Title: A century of invertebrate range extensions in the eastern North Pacific

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Abstract

Aim

Understanding the fundamental drivers of species' range edges has been a core question in ecology and biogeography for centuries and has taken on new urgency in the Anthropocene. Yet, range edges can rapidly shift over large distances, complicating long-term study of their dynamics. This is especially true in marine systems, where ranges may move hundreds of kilometers from one year to the next and where biodiversity monitoring programs are limited.

To fill this gap, we synthesized nearly 120 years of records of marine invertebrate poleward range extensions in the eastern North Pacific to examine their prevalence and association with interannual environmental variability.

Location

Eastern North Pacific Ocean: 23°N - 60°N

Time Period

1903-2020

Major Taxa Studied

Marine invertebrates.

Methods

We collated a database of poleward range extensions of marine invertebrates through a systematic review of peer-reviewed literature and reports from California Cooperative Oceanic Fisheries Investigations. We then analyzed the frequency and geographic distance of range extensions over time and in association with the El Niño Southern Oscillation and the 2014-2016 marine heatwave.

Results

The final dataset comprised 153 poleward range extensions from 68 species. We found that the episodic range extensions were significantly associated with El Niño, and that further extensions occurred during stronger El Niño events. Twenty-two percent of the range extensions were during the 2014-2016 large marine heatwave, far more than in the years preceding or following it.

Main Conclusions

Our synthesis underscored that across many years and taxa, episodic range extensions were not isolated curiosities but signals of how climate variability and warming are continuously reshaping marine ecosystems. Gaining greater insight into short-term redistribution events and their interplay with long-term ecological change including range shifts is essential for forecasting long-term biogeographic change and for designing adaptive management strategies in a warming ocean.

Keywords: climate extreme, coastal ecosystem, historical ecology, marine invertebrate, range limit, species redistribution, California Current

1. Introduction

Marine environments experience environmental variability across daily to interannual timescales, from short-lived extreme events (e.g., marine heatwaves, cold spells) to recurring climate oscillations (e.g., El Niño Southern Oscillation, North Atlantic Oscillation). Species responses to environmental variability include changes in geographic distributions (Pinsky, Selden, & Kitchel, 2020; Harvey, Marshall, Harley, & Russell, 2022; Fredston et al., 2025). These redistributions may be transient, representing dispersal beyond established ranges without successful establishment, or they may constitute the earliest stages of range shifts if repeated arrivals and persistence subsequently occur (Soifer et al., 2025; Bates et al., 2014; Zinmeister, 1974; MacArthur, 1972). Most global change research on range edges has focused on decadal-scale shifts and concordance with ocean warming (Fredston et al., 2021).

Despite their importance, short-term redistributions remain difficult to characterize because they require repeated observations across broad geographic extents that span historical biogeographic boundaries, yet such long-term, large-scale datasets are uncommon (Hughes et al., 2021). Marine systems provide an informative setting for these questions because species exhibit diverse dispersal strategies and constraints, creating the potential for different redistribution responses to the same climatic events (Cowen & Sponaugle 2009). Understanding how environmental variability influences range extensions therefore requires study systems that combine long-term biodiversity observations with recurring environmental variability across broad spatial scales and taxa.

Marine invertebrates are well suited to these questions because they encompass a wide range of dispersal strategies. Many have planktonic larvae that can be transported long distances by changing ocean currents (Cowen & Sponaugle 2009; Shanks, 2009; Pineda, Hare & Sponaugle, 2007; Kinlan & Gaines, 2003), whereas others have short larval durations or direct development. This diversity allows us to examine how species across a wide range of dispersal capacities are responding to the same climatic forcing.

The eastern North Pacific presents an opportunity to study patterns in short term redistribution events because it combines a long history of biodiversity monitoring programs such as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) with recurrent climate events including El Niño Southern Oscillation (ENSO) and marine heatwaves (MHW) (Sanford, Sones, García-Reyes, Goddard, & Largier, 2019; Cavole, Demko, Diner, Giddings & Koester, 2016; Lluch-Belda, Lluch-Cota & Lluch-Cota, 2005; Mearns, 1988; Hubbs,1948). Paleontological records in the eastern North Pacific indicate that many warm-affinity marine taxa occupied more poleward distributions during past warm interglacial periods than they do today, demonstrating that substantial redistributions have occurred repeatedly in this system over geological timescales (Roy, Jablonski, & Valentine, 1995; Muhs et al., 2022). Whereas paleontological records capture the cumulative outcomes of climatic change over thousands of years, recurrent ENSO events and marine heatwaves provide contemporary natural experiments for examining redistribution events as they occur. These events alter ocean circulation and elevate sea surface temperatures by up to 2 °C, allowing evaluation of how short-term environmental variability influences species' range edges (Cavole et al., 2016; Di Lorenzo & Mantua, 2016; Jacox et al., 2016; Gentemann, Fewings & García-Reyes, 2017; Sanford et al., 2019; Harvey et al., 2022; Cimino et al., 2021; Soifer et al., 2025).

Beyond its extensive monitoring history and environmental variability, the eastern North Pacific also contains several well-recognized biogeographic transition zones, including Cape Flattery, Cape Mendocino, Point Conception, and Punta Eugenia, where many species reach historical range limits and community composition changes over relatively short spatial scales (Valentine, 1966; Spalding et al., 2007; Blanchette et al., 2008; Krumhansl et al., 2023, Drake et al., 2011). These transition zones provide

a natural context for evaluating whether environmental variability is associated with temporary excursions beyond established distributions.

Marine invertebrate range shifts associated with environmental variability have been documented globally, including contemporary tropicalization and thermophilization linked to climate warming (Burrows et al., 2019; Zarzyczny, Rius, Williams & Fenberg, 2024b). In the eastern North Pacific, observations spanning more than 75 years have documented distributional changes and poleward range extensions associated with environmental variability, from early reports (Hubbs, 1948; Zinsmeister, 1974; Mearns, 1988; Lluch-Belda et al., 2005) to recent studies of the 2014-2016 marine heatwave and concurrent El Niño (Cavole et al., 2016; Sanford et al., 2019; Cimino et al., 2021; Wonham & Hart, 2018; Starko et al., 2025). Together, these studies demonstrated that climatic anomalies can coincide with rapid species redistributions, but because they largely focused on individual events, habitats, or subsets of taxa, they did not resolve how widespread poleward redistributions are across taxa, how frequently they occurred over recent decades, or whether they consistently coincide with warming events rather than occurring sporadically through time.

Here, we synthesized nearly 120 years of records of marine invertebrate poleward range extensions in the eastern North Pacific from 23°N - 60°N to examine their association with ENSO and the 2014-2016 MHW. We conducted a systematic review of peer-reviewed literature and reports from scientific surveys to generate a synthesized time-series of when, where, and which marine invertebrates were observed to extend poleward. We analyzed whether these events more likely represented predictable biogeographic responses to environmental variability or instead were chance occurrences. More specifically, we tested if more poleward range extensions of marine invertebrates occurred during El Niño events than expected by chance; we tested if stronger El Niño events resulted in geographically further extension distances; and we tested if more poleward range extensions occurred during the 2014-2016 MHW interval than expected by chance.

2. Methods

We collated a database of poleward range extensions, defined as the observation of one or more individuals of a particular species occurring poleward of its historical range edge (see Section 2.4), of marine invertebrates in the eastern North Pacific through a systematic review of reports from scientific surveys and peer-reviewed literature (Fig. 1; Supp. Fig. 1; Supp. Table 1). We extracted narrative records of invertebrate range extensions from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) documents, which describe environmental conditions and living resources of the California Current formally since 1950, capturing observations made before ENSO was widely recognized. These documents contain serendipitous records of unusual species occurrences that were noted by scientists during quarterly oceanographic surveys along established survey lines extending about 500km offshore from San Francisco Bay to San Diego, California. While these surveys are not designed to detect range shifts or novel species, the reports note unusual biological occurrences in the context of the collected oceanographic data by scientific teams familiar to those waters. We combined the observations extracted from the historical reports with observations extracted from a systematic review of the peer-reviewed scientific literature. Together, these sources cover a wide range of habitats and species. CalCOFI primarily contributed observations of pelagic taxa, while the broader literature synthesis included range-extension records across a wider diversity of habitats, including intertidal and nearshore benthic environments. This synthesis assembled a comprehensive time series of poleward range extensions observed within the past 120 years (see Section 2.2).

2.1 Geographic Extent

All records used in this analysis came from onshore or nearshore (i.e., coastal) observations of marine invertebrates with range extensions in the eastern North Pacific (Fig. 1; Supp. Fig. 1; Supp. Table 2). The eastern North Pacific has a high density of systematic and opportunistic oceanographic sampling,

allowing us to minimize the influence of geographic variation in observation effort on reported range extensions. We focused on species whose historical range edges (see Section 2.4) occurred between approximately 23°N and 48°N. This criterion was applied only to the historical range edge; extension events themselves were not geographically constrained, and the furthest north extension captured in this study went to 60°N.

2.2 Systematic Literature Review

2.2.1 California Cooperative Oceanic Fisheries Investigations Review

We manually screened all available CalCOFI documents, including volumes 01-60 of their now-retired publication (1950-2019) and the *State of the California Current Reports* published in *Frontiers in Marine Science* (2020-2021). These sources, which we collectively refer to as the "CalCOFI documents," include narrative-form observations of unusual marine invertebrate occurrences as far back as 1926. We skimmed all sections of the CalCOFI documents until we came across mention of an invertebrate, at which point we did an in-depth reading of the section. Any paragraph or sentence was recorded when the reporting author described an occurrence of an invertebrate that the author thought was unusual or poleward of the species' range. Information from these excerpts were converted into structured data, including species identity, observation location, and observation date for each extension.

2.2.2 Peer Reviewed Literature Search

We systematically reviewed the wider scientific literature base for reports of any poleward extensions in the eastern North Pacific. We developed iterations of search terms to map the literature and maximize the number of relevant documents using the recommended scoping method from Foo, O'Dea, Koricheva, Nakagawa & Lagisz (2021). The search returned articles relevant to the West Coast of North America that included marine- and invertebrate-related terms as well as language indicating range shifts. The search terms and methods regarding taxa name selection can be found in the supplementary documentation.

We performed an additional opportunistic search wherein if poleward extensions discussed in a reviewed article were from a referenced article, the referenced article was also included in the review (Harari, Parola, Hartwell & Riegelman, 2020; Foo et al., 2021). The search resulted in a total of 409 peer reviewed articles.

