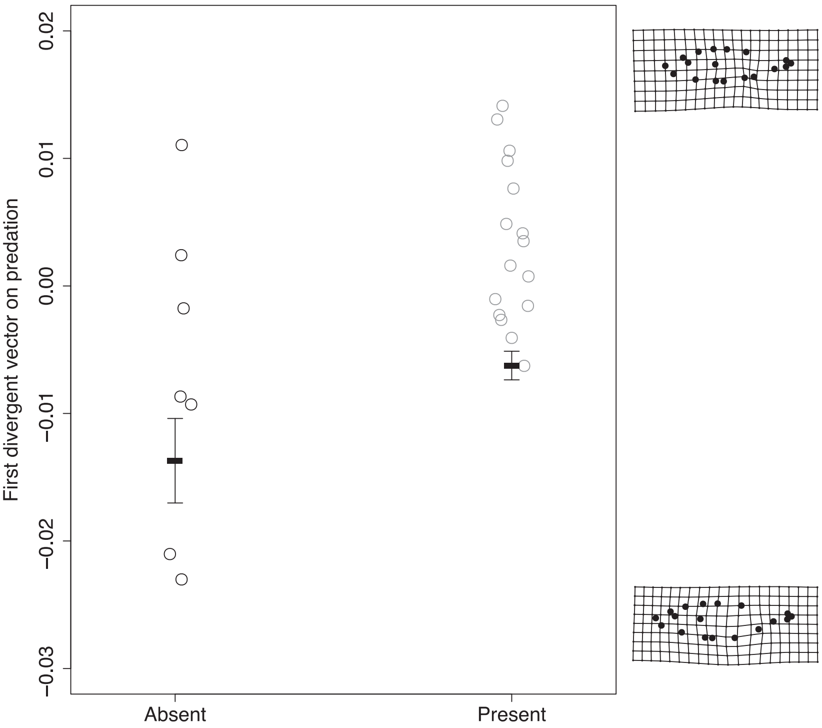

Fig. 4 Divergence scores extracted from the first divergent vector of each population and obtained through a canonical vector analysis (CVA). Each circle depicts the mean value of a particular estuary population in the absence (black) or presence (grey) of predators. Bars represent the overall mean value (± SE) in the presence of absence of predators. Populations with mean negative divergence scores have deeper bodies whereas population scoring positively are more streamlined. Thin-plate spline transformation grids of CVA divergent vectors display the shape difference between positive and negative scores.

regimes. Second, this divergence in armor traits was – as expected from the high gene flow – generally weaker than that observed in other (not bar-built) systems, including among stickleback populations exposed to divergent predator regimes in more temporally stable environments. Third, within-population variation was very high for stickleback in the estuaries, including in comparison to stickleback from other study systems where temporal environmental variation is presumably lower. Fourth, an essential element for ecological stoichiometry (%P) – a trait potentially linked to the ecological effects of stickleback – was strongly associated with armor traits and *Eda* allele frequency. Overall, our results suggest that strong temporal environmental variation – in conjunction with high gene flow – can have important consequences for within- and among-population variation in adaptive traits, and the potential ecological effects of those traits.

Population structure reveals high gene flow between estuaries

Despite frequent breaching events that disrupt the isolation of estuary populations (Allen *et al.*, 2006), we detected some evidence for population structure across the system. The greatest contribution to this structure was that stickleback in several estuaries were clearly distinct from the Bodega Bay marine population, with stickleback in the other estuaries showing apparent admixture between the two genotypic clusters (Fig. 2, Fig. S5). These results concur with the expectation that breaching events promote dispersal between bar-built estuary stickleback and marine stickleback, but not so much as to prevent the latter from diverging genetically in at least some cases. Consistent with this interpretation, we detected weak but significant isolation by distance (Table S2, Fig. S6) and population differentiation (Table S4, Fig. S4), indicating the potential for adaptive divergence among populations. However, it was also clear that many of the estuaries experienced high gene flow with each other and with marine stickleback. Together, these results indicate that gene flow between the bar-built estuaries along this coast is sufficiently low to allow population divergence in at least some cases, but also sufficiently high to constrain the magnitude of that divergence.

Trait differentiation is associated with divergent predator regimes

Spatial variation in the presence of piscivorous fishes was correlated with spatial variation in stickleback armor traits. In particular, when sculpin were present, stickleback had slightly longer spines, more lateral plates, shallower bodies and a higher frequency of the complete *Eda* allele (Fig. 2). Sculpin are well-known predators of stickleback and prey on eggs, fry and adults (Moodie, 1972; Pressley, 1981; Reimchen, 1994; Ingram *et al.*, 2012). These findings parallel many previous studies of stickleback, where populations experiencing greater levels of predation from fish display longer spines, more lateral plates (and therefore a higher

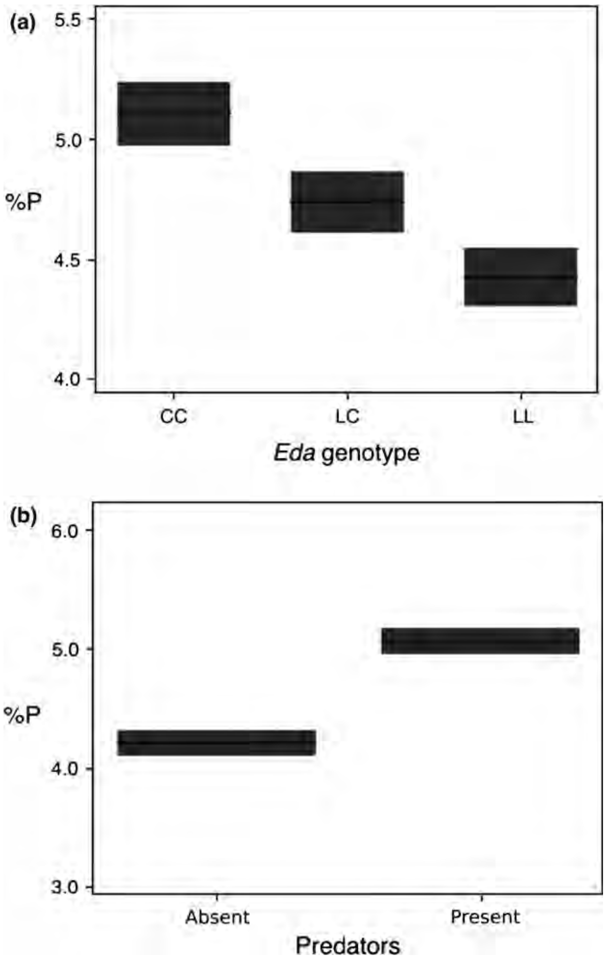

Fig. 5 Modelled relationship between %P and *Eda* from 'phenotype + *Eda*' GLMM (a) and between %P and predation (b). Shaded regions depict ± 1 SE from mean.

frequency of the complete *Eda* allele) and shallower bodies (Reimchen, 1992, 1994; Leinonen *et al.*, 2011; Lescak & von Hippel, 2011), with these patterns being especially strong in the presence of sculpin (Ingram *et al.*, 2012; Miller *et al.*, 2015). In our study, however, the presence of sculpin only modestly affected spine length. Perhaps, one contributor to this comparative subtlety is that longer spines will be less effective against predators without significant gape limitation, such as the Pacific staghorn sculpin (*Leptocottus amatus*), which are able to swallow stickleback with large spines (Moyle, 1976; Hyatt, 1979). Therefore, the only modest effect of sculpin presence on spine length differentiation between estuaries could be due to this trait not providing an effective defence against the functional capabilities of the local predators. Taken together, these results show, despite extreme temporal variation in environmental conditions and high gene flow among estuaries, spatial variation consistent with local adaptation was evident in stickleback armor traits.

Beyond phenotypes, genetic markers associated with *Eda* and *Pitx1* showed evidence for directional and balancing selection, respectively. Consistent with the above results for lateral plates, the frequency of the complete *Eda* allele was higher in the presence of sculpin (Fig. 3d). This pattern is consistent with predation-induced selection, similar to that documented in previous studies of other stickleback systems (Marchinko, 2009; Zeller *et al.*, 2012; Raeymaekers *et al.*, 2014). Although phenotypic plasticity could explain some of this variation in armor phenotypes, its role is likely minimal given that *Eda* explains about 75% of the variation in plate counts (Colosimo *et al.*, 2004; Kitano *et al.*, 2008). Thus, the inferred directional selection at *Eda* likely reflects the importance of lateral plate defence against the predatory sculpin. Interpretations for *Pitx1* are quite different. In other stickleback

Table 2 Results of Tukey *post hoc* test testing for differences in standard deviations between our estuary populations and environmentally stable lake, marine and stream populations for plate counts, *Eda* complete allele count and procrustes variance.

	Plate count				Complete *Eda* allele count				Procrustes variance			
	d.f.	Sum.Sq	Mean.Sq	*F*-value	d.f.	Sum.Sq	Mean.Sq	*F*-value	d.f.	Sum.Sq	Mean.Sq	*F*-value
ANOVA	3	509.30	169.80	**77.06**	3	1.18	0.39	**8.13**	2	0	0	**8.28**
	Diff.	Lower	Upper	*P*-value	Diff.	Lower	Upper	*P*-value	Diff.	Lower	Upper	*P*-value
Estuary–Lake	−5.154	−6.038	−4.269	**< 0.001**	0.104	−0.098	0.306	0.905	−0.006	−0.012	−0.002	**0.010**
Estuary–Marine	−4.246	−5.828	−2.664	**< 0.001**	−0.484	−0.878	−0.091	**0.011**	*na*	*na*	*na*	*na*
Estuary–Stream	−4.787	−5.983	−3.592	**< 0.001**	−0.263	−0.554	0.027	0.087	0.000	−0.012	−0.006	**0.007**
Marine–Lake	0.908	−0.504	2.321	0.343	−0.389	−0.642	−0.138	**< 0.001**	*na*	*na*	*na*	*na*
Marine–Stream	−0.542	−2.166	1.083	0.823	0.073	−0.248	0.395	0.929	*na*	*na*	*na*	*na*
Stream–Lake	0.367	−0.591	1.325	0.753	−0.316	−0.629	−0.003	**0.04**	−0.000	−0.006	0.006	0.991

Mean differences (Diff.), 95% confidence intervals (lower and upper) and *P*-values are reported. Degrees of freedom (d.f.), sum of squares (Sum.Sq), mean sum of squares (Mean.Sq) and *F*-values are reported for a standard ANOVA. $P < 0.05$ and significant *F*-values are in bold.

