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Corresponding author(s): Brent Hughes

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

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☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
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☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We used Google Earth to generate erosional data for tidal creeks.
Data analysis	All sea otter abundance data were analyzed spatially using ArcGIS v. 10. All erosion data were analyzed using ArcGIS v. 10.7 and Google Earth. Statistical analyses were generated using R v. 4.3.0.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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All raw data files and code are available at https://github.com/bbhughes/otters-erosion.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study focused on the effects of trophic interactions on salt marsh vegetation and erosion of tidal creeks in Elkhorn Slough, CA, USA. This study used multiple approaches and combined modeling, observational (spatial and temporal) and experimental procedures to test for the effects of sea otters on salt marsh tidal creeks. Analyses testing for the sea otter impacts to erosion were performed on multiple data sets at multiple scales. Historical analyses examining the relationship between sea otters and erosion (1985-2018) were modeled using 196 permanent creek width locations with sea otter abundance data in the Elkhorn Slough using a Bayesian analysis (Fig. 1). We also ran an analysis on modeled sea otter densities and crab consumption by sea otters by comparing 13 tidal creeks in two periods: pre-otter expansion and post-otter expansion (Fig. 3) and compared bank erosion (averaged from 43-162 permanent creek width stations per creek). Pre- post-otter expansion data were analyzed using Generalized Linear Mixed-Effects Models, treating otter expansion periods (2 levels) as a fixed factor and creek (N = 13) as a random factor. We also examined the relationship between modeled sea otter crab consumption and various marsh and erosional parameters during the period of sea otter expansion (2013-2015, N = 13 tidal creeks). For this spatial analysis we ran analyses on the relationship between: 1) sea otter density with daily rates of sea otter crab consumption, and 2) sea otter crab consumption relationship between belowground marsh biomass (averaged among 5-10 cores collected per creek) and erosion (averaged from 43-162 permanent creek width stations per creek). To test hypotheses related to the mechanisms behind the sea otter-crab-marsh trophic cascade, we ran a predator exclusion experiment over a three year period. We compared areas with sea otter exclusion cages to non-caged areas using a randomized block approach. To test experimental predator removal (predator exclusions v. procedural controls, N = 50) on changes in burrow densities (2014-2015), marsh biomass, sediment bulk density, and sediment accretion rates, we used GLMMs treating sea otter (Otter – no cage v. No Otter - cage) as a fixed factor, and site and block (within site pairings of No Otter and Otter plots) as random factors. Due to differences in the error structure of the various response variables and some variables being either continuous v. integer, we used different error structures: Gamma (bulk density, above- and belowground marsh biomass – continuous data with a log link) or gaussian (change in burrows with an identity link). For changes in shore crab densities, we fit a GAMM (generalized additive mixed-effects model) to the change in shore crab density between the treatment (sea otters excluded) and control (sea otters not excluded) over time with a Gaussian error structure and identity link. We calculated change in crab density as the density at each sampling event minus density at the initial sampling event in May 2014. We found no differences ($P > 0.05$) in shore crab densities between the sea otter exclusions and procedural controls at the beginning of the study. Our model included a treatment fixed effect, a thin plate regression spline with maximum basis dimension ('k') of 3 for day since the start of the experiment, a cyclic cubic regression spline for month (with knots at 0.5, 4.5, 8.5, and 12.5 so that December connected to January), and a random intercept for block ID. We used REML (restricted maximum likelihood) for smoother parameter estimation. For shore crab feeding assays we ran two separate two-sample t-tests, testing for shore crab effects (presence v. absence) on changes in marsh aboveground and belowground marsh biomass, respectively.
Research sample	Our various samples primarily included three biological species: sea otters (Enhydra lutris), marsh crabs (Pachygrapsus crassipes), and pickleweed marsh (Salicornia virginica). Sea otters were sampled using the sampling strategy described below, but sex and age were not considered factors in this study. All sea otter data reported here were observational, we also ran an analysis using video recordings of sea otters in the vicinity of our cage experiment to look at cage effects on sea otter behavior. For our cage experiment we used the same sea otter exclusion plots for examining crab burrows, crab density, and marsh biomass as reported in Beheshti et al. (2021), a study that was looking specifically at crab impacts to the salt marsh. For salt marsh vegetation, we were primarily interested in the biomass as well as sediment mass, and used cores to standardize our sampling to represent biomass on the plot and tidal creek scales. For crab sampling we used pit-fall traps (tennis ball cans) to sample density of crabs in our experimental plots and

along creek banks, size and age were not taken into consideration for crab analyses. For erosional data we used aerial imagery to quantify creek widths at our various tidal creek stations. Our research samples also included measurements of erosion in the system, by supplementing more recent years from data collected by Van Dyke and Wasson (2003).

