Marine Environmental Research 208 (2025) 107149

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Setting the limit: cold rather than hot temperatures limit intertidal distribution of a coastal foundation species

Kerstin Wasson [a,b,*], Kim Cressman [c], Kathryn Beheshti [d], Erin C. Herder [e], Charlie Endris [f], Christopher D.G. Harley [g], Alicia Abadía-Cardoso [h], Rodrigo Beas-Luna [h], Joachim Carolsfeld [i], Andrew L. Chang [j,k], Jeffrey A. Crooks [l], Matthew C. Ferner [m], Edwin D. Grosholz [n], Neil Harrington [o], Jacob Harris [p], Hilary Hayford [q], Alicia R. Helms [r], Julio Lorda [s], Jennifer L. Ruesink [t], Amaia Ruiz de Alegría-Arzaburu [u], Steven S. Rumrill [v], Jenni Schmitt [r], Rachel S. Smith [d], Janet B. Walker [w], Christine R. Whitcraft [x], Sylvia Yang [y], Danielle Zacherl [z], Chela J. Zabin [j,k]

[a] *Elkhorn Slough National Estuarine Research Reserve, 1700 Elkhorn Road, Royal Oaks, CA, 95076, USA*
[b] *University of California, Santa Cruz, Ecology and Evolutionary Biology, CA, 95064, USA*
[c] *Catbird Stats LLC, Gautier, MS, 39553, USA*
[d] *University of California, Santa Barbara, Marine Science Institute, Santa Barbara, CA, 93106, USA*
[e] *Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC, V9T 6N7, Canada*
[f] *Moss Landing Marine Laboratories, Moss Landing, CA, 95039, USA*
[g] *Department of Zoology and Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada*
[h] *Universidad Autónoma de Baja California, Facultad de Ciencias Marinas, Ensenada, Baja California, 22760, Mexico*
[i] *World Fisheries Trust, Victoria, BC, V9A4T5, Canada*
[j] *Smithsonian Environmental Research Center, Tiburon, CA, 94920, USA*
[k] *Estuary & Ocean Science Center, San Francisco State University, Tiburon, CA, 94920, USA*
[l] *Tijuana River National Estuarine Research Reserve, Imperial Beach, CA, 91932, USA*
[m] *San Francisco Bay National Estuarine Research Reserve, San Francisco State University, Tiburon, CA, 94920, USA*
[n] *Department of Environmental Science and Policy, University of California, Davis, CA, 95616, USA*
[o] *Jamestown S'Klallam Tribe, Sequim, WA, 98382, USA*
[p] *Amah Mutsun Land Trust, Santa Cruz, CA, 95062, USA*
[q] *Puget Sound Restoration Fund, Bainbridge Island, WA, 98110, USA*
[r] *South Slough National Estuarine Research Reserve, Coos Bay, OR, 97420, USA*
[s] *Universidad Autónoma de Baja California, Facultad de Ciencias, Ensenada, Baja California, 22760, Mexico*
[t] *Department of Biology, University of Washington, Seattle, WA, 98195, USA*
[u] *Universidad Autónoma de Baja California, Instituto de Investigaciones Oceanológicas, Ensenada, Baja California, 22860, Mexico*
[v] *Oregon Department of Fish and Wildlife, Newport, OR, 97365, USA*
[w] *Southern California Coastal Water Research Project, Costa Mesa, CA, 92626, USA*
[x] *California State University Long Beach, Long Beach, CA, 90840, USA*
[y] *Padilla Bay National Estuarine Research Reserve, Mount Vernon, WA, 98273, USA*
[z] *California State University Fullerton, Fullerton, CA, 92831, USA*

ARTICLE INFO

Keywords:
Thermal tolerance
Heat stress
Climate change
Elevational distribution
Global warming
Intertidal zonation
Latitudinal study
Space-for-time substitution

ABSTRACT

Long-lasting restoration success of foundation species requires understanding their responses to climate change. For species with broad distributions, lower latitudes may serve as a proxy for future warming at higher latitudes. Such space-for-time substitutions are a powerful tool for developing climate change predictions for species distributed along steep elevational gradients. To understand climate resilience of a key coastal foundation species, we examined the upper elevational limit of the native Olympia oyster (*Ostrea lurida*) along its entire range at 26 sites spanning 21° latitude, from British Columbia to Baja California. Counter to our expectations, high air temperatures did not affect variation in the upper limit of Olympia oysters. Indeed, Olympia oysters extended high into the intertidal zone at the warmer southern sites, and shading did not influence the upper

---

[*] Corresponding author. Elkhorn Slough National Estuarine Research Reserve, 1700 Elkhorn Road, Royal Oaks, CA, 95076, USA.
E-mail address: wasson@ucsc.edu (K. Wasson).

https://doi.org/10.1016/j.marenvres.2025.107149
Received 18 January 2025; Received in revised form 10 March 2025; Accepted 8 April 2025

limit. Our models indicated instead that extreme low temperatures set the upper limit for Olympia oysters at higher latitudes. In contrast, neither the Pacific oyster (*Magallana gigas*), a co-occurring global invader, nor barnacles exhibited clear latitudinal patterns. These findings suggest that Olympia oysters and restoration projects aimed at supporting their recovery will be resilient to increased temperatures projected by climate change models. Our results also illustrate the importance of testing the assumption that species on steep elevational gradients are living close to their upper thermal limits and will be negatively impacted by warming; for this foundation species, the assumption was false. Latitudinal studies enhance understanding of species response to climate stressors and are key to the design of climate-resilient conservation strategies.

1. Introduction

Climate change is rapidly altering species distributions and is predicted to do so more dramatically in the future (Lenoir and Svenning, 2015; Thomas, 2010). In addition to affecting the latitudinal and longitudinal components of distribution, climate change can affect elevational distributions (Chen et al., 2011). For example, treelines on mountains where growth is limited by cold temperatures are moving upward with warming (Hansson et al., 2021; Holtmeier and Broll, 2020). In the rocky intertidal, where survival of sessile animals can be affected by heat during low tides, the elevational distribution of mussels is shrinking due to rising air temperature lowering the upper limit, while predation maintains the lower limit (Harley, 2011). Understanding the interplay between horizontal, vertical, and thermal stress gradients is key to understanding the distribution and abundance of species and how they are changing through time.

Physical gradients and elevational distributions of species across them can vary across latitude. For example, some treelines on mountains extend further upward at lower latitudes, an expansion of their vertical range due to warmth (Cogbill and White, 1991; Hansson et al., 2021). Conversely, some barnacles in the rocky intertidal extend further upward at higher latitudes, expanding their upper limit in response to less extreme high temperatures (Kusic Heady, 2013; Wethey, 1983). Biological variation across latitude due to changing temperature gradients can be a useful proxy for change over time with global warming (Sorte et al., 2018). Such space-for-time substitutions can increase understanding by scientists and stakeholders regarding future change in the distribution and abundance of species (Lovell et al., 2023). In the examples of treelines and barnacles, current conditions at lower latitudes may resemble future conditions at higher latitudes, with elevational distributions expanding or contracting with warming, respectively (Fig. 1).

The elevational distribution of many species remains poorly documented, both locally and across entire ranges. For foundation species that are the focus of conservation, understanding elevational limits is critical for appropriate spatial investment of habitat protection, enhancement, and restoration activities, as well as for the design of climate-resilient projects. Improved understanding of climate drivers of elevational distributions can inform conservation planning; information is needed on whether cold or warm temperatures set limits, and whether means or extremes are the most predictive metrics (Clark-Wolf et al., 2023). For example, extreme cold events (freezing) are critical for limiting distributions of plants (Osmond et al., 1987) including cacti (Shreve, 1911) and trees (Körner, 2021), while extreme warm atmospheric events contribute to upper limits of sessile invertebrates and seaweeds in the intertidal zone (Harley and Paine, 2009; Sorte et al., 2018; Tsuchiya, 1983). Latitudinal studies of elevational distribution of single species can be powerful for understanding responsiveness to climate-related drivers and for predicting climate resilience, but very few such latitudinal investigations have been carried out for foundation species of conservation concern. While plants are the main foundation species in terrestrial habitats, sessile animals are often foundation species in the intertidal zone, and can serve as indicators of thermal stress along steep environmental gradients. Oysters are sessile, intertidal foundation species that serve as excellent model systems for examining elevational distributions and how these vary across latitude and as a function of temperature extremes.

As important coastal foundation species, oysters are the focus of intensive restoration investment (Hall and DeAngelis, 2024; Smith and Pruett, 2024), so understanding their current and future distributions is critical. The Olympia oyster (*Ostrea lurida*) is the only native oyster of the Pacific coast of the United States and Canada, found from central British Columbia, Canada to central Baja California, Mexico (Polson and Zacherl, 2009; Raith et al., 2015), a vast expanse with a wide range of environmental conditions. Olympia oyster populations have declined dramatically on this coast due to anthropogenic impacts (Kornbluth et al., 2022; Pritchard et al., 2015). They are considered a Species of Special Concern in Canada (COSEWIC, 2011), and a Species of Greatest Conservation Need in Washington and Oregon (Oregon Department of Fish and Wildlife, 2016; Washington Department of Fish and Wildlife, 2015). Olympia oyster populations are now the focus of enhancement and restoration activities along the coast, with efforts typically involving deployment of hard substrates or spat on shell in the intertidal zone (Ridlon et al., 2021). To maximize the footprint of successful restoration efforts and ensure projects are resilient in a changing climate, a better understanding of the elevational limits and thermal tolerances of

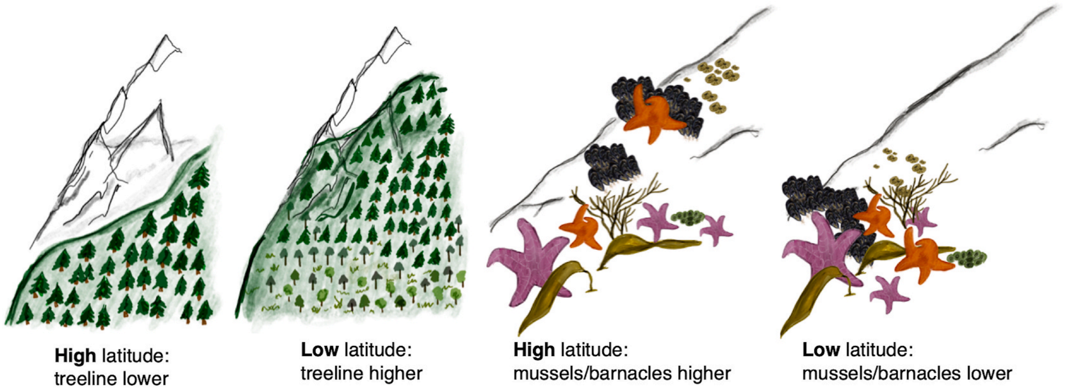

Fig. 1. Schematic illustration of cold air temperatures depressing the upper limit of the treeline at high latitudes along mountain elevation gradients, and at hot air temperatures (low latitude) depressing the upper limit of mussels and barnacles along rocky intertidal elevation gradients (drawing by Kathryn Beheshti).