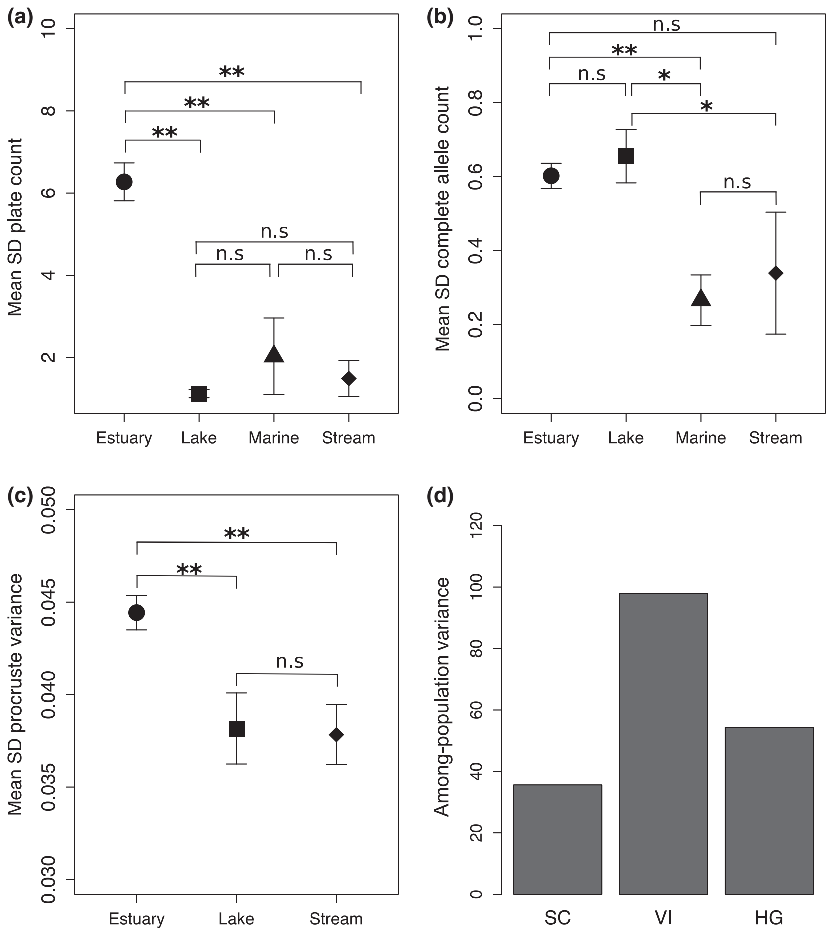

Fig. 6 Within-population mean standard deviations (SD) between Santa Cruz estuaries and less temporally variable lake, marine and stream environments (± SE, panels a–c) and among-population variance in plate counts in the Santa Cruz estuaries (SC), Vancouver Island (VI) and Haida Gwaii (HG) (panel d). *P*-values < 0.01 are presented by two stars, and *P*-values < 0.05 by one star. Nonsignificant differences are represented by n.s.

Table 3 Among-population variance (Variance), total number of populations (*N*) and population sum of squares (Sum.Sq) in the Santa Cruz, Vancouver Island, Haida Gwaii and Iceland systems.

	N	Sum.Sq	Variance
Santa Cruz	23	818.88	35.61
Vancouver Island	49	6002.83	97.86
Haida Gwaii	30	1630.06	54.34
Iceland	10	501.23	50.13

systems, regulatory mutations at *Pitx1* are generally associated with molecular signatures of positive directional selection in pelvic-reduced populations that colonized freshwater from the ocean (Chan *et al.*, 2010). In contrast, we detected evidence of balancing selection at this locus. Balancing selection is thought to be an important mechanism responsible for the maintenance of genetic polymorphism (Hedrick, 1986), especially in heterogeneous environments (Hedrick, 1986; Spichtig & Kawecki, 2004). Thus, whereas patterns for lateral plates likely reflect consistent directional selection on a defensive trait owing to spatial variation in predatory fishes, balancing selection at *Pitx1* could be reflective of the temporal fluctuations in environmental conditions present in these estuaries.

At the same time, it is important to recognize that population divergence in the bar-built system is considerably weaker than that in other stickleback systems (Table 3, Fig. 6d). This contrast among systems is consistent with the expected effects of both temporal variation and gene flow. First, when temporal variation is high, spatial differences are expected to be compromised, as suggested by some previous theoretical and empirical analyses (Kawecki & Ebert, 2004; Siepielski *et al.*, 2009; Bell, 2010; Chevin *et al.*, 2015). Second, when gene flow is high, spatial population divergence is often low, as shown in theory (Slatkin, 1973; Felsenstein, 1976; Kawecki, 2008) and empirical systems including stickleback (e.g. Hendry & Taylor, 2004; Stuart *et al.*, 2017).

One additional consideration is that the relatively high within-population variation observed in these estuary populations could occur because they represent a hybrid zone between marine and stream freshwater populations (e.g. Jones *et al.*, 2006; Vines *et al.*, 2016).

This hypothesis was historically investigated and rejected (Bell, 1976, 1979a, b, 1981, 1982; Baumgartner & Bell, 1984; Baumgartner, 1986, 1992, 1994; Bell & Richkind, 2015). Indeed, a freshwater form was never found upstream of California estuaries, and plate counts were – in fact – often greater upstream than downstream (Bell, 1976, 1979a, b, 1981, 1982). In addition, all of our neutral markers showed no departure from Hardy–Weinberg equilibrium and individuals homozygote 'complete' at *Eda* did not group with the neutral marine cluster of Bodega Bay (Fig. S7). These results confirm historical evidence that our estuaries do not represent hybrid zones but rather coherent populations in their own right. In summary, spatial patterns of phenotypic and genetic variation for stickleback in bar-built estuaries match some important aspects of previous studies, while also suggesting additional nuances and effects.

Trait variation within populations

We found that stickleback in bar-built estuaries of the central California coast exhibits very high levels of within-population variation. This result held for all traits, ranging from spine length to body shape to plate count to *Eda* genotype to %P (Fig. S10). This within-population variation appears much greater than that documented in previous stickleback studies that focused on populations in presumably more stable environments (Table 3, Table S7, Fig. 6a–c). An exception that could prove the rule is the very low among-population differentiation and very high within-population variation in stickleback from ephemeral streams and adjacent vineyard reservoirs in Napa, California (Hendry *et al.*, 2013), another system where temporal environmental variation (and likely gene flow) is extremely high. These differences among systems are consistent with arguments that constantly shifting environmental conditions prevent temporally consistent selection, thereby impeding the ability of directional selection to eliminate variation from the populations (Bell, 2010; Michel *et al.*, 2014). Valuable additional steps would be to examine the fitness consequences of this high genetic variation – such variation could impose a substantial genetic load on populations (Lande & Shannon, 1996; Arnold *et al.*, 2001). On the other hand, high genetic variation should maintain the potential for strong selection and rapid evolutionary responses, which could aid responses to future environmental changes (Mackay, 1981; Kirkpatrick & Barton, 1997; Kawecki & Ebert, 2004).

As alluded to several times already, there are two likely mechanisms driving the observed high within-population and low among-population variation: high temporal environmental variation and high gene flow. Although gene flow could certainly contribute to reduced divergence – as has been inferred by our group for other stickleback systems (e.g. Hendry & Taylor, 2004; Stuart *et al.*, 2017) – we do not think that this mechanism alone explains patterns of variation in the bar-built system. The reason is that high gene flow is most effective at maintaining high within-population variation if among-population variation is also high. In the bar-built system, however, among-population variation is low (Table 3, Fig. 6), which means that gene flow will not be moving novel variants among estuaries and inflating the variation within each of those populations. Hence, we suggest that high temporal variation is responsible for the observed high within-population variance and low among-population variance, as also suggested by some previous theoretical and empirical analyses (Kawecki & Ebert, 2004; Siepielski *et al.*, 2009; Bell, 2010; Chevin *et al.*, 2015).

Elemental composition

Previous studies have shown that investment in bony structures can increase phosphorus demand, which can potentially alter how fish forage and recycle nutrients (El-Sabaawi *et al.*, 2016; Durston & El-Sabaawi, 2017; Leal *et al.*, 2017). We find that, despite dramatic environmental fluctuations, the expected association between %P and armor remains strong. Moreover, we find that genotypes at a single locus (*Eda*) explain a large amount of the variation in %P (Fig. 5a), which is not surprising given that variation in *Eda* explains much of the variation in lateral plates (Colosimo *et al.*, 2004). Importantly, lateral plates and *Eda* vary dramatically within and among the estuaries, generating the high levels of variation in %P. This variation should have a major influence on whole fish elemental ratios and thus the observed variation in %P is likely to influence the balance between excretion rates and diet choice (El-Sabaawi *et al.*, 2016; Durston & El-Sabaawi, 2017). Given that allelic variation at *Eda* appears to be driving variation in elemental composition, and because *Eda* is generally subject to strong natural selection in the wild (Colosimo *et al.*, 2004, 2005; Barrett *et al.*, 2008; Jones *et al.*, 2012), it is likely that elemental composition in %P can evolve just as rapidly as can lateral plates (see Durston & El-Sabaawi, 2017). As a result, this contemporary evolution of elemental composition should then feedback to influence selection on stickleback armor and elemental composition, thus influencing ecological interactions (Leal *et al.*, 2017; individuals with different elemental demands compensate through consumer–resource interactions). These eco-evolutionary hypotheses seem a profitable avenue for future studies.