2.3 *Inclusion Criteria*

To be included in this study, observations from CalCOFI and the peer-reviewed literature had to meet the following criteria: (1) involve a focal species (marine animal that was not a vertebrate, insect, microscopic organism, parasite, or invasive species); (2) occur in or after 1900 and before 2025; (3) be a poleward range extension; and (4) have a historical range edge (see Section 2.4) in the eastern North Pacific (see Section 2.1). Of the 409 peer-reviewed articles, criterion 1 rejected 93 articles; criterion 2 rejected 31; criterion 3 rejected 184 articles; and criterion 4 rejected 34 articles. We excluded six peer-reviewed articles because they were already reviewed in the CalCOFI documents screening. Additionally, we deemed twenty-seven articles as 'inconclusive' (see Supplementary). This yielded 39 peer-reviewed articles containing 272 distinct observations of range extensions of invertebrates in this region. The CalCOFI documents (see Section 2.2.1) contained an additional 64 range extension observations.

For the systematic literature review, we assigned a confidence rating to each observation. If the observation was at a never-before-surveyed or very-infrequently-surveyed location, the extension was considered low confidence. If the observation was made at a frequently but irregularly surveyed location (e.g., data from a citizen science platform), the extension was considered medium confidence. If the observation was made at a frequently surveyed site by an expert, the extension was considered high confidence. All CalCOFI records were classified as high confidence. Only the medium and high confidence range extension observations were included in the analyses, reducing the literature review

observations from 272 to 251. These criteria increase confidence that extension events reflect recent range extensions rather than isolated observations of previously undocumented populations.

Merging the CalCOFI dataset and systematic review dataset, we totalled 315 observations of marine invertebrate range extensions. We retained only the furthest-north observation of a single species in a year to ensure a common temporal resolution (yearly), and if multiple observations occurred at the same latitude, we retained the observation on the earliest date in the year. This de-duplication of the dataset reduced the observations to 237. The exact location of observation was used when it was available. If only general descriptions of the locations were available, we estimated the latitude (e.g. "the San Diegan region" is assigned the latitude for San Diego, California). In a few instances, longitudes were provided in reference to a coastal position (e.g., 45 miles off Coos Bay) and were estimated by hand with spherical geometry. If longitude was not recorded, we snapped the observation latitudes to the coastline (R package 'sf' v. 1.0.20, Pebesma, 2018; Pebesma & Bivand, 2023).

2.4 Historical Range Edge Classification

We defined a "historical range edge" as the poleward range edge position previously described for a species in reference texts and/or the ecological literature. Not all of our primary sources of range extension observations reported species-specific historical range edge locations; thus, we developed a workflow to determine those independently. For each species identified as having a poleward extension meeting our criteria (see section 2.3), we recorded the historical range edge from reference texts on invertebrate distributions as they were available (41 of 68 species), using the extensions' reference article as a secondary source if necessary (27 of 68 species; Supp. Table 2; a list of the data sources is found in Appendix 1). When sources described historical range edges qualitatively within the eastern North Pacific rather than providing exact latitudes, we assigned representative biogeographic latitude values as follows: 'southern California' = 34.5; 'warm to warm-temperate waters' = 34.5; 'southern species' = 34.5; 'tropical Pacific' = 24 'Transition Zone Waters' = 34.5; 'Mexico' = 32.5. For these latitude classifications, we used the most poleward plausible latitude as a conservative estimate to reduce the likelihood of falsely classifying observations as range extensions at the recognized cost of potentially losing real extensions. While the designation of "southern species", and "Transition Zone Waters" is necessarily arbitrary, we selected Point Conception (~34.5°N) for both cases because it represents a major oceanographic and biogeographic transition characterized by strong gradients in temperature, circulation, and species composition along the eastern North Pacific coast (Valentine, 1966; Spalding et al., 2007; Blanchette et al., 2008).

2.5 Filtering of Extension Observations & Extension Event Classification

After establishing historical range edges (see section 2.4), we filtered for observations (see sections 2.2, 2.3) poleward of species' historical range edges, reducing the dataset to 228 observations. These observations beyond historical range edges may have represented either transient occurrences or successful establishment. Of these observations, 195 came from peer-reviewed articles and 33 came from the CalCOFI documents (a list of the data sources is found in Appendix 2). If at least one individual of a species was observed beyond its historical range edge for one or more consecutive years within the synthesized data, this was classified as a single "extension event". We considered the event to end when the species did not have an observation in the synthesized dataset beyond the historical range edge for at least one year (e.g., if pelagic red crab had observations beyond the historical range edge in 2002 and 2014, 2015, and 2016, we assigned two events: 2002 and 2014-2016). The 228 observations became 153 extension events. Some analyses below used only species with at least three distinct extension events, which we termed "episodic extension events" of which there were 95.

2.6 Analyses

We tested whether the annual frequency of poleward extension events changed over time using a hurdle model implemented in the R package pscl (v. 1.5.9; Jackman, 2024), because annual counts included

many zero-event years. The model separately estimated temporal trends in the probability of observing at least one event and in the number of events observed during years with one or more events. In both components, the year index was included as the predictor variable. We compared Poisson and negative binomial hurdle models using Akaike's Information Criterion (AIC) and visual inspection to assess model fit.

For the following analyses, El Niño events were defined by the Oceanic Niño Index (ONI; National Oceanic and Atmospheric Administration, 2024) in which a strong El Niño event is classified when Niño 3.4 SST anomaly (ERSST.v5) exceeds +0.5°C for five consecutive overlapping three-month running averages (available February 1950 - April 2025 at time of analysis; NOAA, 2024). The monthly ONI and associated ENSO classifications by month were acquired using R package 'rsoi' v. 0.5.6 (Albers, 2023). We tested three hypotheses using these ENSO data and the episodic extension events: (1) that extension events occur more frequently in association with El Niño than expected by chance alone, (2) that stronger El Niño events are associated with more extension events, and (3) that stronger El Niño events are associated with further (i.e., more distant) extension events. Of the episodic extensions, only extension events from 1950 onwards aligned with the ONI timeframe and were retained (82 extension events).

First, we used a χ-squared goodness-of-fit test to compare the observed frequency of extension events across all species during El Niño years with the expected frequency based on the long-term proportion of months classified as El Niño (using the reduced dataset of 82 extension events; Fig. 2a). Our sample size precluded us from accounting for differences in taxonomic identity, life history, and event coverage. We classified an extension event as occurring during El Niño if the first year of the extension coincides with either (a) the peak year (i.e., a year containing the maximum number of El Niño months for an event) or (b) the terminal year of an El Niño event.

Second, we tested whether stronger El Niño events (higher ONI values) are associated with an increased number of poleward extension events (using the reduced dataset of 82 extension events). For each of the annual ONI values calculated from our 75-year ONI time-series, we counted up the total number of associated extension events (sometimes across multiple years, if that ONI value occurred more than once), retaining the ONI values with zero extension events. We then fitted models with number of events as the response variable and ONI as the predictor variable, again using a hurdle model (R package 'pscl' v. 1.5.9 Jackman S, 2024) because the response consisted of zero-inflated count data. In both components of the hurdle model, annual mean ONI was included as the predictor variable. We compared Poisson and negative binomial hurdle models using Akaike's Information Criterion (AIC) and visual inspection to assess model fit. We performed a leave-one-species-out analysis to evaluate whether results were driven by any single species. For each iteration, one species was excluded, annual extension counts were recalculated, and the hurdle model was refit.

Third, we tested whether stronger El Niño events (higher ONI values) are associated with geographically further extensions (using the reduced dataset of 82 extension events). For each extension event, our response variable was the maximum observed extension distance within that extension event, which was log-transformed prior to analysis to improve normality and stabilize residual variance. Our predictor variable was the assigned ONI for each extension event, same as above. We evaluated multiple candidate models including linear, quadratic, and GAMs (R package 'mgcv' v. 1.9.1, Wood, 2003, 2004, 2011; Wood et al., 2016; Wood, 2017). We also fitted a linear mixed-effects model with species as a random factor, first with random intercepts only, then with both random intercepts and slopes with respect to ONI (R package 'lme4' 1.1-37, Bates, Mächler, Bolker & Walker, 2015). We then evaluated relative support using AIC. We also tested whether extension distances (log-transformed) differ significantly between high ONI values (≥ 0.5, the El Niño threshold) and low ONI values with a Welch two-sample, two-tailed *t*-test.

Finally, we examined how the 2014-2016 MHW influences extension event frequency (using the full dataset of 153 extension events). We tested whether the number of extension events during 2014-2016 exceeded expectations by chance using a χ-squared goodness-of-fit test, with the expected frequency based on the proportion of years spanned by the heatwave (3 of 117 years of extension data). Due to data limitations, we were unable to account for differences in taxonomic identity and event coverage.

3. Results

The final dataset comprised 153 poleward extension events (21 from CalCOFI documents, 126 from literature search, and 6 identified in both; Supp. Fig. 2; Supp. Table 1) observed from 1903 to 2020 for 68 species (eight phyla). Of these species, 26 were fully pelagic (38%), 27 were benthic as adults with pelagic larval phases (40%), five were benthic with limited dispersal or direct development (7%), and 10 were benthic with unknown developmental traits (15%; Supp. Table 2). The median extension event frequency (pooled across all species) was 0.5 extension events per year (range: 0 - 20 events per year) and the median extension distance was 484 km (range: 3-4,548 km). Of the 26 pelagic species in our synthesized dataset, 21 exhibited median extension distances that were greater than the overall median (Supp. Table 1). Thirty-eight species had only one extension event and 20 species had episodic extension events (3+ extension events). Pelagic red crab (*Pleuroncodes planipes*) had the most recorded extensions with nine events. Between 1903 and 2020, the probability of observing at least one poleward extension event increased significantly through time (zero component: $\beta = 0.035$ per year, $p < 0.001$). Conditional on at least one extension event occurring, the number of extension events also increased significantly through time (count component: $\beta = 0.028$ per year, $p < 0.001$; Supp. Fig. 3). The negative binomial hurdle model was selected over the Poisson hurdle model based on its lower AIC (ΔAIC = 21.2).

We report 82 episodic extension events for 20 species with a median extension distance of 459 km (range: 14-4,548 km; Fig. 1; Supp. Fig. 1; Supp. Table 1). More than two-thirds of the episodic extension events occurred during an El Niño (55 of 82 extension events; 67%), which was over double the expected frequency based on the long-term El Niño baseline (26%; χ-squared = 71.49, df = 1, p-value < 0.001; Fig. 2a and 2b). Four of the 20 species had all of their extension events occur during or just after an El Niño phase: Pacific mole crab (*Emerita analoga*)*, Euphausia eximia,* pelagic red crab *(Pleuroncodes planipes)* and *Velella velella* (Fig. 2b).

Higher ONI increased the probability of at least one extension event occurring (zero component: $\beta = 1.24$ per ONI, $p = 0.005$). Conditional on an extension event occurring, higher ONI was also associated with a greater number of extension events (count component: $\beta = 0.81$ per ONI, $p < 0.001$; Fig. 2c). The Poisson hurdle model was selected over the negative binomial hurdle model based on its lower AIC (ΔAIC = 2). The positive relationship between ONI and extension event frequency was robust to the exclusion of individual species. Despite unequal observations among species, in every leave-one-species-out iteration, ONI remained a significant positive predictor in both the hurdle and count components of the model.

