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

Authors: Jordana K. Sevigny[1], Bella G. Lipsey[1], Theodore T. Tran[1], and Alexa L. Fredston[1]

Affiliations:

1. Department of Ocean Sciences, University of California, Santa Cruz, California, United States of America

Address for correspondence: Jordana K. Sevigny, Department of Ocean Sciences, University of California, Santa Cruz, California, 1156 High Street, Santa Cruz, California 95064. jsevigny@ucsc.edu

Conflict of interest: The authors have no competing interests.

Funding: JKS and AF gratefully acknowledge funding from the Zegar Family Foundation. JKS gratefully acknowledges support from the National Science Foundation grant OCE-2329560.

Data Availability: Data and code is available at https://github.com/jordanasevigny/ca-invert-shifts.git.

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 biodiversity monitoring programs are limited.

To fill this gap, we synthesized nearly 120 years of records of marine invertebrate poleward range extensions in California to examine their prevalence/frequency and association with environmental variability on a year-to-year time horizon.

Location

Eastern North Pacific Ocean

Time Period

1903-2020

Major Taxa Studied

Marine invertebrates.

Methods

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

Results

The final dataset comprises 63 species and 143 poleward range extensions. We found that the episodic range extension events are 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 underscores that across many years and taxa, episodic poleward range extensions are not isolated curiosities but signals of how climate variability and warming can reshape coastal 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.

1. Introduction

The link between long-term ocean warming and shifts in species' range edges is a key frontier in understanding how marine life responds to climate change globally (Fredston *et al.*, 2021; Parmesan & Yohe, 2003; Pecl *et al.*, 2017). Yet species' range edges are dynamic even in the absence of long-term change (MacArthur, 1972). Species experience environmental variability on daily, seasonal, and year-to-year timescales, from short-term extreme events (e.g., marine heatwaves, cold spells) to interannual climatic oscillations (e.g., El Niño Southern Oscillation, North Atlantic Oscillation). Species' responses, including range edge shifts, also occur on multiple timescales (Pinsky *et al.*, 2020, Harvey *et al.*, 2022, Fredston *et al.*, 2025). Gaining greater insight into short-term redistribution events and their interplay with long-term ecological change is essential for forecasting long-term biogeographic change and for designing adaptive management strategies in a warming ocean (Soifer *et al.*, 2025).

An ideal system in which to disentangle these processes is one with recurrent environmental variability and extreme events and minimal long-term warming. This is the case for marine species' range edges in the eastern North Pacific, which experience El Niño Southern Oscillation (ENSO) and marine heatwaves (MHW) (Sanford *et al.*, 2019; Cavole *et al.*, 2016; Lluch-belda *et al.*, 2005; Mearns, The Odd Fish, 1988; Hubbs *et al.*, 1948). Both events change the oceanographic currents and conditions and cause sea surface temperatures up to 2 °C warmer than usual (Cavole *et al.*, 2016; Di Lorenzo & Mantua, 2016; Jacox *et al.*, 2016; Gentemann *et al.*, 2017). Thus, ENSO and MHWs provide natural experiments to evaluate how short-term increases in temperature and shifts in ocean circulation influence species' range edges (Sanford *et al.*, 2019; Harvey *et al.*, 2022; Cimino *et al.*, 2021; Jacox *et al.*, 2016; Soifer *et al.*, 2025). Marine invertebrates are especially informative for studying range edge dynamics associated with warming and circulation shifts because they are sensitive to thermal stress (Pinsky *et al.*, 2020) and, owing to their planktonic early life stages, often rely on ocean currents for dispersal (Cowen and Sponaugle 2009; Shanks 2009; Pineda *et al.*, 2007; Kinlan and Gaines 2003).

Although several studies have reported range shifts of individual marine invertebrate species in relation to environmental variability (Sanford *et al.*, 2019; Lluch-belda *et al.*, 2005; Mearns, The Odd Fish, 1988; Hubbs *et al.*, 1948), these reports have not yet been synthesized across species and time. Much of the evidence for an association between environmental variability and episodic range extensions in the eastern North Pacific comes from a large marine heatwave in 2014-2016 that overlapped with an El Niño event. The 2014-2016 MHW, one of the longest recorded MHW to date, is the leading hypothesized cause for 37 marine species' poleward range extensions in California (Starko *et al.*, 2025; Sanford *et al.*, 2019). Past studies of the impacts of environmental variability on marine species' ranges rarely extend past individual anomalous events if they focus on multiple taxa (Sanford *et al.*, 2019; Williams, 2001) but are more often limited to particular habitat or narrow taxonomic groups (Cimino *et al.*, 2021; Wonham & Hart, 2018, Cavole *et al.*, 2016; Lluch-Belda, 2005; Glynn *et al.*,, 1988; Lenarz *et al.*, 1995; Pearcy, 2002; Mearns, The Odd Fish, 1988; Hubbs, 1948). While valuable, these studies alone cannot reveal how frequently species undergo poleward range shifts in the context of their long-term extension histories, nor whether those shifts consistently align with warming events rather than occurring by chance.