Olympia oysters is needed.

Olympia oysters are known primarily from the low intertidal zone of estuaries, though subtidal populations have been reported from various locations (Baker, 1995; Pritchard et al., 2015). Olympia oyster growth rates and recruitment densities typically increase with decreasing intertidal elevation (Harris et al., 2024; Tronske et al., 2018; Zabin et al., 2016). The upper elevational limit of Olympia oysters is not well-characterized and the mechanisms setting it are not known. The upper limits to intertidal distribution could be the result of physical (heat, cold, desiccation) or biological (predation or competition) factors, or a combination. Both high (Bible et al., 2017; Brown et al., 2004) and low (Davis, 1955) air temperatures are known to negatively affect Olympia oyster survival during low tide exposure, but how temperature affects intertidal distribution has not been studied. Water temperatures are unlikely to affect elevational distribution of Olympia oysters, as Pacific temperatures are moderate relative to Olympia oyster tolerances (Cheng et al., 2015).

While only one oyster is native to the northeast Pacific coast, a second oyster species commonly occurs within the range of the Olympia oyster. The globally invasive Pacific oyster, *Magallana gigas* (=*Crassostrea gigas*), is found in many of the same estuaries as Olympia oysters (Kornbluth et al., 2022), and has increased in abundance in recent years (Beck et al., 2024; Crooks et al., 2015; Wolfe et al., 2024), due at least in part to warming water temperatures increasing reproductive success. Pacific oysters can compete with Olympia oysters but tend to peak in density at higher intertidal elevations, and so restoration projects can be designed to optimize Olympia oysters over the invader (Fuentes et al., 2020; Tronske et al., 2018). Understanding Pacific oyster elevational distribution across latitudes is also of interest in terms of invasion dynamics.

The goal of our investigation was to characterize the upper elevational limit of Olympia oysters across the full latitudinal range of the species, and to determine how this limit varies as a function of air temperature. This research was coordinated by the Native Olympia Oyster Collaborative, a community of practice supporting Olympia oyster recovery across the range of the species. At each of 26 sites from British Columbia to Baja California (Fig. 2), we located the highest live Olympia oysters to identify the upper distributional limit at that site. Where Pacific oysters were present, we also identified their upper elevational limit.

In addition, we identified the upper limit of acorn barnacles at the site as a biological indicator of the upper limit of sessile invertebrate communities in the intertidal zone, analogous to the treeline on mountains. We examined how the upper elevational limits of the two oyster species and barnacles varied across latitudes and as a function of air temperature, obtained from a nearby weather station. We recognize that air temperature does not exactly predict intertidal invertebrate body temperature (Helmuth, 1998), and that substratum temperatures are not perfectly captured by local weather station data (Graae et al., 2012). Nevertheless, differences in air temperature in space and time do correlate with differences in substratum or body temperature, particularly for sessile intertidal organisms with similar sun exposure. We therefore use general patterns in air temperature across many sites to understand large-scale patterns in upper distributional limits (after accounting for substrate size and local shading), without attempting to estimate specific body temperatures at any given site.

Given that other studies have shown negative effects of extreme heat events on intertidal organisms (Harley, 2011; Harley and Paine, 2009; Sorte et al., 2018), we hypothesized that the elevational distribution of these species would be compressed at sites experiencing more frequent high temperatures. Thus, we expected the upper limit of these species to be lower at hotter, lower latitude sites. However, timing of the tides affects exposure to heat events (Helmuth et al., 2002) and sites where the lowest tides in summer occur near midday are exposed to more heat stress than sites where they fall at night or early morning. Consequently, we expected that temperatures during low tide exposure would be a better predictor of the upper limits than temperatures across all time periods. To further explore whether high temperatures might cause mortality near the species' upper limit, we also compared the elevations of the highest dead vs. live Olympia oysters and examined size distributions in relation to elevation for this species. For example, if a recent thermally induced die-off had occurred, dead oysters should occur higher than live oysters, and small, newly settled oysters should occur above larger, older ones. We also expected that the highest oysters at a site would be in shaded rather than sun-exposed microhabitats. Ultimately, the goals of this investigation across an expansive latitudinal range were to improve understanding of the ecology and climate sensitivity of Olympia oysters to inform future restoration planning for this important foundation species, and to serve as a model for evaluating climate resilience of other foundation species that occur along steep environmental gradients.

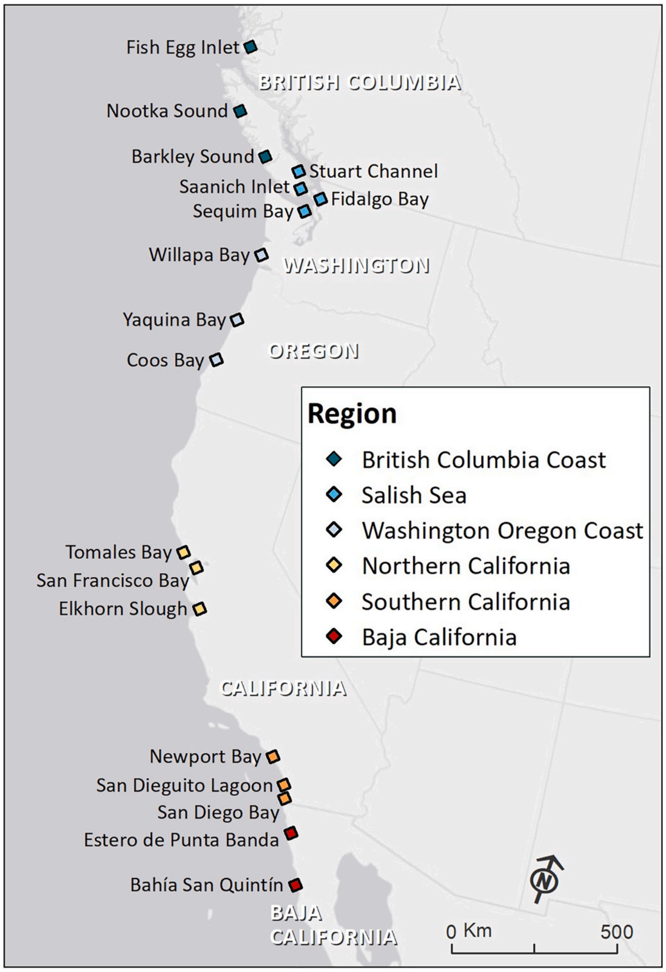

Fig. 2. Map of study estuaries. Details on site locations are in Table S1 and Supplemental File 2 (Google Earth KMZ of the 26 sites).

2. Methods

We conducted surveys at 26 sites located in 18 estuaries across more than 21° latitude, from 30.5° N to 51.6° N (Fig. 2, Table S1). This represents nearly the entire biogeographic range of the species, known from ~28° N (Raith et al., 2015) to ~52° N (Gillespie, 2009). Sampling occurred May–November 2023, mostly in summer (Table S1). This effort was a collaborative project with more than 100 people involved in the field (Fig. S1). We chose sites that had appropriate substrate for oysters distributed across a range of elevations, at least from Mean Lower Low Water (MLLW) to Mean Higher High Water (MHHW); we thus could be confident that the absence of oysters from high elevations was not due to lack of suitable substrata (Fig. 3).

2.1. Characterizing intertidal distributions

2.1.1. Olympia oyster elevational patterns

Our primary focus at all 26 sites was to identify the upper elevational limit of Olympia oysters – to identify their landward boundary in the intertidal zone. At all sites, we placed markers on the highest 10–20 live Olympia oysters that could be found. We only included oysters that were in fairly exposed locations; that is, we excluded oysters that inhabited deep crevices, under cobble, or in seeps or pools that retain water at low tide. These oysters were at least 1 m apart from each other within 100 m of shoreline. In these relatively rapid field surveys for oysters, we would not have detected newly settled juveniles <0.05 cm in size.

We measured the elevation of the highest Olympia oysters flagged at each site. At most sites we used a networked RTK GPS. At the most northern two sites and one Oregon site we used laser leveling from the waterline and estimated relative tidal elevations using the predicted waterline elevation at that time. At the three most southern sites, we used differential GPS. While methods differed, they all were ones known to deliver robust elevation measurements. We surveyed a landmark (known/stable ground control point) at the start and end of our fieldwork at the site, and in most cases these measurements differed by < 3 cm (Table S1 has details on instrumentation used and estimated accuracy based on re-measurement of benchmark).

To compare upper distribution limits of oysters across estuaries with different tidal ranges and different vertical datums, it was critical to use a consistent universal currency (Holmquist and Windham-Myers, 2022). For each site, we obtained an estimate of MLLW and MHHW in the same vertical datum as the field elevation measurements. We used this estimate to standardize all oyster elevation measurements to a relative scale where MLLW had an elevation of 0 and MHHW had an elevation of 1 (see Supplement for details on calculation of relative elevations).

Because we were interested in the upper tolerance limit at each site, we used the highest five elevation values for each site that were within 0.1 unit on the relative scale (where 0 = MLLW, 1 = MHHW) of the highest measurement. We preferred five measurements to a single one, to avoid anomalous outliers. However, at sites with very low oyster densities, sometimes there were fewer than five oysters near the upper limit; in these cases some of the top five measures spanned a large elevational range. To obtain a more accurate estimate of the true upper limit at that site, we only used those within 0.1 elevational unit.

At those sites where the tide was low enough after conducting the above surveys, we also characterized the elevational zone with the densest Olympia oysters, which was always lower than the upper limit. At 12 sites we placed quadrats (15 × 15 cm) in 10 of the densest oyster locations at the site and counted the oysters. We took the elevation of these 10 quadrats as described above. To compare the elevation of the Olympia oyster upper limit vs. the densest zone, we conducted a paired Wilcoxon test for the 12 sites where these data were collected. For this and all subsequently described non-parametric tests (Wilcoxon, Kruskal-Wallis, Kendall) we used ‘ggpubr’ v. 0.6.0 (Kassambara, 2023). These and all analyses in this paper were performed using R version 4.4.1 (R Core Team, 2024). All data used for analyses are available on Dryad at https://doi.org/10.5061/dryad.ngf1vhj4v, and summarized in Table S1.