Extension distance increased 42.5% (95% CI: 2% - 99%) for each one-unit increase in ONI ($\beta = 0.36$; Fig. 3b, Supp. Table 3). The mixed-effects model with species-specific random intercepts provided the best fit based on AIC and is thus reported (ΔAIC $\geqq$ 3.9 relative to all other alternatives). Species identity accounted for a substantial proportion of the variation in maximum extension distance (ICC = 0.64), supporting the inclusion of species as a random intercept. For visualization purposes, we displayed the linear model fit in Fig. 3b. A t-test comparing extension distances between categorically high- and low-ONI years was suggestive but did not provide evidence to reject the null hypothesis of equal extension distances between high ONI years and low ONI years ($t_{60} = 1.21$, $p = 0.23$; Fig. 3a). Pelagic taxa had significantly greater extension distances than limited-dispersal (LD) taxa (5.4-fold; $p < 0.05$), while benthic taxa with pelagic larvae had an estimated 1.7-fold greater extension distance than LD taxa that was not statistically significant ($p > 0.05$; Supp. Fig. 4; Supplementary Methods & Results).

More than one-fifth of all extension events occurred during the 2014-2016 marine heatwave (33 of 153 extension events; 22%), which was about eight times the expected frequency based on the duration of the heatwave (2.6%; χ-squared = 221.38, df = 1, p-value < 0.001; Supp. Fig. 5). In 2015 alone, our dataset recorded 13 extension events, the most in any single year. Nearly half of all species in our full dataset extended their ranges during the 2014-2016 marine heatwave (31 of 68; 46%); 17 of those species had extension events exclusively during the 2014-2016 marine heatwave with no other record (Supp. Table 1).

4. Discussion

Episodic appearances of invertebrate species in the eastern North Pacific are a remarkable part of the region's ecology and history, yet previously a synthesis of these range-extending species was lacking. Our inventory of the scientific and historical records since 1900 shows that many species exhibit episodic extension events (Fig. 1). We also found multiple lines of evidence that episodic extension events were significantly associated with El Niño. The number and distance of range extensions were both positively correlated with El Niño strength (Fig. 2c, 3b) and range extensions were more likely to coincide with El Niño than expected by chance (Fig. 2b). This pattern held across an ecologically and taxonomically diverse set of species, although the species-specific associations between El Niño and extension events differed (Fig. 2b). Building on the extensive literature documenting ecological impacts of the 2014-2016 marine heatwave in the eastern North Pacific (Suryan et al., 2021; Freedman et al., 2020; Sanford et al., 2019), our synthesis identified 33 distinct range extension events during this interval—nearly one quarter of all events compiled across more than a century of observations. Together, these results situate episodic range extensions as a recurring and climatically structured component of the eastern North Pacific's marine biogeography.

Consistent with a transport-based mechanism, pelagic species in our dataset generally exhibited longer extension distances than benthic species (Supp. Table 1 & 2; Supp. Fig. 4; Supplementary Methods & Results). Species whose extensions occurred exclusively during El Niño (Pacific mole crab*, Euphausia eximia,* pelagic red crab, *Vellela velella*) are completely pelagic or have long pelagic larval phases and have all been reported to be associated with anomalous poleward and onshore transport (Sorte, Peterson, Morgan & Emmett, 2001; Lilly & Ohman, 2021; Cimino et al., 2021; Jones, Parrish & Burgess, 2021; Simpson, 1984). The documented failure of these species to persist between El Niños may be because reproduction and recruitment are inhibited under cooler, upwelling-dominated conditions (Williams et al., 2001; Simpson, 1984; Cimino et al., 2021). One notable exception was the dark unicorn whelk (*Mexacanthina lugubris*), which extended poleward repeatedly independent of El Niño despite lacking a pelagic larval stage. Its iterative extensions likely reflect an ongoing climate-driven range expansion rather than anomalous transport events (Wallingford & Sorte, 2022; Fenberg et al., 2023; Muhs et al., 2022).

These species-level patterns are consistent with broader oceanographic theory and empirical observations. In typical years, poleward flow in the California Current is relatively weak during winter, spring, and summer, (Hickey, 1979; Lynn & Simpson, 1987; Melton, Washburn & Gottschalk, 2009; Checkley & Barth, 2009), potentially limiting poleward dispersal for species with short pelagic durations or spawning periods in this seasonal window. During El Niño, however, poleward and onshore flows strengthen and persist for longer periods (Lynn & Bograd, 2002; Durazo & Baumgartner, 2002; Zacherl, Gaines & Lonhart, 2003; Jacox et al., 2016), increasing opportunities for northward transport. Consistent with this mechanism, particle-tracking studies predict substantially greater poleward dispersal for long-duration than short-duration propagules during El Niño (Drake, Edwards & Barth, 2011; Strub et al., 2024; Strub & James, 2025). These mechanisms are consistent with previous work showing that fully pelagic invertebrates extended nearly three times farther than benthic species during the 2014-2016 marine heatwave and concurrent El Niño (Sanford et al., 2019). Our results similarly indicate that species with longer pelagic durations tended to exhibit longer extension distances and that extension events in these

species were more frequently associated with El Niño conditions, supporting the hypothesis that enhanced poleward transport facilitates long-distance dispersal in species that spend more time in the pelagic environment.

Many of the range extensions in our dataset crossed one or more recognized biogeographic boundaries (Supp. Table 4), indicating that these boundaries are not absolute barriers, at least not during periods of anomalous ocean conditions. Because our synthesis did not distinguish between transient observations beyond historical range limits and persistent population establishment, these crossings should not be interpreted as evidence of permanent range shifts (Zinmeister, 1974; Brodie et al., 2025). Rather, they demonstrate that climatic events can facilitate dispersal and occurrence beyond historical distributions.

El Niño amplified the number of extensions of marine invertebrates, as did the 2014-2016 large marine heatwave. While the El Niño Southern Oscillation is a long-term natural climatic phenomenon, the large 2014-2016 marine heatwave was likely fueled, at least in part, by anthropogenic climate change (Jacox et al., 2016 and 2018). During this heatwave, we found a pronounced increase in the frequency of extension events. Seventeen species exhibited poleward range extensions that occurred exclusively during the 2014-2016 MHW and at no other time (Supp. Table 1). This pattern indicates that extreme warming events may drive species to extend their range edges that have not historically done so, even under El Niño conditions, and potentially act as a catalyst for sustained shifts (Soifer et al., 2025). When these species expand poleward, they may disrupt established ecological networks by introducing novel competitive and predator-prey interactions, altering trophic interactions, and potentially reshaping top-down control (Parmesan, 2006; Walther, 2010; Fenberg et al., 2023; Zarzyczny et al., 2024b). The sustained presence of these species and the resulting “tropicalization” of temperate ecosystems could produce cascading and unpredictable ecological consequences (Vergés et al., 2019; Zarzyczny et al., 2024b).

Our synthesis is necessarily constrained by the heterogeneous nature of historical observations. The dataset combined systematic observations from CalCOFI with published reports that differed in sampling design, geographic coverage, taxonomic focus, and reporting effort (Supp. Fig. 2). As a result, observed spatial and temporal patterns likely reflect both biological processes and variation in survey effort, and regions or taxa with few reported extensions should not be interpreted as necessarily lacking climate-mediated redistributions. We did not incorporate biodiversity databases because our goal was to synthesize published observations and augment existing records, and because marine invertebrates remain incompletely represented in many large biodiversity repositories. Similarly, increased scientific attention following major El Niño events may have increased the likelihood that unusual species occurrences were detected and reported, potentially contributing to temporal variation in extension records.

Detection probability also varied through time due to changes in sampling technology, taxonomic expertise, and research priorities. Unresolved taxonomic complexity, inconsistent identification of morphologically similar taxa, and cryptic or rare species may also have contributed to misclassification of some range extension events (Hollister et al., 2025; Zarzyczny et al., 2024a; Hollister et al., 2023). In addition, because most synthesized records documented adult occurrences, the timing of first observation may lag months or even years behind arrival, particularly for long-lived sessile species (Zacherl et al., 2003). Our analyses therefore relate the first documented observation beyond the historical range edge, rather than the timing of arrival, to environmental variability. This uncertainty, together with differences among species in life history, dispersal, and detection probability, would generally be expected to weaken rather than inflate the relationships with El Niño and marine heatwaves that we recorded. Finally, because the synthesis is based on presence-only records, it cannot quantify the true frequency of range extension events, distinguish transient occurrences from permanent establishment, or rule out undocumented extensions in unsurveyed regions.

Range edge dynamics have long been a central focus in biogeography and ecology, as the limits of species distributions define both their environmental tolerances and opportunities for expansion (MacArthur, 1972; Wallace, 1876). Recent studies have highlighted that range edges are often more permeable and dynamic than previously thought, responding rapidly to variability in temperature and habitat availability (Parmesan & Yohe, 2003; Hickling, Roy, Hill, Fox & Thomas, 2006; Burrows et al., 2014; Fredston et al., 2021). Short-term redistribution events are critical yet complex to study in marine systems, where species distributions are three-dimensional, vary across seasons and years, are strongly influenced by ocean circulation, and remain incompletely documented by long-term observations (Fredston et al., 2025). By synthesizing observations across taxa, habitats, and decades, this study broadens our understanding of the frequency, magnitude, and taxonomic breadth of episodic poleward range extensions in a dynamic marine ecosystem.

Long-term monitoring programs such as CalCOFI, the Multi-Agency Rocky Intertidal Network (MARINe, 2018), and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO; Blanchette et al., 2008) provide an essential foundation for detecting biological responses to environmental variability and change (Lindenmayer et al., 2012; Hughes et al., 2017). Because no single monitoring program can provide complete spatial, temporal, or taxonomic coverage, synthesis across long-term surveys, targeted studies, and published observations has become increasingly important for identifying broad ecological patterns and testing hypotheses in rapidly changing ecosystems (Halpern et al., 2020). Our synthesis demonstrates that episodic range extensions are not isolated curiosities but recurrent features of eastern North Pacific ecosystems, with many marine invertebrates shifting their observed distributions by hundreds to thousands of kilometers within a single year. These findings challenge management and conservation strategies that rely on static representations of species' geographic ranges (Melbourne-Thomas et al., 2021) and highlight the importance of sustained monitoring and data synthesis for anticipating ecological responses to ongoing climate variability.