Here, we synthesized nearly 120 years of records of marine invertebrate poleward range extensions in California (CA) 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 novel time-series of when, where, and which marine invertebrates extend poleward. We analyzed whether these events represent predictable biogeographic responses to climate variability or simply transient chance occurrences. More specifically, we tested if more poleward range extensions of marine invertebrates occur during El Niño events than expected by chance; we tested if stronger El Niño events result in geographically further extension distances; and we tested if more poleward range extensions occur during the 2014-2016 MHW interval than expected by chance.

2. Methods

We collated a database of poleward range extensions of marine invertebrates through a systematic literature review of peer-reviewed literature and reports from scientific surveys. Specifically, we used documents from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) starting in 1950, which record decades of observations including many made before ENSO was widely recognized as a climate phenomenon. These documents include serendipitous records of unusual species occurrences noted by scientists during quarterly oceanographic and ecosystem surveys along established survey lines extending about 500km offshore from San Francisco Bay to San Diego, CA. These surveys are not designed to detect range shifts or novel species, but the reports often note unusual biological occurrences in the context of the collected oceanographic data. To expand beyond these historical accounts, we conducted a systematic literature review of peer-reviewed studies, integrating their observations with those from the CalCOFI documents to assemble a comprehensive time-series of poleward range extensions.

All records used in this analysis come from onshore or nearshore (i.e., coastal) observations of species with a historical or novel range edge in California (Figure 1). We centered our analysis on California because the region has a very high density of systematic and opportunistic oceanographic sampling, allowing us to minimize the influence of geographic variation in observation effort on reported range extensions. Vertebrates were excluded from this study because their high mobility allows rapid responses to environmental change, whereas invertebrates are often slow-moving or sessile for part of their life cycle. Our focus is on the dynamics shaping poleward range edges of these less mobile species, whose dispersal potential is expected to remain limited and reliant on oceanographic currents compared to a fully mobile species under changing conditions (Gaylord and Gaines, 2000; Helmuth *et al.*, 2006; Sanford *et al.*, 2019). The relevant data and R scripts associated with this study are available at https://github.com/jordanasevigny/ca-invert-shifts.git.

2.1 Systematic Literature Review

2.1.1 California Cooperative Oceanic Fisheries Investigations Review

We manually screened all historical CalCOFI documents, including volumes 01-60 of their now-retired publication (1950-2019) and the recent *State of the California Current Reports* published in *Frontiers in Marine Science* (2020-2021). These sources, which we collectively call “CalCOFI documents”, include anomalous observations of marine invertebrate presence as far back as 1926 (CalCOFI 1950-2021). Any paragraph or sentence in the documents describing an invertebrate observed north of its expected range was recorded. These excerpts were then converted into data, recording species identity, anomalous observation location, and observation date for each extension.

2.1.2 Broader Peer Reviewed Literature Search & Review

We systematically reviewed the wider scientific literature base for reports of any poleward expansions into, out of, or within California’s coast. We developed iterations of search terms to map the literature and maximize the number of relevant articles using the recommended scoping method from Foo *et al.* (2021). The final abbreviated word search is as follows: TS = (("east* Pacific" OR "northeast* pacific" OR "Alaska" OR "BC" OR "California" OR "Oregon" OR "Washington") AND ("ocean*" OR "sea*" OR "marine*" OR "*tidal" OR "coast*") AND ("invertebrate*" OR (("*tidal" OR "*benthic" OR "*fouling") NEAR/0 ("species" OR "community")) OR [**relevant taxa names - see supplementary documentation]**) AND (("population*" OR "range*" OR "range edge*" OR "geograph*" OR "distribution*" OR "limit*") NEAR/2 ("shift*" OR "extension*" OR "expansion*"))). This search thus returns articles that are relevant to the West Coast of North America; includes a marine-related term; includes an invertebrate-related term; and includes a phrase related to range shifts. The full version of the word search and methods regarding taxa name selection can be found in the supplementary documentation.

An opportunistic backwards search was also performed wherein if poleward extensions discussed in a forward search article were from a referenced article, the referenced article was included in the review (Harari *et al*., 2020; Foo *et al*., 2021). The forward and backwards searches resulted in a final total of 409 peer reviewed articles that were passed through the inclusion criteria below.