The among-population variation in %P was closely associated with predator regime, being higher in stickleback populations coexisting with sculpins. This variation could arise for two main reasons: (i) stickleback evolving with predators are more heavily armored and therefore have greater %P or (ii) stickleback exposed to predators forage less, resulting in lower lipid stores and higher %P due to the lower body mass (Sterner & Elser, 2002). Both effects seem possible here given that (i) predation regime influences stickleback armor traits (Fig. 3c), which then influences %P (Fig. 5b); and (ii) fish condition influences %P (Par. $\eta^2 = 0.24$, $P < 0.001$) and predator presence can lead to lower foraging rates in stickleback (Milinski & Heller, 1978). Here, then, we have the potential for both genetic variation (armor adaptive divergence) and perhaps plasticity (decreased foraging) to jointly influence ecological effects, which has been suggested (Hendry, 2017), but not yet demonstrated. In addition, predator-driven selection on armor traits could lead to changes in environmental stoichiometry, which may then alter selection regimes further, thereby facilitating eco-evolutionary feedbacks (Pelletier *et al.*, 2009; Hendry, 2017).

Conclusions and implications

Our study provides empirical support for the expectation that temporal variation in environmental conditions can maintain high levels of variation in adaptive traits, even in traits that show differentiation associated with spatial variation in predator regime. In this system, breaching events cause each estuary to be periodically open to the ocean, which likely increases within-population variation through two mechanisms that prevent the fixation of adaptive alleles: (i) temporal variation in selection within populations (Kawecki & Ebert, 2004; Bell, 2010) and (ii) high gene flow between populations (Slatkin, 1973; Felsenstein, 1976; Kawecki, 2008). Although the latter effect is likely important, the former is too because gene flow alone is an insufficient explanation for the high within-population variation given only modest among-population variation. Our results thus support the hypothesis that temporal variation helps to maintain variation in adaptive traits within populations.

At the same time, temporal variation and high within-population variation did not eliminate population divergence in response to spatial variation in selection. Specifically, we documented associations between predator regime (presence or absence of sculpin) and stickleback armor traits (lateral plates and the gene that controls them, *Eda*). Although this differentiation is not as great as that found among other stickleback populations experiencing divergent selection regimes, it is notable for occurring in the face of frequent temporal fluctuations and relatively high gene flow. It therefore seems likely that selection occurring during the periods when estuaries are closed from the ocean and isolated from each other is sufficiently strong to drive some differentiation – even if it is later erased or reduced when the estuaries are open to the ocean. Certainly, some other studies have found that adaptive divergence can persist despite temporal variation in selection and high gene flow (Mojica *et al.*, 2012; Gotanda & Hendry, 2014); yet we argue that the divergence documented here is especially noteworthy given the extreme and rapid shifts in environmental conditions that these populations experience (Fig. 1b, Fig. S1).

It has long been debated whether selection in nature is typically ‘strong’ or ‘weak’ (Endler, 1986; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Hereford *et al.*, 2004). What can be safely asserted is that selection should be stronger when environmental conditions change more rapidly (Chevin *et al.*, 2010; Michel *et al.*, 2014). Hence, we predict that these bar-built estuary stickleback population experience extremely strong selection at periodic intervals – and that this selection likely differs depending on temporal proximity to the breaching event. We suggest that selection is constantly driving contemporary evolution in these populations but that this nascent adaptation is frequently impeded or reversed by the rapidly changing conditions (i.e. fluctuating selection generating evolution in ‘fits and starts’). These highly dynamic conditions should provide an excellent system for studies of contemporary evolution and its ecological consequences.

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Contributions

AP, BAW, EPP, APH and RDHB designed the study. BAW, TMA and EPP collected samples. BAW took phenotypic measurements. AP, DH and SK performed the molecular work. LA took geomorphometric measurements. DD and RWE took stoichiometric measurements. AP, BAW, DH, LA and DD analysed the data. AP wrote the manuscript with inputs from DH, RWE, EPP, EPH and RDHB.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1 Population sample size used in each analysis.

Table S2 Pairwise genetic differentiation between estuaries represented by F_{ST} values.

Table S3 Summary statistics of AMOVA test.

Table S4 Results of permutation tests performed on the AMOVA test statistics.

Table S5 For each element of armor morphology: standard deviation (SD) of the random intercepts for estuary for the mixed model, ΔAIC for the comparison of a model without a random effect to the full model, log-likelihood-ratio (LLR), and *P*-value of a likelihood ratio test comparing the full model with a model lacking the random effect of population for each dependent variable.

Table S6 Best models based on AICc for %P. Marginal R^2 for model fit of main effect is .35 (phenotype model) and .43 (phenotype + *Eda* model).

Table S7 Within-population standard deviations from the estuary populations and from known environmentally stable populations.

Table S8 Mean lateral plate counts (Plate) and standard deviations (SD) from six different systems.

Figure S1 Photos and videos of breaching events.

Figure S2 Location of the 18 landmarks for geometric morphometrics.

Figure S3 Representation of correspondence analysis (CA) performed on allele frequencies on axes 1 and 2.

Figure S4 Histograms representing the simulated values of the randomized values of the AMOVA test. The black line represents the observed values. A. Variation within samples, B. Variation between samples, C. Variation between populations.

Figure S5 Hierarchical clustering tree based on a cluster analysis constructed with Edward's genetic distance. The axis is a measure of closeness of clusters (Distance).

Figure S6 Isolation by distance in Santa Cruz estuary populations. Scatter plot of pairwise genetic distances (Edward's) against pairwise geographic distances (km) in our 23 sampling points.

Figure S7 Individual assignment to population structure inferred by STRUCTURE using only fish homozygote 'complete' at *Eda*. Each bar represents an individual. The Y axis represents the probability of classification to a cluster.

Figure S8 Body shape variation on PC1 (top) and PC2 (bottom) of Procrustes residuals.

Figure S9 Relationships between phenotypic traits and %P from the phenotypic GLMM. %P rose significantly ($P < 0.001$) with standard length (Panel A; SL), head length (C) and lateral plate count (D), while declining with condition (B). Shaded regions depict 95% confidence ranges.

Figure S10 Proportion of variance explained (η^2) for the studied traits. Between-population variance is in grey and within-population variance in black.

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Coyote (*Canis latrans*) use of marine resources in coastal California: A new behavior relative to their recent ancestors

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Abstract

Coyotes (*Canis latrans*) are known to consume marine foods, but the importance and persistence of marine subsidies to coyotes is unknown. Recent access to a marine subsidy, especially if gained following apex predator loss, may facilitate coyote expansion along coastal routes and amplify the effects of mesopredator release. Our goal was to quantify and contextualize past and present marine resource use by coyotes on the central coast of California via stable isotope analysis. We measured δ^{13}C and δ^{15}N values in coyotes, their competitors, and their food resources at two modern sites, seven archaeological sites spanning in age from ~3000 to 750 BP, and from historical (AD 1893–1992) coyote and grizzly bear hair and bone sourced from coastal counties. We found evidence for marine resource use by modern coastal California coyotes at one site, Año Nuevo, which hosts a mainland northern elephant seal (*Mirounga angustirostris*) breeding colony. Seals and sea lions account for ~20% of Año Nuevo coyote diet throughout the year and this marine subsidy likely positively impacts coyote population size. Isotopic data suggest that neither historic nor prehistoric coyotes consumed marine-derived foods, even at sites near ancient mainland seal rookeries. Marine resource use by some contemporary California coyotes is a novel behavior relative to their recent ancestors. We hypothesize that human alteration of the environment through extirpation of the California grizzly bear and the more recent protection of marine mammals likely enabled this behavioral shift.

Keywords

carbon isotopes, coyote, diet, interspecific competition, nitrogen isotopes, resource subsidy

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Introduction

The transfer of energy and resources from ocean (Polis and Hurd, 1996) to land can have profound consequences for coastal terrestrial ecosystems (Rose and Polis, 1998; Spiller et al., 2010). One avenue for energy transfer is the consumption of marine foods by terrestrial animals, a phenomenon that is quite common and significant; Carlton and Hodder (2003) reviewed 135 records of marine resource use by 45 different terrestrial mammal species on every continent except Antarctica. Marine resource use is generally sporadic and opportunistic; however, marine subsidies can also significantly contribute to the maintenance (e.g. Roth, 2003) and/or expansion (Killengreen et al., 2011) of predator populations. The recent population increase and range expansion of mesopredators has largely been attributed to top-down release following the widespread loss of apex predators (Prugh et al, 2009; Ripple et al., 2013; Ritchie and Johnson, 2009). But bottom-up effects, including anthropogenic and/or marine resource subsidies, can also contribute to (Killengreen et al., 2011; Polis and Hurd, 1996), attenuate (Elmhagen and Rushton, 2007; Polis and Hurd, 1996; Rose and Polis, 1998; Spiller et al., 2010), or possibly even amplify top-down effects.