5. References

Albers, S. (2023). rsoi: Import Various Northern and Southern Hemisphere Climate Indices. https://CRAN.R-project.org/package=rsoi

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1). https://doi.org/10.18637/jss.v067.i01

Blanchette, C. A., Miner, C. M., Raimondi, P. T., Lohse, D., Heady, K. E. K., & Broitman, B. R. (2008). Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. JOURNAL OF BIOGEOGRAPHY, 35(9), 1593–1607. https://doi.org/10.1111/j.1365-2699.2008.01913.x

Brodie, J. F., Freeman, B. G., Mannion, P. D., & Hargreaves, A. L. (2025). Shifting, expanding, or contracting? Range movement consequences for biodiversity. Trends in Ecology & Evolution, 40(5), 439–448. https://doi.org/10.1016/j.tree.2025.02.001

Brodie, S., Abrahms, B., Bograd, S. J., Carroll, G., Hazen, E. L., Muhling, B. A., Pozo Buil, M., Smith, J. A., Welch, H., & Jacox, M. G. (2021). Exploring timescales of predictability in species distributions. Ecography, 44(6), 832–844. https://doi.org/10.1111/ecog.05504

Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). THE GEOGRAPHIC RANGE: Size, Shape, Boundaries, and Internal Structure. Annual Review of Ecology and Systematics, 27(1), 597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

Burrows, M. T., Hawkins, S. J., Moore, J. J., Adams, L., Sugden, H., Firth, L., & Mieszkowska, N. (2019). Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain. Global Change Biology, 26(4), 2093–2105. https://doi.org/10.1111/gcb.14968

Burrows, M. T., Schoeman, D. S., Richardson, A. J., Molinos, J. G., Hoffmann, A., Buckley, L. B., Moore, P. J., Brown, C. J., Bruno, J. F., Duarte, C. M., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Sydeman, W. J.,

Ferrier, S., … Poloczanska, E. S. (2014). Geographical limits to species-range shifts are suggested by climate velocity. Nature, 507(7493), 492–495. https://doi.org/10.1038/nature12976

California Cooperative Oceanic Fisheries Investigations (CalCOFI). (1950). CalCOFI Reports. California Department of Fish and Game, NOAA Fisheries, and Scripps Institution of Oceanography, 01–60. https://calcofi.org/publications/calcofireports/

Cavole, L. M., Demko, A. M., Diner, R. E., Giddings, A., & Koester, I. (2016). Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific: Winners, Losers, and the Future | Oceanography (Pt. 273-285). 29. https://tos.org/oceanography/article/biological-impacts-of-the-20132015-warm-water-anomaly-in-the-northeast-paci

Checkley, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. Progress in Oceanography, Eastern Boundary Upwelling Ecosystems: Integrative and Comparative Approaches, 83(1), 49–64. https://doi.org/10.1016/j.pocean.2009.07.028

Cimino, M. A., Jacox, M. G., Bograd, S. J., Brodie, S., Carroll, G., Hazen, E. L., Lavaniegos, B. E., Morales, M. M., Satterthwaite, E., & Rykaczewski, R. R. (2021). Anomalous poleward advection facilitates episodic range expansions of pelagic red crabs in the eastern North Pacific. Limnology and Oceanography, 66(8), 3176–3189. https://doi.org/10.1002/lno.11870

Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. Annual Review of Marine Science, 1(Volume 1, 2009), 443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change, 6(11), 1042–1047. https://doi.org/10.1038/nclimate3082

Drake, P. T., Edwards, C. A., & Barth, J. A. (2011). Dispersion and connectivity estimates along the U.S. west coast from a realistic numerical model. Journal of Marine Research, 69(1), 1–37. https://doi.org/10.1357/002224011798147615

Durazo, R., & Baumgartner, T. R. (2002). Evolution of oceanographic conditions off Baja California: 1997–1999. Progress in Oceanography, Observations of the 1997-98 El Nino along the West Coast of North America, 54(1), 7–31. https://doi.org/10.1016/S0079-6611(02)00041-1

Fenberg, P. B., Beas-Luna, R., Igić, B., MacLean, M. A., Paz-García, D. A., Raimondi, P. T., Sones, J. L., Zarzyczny, K. M., & Sanford, E. (2023). Predator-induced defences under tropicalisation: A biogeographic approach. Journal of Biogeography, 50(12), 2148–2159. https://doi.org/10.1111/jbi.14716

Foo, Y. Z., O'Dea, R. E., Koricheva, J., Nakagawa, S., & Lagisz, M. (2021). A practical guide to question formation, systematic searching and study screening for literature reviews in ecology and evolution. Methods in Ecology and Evolution, 12(9), 1705–1720. https://doi.org/10.1111/2041-210X.13654

Fredston, A. L., Tingley, M. W., Neate-Clegg, M. H. C., Evans, L. J., Antão, L. H., Ban, N. C., Chen, I.-C., Chen, Y.-W., Comte, L., Edwards, D. P., Evengard, B., Fadrique, B., Falkeis, S. H., Guralnick, R., Klinges, D. H., Lembrechts, J. J., Lenoir, J., Palacios-Abrantes, J., Pauchard, A., … Scheffers, B. R. (2025). Reimagining species on the move across space and time. Trends in Ecology & Evolution, 40(7), 629–638. https://doi.org/10.1016/j.tree.2025.03.015

Fredston, A., Pinsky, M., Selden, R. L., Szuwalski, C., Thorson, J. T., Gaines, S. D., & Halpern, B. S. (2021). Range edges of North American marine species are tracking temperature over decades. Global Change Biology, 27(13), 3145–3156. https://doi.org/10.1111/gcb.15614

Freedman, R. M., Brown, J. A., Caldow, C., & Caselle, J. E. (2020). Marine protected areas do not prevent marine heatwave-induced fish community structure changes in a temperate transition zone. Scientific Reports, 10(1), 21081. https://doi.org/10.1038/s41598-020-77885-3

Gaylord, B., & Gaines, S. D. (2000). Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. The American Naturalist, 155(6), 769–789. https://doi.org/10.1086/303357

590 Gentemann, C. L., Fewings, M. R., & García-Reyes, M. (2017). Satellite sea surface temperatures
591 along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat
592 wave. Geophysical Research Letters, 44(1), 312–319. https://doi.org/10.1002/2016GL071039
593 Glynn, P. W. (1988). El Niño-Southern Oscillation 1981-1983: Nearshore population, community,
594 and ecosystem responses. Annual Review of Ecology and Systematics, 19(1), 309–346.
595 https://doi.org/10.1146/annurev.es.19.110188.001521
596 Halpern, B. S., Berlow, E., Williams, R., Borer, E. T., Davis, F. W., Dobson, A., Enquist, B. J.,
597 Froehlich, H. E., Gerber, L. R., Lortie, C. J., O'connor, M. I., Regan, H., Vázquez, D. P., &
598 Willard, G. (2020). Ecological Synthesis and Its Role in Advancing Knowledge. BioScience,
599 70(11), 1005–1014. https://doi.org/10.1093/biosci/biaa105
600 Harari, M. B., Parola, H. R., Hartwell, C. J., & Riegelman, A. (2020). Literature searches in
601 systematic reviews and meta-analyses: A review, evaluation, and recommendations. Journal of
602 Vocational Behavior, 118, 103377. https://doi.org/10.1016/j.jvb.2020.103377
603 Harvey, B. P., Marshall, K. E., Harley, C. D. G., & Russell, B. D. (2022). Predicting responses to
604 marine heatwaves using functional traits. Trends in Ecology & Evolution, 37(1), 20–29.
605 https://doi.org/10.1016/j.tree.2021.09.003
606 Helmuth, B., Mieszkowska, N., Moore, P., & Hawkins, S. J. (2006). Living on the Edge of Two
607 Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate
608 Change. Annual Review of Ecology, Evolution, and Systematics, 37(1), 373–404.
609 https://doi.org/10.1146/annurev.ecolsys.37.091305.110149
610 Hickey, B. M. (1979). The California current system—Hypotheses and facts. Progress in
611 Oceanography, 8(4), 191–279. https://doi.org/10.1016/0079-6611(79)90002-8
612 Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a wide
613 range of taxonomic groups are expanding polewards. Global Change Biology, 12(3), 450–455.
614 https://doi.org/10.1111/j.1365-2486.2006.01116.x
615 Hollister, J. D., Cai, X., Horton, T., Price, B. W., Zarzyczny, K. M., & Fenberg, P. B. (2023). Using
616 computer vision to identify limpets from their shells: A case study using four species from the
617 Baja California peninsula. Frontiers in Marine Science, 10.
618 https://doi.org/10.3389/fmars.2023.1167818
619 Hollister, J. D., Paz-García, D. A., Beas-Luna, R., Horton, T., Cai, X., & Fenberg, P. B. (2025).
620 Genes, shells, and AI: Using computer vision to detect cryptic morphological divergence
621 between genetically distinct populations of limpets. Scientific Reports, 16(1), 1051.
622 https://doi.org/10.1038/s41598-025-30613-1
623 Holt, R. d., & Keitt, T. h. (2000). Alternative causes for range limits: A metapopulation perspective.
624 Ecology Letters, 3(1), 41–47. https://doi.org/10.1046/j.1461-0248.2000.00116.x
625 Hubbs, C. L. (1948). Changes in the fish fauna of western North America correlated with changes in
626 ocean temperature. Journal of Marine Research.
627 Hughes, A. C., Orr, M. C., Ma, K., Costello, M. J., Waller, J., Provoost, P., Yang, Q., Zhu, C., &
628 Qiao, H. (2021). Sampling biases shape our view of the natural world. Ecography, 44(9), 1259–
629 1269. https://doi.org/10.1111/ecog.05926
630 Hughes, B. B., Beas-Luna, R., Barner, A. K., Brewitt, K., Brumbaugh, D. R., Cerny-Chipman, E. B.,
631 Close, S. L., Coblentz, K. E., de Nesnera, K. L., Drobnitch, S. T., Figurski, J. D., Focht, B.,
632 Friedman, M., Freiwald, J., Heady, K. K., Heady, W. N., Hettinger, A., Johnson, A., Karr, K.
633 A., … Carr, M. H. (2017). Long-Term Studies Contribute Disproportionately to Ecology and
634 Policy. BioScience, 67(3), 271–281. https://doi.org/10.1093/biosci/biw185
635 Jackman, S. (2024). pscl: Classes and Methods for R Developed in the Political Science
636 Computational Laboratory (Version R package version 1.5.9) [Computer software]. University
637 of Sydney,. https://github.com/atahk/pscl/
638 Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal Upwelling Revisited:
639 Ekman, Bakun, and Improved Upwelling Indices for the U.S. West Coast. Journal of
640 Geophysical Research: Oceans, 123(10), 7332–7350. https://doi.org/10.1029/2018JC014187