2.1.2. Pacific oyster and barnacle upper limits compared to Olympia oysters

At a selection of sites where time and tide permitted, we measured the elevation of the 10 highest live Pacific oysters using the same methods described above. At most (22 of 26) sites, we measured the elevation of the 10 highest barnacles, which represented the highest sessile invertebrates present at the site. At sites with both oyster species present, individuals <7 cm in size were sacrificed following measurement to view diagnostic features for definitive identification. Individuals >7 cm were assumed to be Pacific oysters. To determine whether the upper distribution limit of the two oyster species differed significantly, we conducted a paired Wilcoxon test at the 11 sites that measured both species.

To determine whether the upper limits of Olympia oysters, Pacific oysters, and barnacles varied by latitude and whether such variations

Fig. 3. Examples of the diversity of habitats sampled, from north to south. A) Oyster Bay, Fish Egg Inlet, British Columbia; B) Port Eliza Inlet, Nootka Sound, British Columbia; C) Transfer Beach, British Columbia; D) Port of Peninsula Breakwater, Willapa Bay, Washington; E) Haynes Inlet, Coos Bay, Oregon; F) Berkeley Marina, San Francisco Bay, California; G) Dunphy Park, San Francisco Bay, California; H) Kirby Park, Elkhorn Slough, California; I) Dog Beach Bridge, San Dieguito Lagoon, California; J) RV Park, Estero de Punta Banda, Baja California; K) Molino Viejo, Bahía San Quintín, Baja California; L) La Ventana, Bahía San Quintín, Baja California.

were consistent among species, we constructed a linear mixed model where relative elevation was the response and the predictors were species, latitude, and the interaction between species and latitude. We specified a random intercept for species nested within site, to allow use of multiple measurements for each species at each site. Diagnostic plots of residuals were assessed to ensure the model did not violate assumptions. We used the 'lme4' v. 1.1.35.5 (Bates et al., 2015) and 'lmerTest' v. 3.1.3 (Kuznetsova et al., 2017) R packages for mixed models, then assessed marginal trends for each species and pairwise comparisons of trends by species using the 'emmeans' v. 1.10.4 (Lenth, 2024) and 'modelbased' v. 0.8.8 (Makowski et al., 2020) R packages. In all mixed model comparisons, the Kenward-Roger method was used to calculate degrees of freedom, and the Tukey method was used for p-value adjustments in pairwise comparisons.

2.2. Relationships among air temperature, latitude, and Olympia oyster upper limits

We used the nearest reliable weather stations (listed in Table S1) to obtain hourly air temperature for the five years prior to and including our field surveys (2019–2023) for each site. In a few cases, there were gaps in the datasets. Where these gaps lasted a week or more (South Sequim Bay and Brickyard Park, San Francisco Bay), we substituted data from the next closest weather station. We were unable to fill a 3-month gap (Jan–Mar 2023) at one site (RV Park, Estero Punta Banda). We recognize that air temperatures from the closest weather station do not exactly represent the air temperatures experienced by the oysters in the intertidal zone, but since our focus was on latitudinal gradients across a large geographic scale, these weather data broadly differentiate conditions among sites.

To examine air temperatures during low tide exposure, we also filtered the above dataset of all air temperatures to only include hours when tide level was below MLLW. We used the nearest tide stations (listed in Table S1) for water level estimates to obtain predicted hourly tide levels relative to MLLW for each site for the same five-year period.

We were interested in the role of extreme temperatures in shaping the intertidal distribution of oysters, and in exploring which methods of calculating extreme temperatures would be most ecologically relevant. We therefore examined multiple metrics for characterizing temperatures that were extreme across the range of the Olympia oyster. We recognize that these "extreme" temperatures were not extreme on a global scale, but rather only in relative terms of what organisms at these sites experience. To characterize exposure to these air temperature extremes, we calculated the number of temperature values $< 5\ ^\circ\mathrm{C}$ and $>30\ ^\circ\mathrm{C}$ both before and after filtering data for water levels below MLLW. Due to occasional missing data, we divided that by the number of hourly readings present to get the proportions of readings below 5 °C and above 30 °C. Totals and proportions were for the entire 5-year period of 2019–2023. We used 5 °C and 30 °C as thresholds for extreme temperatures based on inspection of temperatures across the range; we had initially considered using 0 °C and 40 °C, but determined they occur so rarely at most sites as not to be useful for correlative analyses. As an alternative approach, we also examined the 10th and 90th percentile of temperatures for each site both before and after filtering data for water levels below MLLW. The temperature extremes for each site (calculated by various methods) are summarized in Table S1.

To determine the best temperature predictor(s) of Olympia oyster relative elevation, we used an information-theoretic model selection approach (Burnham and Anderson, 2002). The response variable for the models was the average relative elevation of the highest Olympia oysters at each site (site was used as replicate). We constructed 21 models, in which the predictors were various combinations of the calculated metrics listed above, and a null model (Table S5). These models encompassed individual indicators of high and low temperatures, combinations of high and low extremes, and extreme temperatures at low tide vs. extreme temperatures across all readings. Models were fit as simple linear regression models using the lm(.) function of the 'stats' package v. 4.4.1 (R Core Team, 2024), and a model selection table to allow comparison of AICc between models was constructed using the 'MuMIn' package v. 1.48.4 (Bartoń, 2024).

2.3. Within-site variation in upper elevational limits

We collected and analyzed ancillary data to determine whether within-site variation in Olympia oyster elevations showed patterns that would be consistent with mortality associated with extreme high temperature events.

2.3.1. Sun exposure

If high temperatures set the maximum elevation of an intertidal species, upper distributional limits should be related to exposure to sunshine (Miller et al., 2009). For the highest Olympia oysters at each site, we assigned each oyster to one of three levels of exposure, 1) shady: oyster would be mostly shaded at midday, for instance under overhang; 2) exposed: oyster would be mostly in full sun at midday, for instance on top of rock; and 3) partial: somewhere in between shaded and exposed. At some sites, there was no variation (e.g., all of the highest oysters were exposed); at other sites, low tides during our field survey occurred at night and exposure could not be assessed. We examined the effect of exposure on the highest Olympia oysters at the seven sites where there were at least three oysters in each of two (out of the three) exposure categories, and conducted a Kruskal-Wallis test to determine whether elevation of the highest oyster differed by exposure category within each site.

As time permitted, field teams at selected sites also surveyed the site to determine whether Olympia oysters in very protected microhabitats such as deep crevices or seeps were at higher elevations than those in exposed areas. Field teams took the elevations of the highest Olympia oysters found in such microhabitats.

2.3.2. Evidence of recent die-off

If recent die-offs caused by low tide exposure to heat occurred, one would expect to find dead oysters above live oysters at a site. In addition to searching for the highest live Olympia oysters, field teams also searched for the highest dead Olympia oysters when time permitted. We focused on recently dead individuals that were gaping (oysters still cemented to the substrate by the bottom valve, with the top valve still attached). As with live oysters, we identified individuals at least 1 m apart within 100 m of shoreline, and measured elevations as described above. We conducted a paired Wilcoxon test to compare the average elevation of the highest live vs. recently dead Olympia oysters at the 17 sites that collected these data.

If the local populations experienced periodic die-offs of the highest oysters due to heat waves, the highest oysters at a site should be smaller than lower ones. At all except one site, we measured shell sizes (longest dimension) for the highest Olympia oysters while collecting their elevations. We used Kendall's tau correlations to test for associations between Olympia oyster size and elevation at each site.

2.3.3. Substrate size

Large substrates heat up more slowly than small ones during low tide exposure, so if high temperatures were setting the upper limit, the highest oysters might be limited to the largest substrates at the site. We measured the size (maximum linear dimension) of the substrate to which the highest live Olympia oysters were attached. Unattached single oysters were assigned an arbitrary substrate size of 1 cm and oysters on bedrock were assigned a substrate size of 1000 cm. At 20 sites, we conducted a Kendall test for Olympia oyster elevation vs. substrate size within each site; six sites were not included because they had no or virtually no variation in substrate size (all oysters on tiny gravel or all on big bedrock) or because substrate size was not measured.

2.4. *Site characterizations to inform restoration planning*

To characterize the sites more broadly, we estimated the population size of live Olympia and Pacific oysters within the intertidal zone in the 100 m stretch of shoreline to the nearest order of magnitude. We used local knowledge to determine whether there was a substantial subtidal population of each oyster species at each site and whether it was likely to be limited by substrate availability. We also conducted additional elements of site characterization that are summarized in Table S1, such as determining substrate type and noting whether oyster drills (predatory snails) were present.

3. Results

3.1. *Characterizing intertidal distributions*

3.1.1. *Olympia oyster elevational patterns*

The upper elevational limit of Olympia oysters varied greatly across the 21 degrees of latitude represented by the study area, showing a negative relationship with latitude ($p < 0.001$; Figs. 4 and 5A, Table S1; Table S3). On average, the upper limit decreased by 2 % per degree of latitude on our relative scale, which ranges from 0 (MLLW) to 1 (MHHW). The upper limit was lowest at the most northern site, Oyster Bay in Fish Egg Inlet, British Columbia where the highest Olympia oysters were at 0.035 on our relative scale. Thus, Olympia oysters at this site barely occupy any of the vertical extent of the intertidal zone. In contrast, one of the most southern sites, Molino Viejo in San Quintin Bay, Baja California, had the highest elevation of Olympia oysters, 0.78 on our relative scale; here Olympia oysters occupied more than three-quarters of the area between MLLW and MHHW. The slope of the intertidal zone was not quantified but was more often steep at southern than northern sites (Fig. 3). However, there was some within-region variation in slope (Fig. 3 A vs. B or J vs. K), so slope differences do not appear to account for regional patterns in Olympia oyster upper limits.

The upper limit of Olympia oysters was higher than the elevation of the densest oysters at the 12 sites that measured elevations of the densest zone, and this difference was statistically significant ($p < 0.001$) (Fig. S2). The difference in elevation of the upper limit and densest zone was much less pronounced in the north than the south (Table S1). The maximum Olympia oyster density documented at a site varied from 35 to 1017 m^2, with no clear geographic patterns (Table S1).

3.1.2. *Pacific oyster and barnacle upper limits compared to Olympia oysters*

The upper limit of Olympia oysters was lower than that of Pacific oysters, which in turn was lower than that of barnacles, the highest sessile invertebrates in the intertidal zone (Fig. 4, Table S1). The upper limit of Pacific oysters was significantly higher than that of Olympia oysters at the 11 sites where measurements were taken ($p < 0.001$, paired Wilcoxon test; Fig. S3). Pacific oysters and barnacles showed different patterns in their elevational limits across latitude compared to Olympia oysters (interaction term in mixed model $p = 0.003$; pairwise comparisons of coefficients $p = 0.007$ (Pacific oysters) and $p = 0.019$ (barnacles) Table S2, Table S4). While the upper limit of Olympia oysters was negatively related to latitude, neither Pacific oyster nor barnacle upper limits were significantly associated with latitude (Pacific oyster: slope −0.2 % per degree of latitude, $p = 0.595$; barnacles: slope −0.6 % per degree of latitude $p = 0.075$), Table S3).