Coyotes (*Canis latrans*) have a rapidly expanding North and Central American range (Chubbs and Phillips, 2005; Fener et al., 2005; Hidalgo-Mihart et al., 2006; Mendez-Carvajal and Moreno, 2014) and a significant body of research now attributes coyote expansion predominantly to wolf extirpation (e.g. Berger and Gese, 2007; Peterson, 1996; Ripple et al., 2013; Thurber and Peterson, 1991). Coyotes have also been shown to benefit from anthropogenic (Fedriani et al., 2001; Newsome et al., 2015) and marine subsidies (Rose and Polis, 1998; Schwarcz, 1991), and they can have cascading impacts on other predators and prey (Crooks and Soulé, 1999). On the central coast of California, coyotes have been observed consuming marine resources, but the importance of these resources to their diets is unknown. If this marine subsidy has a recent onset, it may be facilitating coyote expansion along coastal routes. Furthermore, if access to a marine subsidy was only gained following the removal of a competitor, a new marine subsidy could intensify the effects of mesopredator release.

Here we aim to quantify the current marine subsidy to coyotes and evaluate its spatial and temporal coverage. Our goals are (1) to characterize the extent and importance of a marine subsidy to modern coyotes on the central California coast and (2) to determine whether this marine subsidy is recent or has roots deeper in

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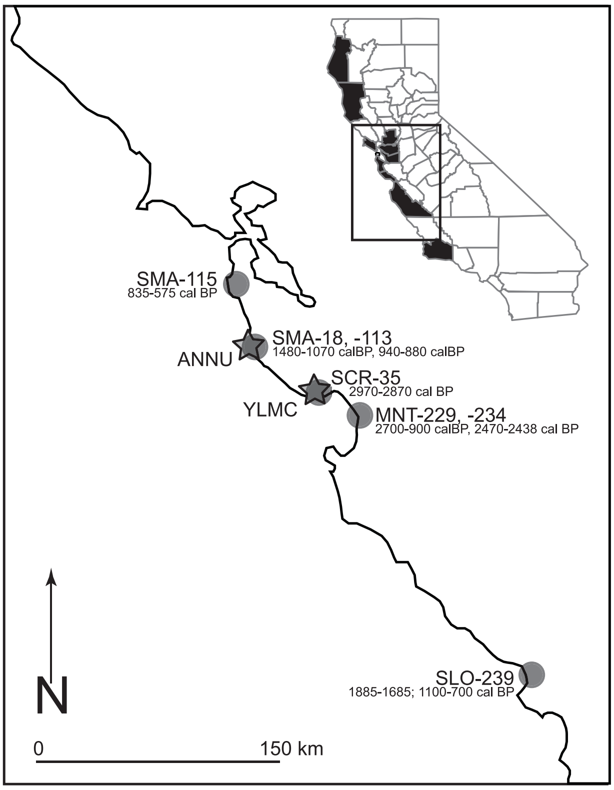

Figure 1. Map of the central California coast illustrating sampling localities: seven archaeological sites used in this study (gray circles) and two modern scat transects (stars with black outlines; ANNU: Año Nuevo, YLMC: Younger Lagoon/Moore Creek). Dates of occupation for the archaeological sites are listed below the site codes: Montara State Beach (CA-SMA-115; Hylkema 1991), Año Nuevo (CA-SMA-18; Hylkema et al., 2006; Newsome et al., 2007), Quiroste Valley (CA-SMA-113; Gifford-Gonzalez, 2011), Davenport (CA-SCR-35; Newsome et al., 2007), Moss Landing (CA-MNT-229; Dietz et al., 1988; Jones, 2002; CA-MNT-234; Newsome et al., 2007), and Morro Bay (CA-SLO-239, Jones et al., 2017). Details regarding the fauna at these archaeological sites are described in the Supplementary Text available online. Coastal counties from which we analyzed historical specimens are shaded in black.

the Holocene. We use coyotes as a test case to examine the possible interplay between top-down (apex predator loss) and bottom-up (resource subsidy) effects on mesopredator expansion. The central California coast is an ideal region to investigate the past and present magnitude of a marine subsidy to coyotes. Not only is the marine environment highly productive, offering numerous opportunities for the delivery of subsidies to adjacent terrestrial communities, but humans have occupied this part of the coast for thousands of years, allowing for the accumulation of subfossil assemblages in archaeological middens.

We present carbon and nitrogen isotope data from coyotes, their competitors, and their potential food resources collected from two present-day coastal sites, seven coastal archaeological sites spanning periods of occupation from ~3000 to 750 BP, and from historical coyote and grizzly bears from coastal California counties (Figure 1). Año Nuevo State Park (San Mateo County, CA) presently supports a dense seasonal concentration of California sea lions (*Zalophus californianus*) as well as a breeding colony of northern elephant seals (*Mirounga angustirostris*) that was established in the 1960s (Le Boeuf and Panken, 1977). Mainland rookery sites such as these likely provide terrestrial predators and scavengers easy access to living and dead seal pups, both of which are possible coyote food sources (Steiger et al., 1989; Way and Horton, 2004). Younger Lagoon Reserve, while also a protected area along the coast, lacks a seal rookery. Looking to the archaeological sites, a preponderance of evidence points to the existence of mainland northern fur seal (*Callorhinus ursinus*) rookeries coincident with ancient human occupation at Moss Landing, CA (CA-MNT-234 and CA-MNT-229; Burton et al., 2001; Gifford-Gonzalez, 2011; Milliken et al., 1999) as well as at Año Nuevo, CA (CA-SMA-18; Gifford-Gonzalez et al., 2006; Hylkema, 2002), allowing for a comparison between past and present sites with very similar resource availabilities. In contrast with northern elephant seals, *C. ursinus* typically comes ashore to pup and breed between June and October (Riedman, 1990), with some hints of a longer span of maternal attendance in prehistoric populations (Newsome et al., 2007). By comparing modern and prehistoric coyote diets in coastal California at sites with and without seal rookeries, we show that marine resource use by some present-day coyotes is a new behavior relative to their recent ancestors. We argue that reduced competition with both grizzly bears and humans likely enabled this behavioral shift, which suggests that the top-down effect of mesopredator release could be amplified by the bottom-up effect of a newly gained resource subsidy.

Methods

Approach

Stable isotope analysis is an ideal approach for assessing the relative importance of marine and terrestrial resources to past and present coyote diets. The δ^{13}C and δ^{15}N values of animal tissues and scat reflect the isotopic composition of an animal's diet, offset by characteristic diet-to-tissue isotopic discrimination factors in both carbon and nitrogen, which can vary depending on the tissue being analyzed (reviewed by Koch, 2007). Marine ecosystems are isotopically distinct from terrestrial ecosystems in part because of baseline differences in the isotopic composition of primary producers; in many regions, including coastal California, marine primary producers are enriched in both ^{13}C and ^{15}N relative to terrestrial plants (Newsome et al., 2010). Furthermore, marine food chains are generally longer than terrestrial food chains, leading to greater trophic enrichments in the heavier isotopes. Apex predators in marine systems thus have δ^{15}N values in the range of +16 to +19 ‰, while terrestrial apex predator δ^{15}N values range between +7 to +12 ‰. Coastal California is dominated by C$_3$ plants (Suits et al., 2005), consequently, its coastal terrestrial food webs are characterized by relatively low δ^{13}C values, ranging from −22 to −28 ‰, while marine-sourced materials tend to have higher values. Consumers relying on a mixture of marine and terrestrial resources will have δ^{13}C and δ^{15}N values between these end members.

Modern sample collection and analysis

Between May 2011 and August 2013, we collected mammalian mesopredator scats quarterly along coast-to-inland transects at Año Nuevo (n = 346, 37.1188ºN, 122.3066ºW; Figure 1) and about 20 miles to the south at Younger Lagoon/Moore Creek (n = 169, 36.9510ºN, 122.0665ºW). Because it is difficult to accurately distinguish among mammalian mesopredator scats by morphology alone, we focused our efforts on a subset of scats that were DNA-verified to species in collaboration with Wildlife Genetics International (WGI) (Reid, 2015). We submitted cotton swabs of the exterior of the scats, which WGI processed as tissue using QIAGEN DNeasy Blood and Tissue Kits. For the species test, WGI performed two variants of a sequence-based analysis of the mitochondrial 16S rRNA gene (Johnson and O'Brien, 1997) using primers that amplify across all mammals or preferentially across Carnivora sequences; results were compared to a reference collection of > 125 mammalian species. From this subset, we identified

29 scats from Año Nuevo and 13 scats from Younger Lagoon as coyote based on mtDNA evidence and/or the presence of coyote guard hairs (Miotto et al., 2007). To increase our sample size, we then used a quadratic discriminant function predictive morphometric model (Reid, 2015) to identify additional scats in our collection as coyote with > 60% probability (15 from Younger Lagoon, 5 from Año Nuevo). Our scat dataset additionally includes DNA-verified gray fox scats (*Urocyon cinereoargenteus, n* = 27; all from Año Nuevo) and bobcat scats (*Lynx rufus, n* = 62; 9 from Younger Lagoon, 53 from Año Nuevo). To enable comparison between the isotopic values of different coyote tissue types, we also opportunistically obtained bone collagen samples from two road kill coyotes collected on CA Hwy 1 adjacent to Año Nuevo as well as two road kill individuals collected adjacent to Younger Lagoon Reserve (California Fish and Game permit SC-11995).

We used the results of our previous work on coyote scat contents (Reid and Koch, 2017) to identify coyote food sources for isotopic characterization, including marine mammals, deer, small mammals, berries, arthropods, reptiles, birds, anthropogenic foods, and other mammalian mesopredators. When possible, we sourced local isotopic data for these food items from the literature, but we also opportunistically collected berry and insect samples along the transects and sampled hair from live-trapped small mammals at Año Nuevo. We followed the guidelines of the American Society of Mammalogists (Sikes and Gannon, 2011) for all of our work with animals, which was approved by the UC Santa Cruz Institutional Animal Care and Use Committee (permits Kochp1105 and Kochp1211).