641 Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., & Bograd,
642 S. J. (2016). Impacts of the 2015–2016 El Niño on the California Current System: Early
643 assessment and comparison to past events. Geophysical Research Letters, 43(13), 7072–7080.
644 https://doi.org/10.1002/2016GL069716
645 Jones, T., Parrish, J. K., & Burgess, H. K. (2021). Long-term patterns of mass stranding of the
646 colonial cnidarian Velella velella: Influence of environmental forcing. Marine Ecology Progress
647 Series, 662, 69–83. https://doi.org/10.3354/meps13644
648 Kinlan, B. P., & Gaines, S. D. (2003). Propagule Dispersal in Marine and Terrestrial Environments:
649 A Community Perspective. Ecology, 84(8), 2007–2020. https://doi.org/10.1890/01-0622
650 Krumhansl, K., Gentleman, W., Lee, K., Ramey-Balci, P., Goodwin, J., Wang, Z., Lowen, B.,
651 Lyons, D., Therriault, T. W., & DiBacco, C. (2023). Permeability of coastal biogeographic
652 barriers to marine larval dispersal on the east and west coasts of North America. Global
653 Ecology and Biogeography, 32(6), 945–961. https://doi.org/10.1111/geb.13654
654 Lenarz, W. H., Ventresca, D. A., Schwing, F. B., Chavez, F., & Graham, W. M. (1995). Explorations
655 of El Niño Events and Associated Biological Population Dynamics off Central California.
656 CalCOFI Reports, 36.
657 Lilly, L. E., & Ohman, M. D. (2021). Euphausiid spatial displacements and habitat shifts in the
658 southern California Current System in response to El Niño variability. Progress in
659 Oceanography, 193, 102544. https://doi.org/10.1016/j.pocean.2021.102544
660 Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C.
661 R., Hoffmann, A. A., Keith, D. A., Liddell, M. J., Lowe, A. J., Metcalfe, D. J., Phinn, S. R.,
662 Russell-Smith, J., Thurgate, N., & Wardle, G. M. (2012). Value of long-term ecological studies.
663 Austral Ecology, 37(7), 745–757. https://doi.org/10.1111/j.1442-9993.2011.02351.x
664 Lluch-Belda, D., Lluch-Cota, D. B., & Lluch-Cota, S. E. (2005). Changes in marine faunal
665 distributions and ENSO events in the California Current. Fisheries Oceanography, 14(6), 458–
666 467. https://doi.org/10.1111/j.1365-2419.2005.00347.x
667 Lynn, R. J., & Bograd, S. J. (2002). Dynamic evolution of the 1997–1999 El Niño–La Niña cycle in
668 the southern California Current System. Progress in Oceanography, Observations of the 1997-
669 98 El Nino along the West Coast of North America, 54(1), 59–75.
670 https://doi.org/10.1016/S0079-6611(02)00043-5
671 Lynn, R. J., & Simpson, J. J. (1987). The California Current system: The seasonal variability of its
672 physical characteristics. Journal of Geophysical Research: Oceans, 92(C12), 12947–12966.
673 https://doi.org/10.1029/JC092iC12p12947
674 MacArthur, R. H. (1972). Geographical Ecology: Patterns in the Distribution of Species. Harper &
675 Row.
676 MARINe. (2018). https://marine.ucsc.edu/explore-the-data/#data-use
677 Mearns, A. J. (1988). The “Odd Fish”: Unusual Occurrences of Marine Life as Indicators of
678 Changing Ocean Conditions. In D. F. Soule & G. S. Kleppel (Eds.), Marine Organisms as
679 Indicators (pp. 137–176). Springer. https://doi.org/10.1007/978-1-4612-3752-5_7
680 Melbourne-Thomas, J., Audzijonyte, A., Brasier, M. J., Cresswell, K. A., Fogarty, H. E., Haward,
681 M., Hobday, A. J., Hunt, H. L., Ling, S. D., McCormack, P. C., Mustonen, T., Mustonen, K.,
682 Nye, J. A., Oellermann, M., Trebilco, R., van Putten, I., Villanueva, C., Watson, R. A., & Pecl,
683 G. T. (2022). Poleward bound: Adapting to climate-driven species redistribution. Reviews in
684 Fish Biology and Fisheries, 32(1), 231–251. https://doi.org/10.1007/s11160-021-09641-3
685 Melton, C., Washburn, L., & Gotschalk, C. (2009). Wind relaxations and poleward flow events in a
686 coastal upwelling system on the central California coast. Journal of Geophysical Research:
687 Oceans, 114(C11), 2009JC005397. https://doi.org/10.1029/2009JC005397
688 Milanesi, P., Della Rocca, F., & Robinson, R. A. (2019). Integrating dynamic environmental
689 predictors and species occurrences: Toward true dynamic species distribution models. Ecology
690 and Evolution, 10(2), 1087–1092. https://doi.org/10.1002/ece3.5938

691 Muhs, D. R. (2022). MIS 5e sea-level history along the Pacific coast of North America. Earth
692 System Science Data, 14(3), 1271–1330. https://doi.org/10.5194/essd-14-1271-2022
693 National Oceanic and Atmospheric Administration (NOAA). (2024). Oceanic Niño Index (ONI) and
694 ERSSTv5 data (NOAA National Centers for Environmental Information.) [Dataset].
695 https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php
696 Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. Annual
697 Review of Ecology, Evolution, and Systematics, 37(Volume 37, 2006), 637–669.
698 https://doi.org/10.1146/annurev.ecolsys.37.091305.110100
699 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across
700 natural systems. Nature, 421(6918), 37–42. https://doi.org/10.1038/nature01286
701 Pearcy, W. G. (2002). Marine nekton off Oregon and the 1997–98 El Nino. Progress in
702 Oceanography, Observations of the 1997-98 El Nino along the West Coast of North America,
703 54(1), 399–403. https://doi.org/10.1016/S0079-6611(02)00060-5
704 Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. The R
705 Journal, 10(1), 439–446. https://doi.org/10.32614/RJ-2018-009
706 Pebesma, E., & Bivand, R. (2023). Spatial Data Science: With applications in R. Chapman and
707 Hall/CRC. https://doi.org/10.1201/9780429459016
708 Pineda, J., Hare, J. A., & Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean
709 and Consequences for Population Connectivity. In OCEANOGRAPHY (Vol. 20, Issues 3, SI,
710 pp. 22–39). OCEANOGRAPHY SOC. https://doi.org/10.5670/oceanog.2007.27
711 Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-Driven Shifts in Marine Species
712 Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science,
713 12(Volume 12, 2020), 153–179. https://doi.org/10.1146/annurev-marine-010419-010916
714 Roy, K., Jablonsk, D., & Valentine, J. W. (1995). Thermally anomalous assemblages revisited:
715 Patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. Geology,
716 23(12), 1071. https://doi.org/10.1130/0091-
717 7613(1995)023%253C1071:TAARPI%253E2.3.CO;2
718 Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H. R., & Largier, J. L. (2019). Widespread
719 shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves.
720 Scientific Reports, 9(1), 4216. https://doi.org/10.1038/s41598-019-40784-3
721 Shanks, A. L. (2009). Pelagic Larval Duration and Dispersal Distance Revisited. The Biological
722 Bulletin, 216(3), 373–385. https://doi.org/10.1086/BBLv216n3p373
723 Simpson, J. J. (1984). El Nino-induced onshore transport in the California Current during 1982-
724 1983. Geophysical Research Letters, 11(3), 233–236.
725 https://doi.org/10.1029/GL011i003p00233
726 Soifer, L. G., Lockwood, J. L., Lembrechts, J. J., Antão, L. H., Klinges, D. H., Senior, R. A., Ban, N.
727 C., Evengard, B., Fadrique, B., Falkeis, S., Fredston, A. L., Guralnick, R., Lenoir, J., Neate-
728 Clegg, M. H. C., Palacios-Abrantes, J., Pecl, G., Pinsky, M. L., Smith, J. E., Stys, B., …
729 Scheffers, B. R. (2025). Extreme events drive rapid and dynamic range fluctuations. Trends in
730 Ecology & Evolution, 40(9), 862–873. https://doi.org/10.1016/j.tree.2025.06.009
731 Sorte, C. J., Peterson, W. T., Morgan, C. A., & Emmett, R. L. (2001). Larval dynamics of the sand
732 crab, Emerita analoga, off the central Oregon coast during a strong El Niño period. Journal of
733 Plankton Research, 23(9), 939–944. https://doi.org/10.1093/plankt/23.9.939
734 Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B.
735 S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia,
736 C. A., & Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of
737 Coastal and Shelf Areas. BioScience, 57(7), 573–583. https://doi.org/10.1641/B570707
738 Starko, S., Epstein, G., Chalifour, L., Bruce, K., Buzzoni, D., Csordas, M., Dimoff, S., Hansen, R.,
739 Maucieri, D. G., McHenry, J., Tietjen, K. L., Timmer, B., & Baum, J. K. (2025). Ecological
740 Responses to Extreme Climatic Events: A Systematic Review of the 2014–2016 Northeast

741 Pacific Marine Heatwave. In B. D. Russell & P. A. Todd, Oceanography and Marine Biology
742 (1st ed., pp. 42–96). CRC Press. https://doi.org/10.1201/9781003589600-2
743 Strub, P. T., & James, C. (2025). Altimeter-Derived poleward Lagrangian pathways in the California
744 Current System: Part 2 – 2-D patterns of parcel transports. Progress in Oceanography, 235,
745 103495. https://doi.org/10.1016/j.pocean.2025.103495
746 Strub, P. T., James, C., Fisher, J. L., Fewings, M. R., Zeman, S. M., Combes, V., Garwood, J. C.,
747 Bolm, A. E., & Scherer, A. (2024). Altimeter-derived poleward Lagrangian pathways in the
748 California Current System: Part 1. Progress in Oceanography, 229, 103353.
749 https://doi.org/10.1016/j.pocean.2024.103353
750 Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J.,
751 Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing,
752 D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H.,
753 … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave.
754 Scientific Reports, 11(1), 6235. https://doi.org/10.1038/s41598-021-83818-5
755 Thompson, A. R., Bjorkstedt, E. P., Bograd, S. J., Fisher, J. L., Hazen, E. L., Leising, A., Santora, J.
756 A., Satterthwaite, E. V., Sydeman, W. J., Alksne, M., Auth, T. D., Baumann-Pickering, S.,
757 Bowlin, N. M., Burke, B. J., Daly, E. A., Dewar, H., Field, J. C., Garfield, N. T., Giddings, A.,
758 … Weber, E. D. (2022). State of the California Current Ecosystem in 2021: Winter is coming?
759 Frontiers in Marine Science, 9. https://doi.org/10.3389/fmars.2022.958727
760 Valentine, J. W. (1966). Numerical Analysis of Marine Molluscan Ranges on the Extratropical
761 Northeastern Pacific Shelf. Limnology and Oceanography, 11(2), 198–211.
762 Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M. A., Wernberg, T., Ainsworth, T., &
763 Steinberg, P. D. (2019). Tropicalisation of temperate reefs: Implications for ecosystem
764 functions and management actions. Functional Ecology, 33(6), 1000–1013.
765 https://doi.org/10.1111/1365-2435.13310
766 Wallace, A. R. (1876). The geographical distribution of animals; with a study of the relations of
767 living and extinct faunas as elucidating the past changes of the Earth's surface (Vol. 1–1). New
768 York: Harper & Brothers.
769 Wallingford, P. D., & Sorte, C. J. B. (2022). Dynamic species interactions associated with the range-
770 shifting marine gastropod Mexacanthina lugubris. Oecologia, 198(3), 749–761.
771 https://doi.org/10.1007/s00442-022-05128-5
772 Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. Philosophical
773 Transactions of the Royal Society of London. Series B, Biological Sciences, 365(1549), 2019–
774 2024. https://doi.org/10.1098/rstb.2010.0021
775 Weber, E. D., Auth, T. D., Baumann-Pickering, S., Baumgartner, T. R., Bjorkstedt, E. P., Bograd, S.
776 J., Burke, B. J., Cadena-Ramírez, J. L., Daly, E. A., De La Cruz, M., Dewar, H., Field, J. C.,
777 Fisher, J. L., Giddings, A., Goericke, R., Gomez-Ocampo, E., Gomez-Valdes, J., Hazen, E. L.,
778 Hildebrand, J., … Zeman, S. M. (2021). State of the California Current 2019–2020: Back to the
779 Future With Marine Heatwaves? Frontiers in Marine Science, 8, 709454.
780 https://doi.org/10.3389/fmars.2021.709454
781 Wetherall, J. A. (n.d.). Biology, Oceanography, and Fisheries of the North Pacific Transition Zone
782 and Subarctic Frontal Zone.
783 Williams, G. D., West, J. M., & Zedler, J. B. (2001). Shifts in Fish and Invertebrate Assemblages of
784 Two Southern California Estuaries during the 1997-98 El Niño. Southern California Academy
785 of Sciences, 212–237.
786 Wonham, M. J., & Hart, M. W. (2018). El Niño Range Extensions of Pacific Sand Crab (Emerita
787 analoga) in the Northeastern Pacific. Northwest Science, 92(1), 53–60.
788 https://doi.org/10.3955/046.092.0106
789 Wood, S. N. (2003). Thin-plate regression splines. Journal of the Royal Statistical Society (B), 65(1),
790 95–114.

Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association, 99(467), 673–686.
Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B), 73(1), 3–36.
Wood, S. N. (2017). Generalized Additive Models: An Introduction with R (2nd ed.). Chapman and Hall/CRC.
Wood, S. N., N., Pya, & S"afken, B. (2016). Smoothing parameter and model selection for general smooth models (with discussion). Journal of the American Statistical Association, 111, 1548–1575.
WoRMS Editorial Board. (2025). World Register of Marine Species [Dataset]. https://doi.org/10.14284/170
Zacherl, D., Gaines, S. D., & Lonhart, S. I. (2003). The limits to biogeographical distributions: Insights from the northward range extension of the marine snail, Kelletia kelletii (Forbes, 1852). Journal of Biogeography, 30(6), 913–924. https://doi.org/10.1046/j.1365-2699.2003.00899.x
Zarzyczny, K. M., Hellberg, M. E., Lugli, E. B., MacLean, M., Paz-García, D. A., Rius, M., Ross, E. G., Treviño Balandra, E. X., Vanstone, J., Williams, S. T., & Fenberg, P. B. (2024). Opposing genetic patterns of range shifting temperate and tropical gastropods in an area undergoing tropicalisation (Pt. 246–262). 51. https://doi.org/10.1111/jbi.14744
Zarzyczny, K. M., Rius, M., Williams, S. T., & Fenberg, P. B. (2024). The ecological and evolutionary consequences of tropicalisation. Trends in Ecology & Evolution, 39(3), 267–279. https://doi.org/10.1016/j.tree.2023.10.006
Zinsmeister, W. J. (1974). A New Interpretation of Thermally Anomalous Molluscan Assemblages of the California Pleistocene. Journal of Paleontology, 48(1), 84–94.

6. Data Availability: Data and code is available at https://anonymous.4open.science/r/ca-invert-shifts-anon (reviewer link) and will be archived in a stable repository (e.g., Dryad) upon manuscript acceptance.

7. Figures

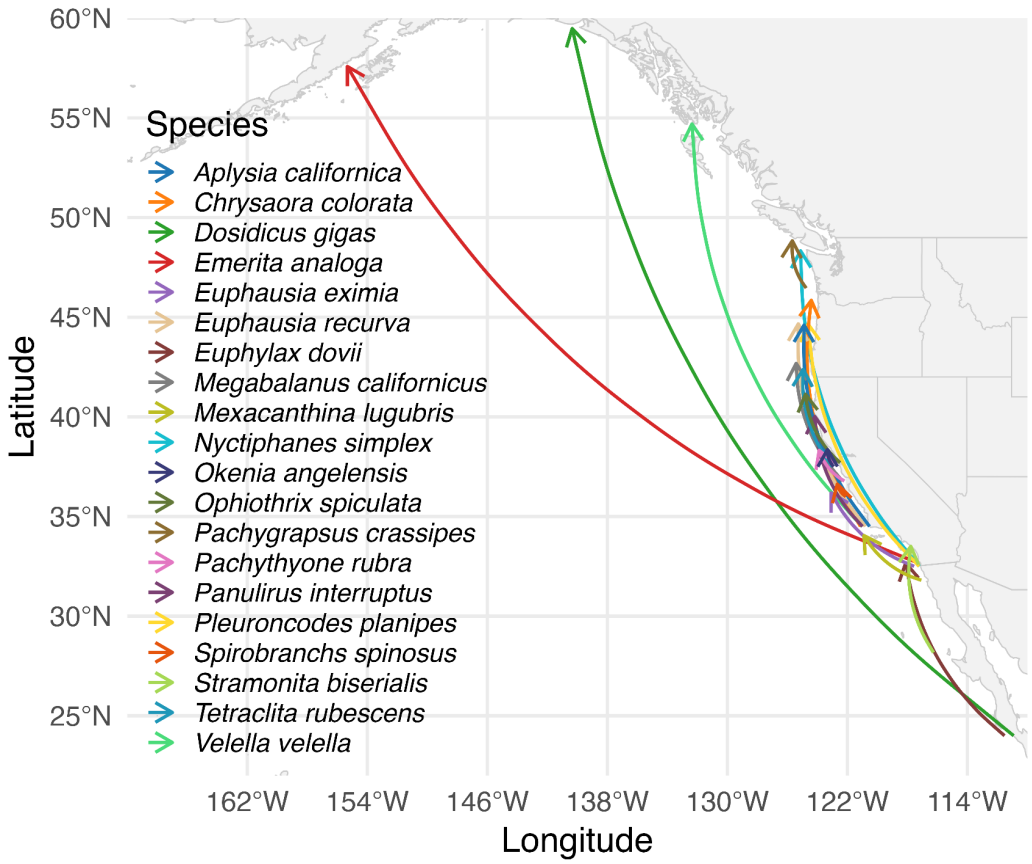

Figure 1. Marine invertebrates in the eastern North Pacific repeatedly extended their ranges hundreds of kilometers beyond historical poleward edge, based on our >100-year synthesized dataset. Each arrow represents one species. The arrow origin is the historical poleward range edge (see Supp. Table 2 with the historical range edge data), and the arrow destination is the northernmost point of anomalous observation of the species. Up to -1 degree of jitter is added to the arrow longitudes to reduce overlap. The 95 episodic extension events of these 20 species have a median distance of 459 km (range: 14km - 4,548 km).

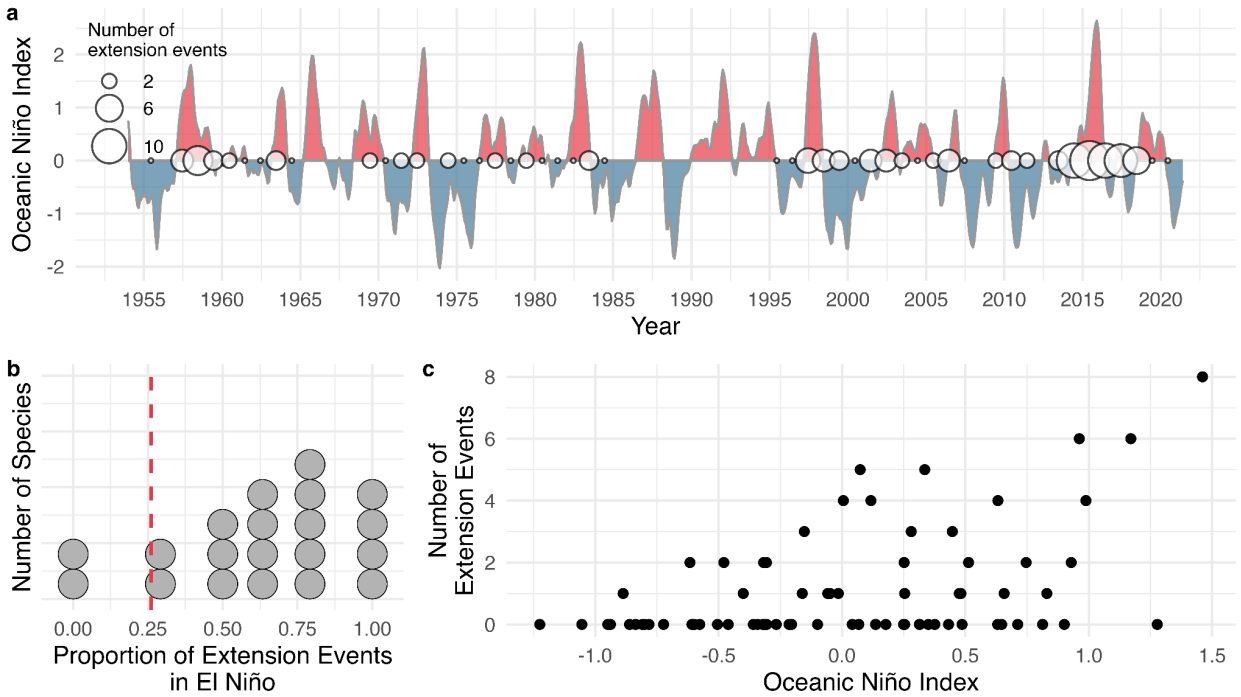

Figure 2. Range extensions of marine invertebrates in our synthesized dataset were more frequent the stronger the El Niño events. a. Time-series of the Oceanic Niño Index (ONI; National Oceanic and Atmospheric Administration, 2024) where red is positive ONI, or an El Niño event if greater than 0.5, and blue is negative ONI, or a La Niña event if less than -0.5. The number of extension events (when a species appears north of its historical range edge for a year or set of consecutive years) per year for species with 3+ extension events is depicted by the diameter of the overlaid white circles. b. The proportion of extension events occurring during the peak or at the end of an El Niño event, for each species with 3+ extension events (20 species; one gray circle per species). Over two-thirds of all 1950-2020 episodic extension events (55 of 82; 67%) occur during El Niño years, which is more than double the expected frequency based on the long-term El Niño baseline (26%; dotted red line). c. Each black point represents the number of extension events (y-axis) associated with a given ONI (x-axis).