3.2. *Relationships among air temperature, latitude, and Olympia oyster upper limits*

Extreme high air temperatures did not predict variation in the upper elevational limit of Olympia oysters. Models that included only ‘proportion of temperatures above 30 °C’ metrics as predictors had the least support of the 22 models we tested (AICc 8.4–9.8 higher than the top model; Fig. 6A; Table S6). The model using the 90th percentile of air temperatures was ranked 4th (slope 0.032, R^2 0.27, AICc difference 1.97; Table S6) but had the reverse relationship as hypothesized, a positive rather than negative association with Olympia oyster upper elevational limits.

Contrary to our hypothesis, extreme low air temperatures best predicted variation among sites in the upper distribution limits of Olympia oysters, with the upper Olympia oyster limit decreasing as frequency of extreme low temperatures increased (Fig. 6B). This pattern held across the different metrics of extreme low temperatures. There were no strong differences among these models: 3 models had an AICc difference less than 2 from the top model, and 13 more had AICc differences less than 6.

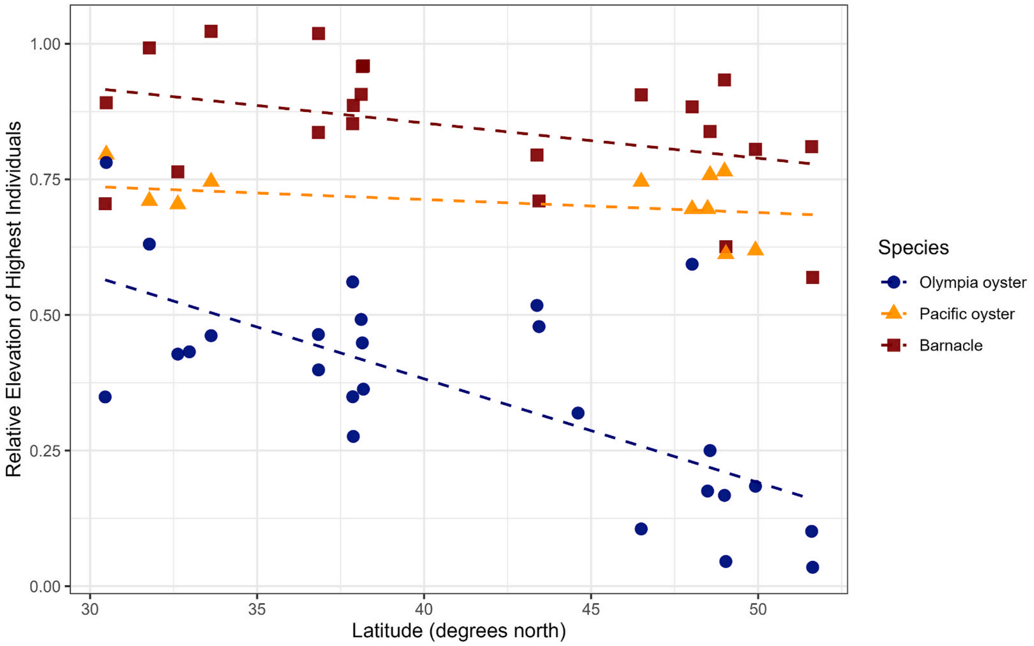

Fig. 4. *Species’ relative elevation by latitude, with the best-fit line from the linear mixed model. Each point represents the average elevation of the five highest individuals of each species at one site. Confidence intervals and statistical model outputs can be found in* Table S3.

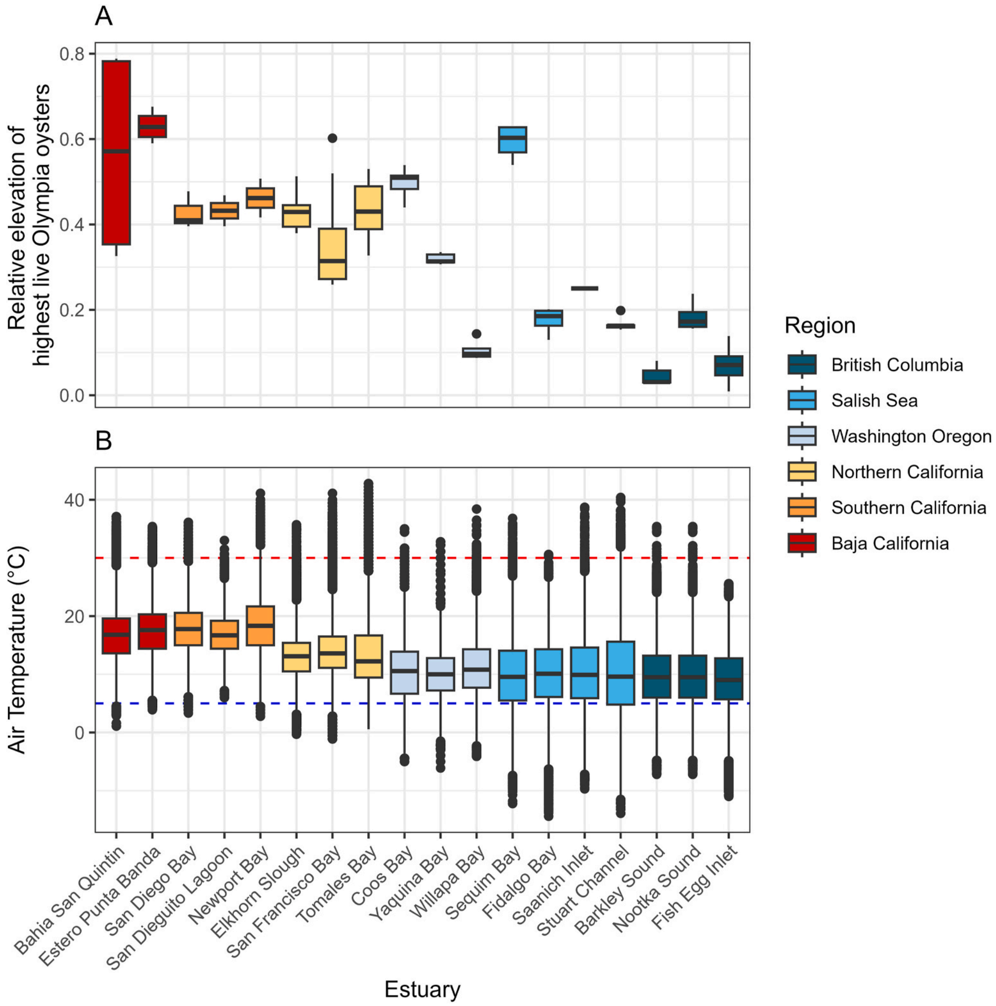

Fig. 5. Regional patterns in A) the upper limit of Olympia oysters and B) air temperatures. Regions run from south to north on the X axis and correspond to the groupings shown in Fig. 2. The lower and upper edges of the boxes represent the 25th and 75th percentiles of the data in that category; the horizontal line is the median. Whiskers extend out from each edge to the furthest value that is no more than 1.5 * IQR (interquartile range, distance between box edges) from the edge. Points are displayed for values outside that range.

The top model used a single predictor, proportion of temperatures below 5 °C at all tides (slope −1.173, R^2 0.32, Table S6). The model using the single predictor proportion of temperatures below 5 °C at low tides was ranked 7th out of the 22 models (slope −0.979, R^2 0.24, AICc difference 2.8; Table S6). Thus there was no support for our hypothesis that low tide temperatures would predict oyster elevations better than all temperatures (Fig. S4). Using the 10th percentile of air temperatures to represent low temperatures yielded similar R^2 values to the proportion of time temperatures were below 5 °C (Table S6).

Air temperatures varied across estuaries (Fig. 5B), with median air temperatures increasing and extreme low temperatures decreasing with decreasing latitude. Extreme high air temperatures did not show as clear a latitudinal pattern, with high temperatures occurring even far north, and with some Southern California, USA sites hotter than those in Baja California, Mexico (Fig. 5B). The proportion of time that temperatures were below 5 °C during all tides and proportion of time below 5 °C during low tides correlated well (Spearman correlation coefficient 0.96; Fig. S5), although the Salish Sea had relatively more cold extremes at low tide than over all periods. For high temperature metrics, the correlation between the proportion of time above 30 °C during all tides and the proportion of time above 30 °C during low tides was only 0.05, likely because extreme heat was uncommon (<1.5 % of the time in all cases; Fig. S6). Seasonal timing of extreme temperatures during low tide varied across latitudes; hottest low tide air temperatures occurred in June in the north, but in Sept–Oct in the south, because the lowest tides occur at midday in summer the north but not south (Fig. S7).

3.3. Within-site variation in upper elevational limits

We found no evidence of spatial patterns of exposure, dead vs. live oysters, or substrate size consistent with extreme high temperatures setting the elevational upper limit of Olympia oysters.

3.3.1. Sun exposure

There was no significant difference in elevation among oysters in exposed, partially shaded or shaded sites (Fig. 7A), contrary to the expectation of a strong difference if exposure to heat had caused mortality near the upper limit; and sun exposure did not significantly affect elevation of the highest live Olympia oysters at any of the seven sites examined (Fig. S8). At no site were oysters found at higher elevations in protected microhabitats (crevices, seeps) than elsewhere in the general search area.