We prepared samples for isotopic analysis following published protocols. For scat samples, we analyzed the fine-grained matrix material (Reid and Koch, 2017), which we extracted by sieving and cleaned by rinsing with Milli-Q water, 0.1N HCl to remove inorganic $CaCO_3$, and again with Milli-Q. After drying and homogenizing the scat samples, we weighed ~5 mg of scat matrix into 5 mm × 9 mm tin boats for isotopic analysis. We prepared hair samples following the methods of O'Connell and Hedges (1999); samples were rinsed with Milli-Q water, immersed in petroleum ether, and sonicated for 15 min, rinsed again with Milli-Q water (five times), and dried in a 60°C oven overnight. Our collagen extraction methods followed Brown et al. (1988); bone fragments were decalcified in 0.5N HCl for ~72 h, treated in 0.1N NaOH for 24 h, lipid extracted using petroleum ether (Dobush et al., 1985), rinsed five times with Milli-Q, and freeze dried overnight. Arthropod and berry samples were repeatedly rinsed and sonicated in Milli-Q water (4× for 15 min), dried (60°C overnight), and then crushed with an agate mortar and pestle. For hair, collagen, and arthropod samples, we weighed ~0.7 mg of material into 5 mm × 9 mm tin capsules. Berry samples were weighed separately for C and N isotope analysis (~0.4 mg for carbon and ~3 mg for nitrogen) and also sealed into 5 mm × 9 mm tin capsules.

We subjected samples to Dumas combustion using a Carlo Erba 1108 elemental analyzer and then measured $\delta^{13}C$ and $\delta^{15}N$ values on a ThermoFinnigan Delta Plus XP continuous flow isotope ratio mass spectrometer at the UC Santa Cruz Stable Isotope Laboratory. Sample isotopic values were corrected using two-point normalization and adjusted for size, drift, and source stretching effects. Based on the standard deviation of 38 replicates of an in-house standard (Acetanilide), the average analytical precision was < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. We estimated the atomic carbon and nitrogen elemental composition of samples based on standards of known elemental composition (PUGel and Acetanilide); precision of these known compounds is better than 1%. The atomic C/N ratios in the proteinaceous tissue samples (hair and bone) fell within the ranges expected for well-preserved samples (Ambrose, 1990; O'Connell and Hedges, 1999).

We performed all data analyses in R version 3.4.1 (R Core Team, 2017). We used Hotelling's T^2-test (R-package ICSNP) to evaluate whether coyotes from Año Nuevo and Younger Lagoon have statistically different multivariate C and N isotope means. We used MixSIAR (R-package MixSIAR) (Stock and Semmons, 2016a), a Bayesian stable isotope mixing model, to estimate the proportional contributions of isotopically distinct food resources to coyote diets. We conducted Markov Chain Monte Carlo (MCMC) sampling within MixSIAR, primarily using the 'normal' setting, which included running three replicate chains (each with 100,000 draws), a burn-in of 50,000, and a thinning rate of 50. Because coyotes are omnivores and eat foods with different proportions of digestible [C] and [N], we included concentration dependence in our models to reduce bias (Phillips and Koch, 2002) and followed the recommendations of Koch and Phillips (2002) to derive digestible [C] and [N] values for coyote food sources from the USDA nutrient database. We used a multiplicative error structure in our models (Resid*Process; Stock and Semmons, 2016b) and, for Año Nuevo, we included informative priors (Moore and Semmons, 2008; Ward et al., 2010) based on previously dissected scat samples (Reid and Koch, 2017). To calculate the informative priors, we re-classified dietary items found in 12 previously fully dissected scat samples into the six isotopically distinct dietary categories presented below, determined their frequency of occurrence within the scat samples, and then scaled the prior to have a weight of 6 (a = (0.3, 0.5, 1.4, 0.3, 2.7, 0.9)), which is equal to the weight in the uninformative prior (a = (1, 1, 1, 1, 1, 1)). We used both the Gelman–Rubin diagnostic and Geweke diagnostic to assess model convergence.

To convert stable isotope values measured in a variety of tissues to coyote diet space (i.e. the muscle tissue that is digested and assimilated), we applied published organism- and tissue-specific discrimination factors (Supplementary Table 1, available online). For the Año Nuevo coyotes, we grouped dietary items a priori into six categories based on the similarity of their isotopic values: anthropogenic foods, California mouse (*Peromyscus californicus*), marine foods, plants, terrestrial herbivores, and terrestrial omnivores (Supplementary Table 2, available online; Supplementary Figure 1, available online). We used MANOVA to test for differences in multivariate means in the grouping process. For the Younger Lagoon coyotes, we separately considered two additional dietary items, vole (*Microtus californicus*) and brush mouse (*Peromyscus boylii*), the inclusion of which brought the majority of the coyote scat samples into the dietary mixing space, an important requirement for stable isotope mixing models (Phillips et al., 2014). We individually adjusted the coyote scat isotope values for discrimination by adding 1.5 ± 1.6 ‰ for $\delta^{13}C$ values and subtracting 2.3 ± 1.3 ‰ for $\delta^{15}N$ values (Reid and Koch, 2017). We also adjusted the road kill coyote collagen samples to diet using collagen-to-diet discrimination factors derived by combining coyote tissue-to-tissue apparent enrichment factors (Reid and Koch, 2017) with published hair-to-diet discrimination factors for a similar canid (Roth and Hobson, 2000), resulting in an adjustment of −2.8 ± 1.6 ‰ for $\delta^{13}C$ values and −3.5 ± 0.7 ‰ for $\delta^{15}N$ values (Reid and Koch, 2017).

To compare isotopic niche breadths across different sites, we used SIBER (Stable Isotope Bayesian Ellipses in R) metrics (Jackson et al., 2011). These metrics are unbiased with respect to sample size and take into account uncertainty in the sampled data. We calculated the sample size standard ellipse area for each subgroup ($SEA.B_1$) and assessed whether they were significantly different by comparing their Bayesian 95% credible limits; ellipse areas are significantly different when the limits do not overlap. Given that scat integrates diet over a relatively short timescale, we also calculated the standard ellipse areas for each modern site based on seasonal averages ($SEA.B_2$) to reduce some of the short-term temporal variability. We included the road kill coyote bone

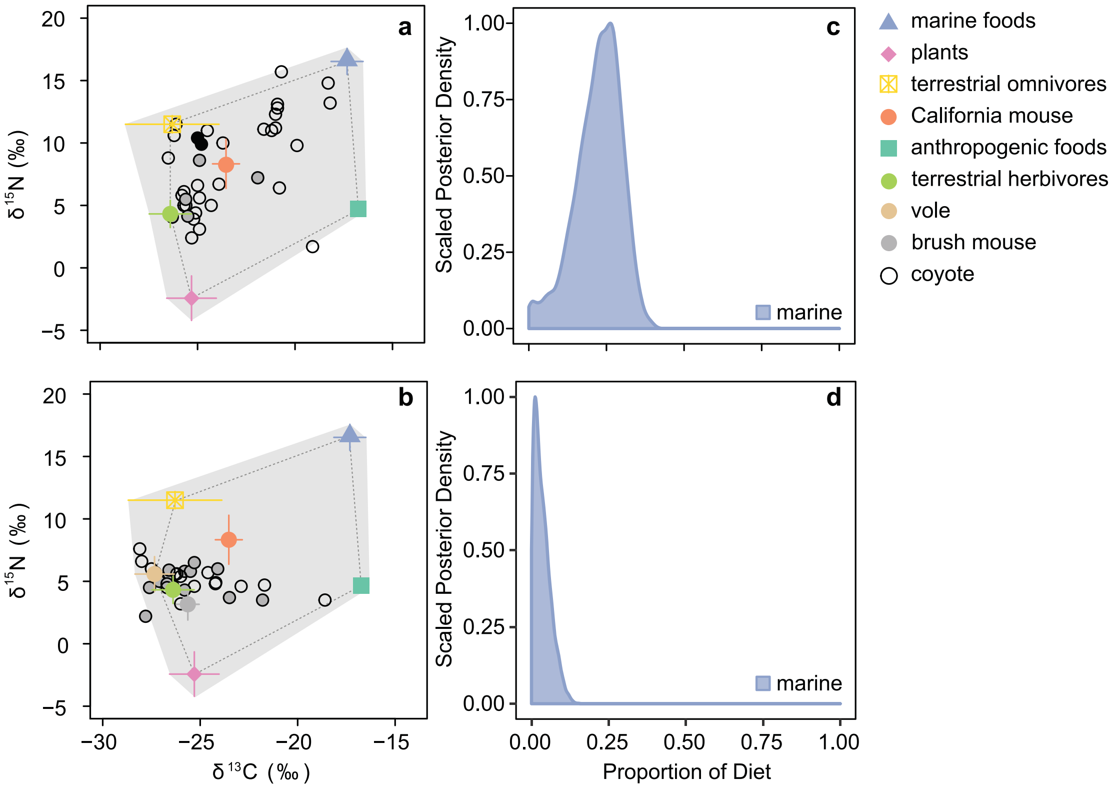

Figure 2. δ^{13}C and δ^{15}N values measured in coyote food resources and coyote scat and bone collagen at (a) Año Nuevo and (b) Younger Lagoon/Moore Creek. Coyote samples are adjusted for discrimination as described in the Methods. Coyote samples illustrated in black are measured in bone collagen, white open circles are DNA-verified scats, and those in gray are model-identified scats. The minimum convex hull of the dietary mixing space is depicted with a medium gray dashed line and the maximum convex hulls are shaded in light gray. Posterior plots of the predicted contributions of marine resources to coyote diets are shown for (c) Año Nuevo and (d) Younger Lagoon/Moore Creek.

collagen values in these calculations as individual points after adjusting collagen-to-scat (–4.3 ± 2.7 ‰ for δ^{13}C and −0.9 ± 1.3 ‰ for δ^{15}N (Reid and Koch, 2017)).