Sampling strategy

We quantified sea otter distribution and trophic interactions within tidal creeks using two well-established methodologies: distributional surveys and observational foraging data. From 1985–2013, sea otter distribution within Elkhorn Slough was recorded once per year as part of range-wide sea otter surveys by USGS. From 2013–2017, we achieved increased temporal resolution of sea otter distribution by conducting bi-monthly surveys of sea otter distribution within Elkhorn Slough. For both these survey data sets, a similar methodology was used, whereby the study area was scanned carefully with binoculars and high-powered telescopes, and the location of each sea otter or group of sea otters was marked onto a 1:25,000 topographic map. Observers used natural features aided by compasses and laser rangefinders, when necessary, to ensure that the marked location of each otter was accurate to within 20 m. To ensure full coverage of the area and to avoid double-counting, five teams of observers were distributed at vantage points around the Slough, each with a predefined area to survey, and survey teams initiated their counts simultaneously in the morning. The resulting survey maps of otter locations were then digitized into ArcGIS prior to analysis. The second monitoring method involved collection of observational data on sea otter foraging behavior and diet. Daily between August 2013 and October 2016, trained observers visited sites distributed throughout the Slough and opportunistically selected sea otters for which to record foraging data. Sea otters were selected haphazardly for observation (the only criteria being that an otter was feeding and within visible range of the observer), and a contiguous sequence of >20 feeding dives were monitored and recorded using standardized methods. Specifically, we recorded the duration (seconds) of each sub-surface dive interval (when prey were captured) and subsequent surface interval (when prey were handled and consumed), the taxonomic identity of each prey item captured, number of items, size class (maximum linear dimension relative to the otter's paw width, ~4.75 cm), and time required to process each item. These variables were recorded into a standardized database for later analysis. A total of 26,040 foraging dives were recorded for the 2013–16 period. We combined this with a previously published data set of 10,349 recorded foraging dives for the 1998–2011 period for a total of 36,389 foraging dives from 1,317 individual feeding bouts recorded over a 19-year period (1998–2017).

For erosion monitoring, first, we assessed erosion using the methods and data from Van Dyke and Wasson (2005), who used a series of georeferenced aerial images from the 1930s to 2003 to measure the cross-section width at 196 locations in the tidal creeks at Elkhorn Slough. They defined cross-section width as "the distance to the nearest remaining recognizable fragment of marsh vegetation where remnants were still visible" in each photograph. We extended this time series by first repositioning the original point locations in ArcGIS v10.764 to accommodate for plate movement since 2003 (approximately 4 cm yr-1 to the northwest). We selected the highest resolution orthoimagery from 2009 (30 cm) and 2017 (15 cm) and used ArcGIS v10.7 to digitize and measure the shortest straight-line distance that passed through each point and the remaining vegetation on either side of the creek. We did not attempt to measure a cross-section if no vegetation was present or if creekbanks were submerged in the imagery.
We used more detailed mapping of erosion to investigate spatial patterns in 13 tidal creeks (Fig. 2A) in relation to sea otter foraging and salt marsh stability indicators (creekbank erosion and belowground biomass). Mapping of creekbank erosion (interface of vegetation and tidal creek) was completed in Google Earth due to the availability of historical aerial photography over the time period of interest (2009-2017), at the 13 tidal creeks (Fig. 2A). A scale of 1:300 was used for interpretation based on the highest possible resolution at which the channel edge was still resolvable for all image years. The edge of the channels was drawn using the polygon tool in Google Earth and each polygon was saved as a .kmz file for import into the ESRI software program, ArcMap.
Channel widths were calculated at 1 m intervals, normal to the centerline of each channel. The process for centerline creation involved the use of topographic data in conjunction with both built-in and custom tools within the ArcMap toolbox. LIDAR data were obtained from NOAA's Data Access Viewer web portal (https://www.coast.noaa.gov/dataviewer/#/), which is managed by the NOAA Office for Coastal Management and provides free downloads of elevation, imagery, and land cover data for the coastal U.S. and its territories. The LIDAR data were used to generate a topographic surface covering all observational transect sites, and contours were generated from the surface. Sets of contours which delineated the channel edges for each study area were extracted. Note that these contours only represent approximate channel edges for a set point in time (only the period during which the LIDAR data were collected) but these were adequate for use in centerline creation. For each tidal creek, a polygon was created with edges delineated by the channel edge contours. The 'polygon to centerline' toolset was run on the polygons thus resulting in a centerline for each observational transect sites. The 'smooth line' tool was run on each centerline with a 5 m smoothing tolerance. Further smoothing was done manually by removing excess nodes from line segments that appeared unnaturally jagged. Each centerline was split into 1 m segments using a custom tool that allows a line to be divided into segments of a given length. The 'add geometry attributes' tool was used to add centroid and line bearing to each line segment and the resulting bearing value was manipulated to create a set of bearings both normal to the line segment and 1800 opposed to one another. A distance field was added to the attribute table and populated with a distance of 20 m. The tool 'bearing distance to line' was then used to obtain two sets of lines for each centerline line segment and running outward normal to the segment and these were merged to create cross-stream profiles at 1 m intervals for each observational transect sites. Any lines that did not reasonably capture a stream cross-section were removed. Finally, the 'clip' tool was used to clip the cross-stream profiles by the channel edge polygons imported from Google Earth resulting in a set of cross-stream lengths taken at 1 m intervals along each study area. Annual rates of erosion were calculated as (WidthYear2 – WidthYear1)/(Year2 – Year1). This resulted in 43-162 points per observational transect or experimental site, depending on the site and the quality of imagery. These annual rates of change were converted to an average for each creek for each year, which were used as replicates in the final analysis.