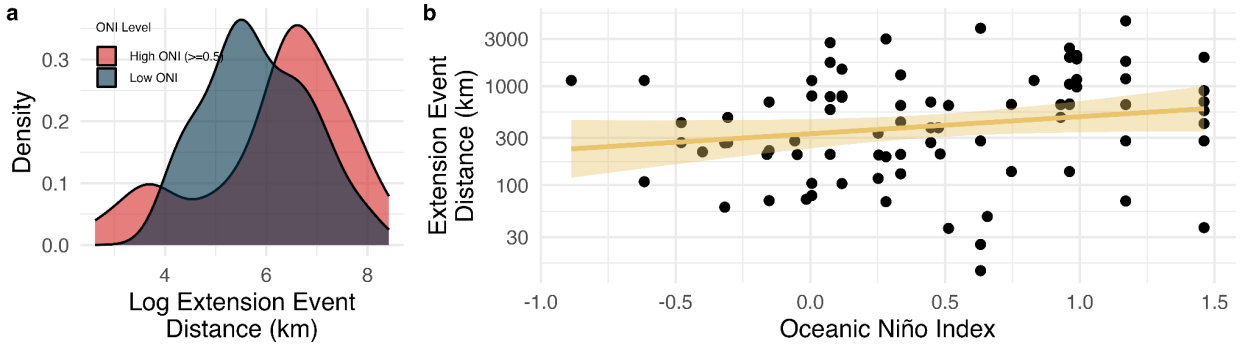

Figure 3. Range extensions of marine invertebrates in our synthesized dataset covered more distance with stronger El Niño events. a. The probability density function (y-axis) of the distance of each extension event (x-axis) for extension events occurring during a high Oceanic Niño Index (ONI) period (red, >=0.5; 36 extension events) and distance of extension events occurring during a low ONI period (blue, <0.5; 46 extension events; $t_{60} = 1.21$, $p = 0.23$). Extension event distance is the distance in kilometers from the historical range edge of the marine invertebrate to the furthest poleward point at which they were found during an extension event. b. Each black point represents an extension event with its distance on the y-

axis and its associated ONI on the x-axis. The yellow line represents the overall trend with the ribbon indicating the 95% confidence interval; statistical inference was based on the mixed-effects model with species-specific random intercepts where extension distance increased 42.5% (95% CI: 2% - 99%) for each one-unit increase in ONI ($\beta = 0.36$).

Appendix 1 - Data sources for historical range edges

Abbott, R. T. (1954). *American seashells*. New York, Van Nostrand.

Alvariño, A. (1965). Chaetognaths. *Oceanography and Marine Biology, An Annual Review.*, (3), 115–194.

Bastida-Zavala, J. R., McCann, L. D., Keppel, E., & Ruiz, G. M. (2017). The fouling serpulids (Polychaeta: Serpulidae) from United States coastal waters: an overview. *European Journal of Taxonomy*, (344). https://doi.org/10.5852/ejt.2017.344

Berner, L. D. (1960). Unusual Features in the Distribution of Pelagic Tunicates in 1957 and 1958. *CalCOFI Reports*, *7*.

Bertsch, H., Gosliner, T., Wharton, R., & Willaims, G. (1972). Natural history and occurrence of opisthobranch gastropods from the open coast of San Mateo County, California. *Veliger -Berkeley-*, *14*, 302–314.

Bieri, R. (1959). The Distribution of the Planktonic Chaetognatha in the Pacific and their Relationship to the Water Masses. *Limnology and Oceanography*, *4*(1), 1–28. https://doi.org/10.4319/lo.1959.4.1.0001

Brinton, E. (1960). Changes in the Distribution of the Euphausiid Crustaceans in the Region of the California Current. *CalCOFI Reports*, *7*.

Brinton, E. (1962). *The distribution of Pacific euphausiids*. https://escholarship.org/uc/item/6db5n157

Brinton, E., & Townsend, A. (2003). Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep Sea Research Part II: Topical Studies in Oceanography, CalCOFI: A Half Century of Physical, Chemical and Biological Research in the California Current System*, *50*(14), 2449–2472. https://doi.org/10.1016/S0967-0645(03)00126-7

Carlton, J. T. (Ed.). (2007). *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon* (4th ed.). University of California Press. https://doi.org/10.2307/jj.5973107

Fenberg, P. B., Posbic, K., & Hellberg, M. E. (2014). Historical and recent processes shaping the geographic range of a rocky intertidal gastropod: Phylogeography, ecology, and habitat availability. *Ecology and Evolution*, *4*(16), 3244–3255. https://doi.org/10.1002/ece3.1181

Goddard, J. H. R., Gosliner, T. M., & Pearse, J. S. (2011). Impacts associated with the recent range shift of the aeolid nudibranch Phidiana hiltoni (Mollusca, Opisthobranchia) in California. *Marine Biology*, *158*(5), 1095–1109. https://doi.org/10.1007/s00227-011-1633-7

Goddard, J., Treneman, N., Pence, W., Mason, D., Dobry, P., Green, B., & Hoover, C. (2016). Nudibranch Range Shifts Associated with the 2014 Warm Anomaly in the Northeast Pacific. *Bulletin, Southern California Academy of Sciences*, *115*, 15–40. https://doi.org/10.3160/soca-115-01-15-40.1

Gosliner, T., & Williams, G. (1970). The Opisthobranch Mollusks of Marin County, California. *Veliger -Berkeley-*, *13*, 175–180.

Haddock, S. H. D., & Case, J. F. (1999). Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: Ctenophores, medusae and siphonophores. *Marine Biology*, *133*(3), 571–582. https://doi.org/10.1007/s002270050497

Hendrickx, M. E. (1995). Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Bulletin de l'Institut Royal Des Sciences Naturelles de Belgique, Biologie, Brussels: Royal Belgian Institute of Natural Sciences*, *65*, 125–150.

Hendrickx, M. E., & Harvey, A. W. (1998). Checklist of anomuran crabs (Crustacea: Decapoda) from the eastern Tropical Pacific. *Belgian Journal of Zoology*, *129*(2), 363–389.

Hubbard Jr., L. T., & Pearcy, W. G. (1971). Geographic Distribution and Relative Abundance of Salpidae off the Oregon Coast. *Journal of the Fisheries Research Board of Canada*, *28*(12), 1831–1836. https://doi.org/10.1139/f71-276

Jaeckle, W. B. (1983). Additions to the opisthobranch mollusk fauna of Marin County, California, with notes on the biology of certain species. *The Veliger*, (26), 93–95.

Jaeckle, W. B. (1984). The opisthobranch mollusks of Humboldt County, California. *The Veliger*, *26*, 207–213.

Jensen, G. C. (1995). *Pacific Coast Crabs and Shrimps*. Sea Challengers.

Keen, A. M. (Angeline M. (with Internet Archive). (1958). *Sea shells of tropical west America; marine mollusks from Lower California to Columbia*. Stanford, Calif., Stanford University Press. http://archive.org/details/seashellsoftropi0000unse

Keister, J., Johnson, T., Morgan, C., & Peterson, W. (2005). Biological indicators of the timing and direction of warm-water advection during the 1997/1998 El Niño off the central Oregon coast, USA. *Marine Ecology Progress Series*, *295*, 43–48. https://doi.org/10.3354/meps295043

Lavaniegos, B. E., & Ohman, M. D. (2003). Long-term changes in pelagic tunicates of the California Current. *Deep Sea Research Part II: Topical Studies in Oceanography*, *50*(14–16), 2473–2498. https://doi.org/10.1016/S0967-0645(03)00132-2

Mearns, A. J. (1988). The "Odd Fish": Unusual Occurrences of Marine Life as Indicators of Changing Ocean Conditions. In D. F. Soule & G. S. Kleppel (Eds.), *Marine Organisms as Indicators* (pp. 137–176). Springer. https://doi.org/10.1007/978-1-4612-3752-5_7

Morris, P. A. (1974). *Field Guide to Pacific Coast Shells* (2nd ed.). Houghton Mifflin Harcourt Publishing Company.

Ott, B., Mcdaniel, N., & Humphrey, E. (2024). Fourteen new species of demosponges (Porifera) from three coastal fjords in southern British Columbia, Canada. *Zootaxa*, *5463*(2), 151–200. https://doi.org/10.11646/zootaxa.5463.2.1

Ricketts, E. F., & Calvin, J. (1985). *Between Pacific Tides | Stanford University Press*.

Roesler, C. S., & Chelton, D. B. (1987). California Current Zooplankton Variability. *CalCOFI Reports*, *28*.

Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H. R., & Largier, J. L. (2019). Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports*, *9*(1), 4216. https://doi.org/10.1038/s41598-019-40784-3

Turner, R. D. (1955). The family Pholadidae in the western Atlantic and eastern Pacific. Part II - Martesiinae, Jouannetiinae and Xylophaginae. (Pt. 65-160). *Johnsonia*, *3*(34).

Wrobel, D. (1998). *Pacific Coast pelagic invertebrates*. Sea Challengers.

Appendix 2 - Data sources for range extensions included in the analyses

Bastida-Zavala, J. R., McCann, L. D., Keppel, E., & Ruiz, G. M. (2017). The fouling serpulids (Polychaeta: Serpulidae) from United States coastal waters: an overview. *European Journal of Taxonomy*, (344). https://doi.org/10.5852/ejt.2017.344

Berner, L. D. (1960). Unusual Features in the Distribution of Pelagic Tunicates in 1957 and 1958. *CalCOFI Reports*, *7*.

Bjorkstedt, E. P., Goericke, R., McClatchie, S., Weber, E., Watson, W., Lo, N., Peterson, B., Emmett, B., Peterson, J., Durazo, R., Gaxiola-Castro, G., Chavez, F., Pennington, J. T., Collins, C. A., Field, J., Ralston, S., Sakuma, K., Bograd, S., Schwing, F., … Munger, L. (2010). State of the California Current 2009-2010: Regional Variation Persists Through Transition from La Niña to El Niño (And Back?). *CalCOFI Reports*, *51*.

Blackburn, M. (1979). Thaliacea of the California Current Region: Relations to Temperature, Chlorophyll, Currents and Upwelling. *CalCOFI Reports*, *20*.

Boulding, E. G., Behrens Yamada, S., Schooler, S. S., & Shanks, A. L. (2020). Periodic invasions during El Niño events by the predatory lined shore crab (Pachygrapsus crassipes): Forecasted effects of its establishment on direct-developing indigenous prey species (Littorina spp.). *Canadian Journal of Zoology*, *98*(12), 787–797. https://doi.org/10.1139/cjz-2019-0250

Braid, H. E., Deeds, J., DeGrasse, S. L., Wilson, J. J., Osborne, J., & Hanner, R. H. (2012). Preying on commercial fisheries and accumulating paralytic shellfish toxins: A dietary analysis of invasive Dosidicus gigas (Cephalopoda Ommastrephidae) stranded in Pacific Canada. *Marine Biology*, *159*(1), 25–31. https://doi.org/10.1007/s00227-011-1786-4

Brinton, E. (1960). Changes in the Distribution of the Euphausiid Crustaceans in the Region of the California Current. *CalCOFI Reports*, *7*.