3.3.2. Evidence of recent die-off

The highest dead Olympia oysters were generally at a similar elevation to the highest live oysters. There was no significant difference ($p = 0.59$; paired Wilcoxon test) in the elevation of the highest live and dead Olympia oysters at the 17 sites that measured both live and dead

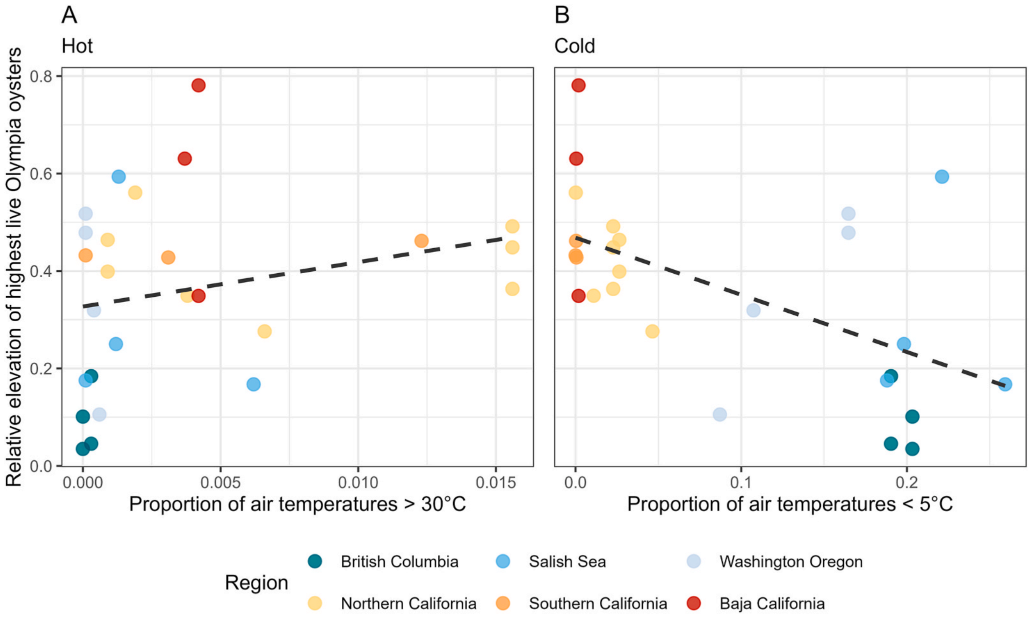

Fig. 6. Relationship between Olympia oyster upper limit and extreme temperatures. A) Correlation with proportion of time that temperatures were above 30 °C (note these are all low, under 2 % of time), R^2 0.06. B) Correlation with proportion of time that temperatures were below 5 °C, R^2 0.32. Each point represents one site.

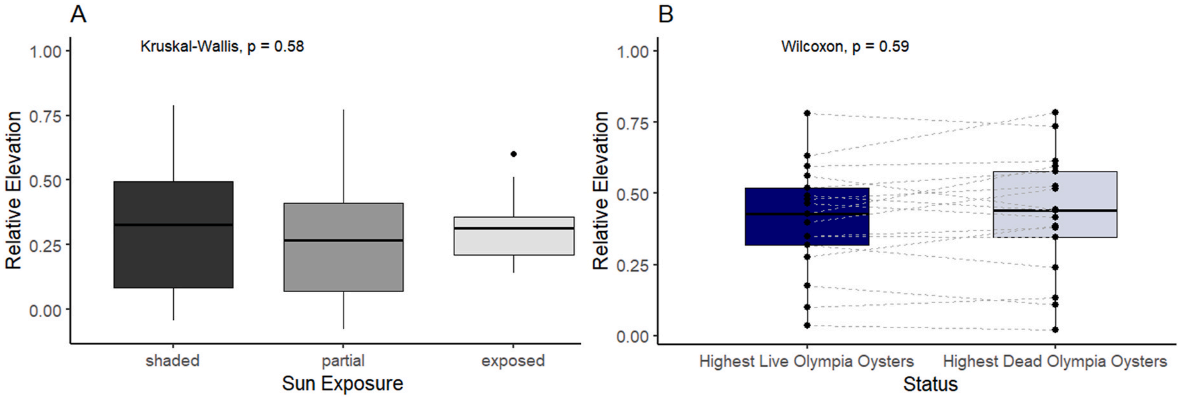

Fig. 7. A) Elevation of the highest Olympia oysters did not differ as a function of sun exposure in a Kruskal-Wallis test for seven sites combined (see Supplement for tests at individual sites). B) The elevation of the highest live and dead oysters did not differ in a paired Wilcoxon test of 17 sites.

oysters (Fig. 7B). Overall there was no relationship between Olympia oyster size and elevation for these oysters near the upper limit; none of the 21 sites had a significant relationship (Fig. S9).

3.3.3. Substrate size

Overall, we found no positive relationship between substrate size and Olympia oyster elevation for oysters near the upper limit. At 17 sites there was no relationship; at 3 sites there was a significant ($p < 0.05$) positive relationship (Fig. S10).

3.4. Site characterizations to inform restoration planning

3.4.1. Oyster site abundance

Abundance of Olympia oysters varied among sites with no conspicuous latitudinal trends (Table S1). Order of magnitude estimates of the number of intertidal Olympia oysters within a 100-m stretch of intertidal coastline centered on the study area showed that 77 % of sites had either 100s or 1000s of oysters present. Only 7 % of sites had over 10,000 oysters present, while 15 % of sites had only 10s of oysters present. Abundance of Pacific oysters was generally lower, with 50 % of sites having zero or 10s at the site.

3.4.2. Subtidal populations and substrate limitation

At all sites where low tide conditions permitted assessment, Olympia oysters extended lower than MLLW. However, presence of a subtidal Olympia oyster population was confirmed for only 35 % of sites. At 42 % of sites subtidal populations were considered absent or rare and at 23 % of sites, considered unknown (Table S1). At 69 % of sites, the local experts indicated that substrate limitation (lack of attachment substrates large enough to prevent burial in mud) was likely a major factor limiting subtidal oyster population sizes (Table S1).

4. Discussion

4.1. Geographic variation in elevational distribution and thermal stress

Latitudinal studies provide a powerful mechanism for examining thermal effects on species distributions, using a space-for-time substitution of low latitudes as a proxy for future warming at higher latitudes. Our study focused on elevational distributions across latitudes, in contrast to most latitudinal studies that focus on the horizontal components of distributions. While some broad geographic surveys of elevation have been conducted, for example of treelines in mountains

(Cogbill and White, 1991) and of rocky intertidal species on the open coast (Kaplanis et al., 2024), most studies of elevational distributions are local. For estuaries, marsh plant elevations have been characterized across a large latitudinal range (Janousek et al., 2019), but the elevations of estuarine animals, including foundation species such as oysters, have not been consistently measured across latitudes. We characterized the elevational distribution of Olympia oysters, Pacific oysters, and barnacles across 21 degrees of latitude, sampling in five states or provinces in three countries. The latitudinal patterns and thermal relationships we found differed by taxa, and the patterns we detected were unexpected.

Our expectation was that high temperatures would limit high intertidal distribution of oysters on the Pacific coast of North America, leading to oysters found lower in the intertidal at lower latitudes. Evidence for such patterns has been found for various other sessile marine invertebrates. For example, an early coastal ecology study found an infaunal clam (*Gemma gemma*) limited to the lower intertidal at lower latitude than higher latitude on the Atlantic coast of North America and attributed this to high summer temperatures (Green and Hobson, 1970). Another early study on the same coast found that a barnacle (*Semibalanus balanoides*) had a lower intertidal distribution at lower latitudes than higher latitudes, implicating thermal stress as the driver (Wethey, 1983). The upper limits of mussel distributions have also been linked to thermal gradients, lower at lower latitudes and/or hotter regions (Blanchette and Gaines, 2007; Sorte et al., 2018; Zardi et al., 2015). Analysis of an extensive database of rocky intertidal data revealed that various species of barnacles, mussels, and algae were found lower on the shore at low latitudes along the Pacific coast of North America (Kusic Heady, 2013).

Contrary to our expectations, the upper limit of Olympia oysters did not decline with latitude or as a function of frequency of extreme high temperatures. Indeed, some of the highest Olympia oysters were found in Southern California and Baja California where temperatures were highest. Furthermore, other indications of thermal stress setting the upper limit were lacking. The highest Olympia oysters were just as likely to be found in exposed areas on the top of rocks (or other substrates) as they were in shaded areas. We did not find evidence of recent mortality at the upper limit – dead oysters were not higher than live oysters – even though major heat waves had occurred. Overall, Olympia oysters appeared fairly tolerant of the highest air temperatures likely to be commonly encountered. However, very high air temperatures can cause mortality. For example, 39 °C was documented to result in 100 % mortality of Olympia oysters in one study (Brown et al., 2004), though another found much lower mortality (24 %) after exposure to 40 °C (Bible et al., 2017). Temperatures above 40 °C are extremely rare on this coast (Fig. 5B). A recent "heat dome" in 2021 in the Pacific Northwest involved extremely high air and water temperatures that had a negative impact on various intertidal species (Raymond et al., 2022), but there was no evidence of a decline in density of Olympia oysters at Vancouver Island sites surveyed before and after the heat dome (Herder and Bureau, 2023).

High air temperatures also did not appear to set the upper limit of the other two taxa examined in our study – the globally invasive Pacific oyster and barnacles. Other taxa may be similarly insensitive to temperature at their upper limits across a broad geographic range; the lethal body temperature of the mussel *Mytilus californianus* was only predicted to be exceeded at its vertical upper limit at two sites (neither near the southern range limit) out of 15 outer coast sites considered from southern California to northern Washington State (Mislan et al., 2014). Like *M. californianus*, Pacific oysters are tolerant of high temperatures in the intertidal and demonstrate phenotypic plasticity that allows survival at higher intertidal heights (Dupoué et al., 2023). For individual barnacle species, high temperatures have been documented as setting the upper elevational limit which is generally lower at warmer sites (Harley, 2011; Harley and Helmuth, 2003; Wethey, 1983, 2002). In our study, we did not identify barnacles to species, so it possible that species more sensitive to high temperatures (e.g., *Balanus glandula*) were replaced by more tolerant species (e.g., *Chthamalus* spp.) in areas with the highest temperature exposure. However, the barnacle line can be considered analogous to the treeline on mountains – the upper elevational limit of various foundation species – and it is interesting that this community upper limit is fairly constant among latitudes, unlike many treelines.

To our surprise, we found that the upper limit of Olympia oysters decreased with increasing latitude and our models identified negative relationships between the upper elevational limit of Olympia oysters and the frequency of extreme low temperatures. Cold temperatures thus appear to be one important factor affecting the upper limit, though other factors such as wave exposure (affecting desiccation stress) may also be important and explain some of the observed variation within regions with similar temperatures. Freezing events in the 1800s had negative effects on commercial Olympia oyster farms in Willapa Bay (Blake and Zu Ermgassen, 2015), and Olympia oysters transplanted to Connecticut died during the cold winter there (Davis, 1955). However, these documentations of negative effects of freezing were limited to aquaculture settings and did not examine elevational gradients. Our study provides the first evidence of low temperatures setting the upper limit of Olympia oysters.