Subfossil and historical sample collection and analysis

To evaluate marine resource use by past coyotes, we sampled historical (AD 1893–1992) coyote fur and bone collagen specimens from coastal California counties (n = 15) and subfossil coyote bone collagen samples from seven coastal archaeological sites ($n = 28$; Figure 1, Supplementary Table 3, available online). When available, we also sampled bone collagen from potential competitors (grizzly bears, *Ursus arctos*; bobcats; and mountain lions, *Puma concolor*) and possible prey (ruminants, small mammals, pinnipeds, fish) from the same archaeological sites (Supplementary Tables 2 and 3, available online). These samples were acquired from the UC Santa Cruz Monterey Bay Archaeology Archives, Moss Landing Marine Lab, and the California Academy of Sciences. Subfossil and historical collagen and hair samples were prepared and analyzed in the same manner as modern samples. We did not consider wolves (*Canis lupus*) in this study because there was no evidence from the archaeological sites we analyzed that wolves were present on the central coast at the time the sites were occupied. While there is some historical evidence for wolves in coastal California based on written accounts of sightings between 1750 and 1850 (Schmidt, 1991), by the time of their extirpation from the state after 1901, confirmed records of wolves were confined to just San Bernardino and Lassen counties, hundreds of kilometers from the study region.

As with the modern samples, we used MixSIAR (Stock and Semmons, 2016a) to estimate the proportional contributions of isotopically distinct food resources to past coyote diets. We ran models separately for each site. Because all isotopic values for both coyotes and their potential prey were measured in collagen, we adjusted the coyotes for discrimination using published canid collagen-to-collagen discrimination factors, subtracting 1.3 ‰ for δ^{13}C (Fox-Dobbs et al., 2007) and 2.7 ‰ for δ^{15}N (Schwarcz, 1991). These values are also quite similar to recently reported collagen-to-collagen discrimination factors for adult red foxes (Δ^{13}C = +1.1 ± 1.1 ‰ and Δ^{15}N = +3.2 ± 1.8 ‰; Krajcarz et al., 2018). We estimated isotopic values for Holocene berries by correcting modern berry data for the Suess effect (the ^{13}C-depletion of surface carbon reservoirs due to fossil fuel burning; Quay et al., 1992; Sonnerup et al., 1999) by adding 1.8 ‰ to δ^{13}C values. Previously, authors have estimated plant values for the Holocene by assuming C_3 plants had δ^{13}C and δ^{15}N values that were 5 and 3 ‰ below ungulate browsers, respectively (Newsome et al., 2004), which is advantageous because it is based on the isotope ratios of a consumer within the Holocene food web. Ungulate browsers, however, primarily consume leaves while coyotes consume fruit and/or berries and these plant tissues can differ significantly isotopically (e.g. Kolb and Evans, 2002). We therefore felt it was more appropriate to estimate berry values from modern data, despite the fact that C_3 plant isotopic values are also sensitive to environmental factors (Farquhar et al., 1989). As with the modern samples, because they are not the consumers being considered in our mixing models, we did not adjust bobcat, mountain lion, or grizzly bear isotope values for trophic discrimination.

To enable direct comparison between the historical and subfossil samples, we corrected the subfossil samples for the Suess effect. We did this by fitting a spline function to the combined atmospheric δ^{13}C records from Rubino et al. (2013) and Indermühle et al. (1999) and predicting the δ^{13}C value of the atmosphere at the time each sample was collected. We then standardized

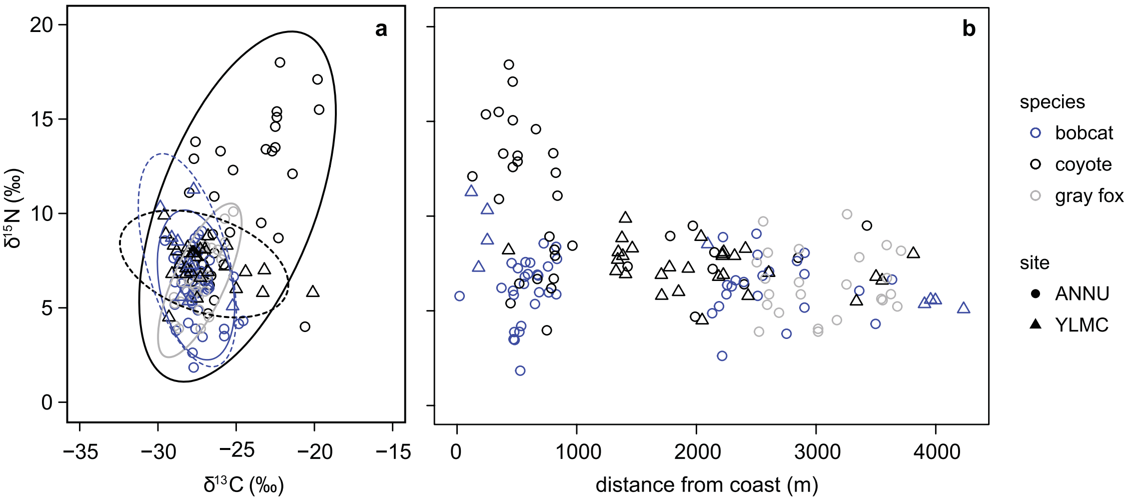

Figure 3. δ^{13}C and δ^{15}N values measured in species-verified mammalian mesopredator scats (Supplementary Table 3, available online) illustrating (a) isotopic dietary niche and (b) variation in δ^{15}N values with distance from the coast. None of the samples are adjusted for discrimination. In (a) standard ellipses depicted with a solid line correspond to samples from Año Nuevo while those depicted with dashed lines correspond to samples from Younger Lagoon/Moore Creek; there were no gray fox scats identified at Younger Lagoon/Moore Creek.

the δ^{13}C values to the time period of interest. For the historical samples, we corrected to 700 BP, which required the addition of between 0.3 ‰ for the samples from the late 1800s to 1.5 ‰ for the sample from 1991. To compare changes in isotopic niche breadth from the Holocene to present, we again used SIBER metrics (Jackson et al., 2011).

Results

Modern samples

We collected a total of 346 scats at Año Nuevo and 169 scats at Younger Lagoon/Moore Creek. The Año Nuevo coyote scats (n = 34) had a mean δ^{13}C value of −24.9 ‰ (±2.6 ‰ standard deviation (SD)) and mean δ^{15}N value of 10.4 ± 3.8 ‰ and the multivariate means were significantly different from those for Younger Lagoon coyote scats ($n = 28$, $\delta^{13}\text{C} = -27.1 \pm 2.2$ ‰ and $\delta^{15}\text{N} = 7.4 \pm 1.1$ ‰; $F_{2,63} = 11.4$, $p = 5.8^{-05}$; Figure 2a and b; Supplementary Table 3, available online). Coyotes at Año Nuevo also had a significantly greater isotopic dietary breadth (SEA.B$_1$ = 26.7 ‰^{2}, 95% confidence interval (CI): 17.7–36.0 ‰^{2}) than those at Younger Lagoon (SEA.B$_1$ = 7.5 ‰^{2}, 95% CI: 4.9–10.4 ‰^{2}). Isotopic dietary breadth assessed from seasonal averages remained significantly higher at Año Nuevo (SEA.B$_2$ = 10.8 ‰^{2}, 95% CI: 5.2–22.4 ‰^{2}) relative to Younger Lagoon (SEA.B$_2$ = 2.2 ‰^{2}, 95% CI: 1.1–4.9 ‰^{2}). Of the 29 verified coyote scats collected at Año Nuevo, 46% contained evidence of marine resource consumption (Supplementary Table 3, available online) while none of the Younger Lagoon coyote scats contained identifiable marine material. Marine material (mainly elephant seal and sea lion hair) was furthermore present in scats collected during all seasons at Año Nuevo (Supplementary Table 3, available online). The two road kill coyote specimens from Año Nuevo similarly had isotopic values suggestive of marine resource use (δ^{13}C = −22.2 and −22.0 ‰, δ^{15}N = 13.9 and 13.4 ‰; Figure 2a, Supplementary Table 3, available online) while the two individuals collected near Younger Lagoon did not (δ^{13}C = −21.4 and −21.7 ‰, δ^{15}N = 8.3 and 10.2 ‰; Figure 2b, Supplementary Table 3, available online).

Based on the results of the isotope mixing models, pinnipeds comprised the second greatest mean dietary component (22%, 95% CI: 4–34%) for coyotes at Año Nuevo, behind terrestrial herbivores (31%, CI: 9–54%; Figure 2c, Supplementary Table 4, available online). This relatively high reliance on marine resources was corroborated by scat dissections, which similarly indicated that pinnipeds made up 22 ± 8% of coyote diet at Año Nuevo based on the percent-by-volume of marine material in the scats (Reid and Koch, 2017). In contrast, mixing model predictions for coyote diets at Younger Lagoon suggested that pinnipeds were unimportant dietary components (4%, CI: 0–9%; Figure 2d). Instead, Younger Lagoon coyotes were predicted to have diffuse diets with various terrestrial herbivores and small mammals making up nearly equal proportions (~19% each; Supplementary Table 4, available online).