Brinton, E. (1981). Euphausiid Distributions in the California Current During the Warm Winter-Spring of 1977-78, in the Context of a 1949-1966 Time Series. *CalCOFI Reports*, *22*.

Brinton, E., & Townsend, A. W. (1980). Euphausiids in the Gulf of California—The 1957 Cruises. *CalCOFI Reports*, *21*.

Brodeur, R., Perry, I., Boldt, J., Flostrand, L., Galbraith, M., King, J., Murphy, J., Sakuma, K., & Thompson, A. (2018). *An unusual gelatinous plankton event in the NE Pacific: The Great Pyrosome Bloom of 2017*. *26*(1).

Burnham, R. E., Meland, K., & Duffus, D. A. (2017). First record of the marine mysid Hippacanthomysis platypoda Murano & Chess, 1987 in coastal waters of British Columbia, Canada. *Journal of Crustacean Biology*, *37*(4), 496–498. https://doi.org/10.1093/jcbiol/rux047

Cassone, B. J., & Boulding, E. G. (2006). Genetic structure and phylogeography of the lined shore crab, Pachygrapsus crassipes, along the northeastern and western Pacific coasts. *Marine Biology*, *149*(2), 213–226. https://doi.org/10.1007/s00227-005-0197-9

Cimino, M. A., Jacox, M. G., Bograd, S. J., Brodie, S., Carroll, G., Hazen, E. L., Lavaniegos, B. E., Morales, M. M., Satterthwaite, E., & Rykaczewski, R. R. (2021). Anomalous poleward advection facilitates episodic range expansions of pelagic red crabs in the eastern North Pacific. *Limnology and Oceanography*, *66*(8), 3176–3189. https://doi.org/10.1002/lno.11870

Clarke, F. N., & Phillips, J. B. (1936). Commercial use of the jumbo squid, Dosidicus gigas. *California Fish and Game*, *22*, 143–144.

Cosgrove, J. (2005). The first specimens of Humboldt squid in British Columbia. *Pices Press*.

Cross, J. N. (1987). Demersal Fishes of the Upper Continental Slope off Southern California. *CalCOFI Reports*, *28*.

Dawson, M. N., Grosberg, R. K., Stuart, Y. E., & Sanford, E. (2010). Population genetic analysis of a recent range expansion: Mechanisms regulating the poleward range limit in the volcano barnacle *Tetraclita rubescens*. *Molecular Ecology*, *19*(8), 1585–1605. https://doi.org/10.1111/j.1365-294X.2010.04588.x

Drumm, D. T., Lauth, R. R., Clark, R. N., & Orr, J. W. (2013). Northern range extensions and biological notes for three decapods in the eastern North Pacific. *Crustaceana*, *86*(13–14), 1572–1585. https://doi.org/10.1163/15685403-00003249

Fenberg, P. B., Posbic, K., & Hellberg, M. E. (2014). Historical and recent processes shaping the geographic range of a rocky intertidal gastropod: Phylogeography, ecology, and habitat availability. *Ecology and Evolution*, *4*(16), 3244–3255. https://doi.org/10.1002/ece3.1181

Haderlie, E. C. (1979). *Range Extension for Penitella fitchi Turner, 1955 (Bivalvia: Pholadidae)*. *v.22 (1979-1980)*, 85.

Helmuth, B., Mieszkowska, N., Moore, P., & Hawkins, S. J. (2006). Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149

Herrlinger, T. (1981). Range Extension of Kelletia-Kelletii. *The Veliger*, *24*.

Hubbard Jr., L. T., & Pearcy, W. G. (1971). Geographic Distribution and Relative Abundance of Salpidae off the Oregon Coast. *Journal of the Fisheries Research Board of Canada*, *28*(12), 1831–1836. https://doi.org/10.1139/f71-276

Keister, J., Johnson, T., Morgan, C., & Peterson, W. (2005). Biological indicators of the timing and direction of warm-water advection during the 1997/1998 El Niño off the central Oregon coast, USA. *Marine Ecology Progress Series*, *295*, 43–48. https://doi.org/10.3354/meps295043

Leising, A. W., Schroeder, I. D., Bograd, S. J., Abell, J., Durazo, R., Gaxiola-Castro, G., Bjorkstedt, E. P., Field, J., Sakuma, K., Robertson, R. R., Goericke, R., Peterson, W. T., Brodeur, R. D., Barceló, C., Auth, T. D., Daly, E. A., Suryan, R. M., Gladics, A. J., Porquez, J. M., … Warybok, P. (2015). State of the California Current 2014-15: Impacts of the Warm-Water "Blob." *CalCOFI Reports*, *56*.

Litz, M. N., Phillips, A. J., Brodeur, R. D., & Emmett, R. L. (2011). Seasonal Occurences of Humboldt Squid. *CalCOFI Reports*, *52*.

Lluch-Belda, D., Lluch-Cota, D. B., & Lluch-Cota, S. E. (2003). Scales of Interannual Variability in the California Current System: Associated Physical Mechanisms and Likely Ecological Impacts. *CalCOFI Reports*, *44*.

Longhurst, A. R. (1967). The Pelagic Phase of Pleuroncodes planipes Stimpson (Crustacea Galatheidae) in the California Current. *CalCOFI Reports*, *11*.

Lonhart, S. I., Jeppesen, R., Beas-Luna, R., Crooks, J. A., & Lorda, J. (2019). Shifts in the distribution and abundance of coastal marine species along the eastern Pacific Ocean during marine heatwaves from 2013 to 2018. *Marine Biodiversity Records*, *12*(1), 13. https://doi.org/10.1186/s41200-019-0171-8

McClatchie, S., Goericke, R., Leising, A. W., Auth, T. D., Bjorkstedt, E. P., Robertson, R. R., Brodeur, R. D., Du, X., Daly, E. A., Morgan, C. A., Chavez, F. P., Debich, A. J., Hildebrand, J., Field, J., Sakuma, K., Jacox, M. G., Kahru, M., Kudela, R., Anderson, C., … Jahncke, J. (2016). State of the California Current 2015-16: Comparisons with the 1997-98 El Niño. *CalCOFI Reports*, *57*.

Mearns, A. J. (1988). The "Odd Fish": Unusual Occurrences of Marine Life as Indicators of Changing Ocean Conditions. In D. F. Soule & G. S. Kleppel (Eds.), *Marine Organisms as Indicators* (pp. 137–176). Springer. https://doi.org/10.1007/978-1-4612-3752-5_7

Pearcy, W., Fisher, J., Brodeur, R., & Johnson, S. (1985). Effects of the 1983 El Niño on Coastal Nekton off Oregon and Washington. *Washington Sea Grant Program University of Washington*.

Pearcy, W. G., & Schoener, A. (1987). Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern Subarctic Pacific Ocean. *Journal of Geophysical Research: Oceans*, *92*(C13), 14417–14428. https://doi.org/10.1029/JC092iC13p14417

Radovich, J. (1960). Redistribution of Fishes in the Eastern North Pacific Ocean in 1957 and 1958. *CalCOFI Reports*, *7*.

Radovich, J. (1961). Fish Bulletin No. 112. Relationships of Some Marine Organisms of the Northeast Pacific to Water Temperatures Particularly During 1957 Through 1959. *State of California Department of Fish and Game Marine Resrouces Operations*.

Roesler, C. S., & Chelton, D. B. (1987). California Current Zooplankton Variability. *CalCOFI Reports*, *28*.

Sadowski, J. S., Gonzalez, J. A., Lonhart, S. I., Jeppesen, R., Grimes, T. M., & Grosholz, E. D. (2018). Temperature-induced range expansion of a subtropical crab along the California coast. *Marine Ecology*, *39*(5), e12528. https://doi.org/10.1111/maec.12528

Sakuma, K. M., Field, J. C., Mantua, N. J., Ralston, S., Marinovic, B. B., & Carrion, C. N. (2016). Anomalous Epipelagic Micronekton Assemblage Patterns in the Neritic Waters of the California. *CalCOFI Reports*, *57*.

Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H. R., & Largier, J. L. (2019). Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports*, *9*(1), 4216. https://doi.org/10.1038/s41598-019-40784-3

Stull, J. K., & Tang, C.-L. (1996). Demersal Fish Trawls off Palos Verdes, Southern California, 1973-1993. *CalCOFI Reports*.

Sutherland, K. R., Sorensen, H. L., Blondheim, O. N., Brodeur, R. D., & Galloway, A. W. E. (2018). Range expansion of tropical pyrosomes in the northeast Pacific Ocean. *Ecology*, *99*(10), 2397–2399. https://doi.org/10.1002/ecy.2429

Thompson, A. R., Schroeder, I. D., Bograd, S. J., Hazen, E. L., Jacox, M. G., Leising, A., Wells, B. K., Fisher, J., Jacobson, K., Zeman, S., Bjorkstedt, E. P., Robertson, R. R., Kahru, M., Goericke, R., Peabody, C. E., Baumgartner, T., Lavaniegos, B. E., Miranda, L. E., Gomez-Ocampo, E., … Melin, S. R. (2019). State of the California Current 2018-19: A Novel Anchovy Regime and a New Marine Heat Wave? *CalCOFI Reports*, *60*.

Wallingford, P. D., & Sorte, C. J. B. (2022). Dynamic species interactions associated with the range-shifting marine gastropod Mexacanthina lugubris. *Oecologia*, *198*(3), 749–761. https://doi.org/10.1007/s00442-022-05128-5

Wells, B. K., Schroeder, I. D., Bograd, S. J., Hazen, E. L., Jacox, M. G., Leising, A. W., Mantua, N., Santora, J. A., Fisher, J., Peterson, W. T., Bjorkstedt, E. P., Robertson, R. R., Chavez, F. P., Goericke, R., Kudela, R., Anderson, C., Lavaniegos, B. E., Gomez-Valdes, J., Brodeur, R. D., … Thayne, B. (2017). State of the California Current 2016-17: Still Anything but "Normal" in the North. *CalCOFI Reports*, *58*.

Wonham, M. J., & Hart, M. W. (2018). El Niño Range Extensions of Pacific Sand Crab (*Emerita analoga*) in the Northeastern Pacific. *Northwest Science*, *92*(1), 53–60. https://doi.org/10.3955/046.092.0106

Zeidberg, L. D., & Robison, B. H. (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas* , in the eastern North Pacific. *Proceedings of the National Academy of Sciences*, *104*(31), 12948–12950. https://doi.org/10.1073/pnas.0702043104