To measure marsh biomass and sediment bulk density, we took measurements of marsh biomass within a 50 cm * 50 cm quadrat in the central part of the plot. We took burrow counts (burrow size > 3 cm) within 2 - 50 cm x 50 cm quadrats in the central part of the plot in August 2014 and 2015 to track shore crab changes over time. Crab trapping was conducted in both our experimental plots and along our 100 m transects (N = 10 traps per creek, each separated by ~10 m) using pitfall traps (tennis ball cans), buried into the ground with the lip of the can at the sediment surface. The traps were uncapped for 24 h and all trapped crabs were identified down to species and carapace length was recorded. We collected cores from each of our experimental sites and transect plots. The core protocol was as follows, the beveled 10 cm (diameter) * 10 cm (depth) cylindrical core was carefully placed into the marsh substrate without sorting rooted versus overhanging aboveground vegetation and placed in a sealed plastic bag and brought to the lab for post-processing. The core depth was recorded if shorter than 10 cm, and all cores longer than 10 cm were cut with a knife to a depth of 10 cm. We made the core depth to be no greater than 10 cm because that is the maximum depth we observed live belowground marsh vegetation as well as shore crab burrowing activity. Next, all aboveground material was cut flush to the sediment surface and placed in a separate container. Each core, now trimmed of any aboveground material, was measured on the scale to record bulk density of the core and any observable burrows in the collected sample were noted. The sediment core was then broken into small pieces and cleaned and drained with a fine mesh strainer until the water-soaked roots and root hairs were draining clear water.

Following a thorough rinse of the root material extracted from the sediment core, we placed the belowground root material on a pre-weighed and labeled piece of aluminum foil. Once the aboveground tissue was thoroughly rinsed and sorted, we placed them each in the labeled foils that corresponded to the sample being processed and placed them into the dehydrating oven. Samples were placed in the oven at 60 degrees C until dry, for aboveground samples this varied from 24 to 48 h, for belowground samples it took between 72 and 144 h. Dried samples were then weighed and recorded.

In addition to our biological collections in our cage experiment, we addressed the effect of caged vs uncaged treatments on sea otter utilization of those areas using camera traps that had been deployed at our site after our experiment was completed, but cages were still fully intact. To accomplish remote assessment of treatment effects on sea otter utilization, a series of camera traps (n =3 per site) was placed around two of our experimental locations for five (5) consecutive months (June-November, 2020) in 2020. We could not assess this with an in-person observer, as observing sea otter behaviors around the experimental areas presented challenges due to the narrow channels providing little camouflage for the observer. Encounters that are this close are known to disturb sea otters. The use of camera traps provides an opportunity to observe sea otters without bias from observer disturbance to their behavior.
We secured each camera trap to the top of a 1.5 m tall PVC pipe and staked the pipe into the edge of the salt marsh creekbank, ensuring that the camera rested at least 1 m above the vegetation to avoid flooding during high tide. We focused the camera's lens on the salt marsh tidal creek channels, in which the channel and adjacent salt marsh creekbanks were visible. We set each camera trap to a high sensitivity setting and to record 30 second videos when triggered, with a 1-minute resting interval in between each event. We set each camera trap to record continuously to include both daytime and nocturnal videos of sea otter behavior at the sites. We visited the camera traps every 1 - 2 weeks during the sampling period to relocate the cameras to random positions to sample each experimental site evenly. At each camera trap visit, we replaced the memory card and batteries as needed.
We manually viewed all 16,732 videos collected during the sampling period and classified the organisms and behaviors present. For videos containing sea otters, we classified the behaviors as foraging, swimming/travel, grooming, hauling out, social, or unidentified. We further identified videos in which raccoons were visible in the sites to assess their impact as predators in the salt marsh. We retained only the camera trap data that focused on our experimental locations.