Extreme low temperatures are well known to affect upper elevational limits of montane species (Hansson et al., 2021; Holtmeier and Broll, 2020). But much less is known about the effects of cold on intertidal organisms, even though exposure to extended low temperatures during low tides increases from the low to high intertidal (Reid and Harley, 2021). Many coastal invertebrates are freeze-tolerant, including Pacific oysters and some barnacles (Gill et al., 2024), consistent with our findings of no latitudinal differences in the upper limits for these taxa. There are few examples of the elevational limit of intertidal species being set by low temperatures at high latitudes, as we found for Olympia oysters. Graphical representations of upper limits of various rocky intertidal species suggested that two barnacle and one algal species have lower limits at high latitudes (Kusic Heady, 2013), which could be related to freezing. There are other examples where cold has negatively affected coastal species, but without specific examination of elevational distributions. For example, mussels in Nova Scotia had high mortality following a winter cold snap (Scrosati and Cameron, 2024). Thus, while global warming is expected to reduce the range of some heat-sensitive intertidal species, it may also expand the distribution of species whose limits are set by freezing. Mangroves are an example of a group of intertidal organisms whose distribution is set by the frequency of freeze events and which are expanding to higher latitudes with warming (Osland et al., 2017; Saintilan et al., 2014). Although there are various studies documenting positive latitudinal and altitudinal shifts in response to warming and the presumed alleviation of cold stress (Parmesan and Yohe, 2003), our study uniquely predicts a potential positive elevational shift in the intertidal zone where climate change is much more commonly associated with higher stress and negative elevational shifts (e.g., Harley, 2011). Understanding changes to elevational distributions is critical for organisms that occur along steep elevational gradients such as in the intertidal zone.

For intertidal organisms, exposure to extreme hot or cold air temperatures occurs during low tide, and the most extreme conditions occur in places where the lowest tides in summer occur near midday and the lowest tides in winter occur in the middle of the night. Therefore, while temperatures generally show latitudinal gradients, geographic variation in the timing of tides also affects thermal exposure and upper limits of intertidal organisms (Harley, 2011; Helmuth et al., 2002). We had expected to find a stronger relationship between the upper limits of Olympia oysters with extreme air temperatures during local low tide exposure compared to all time periods, but that was not the case. We suspect that the much lower intertidal distribution of Olympia oysters at high vs. low latitudes is set largely by pre-settlement processes and that local adaptation allows larvae to use settlement cues to settle in thermally safe elevational zones that differ regionally. This idea is consistent with a study from California that found that Olympia and Pacific oyster larvae settled differentially to lower vs. higher elevations (Perog et al., 2023), rather than this pattern being caused by post-settlement mortality. Such pre-settlement factors determining elevational limits have been documented for other oyster species (Wang et al., 2020) and are consistent with our finding of a stronger correlation between the upper elevational limit and all extreme temperatures compared to only the low-tide extremes. Using all extreme temperatures rather than only those from low tide exposure may have better characterized site conditions to which the oysters were locally adapted.

4.2. Conservation and restoration implications for Olympia oysters

This investigation was led by the Native Olympia Oyster Collaborative specifically in order to obtain critical information to support recovery of the species across its range. Efforts are underway along the Pacific coast to enhance and restore local populations of Olympia oysters (Ridlon et al., 2021), and this study further highlights the widespread need for recovery – only 8 % of the studied sites had >10,000 oysters in a 100 m stretch of shoreline, which is the bare minimum for a functioning oyster bed of ecological significance – high oyster densities are critical for ecological function (Kimbro and Grosholz, 2006). Conservation planners and restoration practitioners need to know the appropriate intertidal elevations for placing suitable substrata or hatchery-raised juveniles. Our findings make it clear that local elevational limits differ geographically, across latitudes, and even within estuaries. Olympia oysters occur, and restoration should focus, much lower in the intertidal zone in the northern part of this species range. This result might suggest that northern sites have more limited potential restoration habitat than southern sites. However, slopes were often steeper at southern sites than northern sites. While potential restoration sites in the north are limited to a much narrower vertical band, this area often stretches extensively horizontally (Fig. 3).

We found the globally invasive Pacific oyster significantly higher in the intertidal zone than the native Olympia oyster. This result has implications for shoreline protection services offered by the two species, and for placement of restoration substrata targeted at enhancing one but not the other species. Our results support earlier recommendations that at sites where both Olympia and Pacific oysters co-occur, restoration of Olympia oysters is best conducted in the very low intertidal zone to decrease settlement of and competition from Pacific oysters (Fuentes et al., 2020; Tronske et al., 2018).

Understanding the lower limits of coastal species is also important for climate adaptation planning. While our main focus was on the upper limit, we also attempted to obtain information on the lower elevational limits of Olympia oysters. Most team members indicated lack of data about subtidal populations at the 26 sites surveyed, and for most sites, they suspected that subtidal populations were absent or at very low abundance due to lack of available attachment substrates sufficiently large to prevent burial in mud. Almost all Olympia oyster restoration has occurred intertidally (Ridlon et al., 2021), primarily for logistical reasons, but the above expert assessments suggest that testing subtidal restoration strategies involving substrate addition might prove fruitful.

Overall, our results suggest that Olympia oysters are likely to be fairly resilient to global warming. They should benefit from decreased freezing in the north with climate warming, which should increase the vertical extent of intertidal habitat available to them and thus their elevational distribution (Fig. 8). Using latitude as a proxy for warming suggests resilience to warming – even in the southern part of the range where high air temperatures are common, Olympia oysters extend high into the intertidal, and they are equally high in sunny as in shady spots. While this study focused exclusively on air temperatures, other studies have found that Olympia oysters appear to benefit from warming water temperatures, growing faster and surviving well at water temperatures consistent with predicted future warming (Cheng et al., 2015). Warming waters should also favor reproduction, since cold summer water

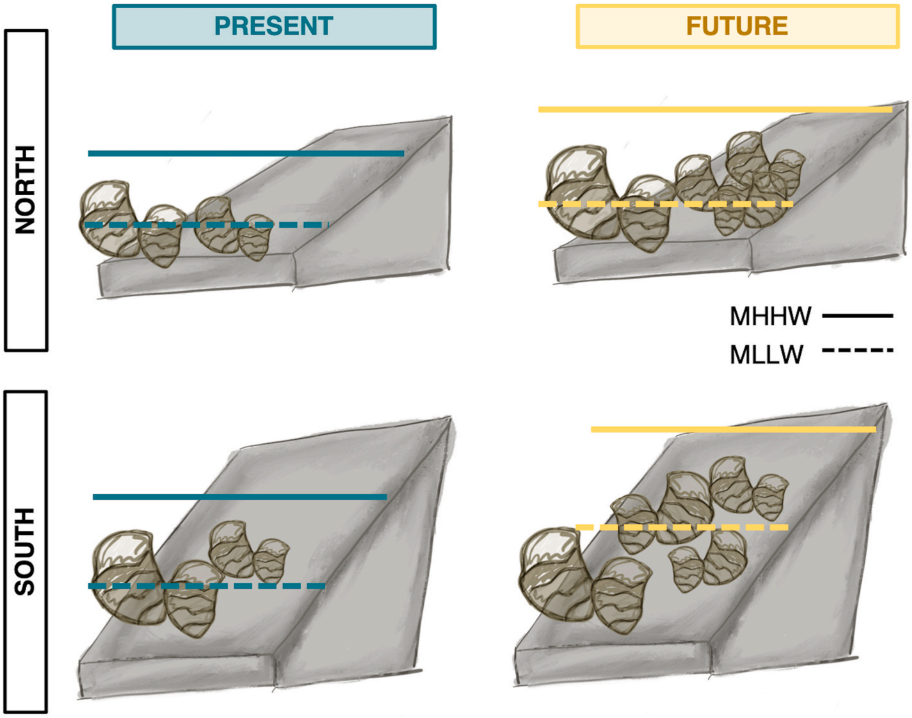

Fig. 8. Differences in intertidal distribution of Olympia oysters in the present and future, at northern vs. southern end of their latitudinal distribution. Present distribution is based on current conditions detected by this study, future conditions are projections incorporating sea level rise and global warming. PRESENT: current Olympia oyster distribution is limited to the very lowest part of the intertidal zone in the north, but slope is often gentle; distribution extends midway through the intertidal zone in the south, but slope is often steeper. FUTURE: Olympia oysters have migrated landward, tracking rising seas in both north and south; due to decrease in cold stress, oysters occupy much more of the intertidal zone in the north compared to present distribution (drawing by Kathryn Beheshti).

temperatures were a top predictor of estuary-wide reproductive failure (Wasson et al., 2016) and unusually warm years have been shown to increase the reproductive period (Chang et al., 2018).

Besides tolerating or even benefiting from some warming, Olympia oysters also appear to be quite resilient to other aspects of climate change. Rising sea level can provide a benefit in some areas, as hard substrates can be a limiting factor at some sites where Olympias occur and there are often more human-placed hard substrates (e.g., rip rap) higher up in the intertidal zone. Since we found that Olympia oysters are larger and denser lower in the intertidal than higher, sea level rise should pose no immediate threat. Olympia oysters also are less vulnerable than Pacific oysters to acidification, another potential threat related to global climate change (Hollarsmith et al., 2020; Lawlor and Arellano, 2020; Waldbusser et al., 2016). There will likely be some negative impacts to Olympia oysters from climate change, such as increasing hypoxia and low salinity events during storms, to which they are sensitive (Cheng et al., 2015, 2016). In addition, Olympia oysters could become increasingly susceptible to negative interactions with introduced species from warmer climates, such as competition with the Pacific oyster or predation by oyster drills. But on balance, it seems Oylmpia oysters may actually be winners in the face of climate change (at least initially), expanding their elevational distribution as water and air temperatures increase and seas rise. Despite having suffered such devastating losses in distribution and abundance due to anthropogenic activities including overharvesting, diking, sedimentation, and eutrophication (Baker, 1995; Kornbluth et al., 2022; Pritchard et al., 2015) – there is hope for Olympia oysters for the future. Our study suggests that activities to enhance Olympia oysters should be resilient to climate change, and re-establishing populations through conservation aquaculture or by placing substrata at suitable elevations is a solid investment in the near and long term recovery of this species.

4.3. Conclusions

Our study provides a powerful example of the use of space-for-time substitution to predict climate change impacts on a foundation species. The focus on elevational distributions across latitudes is rare and can serve as a model for studies of other species occurring along steep elevational gradients. The results of this study suggest that climate change resilience will vary among co-occurring species in Pacific estuaries. We found that two oyster species showed different latitudinal patterns in their upper limits in the intertidal zone. Further investigation is needed to characterize elevational distributions across latitudes for other taxa of conservation concern. In estuaries, much more is known about the elevational distribution of marsh plants than of invertebrates. Oyster restoration is a major focus in many estuaries, and studies of their elevational distribution across latitudes can inform restoration planning for other oyster species globally.

Anthropogenically caused warming has already been documented in many ecosystems and further shifts are predicted into the future. Consequently, it is expected that increased heat will have negative impacts on species of conservation concern, many of which are already challenged by multiple human stressors and may have little resilience to additional stress. Air temperature is likely one of the climate change induced factors of particular importance to intertidal marine organisms. A reasonable assumption for latitudinal studies of sessile intertidal organisms is that high air temperatures at low latitudes are already functioning as stressors, and that this stress response provides a prediction of increased heat stress in the future at higher latitudes. Our study is a good reminder of the importance of testing such assumptions.