Coyotes at Año Nuevo and Younger Lagoon had divergent relationships with other mammalian mesopredators (Figure 3a). At Año Nuevo, coyote scats had significantly different multivariate isotopic means from both bobcat ($n = 53$; $\delta^{13}\text{C} = -27.6 \pm 1.0$ ‰ and $\delta^{15}\text{N} = 6.2 \pm 1.6$ ‰; $F_{2,86} = 36.6$, $p = 3.08^{-12}$) and gray fox scats ($n = 27$; $\delta^{13}\text{C} = -27.3 \pm 1.1$ ‰ and $\delta^{15}\text{N} = 6.5 \pm 1.7$ ‰; $F_{2,60} = 15.4$, $p = 4.01^{-6}$). Coyote scats at Younger Lagoon, however, did not differ significantly from bobcat scats ($n = 9$; $\delta^{13}\text{C} = -28.1 \pm 1.3$ ‰ and $\delta^{15}\text{N} = 7.5 \pm 2.3$ ‰; $F_{2,36} = 1.18$, $p = 0.321$) and there were no DNA-verified gray fox scats collected at Younger Lagoon. The Año Nuevo coyote scats also occupied a significantly greater isotopic niche than the other analyzed mesopredators at both Año Nuevo and Younger Lagoon (Figure 3a).

Subfossil and historical samples

Pooled subfossil and Suess-corrected historical coyote bones (n = 35) had a mean δ^{13}C value of −19.6 ‰ (± 1.1 ‰ SD) and mean δ^{15}N value of 7.5 ± 2.0 ‰ while Suess-corrected historical coyote hair samples (n = 9) had a mean δ^{13}C value of −20.7 ± 0.9 ‰ and mean δ^{15}N value of 7.9 ± 0.9 ‰ (Supplementary Table 3, available online). There was little to no evidence for marine resource use by coastal coyotes across these time periods; coyote collagen δ^{13}C and δ^{15}N values fell squarely in the range expected for an exclusively terrestrial diet at all seven archaeological sites and continued to do so into historical times (Figure 4). Isotope mixing model results also consistently indicated that marine foods were unlikely to have contributed to past coyote diets (mean contributions $\leqslant$ 10% – although SCR-35 was an exception at 14%; Figure 4, Supplementary Table 4, available online). Direct comparison between modern Año Nuevo coyotes and those from the Moss Landing archaeological sites (MNT-229 and MNT-234), both of which were adjacent to a mainland seal rookery at the time of occupation, suggested that coastal coyote dietary breadth has expanded into the present (SEA.B$_1$ = 26.7 ‰^{2}, 95% CI: 17.7–36.0 ‰^{2} and SEA.B$_2$ = 10.8 ‰^{2}, 95% CI: 5.2–22.4 ‰^{2} at Año Nuevo

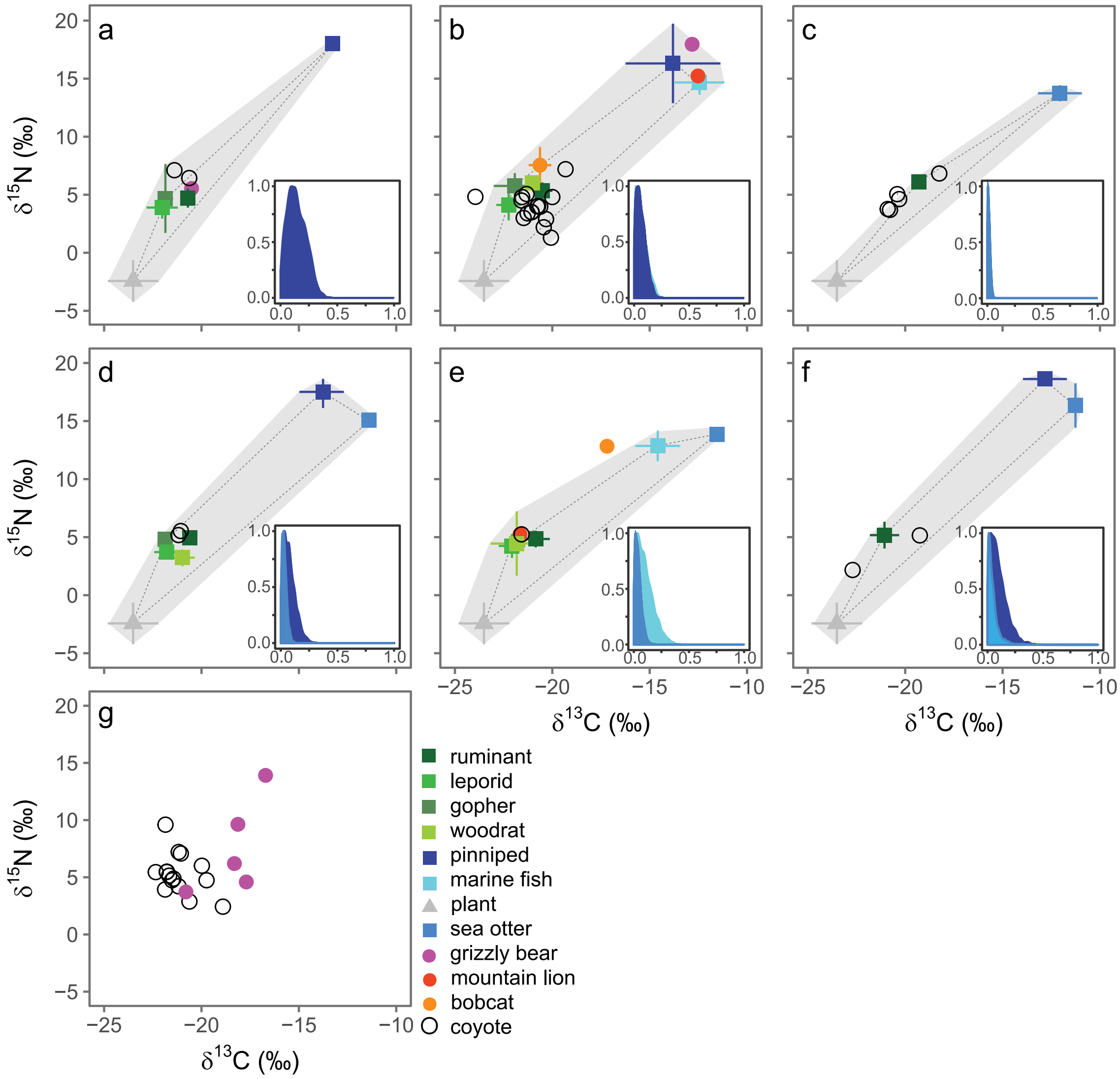

Figure 4. δ^{13}C and δ^{15}N values measured in archaeological and historical bone collagen at (a) SCR-35, (b) Moss Landing (MNT-229 and MNT-234), (c) SLO-239, (d) SMA-18, (e) SMA-113, (f) SMA-115, and (g) historical samples from coastal CA counties. Coyote values are corrected for trophic discrimination and their potential food sources are adjusted to diet space as described in the Methods (Supplementary Table 1, available online). The historical samples are Suess-corrected to 700 BP. The minimum convex hulls of the dietary mixing space are depicted with gray dashed lines and the maximum convex hulls are shaded in light gray. Insets depict the modeled proportional contribution of marine materials to coyote diets (Supplementary Table 4, available online).

today vs 4.7 ‰^{2}, 95% CI: 2.5–7.0 ‰^{2} at the Moss Landing archaeological sites).

Archaeological and historical coyote competitors, including grizzly bears (*Ursus arctos californicus*), mountain lions (*Puma concolor*), and bobcats (*Lynx rufus*) displayed a broad range of isotopic values (Supplementary Table 3, available online). The grizzly bear sample from the oldest site, SCR-35, was consistent with a low trophic-level, purely terrestrial diet (Figure 4a, Sample #101892; δ^{13}C = −20.5 ‰ and δ^{15}N = 5.5 ‰). Both the grizzly bear and mountain lion samples from Moss Landing (MNT-234 and MNT-229), however, plotted with the pinnipeds, suggesting that they consumed a significant proportion of marine foods (Figure 4b, Sample #1242; δ^{13}C = −12.8 ‰ and δ^{15}N = 18.0 ‰, Sample #698; δ^{13}C = −12.5 ‰ and δ^{15}N = 15.2 ‰). Bobcats at Moss Landing were similar to coyotes with a mean δ^{13}C value of −20.6 ± 0.6 ‰ and mean δ^{15}N value of 7.6 ± 1.6 ‰ (Figure 4b). At SMA-113, the bobcat sample appears to reflect some degree of marine resource use (Figure 4e, Sample #2979; δ^{13}C = −17.2 ‰ and δ^{15}N = 12.8 ‰) while the mountain lion sample was not different from the coyotes (Sample #2389; δ^{13}C = −21.7 ‰ and δ^{15}N = 5.2 ‰). Of the five historical California grizzly bear samples, two exhibit isotopic values indicative of marine resource consumption (CAS 24360 and 27342, Figure 4g), both of which were from the San Francisco Bay area and of unknown age. The remaining three historical grizzly samples had isotopic signatures suggesting purely terrestrial diets (Figure 4g).

Discussion

Our analysis reveals that marine foods are important dietary resources for modern coastal coyotes at Año Nuevo, which is adjacent to an elephant seal rookery, and not at Younger Lagoon/Moore Creek. While it is possible for high δ^{13}C values to be sourced from anthropogenic food resources derived from C$_4$ plants, the combination of high δ^{13}C and δ^{15}N values we observe in Año Nuevo coyotes can only be accounted for by marine resource use; the mixing models predicted that anthropogenic food resources made up only 3–4% of coyote diet at both Año Nuevo and Younger Lagoon. Scat dissections confirm that marine foods, primarily northern elephant seal and California sea lion, are the source of these high δ^{13}C and δ^{15}N values (Supplementary Table 3, available online). At Año Nuevo, marine resources are consistently available throughout the year. Peaks in harbor seal strandings in Monterey Bay coincide with their breeding season in early spring (Nevins et al., 2011), while California sea lion stranding rates are highest in the summer/early fall (Greig et al., 2005), and elephant seals begin pupping in the winter (Le Boeuf and Panken, 1977). Año Nuevo Island is a favored haul out for sea lions and consequently dead sea lions wash up on the mainland beach with regularity (Burton and Koch, 1999). Elsewhere around Monterey Bay, marine mammal strandings are not uncommon, but are less frequent (Nevins et al., 2011). Coyotes at other coastal sites may also readily consume marine foods if given the opportunity, but opportunities at any one locality are rare. Beaches may also need to be free of human activity long enough for coyotes to be comfortable feeding on stranded carcasses too large for them to transport to a safe locale, further reducing opportunities. Año Nuevo is unique in that it is protected from human interference in addition to having abundantly available marine food resources.