Data collection

Data collection procedures are noted above, due to the multiple time scales we refer to in Extended Data Table 2 that describes the various time scales for data collection. Sea otter data were collected by the co-authors, as well as other USGS staff and volunteers from the Monterey Bay Aquarium and the Elkhorn Slough National Estuarine Research Reserve. Erosional data from 1937-2003 were reported in Van Dyke and Wasson (2003), and the more recent years were collected by the co-authors. All other data (biological and sediment) were collected by the co-authors.

Timing and spatial scale

All timing (sampling periods), sample sizes and sample frequencies are reported in Extended Data Table 2.

Data exclusions

We excluded one tidal creek from our analyses among the data that we originally collected. Those data were removed because the creek ultimately did not meet the a priori standards (creek width, continuous marsh cover along the bank) we established. No other data were excluded from this study.

Reproducibility

There were no repeats of experimental procedures.

Randomization

Much of the sampling design for this study was systematic, meaning we sought out to conduct our various experiments and observations using a balanced replicated design. For sea otter observations, we either used population-level abundance data or observations from sitings and video recordings, where randomization is not possible. For analyses involving our 13 creeks, we selected nearly every creek in Elkhorn Slough that met our a priori selection criteria. For sampling along our marsh creek transects we standardized sampling along 100 m sections, systematically sampling plots every 10 m. To account for creek-level differences in any of our response variables we included the tidal creek identity as a random factor. Our field experimental locations were chosen based on several criteria with the intention of standardizing the plots, while also covering the greatest area of the estuary. For this, experimental sites were selected also to incorporate a range of sea otter use, which we ultimately found can change from year to year. Samples that were randomly selected include: marsh biomass cores that were randomly selected within a plot, we also randomly selected crab to cover a range of sizes for our laboratory feeding assay.

Blinding

There were no blinding protocols that were prepared a priori for this study. However, data collection/entry and analysis were performed independently. Also, the gathering of data sets, e.g., sea otter abundance and erosion, were ultimately performed blindly as our sea otter team did not interact with our geology team, and therefore there was no bias introduced into the generation of data. Also, many of our analyses were performed by one of the co-authors without a priori knowledge of the system and without biases towards any of the data or results.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

Field conditions varied at the study site because we sampled at various periods for several years across all seasons. Often tides were our biggest consideration for determining when and where we could access our sites. Air temperature ranged from near freezing to 35 degrees C on warm summer days. Coastal fog can also play an important role in field conditions, as sites closer to the mouth of the Pacific Ocean can often remain cold and overcast even in the summer time. Field conditions were often wet and muddy.

Location

The study location was Elkhorn Slough, which is a tidal estuary located in Monterey Bay, California. It is characterized by a full tidal exchange (in our study locations), and is dominated by pickelweed marshes, eelgrass beds, and green algal blooms. The study location can be found in Fig. 1A.

Access & import/export	Access to the study locations required a boat and knowledge of the system. Special access to one of our study locations required a research permit from the Elkhorn Slough National Estuarine Research Reserve, (Site J in Fig. 1 A), which also allowed for the placement of our experimental cages in the marsh. We also performed this study under a collection permit (for marsh and crab collections) from California Department of Fish and Wildlife to B. Hughes (#SC-6563). Permission to perform cage exclusion experiments with sea otters was granted by U.S. Fish and Wildlife Service.
Disturbance	Due to the close proximity to sea otters, listed as threatened under the U.S. Endangered Species Act, we followed all guidelines and protocols established with the disturbance of marine mammals, including maintaining safe distances and maintaining boat headings away from sea otters. For marshes we visited infrequently (seasonally to annually) to minimize trampling effects on the marsh.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	We used shore crabs (Pachygrapsus crassipes) for our marsh feeding experiment.
Wild animals	There were two main study species that were studied, sea otters (Enhydra lutris) and shore crabs (Pachygrapsus crassipes). There were no collections of sea otters for this study, just observations from shore observers and remote video cameras. Pachygrapsus crabs were collected with tennis ball can pit-fall traps. Trapped crabs were measured and released. Wild shore crabs used in our feeding experiment were returned to Elkhorn Slough at the conclusion of the experiment.
Reporting on sex	Sex was not a factor for the animals used in our studies.
Field-collected samples	Shore crabs were collected from Elkhorn Slough and brought back to the University of California - Santa Cruz's Coastal Science Campus, where each individual was placed in a 473 ml mason jar with 10 ml of fresh seawater and starved for 72 h at room temperature. Crabs were then fed pickleweed for 72 hours before being returned to the field.
Ethics oversight	Permission was granted under California Department of Fish and Wildlife (#SC-6563) for crab collections. Sea otter observations were performed under permission from the U.S. Fish and Wildlife Service, as well as from the Institutional Animal Care and Use Committee (IACUC) at the University of California, Santa Cruz (# TINKT1510), and Sonoma State University (#2019-60).

Note that full information on the approval of the study protocol must also be provided in the manuscript.