We developed a series of hypotheses based on the assumption that extreme high air temperatures set the upper elevational limit of oysters, as they do for other sessile intertidal animals. However, that assumption was wrong, and not a single one of our heat-related hypotheses was supported. We found just the opposite latitudinal pattern – Olympia oysters extended higher and occupied much more of the intertidal zone at lower latitudes. We found no statistical relationship of variation in the upper limit with extreme high temperatures, no evidence for recent die-offs related to documented heat waves, and oysters at the highest elevation at a site were as likely to be in sunny microhabitats as in shady microhabitats. Not only do Olympia oysters appear resilient to warming, our study suggests they may benefit from it at least initially, expanding their currently very compressed intertidal distribution in the north (Fig. 8). Climate change will have winners and losers – though likely fewer winners than losers – and careful investigations are required to predict how individual species will fare. Latitudinal studies across elevation gradients will help inform restoration planning in a changing world, so investments can be made in the right places to be resilient today and tomorrow.

CRediT authorship contribution statement

Kerstin Wasson: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kim Cressman:** Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Kathryn Beheshti:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Erin C. Herder:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Charlie Endris:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation. **Christopher D.G. Harley:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Alicia Abadía-Cardoso:** Writing – review & editing, Methodology, Investigation. **Rodrigo Beas-Luna:** Writing – review & editing, Methodology, Investigation. **Joachim Carolsfeld:** Writing – review & editing, Methodology, Investigation. **Andrew L. Chang:** Writing – review & editing, Methodology, Investigation. **Jeffrey A. Crooks:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Matthew C. Ferner:** Writing – review & editing, Methodology, Investigation. **Edwin D. Grosholz:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Neil Harrington:** Writing – review & editing, Methodology, Investigation. **Jacob Harris:** Writing – review & editing, Methodology, Investigation. **Hilary Hayford:** Writing – review & editing, Methodology, Investigation. **Alicia R. Helms:** Writing – review & editing, Methodology, Investigation. **Julio Lorda:** Writing – review & editing, Methodology, Investigation. **Jennifer L. Ruesink:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Amaia Ruiz de Alegría-Arzaburu:** Writing – review & editing, Methodology, Investigation. **Steven S. Rumrill:** Writing – review & editing, Methodology, Investigation. **Jenni Schmitt:** Writing – review & editing, Methodology, Investigation. **Rachel S. Smith:** Writing – review & editing, Methodology, Investigation. **Janet B. Walker:** Writing – review & editing, Methodology, Investigation. **Christine R. Whitcraft:** Writing – review & editing, Methodology, Investigation. **Sylvia Yang:** Writing – review & editing, Methodology, Investigation. **Danielle Zacherl:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Chela J. Zabin:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Kerstin Wasson reports financial support was provided by The Nature Conservancy. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This investigation was led by the Native Olympia Oyster

Collaborative, with support from The Nature Conservancy. Many people generously helped in the field, with elevations, and with tidal datums and weather: B Allen, M Almeida, S Anthony, C Ashbrook, J Belanger, J Beaubier-Brulotte, D Bureau, C Cabrera, J Collucci, L Curtis, A Dalton, L DeLeon, A Deza, D Diaz, A, M & S Ferner, A Ferreira, W Gamperl, D Gavriel, M Gelhaus, E Grason, E Grout, G Hofmann, S Hunter, J Iverson, R Jeppesen, C Johnson, K Johnson, S Johnston, N Kaefer, J Kirkland, J Lisaingo, G Limon, J McClaren, E Moellenhoff, M Morley, J Peters, J Phoncharern, D Rudd, T Schneider, D Shean, S Shull, D Slone, K Swanson. Funding for authors KC, CRW and CZ was provided by The Nature Conservancy, California Oceans Program; all co-author institutions provided additional support.

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.marenvres.2025.107149.

Data availability

The data are publicly available on Dryad. https://doi.org/10.5061/dryad.ngf1vhj4v

References

Baker, P., 1995. Review of ecology and fishery of the Olympia oyster, *Ostrea lurida* with annotated bibliography. J. Shellfish Res. 14, 501–518.

Bartoń, K., 2024. MuMIn: multi-model inference. R package version 1.48.4. https://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beck, E.L., Ruesink, J., Troyer, S., Behrens, M., 2024. Wild populations of Pacific oysters (Magallana gigas) emerge during the blob heatwave in south Puget Sound, Washington USA. Front. Mar. Sci. 11. https://doi.org/10.3389/fmars.2024.1292062.

Bible, J.M., Cheng, B.S., Chang, A.L., Ferner, M.C., Wasson, K., Zabin, C.J., Latta, M., Sanford, E., Deck, A., Grosholz, E.D., 2017. Timing of stressors alters interactive effects on a coastal foundation species. Ecology 98, 2468–2478. https://doi.org/10.1002/ecy.1943.

Blake, B., Zu Ermgassen, P.S., 2015. The history and decline of *Ostrea lurida* in Willapa Bay, Washington. J. Shellfish Res. 34, 273–280.

Blanchette, C.A., Gaines, S.D., 2007. Distribution, abundance, size and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. J. Exp. Mar. Biol. Ecol. 340, 268–279. https://doi.org/10.1016/j.jembe.2006.09.014.

Brown, H.M., Briden, A., Stokell, T., Griffin, F.J., Cherr, G.N., 2004. Thermotolerance and Hsp70 profiles in adult and embryonic California native oysters, *Ostreola conchaphila* (Carpenter, 1857). J. Shellfish Res. 23, 135–141.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. Springer, New York. https://doi.org/10.1007/b97636.

Chang, A.L., Deck, A.K., Sullivan, L.J., Morgan, S.G., Ferner, M.C., 2018. Upstream—downstream shifts in peak recruitment of the native Olympia oyster in San Francisco Bay during wet and dry years. Estuaries Coasts 41, 65–78.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026. https://doi.org/10.1126/science.1206432.

Cheng, B.S., Bible, J.M., Chang, A.L., Ferner, M.C., Wasson, K., Zabin, C.J., Latta, M., Deck, A., Todgham, A.E., Grosholz, E.D., 2015. Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. Glob. Change Biol. 21, 2488–2499.

Cheng, B.S., Chang, A.L., Deck, A., Ferner, M.C., 2016. Atmospheric rivers and the mass mortality of wild oysters: insight into an extreme future? Proc. R. Soc. A B 283, 20161462.

Clark-Wolf, T., Dee Boersma, P., Rebstock, G.A., Abrahms, B., 2023. Climate presses and pulses mediate the decline of a migratory predator. Proc. Natl. Acad. Sci. 120, e2209821120.

Cogbill, C.V., White, P.S., 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. Vegetatio 94, 153–175. https://doi.org/10.1007/BF00032629.

COSEWIC, 2011. Assessment and status report on the Olympia oyster Ostrea lurida in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 56 pp. (ww.sararegistry.c.ca/status/status_e.cfm).

Crooks, J.A., Crooks, K.R., Crooks, A.J., 2015. Observations of the non-native Pacific oyster (Crassostrea gigas) in San Diego county, California. Calif. Fish Game 101, 101–107.

Davis, H.C., 1955. Mortality of Olympia oysters at low temperatures. Biol. Bull. 109, 404–406.

Dupoué, A., Mello, D.F., Trevisan, R., Dubreuil, C., Queau, I., Petton, S., Huvet, A., Guével, B., Com, E., Pernet, F., Salin, K., Fleury, E., Corporeau, C., 2023. Intertidal limits shape covariation between metabolic plasticity, oxidative stress and telomere dynamics in Pacific oyster (*Crassostrea gigas*). Mar. Environ. Res. 191, 106149. https://doi.org/10.1016/j.marenvres.2023.106149.

Fuentes, C.M., Whitcraft, C.R., Zacherl, D.C., 2020. Adaptive restoration reveals potential effect of tidal elevation on oyster restoration outcomes. Wetlands 40, 93–99.

Gill, L.T., Kennedy, J.R., Box, I.C.H., Marshall, K.E., 2024. Ice in the intertidal: patterns and processes of freeze tolerance in intertidal invertebrates. J. Exp. Biol. 227, jeb247043. https://doi.org/10.1242/jeb.247043.

Gillespie, G.E., 2009. Status of the Olympia oyster, *Ostrea lurida* Carpenter 1864, in British Columbia, Canada. J. Shellfish Res. 28, 59–68.

Graae, B.J., De Frenne, P., Kolb, A., Brunet, J., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I., Milbau, A., 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. Oikos 121, 3–19. https://doi.org/10.1111/j.1600-0706.2011.19694.x.

Green, R.H., Hobson, K.D., 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on Gemma gemma (Pelecypoda: Mollusca). Ecology 51.

Hall, E., DeAngelis, B.M., 2024. The business of oyster restoration: using traditional market-based approaches to estimate the oyster restoration economy. Restor. Ecol. n/a, e14143. https://doi.org/10.1111/rec.14143.

Hansson, A., Dargusch, P., Shulmeister, J., 2021. A review of modern treeline migration, the factors controlling it and the implications for carbon storage. J. Mt. Sci. 18, 291–306. https://doi.org/10.1007/s11629-020-6221-1.

Harley, C.D.G., 2011. Climate change, keystone predation, and biodiversity loss. Science 334, 1124–1127. https://doi.org/10.1126/science.1210199.

Harley, C.D.G., Helmuth, B.S.T., 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnol. Oceanogr. 48, 1498–1508. https://doi.org/10.4319/lo.2003.48.4.1498.

Harley, C.D.G., Paine, R.T., 2009. Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. Proc. Natl. Acad. Sci. 106, 11172–11176. https://doi.org/10.1073/pnas.0904946106.

Harris, J., Gardner, L., Kahn, A.S., Ridlon, A.D., Wasson, K., 2024. Experiments in conservation aquaculture to optimize restoration for Olympia oysters Ostrea lurida in Elkhorn Slough, CA, USA. Mar. Ecol. Prog. Ser. 734, 45–64. https://doi.org/10.3354/meps14563.

Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., Blanchette, C.A., 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science 298, 1015–1017. https://doi.org/10.1126/science.1076814.

Helmuth, B.S.T., 1998. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. Ecol. Monogr. 68, 51–74. https://doi.org/10.1890/0012-9615(1998)068[0051:IMMPTB]2.0.CO;2.

Herder, E., Bureau, D., 2023. Surveys for Olympia oysters (Ostrea lurida Carpenter, 1864) at six index sites in British Columbia 2010-2022. Chapter 22 in Boldt, J.L., Joyce, E., Tucker, S., and Gauthier, S. (Eds.). 2023. State of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems in 2022. Can. Tech. Rep. Fish. Aquat. Sci. 3542, 312.