Scats provide a relatively short snapshot of coyote diet, on the order of several days to weeks. Canid gut retention times are just 2–3 days (Weaver, 1993); however, the incorporation rate of epithelial cells into the scat matrix may be an order of magnitude slower (Codron et al., 2011). Isotopic turnover in bone collagen, on the other hand, takes years (e.g. Hobson and Clark, 1992) instead of days or weeks. Given the significant difference in timescales represented by these different tissues, we have adjusted our sampling (by collecting scats over a 2-year period) to ensure comparability between ancient and modern samples. Previous research suggests that 50–59 scats are required to identify principal prey occurring in > 5% of scats (Trites and Joy, 2005; Windberg and Mitchell, 1990). Our species-verified sample sizes fall below these suggested minima; however, if we consider our full sample of mesopredator scats at each site, which undoubtedly includes additional un-verified coyote scats, we see the same result – marine resources are important to mesopredator diets at Año Nuevo, but not at Younger Lagoon (Supplementary Figure 2, available online). We additionally found that $\delta^{13}C$ and $\delta^{15}N$ values measured in coyote bone collagen from two modern road kill coyotes collected near Año Nuevo were indicative of marine resource consumption (Figure 2a). These collagen isotope values corroborate our findings based on coyote scat and confirm that some individuals at Año Nuevo consistently rely on marine foods throughout their lifetimes.

In contrast to their modern counterparts, subfossil and historical coyote diets did not feature marine resources as important components (Figure 4). Even at sites where mainland northern fur seal rookeries were present (Moss Landing: MNT-234 and MNT-229 and Año Nuevo: SMA-18), it appears that coyotes were not consistently consuming marine mammals (Figure 4b and d). We used power analysis to determine the number of samples required to detect marine resource use by past coyotes, given an effect size of 1.6 (Cohen's *d*; based on the mean difference between $\delta^{13}C$ and $\delta^{15}N$ values of modern coyotes consuming some marine vs exclusively terrestrial foods). Assuming that significance (α) = .05 and that the power level ($1 - \beta$) = .95, 23 samples are required; our sample of 28 subfossil coyotes is above this threshold. At all but one Holocene site, the mixing models estimated marine resources to comprise $\leqslant$ 10% of coyote diet. CA-SCR-35 is the exception to this, with the two coyotes there predicted to have a 14% mean dietary proportion of marine resources (Figure 4a). We argue, however, that this estimate is likely inflated because the mixing space is incomplete. Indeed, one of the two coyote samples falls outside of the mixing space, which would be more complete if we had isotopic data for other terrestrial omnivores, insects, and additional small mammals, such as the California mouse. Although we do not have samples of contemporaneous prey with which to compare the historical coyote specimens, historical coyotes continue to display relatively low $\delta^{13}C$ and $\delta^{15}N$ values, suggesting that marine resources were not incorporated into their diets (Figure 4g). Our results imply that, relative to their recent ancestors, the consumption of marine food by modern coyotes at Año Nuevo is a novel behavior.

What caused this shift in behavior? We hypothesize that relaxed interspecific competition with grizzly bears, humans, and dogs, or more likely a combination of these, allowed some modern coyotes to broaden their dietary niche. Brown bears in Alaska are known to limit marine resource use by wolves when they co-occur (Darimont et al., 2009). Historical evidence suggests that California grizzlies were abundant along the coast and that they consumed marine foods (Storer and Tevis, 1996), so it is possible that the extirpation of the California grizzly bear afforded coyotes the opportunity to change their diets and move into the grizzlies' former niche. Although we were only able to obtain isotopic data from two subfossil grizzly bears, the absence of dietary overlap between the grizzly (sample #1242) and mountain lion (sample #698) at Moss Landing, on one hand, and co-occurring coyotes, on the other, is in line with expectations for competitive exclusion (Figure 4b, Huey et al., 1974; Schmitt and Coyer, 1983). Given that grizzlies displayed a variety of dietary preferences into the historical period, however, it is unlikely that this is the only explanation. Humans were without question relying heavily on marine resources in the past (Bartelink, 2009; Beasley et al., 2013; Newsome et al., 2004) and the presence of their camps and dogs on the coast could have deterred coyotes. For example, Hofman et al. (2016) found that both ancient humans and their dogs consumed marine resources in high proportions in the Channel Islands off the coast of southern California; however, they found little to no evidence for marine resource use by island foxes (*Urocyon littoralis*), which was likely a consequence of interference competition with domestic dogs. In contrast to Holocene peoples, modern humans are trying to reduce exploitation of coastal resources by creating coastal parks, marine sanctuaries, and enacting wildlife protection programs, making marine resources more available to coyotes today.

Regardless the reason for modern coyote dietary niche expansion, the marine subsidy to some coastal California coyotes clearly has a recent onset. How then is this new subsidy affecting coyotes and the greater coastal ecosystem? We were not able to successfully extract nuclear DNA from our scat samples; however, two lines of indirect evidence (camera traps and scat deposition rates) suggest that the coyote density near the coast at Año Nuevo is elevated relative to further inland and relative to Younger Lagoon (Supplementary Tables 5 and 6, available online). Given that coyotes at Año Nuevo continue to consume terrestrial foods in significant proportions in addition to marine resources, theory predicts that this increased consumer density could depress local terrestrial resources (Gompper and Vanak, 2008; Polis et al., 1997; Rand and Louda, 2006; Rose and Polis, 1998). The possibility also exists that other mesopredators, such as bobcats and gray foxes, are supported in greater numbers at Año Nuevo because coyotes have shifted out of otherwise contested niche space (e.g. Gomez et al., 2010). By comparing coyote scat isotope values with those measured in DNA-verified bobcat and gray fox scats at both sites, it's apparent that coyotes at Año Nuevo have significantly greater isotopic dietary niches than the other mesopredators (Figure 3a, Supplementary Table 3, available online). It is also clear that these different mammalian mesopredators are partitioning dietary and spatial resources (Figure 3a and b). First, only coyotes at Año Nuevo appear to be consuming marine resources; this is different from the past, when we see evidence for one bobcat consuming marine foods at CA-SMA-113 (Figure 4e). Furthermore, scats found close to the coast were exclusively from bobcats and coyotes while gray fox scats were found further inland where the vegetation along the transects is characterized by mixed evergreen forest. A more detailed assessment of dietary and spatial niche partitioning by mesopredators at Año Nuevo will be necessary to more thoroughly delineate how the marine subsidy to coyotes is impacting their competitors.

Narratives of coyote expansion have primarily invoked a combination of apex predator extirpation and deforestation as the key drivers (Hody and Kays, 2018; Ripple et al., 2013). Coyotes are also recognized as synanthropes, appearing to do well in highly modified suburban and urban environments (e.g. Gehrt et al., 2011). Our results add an additional piece to these narratives, suggesting that release from competition in coastal areas can confer the benefit of access to a resource subsidy (when it is abundantly available, as at Año Nuevo), making coastal routes potentially lucrative for range expansion. There is mounting evidence from elsewhere in North and Central America that coyotes benefit from the sea in many coastal areas (Alvarez-Castaneda and Gonzalez-Quintero, 2005; Atencio, 1994; Eckrich and Owens, 1995). For example, at the very edge of their range in Panama, where coyotes first arrived in 1995, they are observed more frequently in coastal areas than in the interior (Mendez-Carvajal and Moreno, 2014). The same is true at the other end of their expanding range in Labrador (Chubbs and Phillips, 2005). We therefore suspect that marine resources are important for coyotes along this expanding edge and may offer the means by which coyotes expand their range into South America.

We have shown that marine subsidies to coyotes in coastal California have a very recent onset and that coyotes are likely positively impacted by a marine subsidy where it occurs. Today, marine resources comprise ~20% of coyote diets at Año Nuevo, where there is an active northern elephant seal rookery and an essentially constant delivery of marine resources to land. In contrast, coyotes did not consume marine resources in significant enough proportions for us to detect at Younger Lagoon, where marine resources are scarcer. In the past, coyotes did not consume marine foods in significant proportions, even at localities adjacent to mainland eared seal rookeries, such as Moss Landing (MNT-229 and MNT-234) and Año Nuevo (SMA-18). Past peoples (Bartelink, 2009; Beasley et al., 2013; Newsome et al., 2004), their dogs (Hofman et al., 2016), and California grizzly bears (Storer and Tevis, 1996) did, however, rely on marine resources and could have prevented coyotes from gaining access to a subsidy from the sea. The onset of heavy marine resource use by coyotes at Año Nuevo appears to have been delayed until marine mammal populations began to recover following the Marine Mammal Protection Act and designation of marine sanctuaries. Finally, this newly gained access to marine resources has implications for coyote range expansion – it may be that coastal routes lacking former apex predators provide coyotes with relatively easy pathways by which to extend their territory. Further study of additional coastal coyote populations, particularly from coastal locations along their expanding edge, will clarify the importance of a marine subsidy to coyotes more broadly.

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Data accessibility

All data supporting the results reported here are currently available in the supplementary material and will be archived in the Neotoma database (www.neotomadb.org).

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