Hollarsmith, J.A., Sadowski, J.S., Picard, M.M.M., Cheng, B., Farlin, J., Russell, A., Grosholz, E.D., 2020. Effects of seasonal upwelling and runoff on water chemistry and growth and survival of native and commercial oysters. Limnol. Oceanogr. 65, 224–235. https://doi.org/10.1002/lno.11293.

Holmquist, J.R., Windham-Myers, L., 2022. A conterminous USA-scale map of relative tidal marsh elevation. Estuaries Coasts 45, 1596–1614. https://doi.org/10.1007/s12237-021-01027-9.

Holtmeier, F.-K., Broll, G., 2020. Treeline research—from the roots of the past to present time. A review. Forests 11, 38. https://doi.org/10.3390/f11010038.

Janousek, C.N., Thorne, K.M., Takekawa, J.Y., 2019. Vertical zonation and niche breadth of tidal marsh plants along the northeast Pacific coast. Estuaries Coasts 42, 85–98. https://doi.org/10.1007/s12237-018-0420-9.

Kaplanis, N.J., Denny, M.W., Raimondi, P.T., 2024. Vertical distribution of rocky intertidal organisms shifts with sea-level variability on the northeast Pacific coast. Glob. Change Biol. 30, e17527. https://doi.org/10.1111/gcb.17527.

Kassambara, A., 2023. ggpubr: "ggplot2" based publication ready plots. R package, version 0.6.0. https://rpkgs.datanovia.com/ggpubr/.

Kimbro, D.L., Grosholz, E.D., 2006. Disturbance influences oyster community richness and evenness, but not diversity. Ecology 87, 2378–2388.

Kornbluth, A., Perog, B.D., Crippen, S., Zacherl, D., Quintana, B., Grosholz, E.D., Wasson, K., 2022. Mapping oysters on the Pacific coast of North America: a coast-wide collaboration to inform enhanced conservation. PLoS One 17, e0263998. https://doi.org/10.1371/journal.pone.0263998.

Körner, C., 2021. The cold range limit of trees. Trends Ecol. Evol. 36, 979–989. https://doi.org/10.1016/j.tree.2021.06.011.

Kusic Heady, K., 2013. Latitudinal Gradients of Rocky Intertidal Community Structure along the Northeast Pacific coast:Patterns of Distributions, Abundance and Diversity (Ph.D.). University of California, Santa Cruz, United States – California.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. Lmertest package: tests in linear mixed effects models. J. Stat. Software 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Lawlor, J.A., Arellano, S.M., 2020. Temperature and salinity, not acidification, predict near-future larval growth and larval habitat suitability of Olympia oysters in the Salish Sea. Sci. Rep. 10, 13787. https://doi.org/10.1038/s41598-020-69568-w.

Lenoir, J., Svenning, J., 2015. Climate-related range shifts–a global multidimensional synthesis and new research directions. Ecography 38, 15–28.

Lenth, R., 2024. Emmeans: estimated marginal means, aka least-squares means_. R package version 1.10.4. https://cran.r-project.org/package=emmeans.

Lovell, R.S.L., Collins, S., Martin, S.H., Pigot, A.L., Phillimore, A.B., 2023. Space-for-time substitutions in climate change ecology and evolution. Biol. Rev. 98, 2243–2270. https://doi.org/10.1111/brv.13004.

Makowski, D., Ben-Shachar, M., Patil, I., Lüdecke, D., 2020. Modelbased Estimation of Model-Based Predictions, Contrasts and Means. CRAN.

Miller, L.P., Harley, C.D., Denny, M.W., 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, Lottia gigantea. Funct. Ecol. 23, 756–767.

Mislan, K., Helmuth, B., Wethey, D.S., 2014. Geographical variation in climatic sensitivity of intertidal mussel zonation. Global Ecol. Biogeogr. 23, 744–756.

Oregon Department of Fish and Wildlife, 2016. Oregon conservation strategy. https://www.oregonconservationstrategy.org/overview/.

Osland, M.J., Day, R.H., Hall, C.T., Brumfield, M.D., Dugas, J.L., Jones, W.R., 2017. Mangrove expansion and contraction at a poleward range limit: climate extremes and land-ocean temperature gradients. Ecology 98, 125–137. https://doi.org/10.1002/ecy.1625.

Osmond, C.B., Austin, M.P., Berry, J.A., Billings, W.D., Boyer, J.S., Dacey, J.W.H., Nobel, P.S., Smith, S.D., Winner, W.E., 1987. Stress physiology and the distribution of plants. Bioscience 37, 38–48. https://doi.org/10.2307/1310176.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. https://doi.org/10.1038/nature01286.

Perog, B.D., Bowers-Doerning, C., Lopez Ramirez, C.Y., Marks, A.N., Torres, Jr.R.F., Wolfe, M.L., Zacherl, D.C., 2023. Shell cover, rugosity, and tidal elevation impact native and non-indigenous oyster recruitment: implications for reef ball design. Ecol. Eng. 192, 106969. https://doi.org/10.1016/j.ecoleng.2023.106969.

Polson, M.P., Zacherl, D.C., 2009. Geographic distribution and intertidal population status for the Olympia oyster, Ostrea lurida Carpenter 1864, from Alaska to Baja. J. Shellfish Res. 28, 69–77.

Pritchard, C., Shanks, A., Rimler, R., Oates, M., Rumrill, S., 2015. The Olympia oyster *Ostrea lurida*: recent advances in natural history, ecology, and restoration. J. Shellfish Res. 34, 259–271.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Raith, M., Zacherl, D.C., Pilgrim, E.M., Eernisse, D.J., 2015. Phylogeny and species diversity of Gulf of California oysters (Ostreidae) inferred from mitochondrial DNA. Am. Malacol. Bull. 33, 263–283.

Raymond, W., Barber, J., Dethier, M., Hayford, H., Harley, C., King, T., Paul, B., Speck, C., Tobin, E., Raymond, A., McDonald, P., 2022. Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. Ecology 103. https://doi.org/10.1002/ecy.3798.

Reid, H.B., Harley, C.D.G., 2021. Low temperature exposure determines performance and thermal microhabitat use in an intertidal gastropod (Littorina scutulata) during the winter. Mar. Ecol. Prog. Ser. 660, 105–118. https://doi.org/10.3354/meps13588.

Ridlon, A.D., Marks, A., Zabin, C.J., Zacherl, D., Allen, B., Crooks, J., Fleener, G., Grosholz, E., Peabody, B., Toft, J., Wasson, K., 2021. Conservation of marine foundation species: learning from native oyster restoration from California to British Columbia. Estuaries Coasts. https://doi.org/10.1007/s12237-021-00920-7.

Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob. Change Biol. 20, 147–157.

Scrosati, R.A., Cameron, N.M., 2024. Recolonization of intertidal mussels in Nova Scotia (Canada) after their mass disappearance following the severe 2023 winter cold snap. Diversity 16, 503. https://doi.org/10.3390/d16080503.

Shreve, F., 1911. The influence of low temperatures on the distribution of the giant cactus. Plant World 14, 136–146.

Smith, R.S., Pruett, J.L., 2024. Oyster restoration to recover ecosystem services. https://doi.org/10.1146/annurev-marine-040423-023007.

Sorte, C.J.B., Bernatchez, G., Mislan, K.A.S., Pandori, L.L.M., Silbiger, N.J., Wallingford, P.D., 2018. Thermal tolerance limits as indicators of current and future intertidal zonation patterns in a diverse mussel guild. Mar. Biol. 166, 6. https://doi.org/10.1007/s00227-018-3452-6.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488–495.

Tronske, N.B., Parker, T.A., Henderson, H.D., Burnaford, J.L., Zacherl, D.C., 2018. Densities and zonation patterns of native and non-indigenous oysters in southern California bays. Wetlands 38, 1313–1326.

Tsuchiya, M., 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. Caused by high temperature on rocky shores. J. Exp. Mar. Biol. Ecol. 66, 101–111. https://doi.org/10.1016/0022-0981(83)90032-1.

Waldbusser, G.G., Gray, M.W., Hales, B., Langdon, C.J., Haley, B.A., Gimenez, I., Smith, S.R., Brunner, E.L., Hutchinson, G., 2016. Slow shell building, a possible trait for resistance to the effects of acute ocean acidification: slow Shell Building. Limnol. Oceanogr. 61, 1969–1983. https://doi.org/10.1002/lno.10348.

Wang, T., Fan, R., Cheng, Q., Sun, Z., Fan, X., Li, N., Li, X., Quan, W., 2020. Intertidal zonation of the Suminoe oyster Crassostrea ariakensis and the Kumamoto oyster Crassostrea sikamea on the coast of the northern East China sea. J. Shellfish Res. 39, 31–41. https://doi.org/10.2983/035.039.0104.

Washington Department of Fish and Wildlife, 2015. Washington's state Wildlife action plan: 2015 update. Washington Department of Fish and Wildlife, Olympia, Washington, USA. https://wdfw.wa.gov/sites/default/files/publications/01742/wdfw01742.pdf.

Wasson, K., Hughes, B.B., Berriman, J.S., Chang, A.L., Deck, A.K., Dinnel, P.A., Endris, C., Espinoza, M., Dudas, S., Ferner, M.C., 2016. Coast-wide recruitment dynamics of Olympia oysters reveal limited synchrony and multiple predictors of failure. Ecology 97, 3503–3516.

Wethey, D.S., 2002. Biogeography, competition, and microclimate: the barnacle Chthamalus fragilis in New England. Integr. Comp. Biol. 42, 872–880. https://doi.org/10.1093/icb/42.4.872.

Wethey, D.S., 1983. Geographic limits and local zonation: the barnacles Semibalanus (balanus) and Chthamalus in new england. Biol. Bull. 165, 330–341. https://doi.org/10.2307/1541373.

Wolfe, M.L., Bowers-Doerning, C.M., Espinosa, A., Frantz, T., Hoese, W.J., Lam, J.G., Lamp, K.R., Lyons, R.A., Nguyen, J.K., Keyes, B.D., Smith, J., Suther, H.L., Swintek, M., Vannordstrand, J.C., Zacherl, D.C., 2024. Intra-decadal increase in globally-spread Magallana gigas in southern California estuaries. PLoS One 19, e0302935. https://doi.org/10.1371/journal.pone.0302935.

Zabin, C.J., Wasson, K., Fork, S., 2016. Restoration of native oysters in a highly invaded estuary. Biol. Conserv. 202, 78–87.

Zardi, G.I., Nicastro, K.R., McQuaid, C.D., Castilho, R., Costa, J., Serrão, E.A., Pearson, G. A., 2015. Intraspecific genetic lineages of a marine mussel show behavioural divergence and spatial segregation over a tropical/subtropical biogeographic transition. BMC Evol. Biol. 15, 100. https://doi.org/10.1186/s12862-015-0366-5.