2.2 *Inclusion Criteria*

To be included in this study, observations (both from CalCOFI and from the systematic literature review) had to meet the following criteria: (1) involve a marine species, excluding vertebrates, insects, microscopic organisms, parasites, and known invaders; (2) represent poleward extensions into, within, or from California; and (3) occur in or after 1900. Of the 409 peer-reviewed articles, criterion 1 rejected 88; criterion 2 rejected an additional 238; and criterion 3 rejected an additional 28. Five peer-reviewed articles were excluded because they were included in the CalCOFI documents. Sixteen articles were deemed ‘inconclusive’ due to the following reasons: the time range for the observation was at a temporal resolution greater than a year (2 articles); the taxonomic resolution was too coarse (e.g., phylum level, 1 article); the article was not able to be obtained (4 articles); the data was recorded from a different article (6 articles); the data was an abundance shift rather than an occurrence observation (2 articles); or the article was not peer-reviewed (1 article). This yielded 34 peer-reviewed articles that contained 247 distinct observations of range extensions of invertebrates in this region. The CalCOFI documents (see 2.2.1) contained an additional 64 range extension observations.

For the systematic literature review, a confidence rating was assigned to each observation. If the anomalous observation was at a never-before-surveyed or very-infrequently-surveyed location, the extension was considered low confidence ("Opportunistic"). If the observation was made at a frequently but irregularly surveyed location by a non-expert, the extension was considered medium confidence ("Opportunistic+"). If the observation was made at a frequently and regularly surveyed site by an expert, the extension was considered high confidence ("Long-term monitoring site"). These ratings were not applied to the CalCOFI dataset since all observations were made by experts at regularly surveyed sites. Only the medium and high confidence extensions were included in the analyses, reducing the observations from 247 to 234).

Merging the CalCOFI dataset and systematic review datasets we total 298 observations of marine invertebrate range extensions. We de-duplicated the observations by retaining only the furthest-north observation of a single species in a year, and if multiple observations occurred at the same latitude, retaining the observation on the earliest date in the year. This reduced the observations from 298 to 221. 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, CA according to Google Maps). 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, the observation latitudes were snapped to the coastline.

2.3 Historical Range Edge Classification

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 2.2), we recorded the historical northern range edge from textbooks on invertebrate distributions as available (45 of 63 species), using the extension article as a secondary source if necessary (18 of 63 species; Supp. Table 2). Two species, *Thetys vagina* and *Sagitta pseudoserratodentata*, are found offshore north of 42°N but not typically onshore north of 42°N; we classified their historical northern range edge as 42°N. When exact latitudes were not available, historical ranges were assigned as follows: 'southern California' = 34.5;' warm waters' = 34.5; 'southern species' = 34.5; 'tropical Pacific' = 32.5; 'Transition Zone Waters' = 34.5; 'Mexico' = 32.5; 'temperate waters' = 40.

2.4 Cleaning and Filtering of Dataset & Extension Event Classification

After confirming historical range edges with third-party sources (see section 2.3), we filtered the observations dataset (see sections 2.1, 2.2) for records that were north of species' historical range edge latitudes. This reduced the dataset from 221 to 212 observations and from 147 to 143 'extension events', which we define as any year when the species appeared north of its historical range after not being recorded there the previous year. Once an extension event began, we counted it as a single event regardless of how many consecutive years afterward the species continued to occur beyond its historical range edge. We considered the event to end when the species was absent north of the historical range edge for at least one year (e.g., if pelagic red crab occurred in 2002 and 2014, 2015, and 2016, we assigned two events: 2002 and 2014-2016). Some analyses used only species with at least three distinct extension events (18 species of 4 phyla, 88 extension events), which we termed "episodic extension events.".

2.5 Analyses

We first computed summary statistics of the dataset to calculate mean extension frequency per year. We then tested whether observation frequency increased over time with a linear regression. Then, we specifically tested whether extension patterns were associated with ENSO and/or the 2014-2016 MHW.

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 1950-present; 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 data and our episodic extension event dataset: (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 range extensions, and (3) that stronger El Niño events are associated with further (i.e., more distant) range extensions. The episodic extension event dataset used to test these hypotheses retained only extension events from 1950 onwards to align with the ONI timeframe (18 species of 4 phyla, 76 extension events).

First, we compared the observed frequency of extension events during El Niño years with the expected frequency based on the long-term proportion of months classified as El Niño with a χ-squared goodness-of-fit test (Figure 2a and 2b; using the reduced dataset of 76 extension events). For the χ-squared test, an extension event was classified as occurring during El Niño if the first year of the extension coincides with either (a) the peak year (the year containing the maximum number of El Niño months for that event) or (b) the terminal year of an El Niño event. Extensions were treated as independent events in order to test our hypothesis that El Niño is related to extension frequency regardless of species identity.

Second, we tested whether stronger El Niño events (higher ONI values) are associated with an increased number of poleward extensions (Fig. 2c; using the reduced dataset of 76 extension events). Our response variable was the number of extensions to occur. Each extension event was matched with one predictor ONI value, representing the maximum ONI (calculated as a calendar year average) in the year(s) of the range extension *or* the year before. For multi-year range extensions that were categorized as a single "event" (see Section 2.4), e.g., range extensions of a species recorded in 2014, 2015, and 2016, we used the maximum ONI (calculated as a calendar year average) of that entire time period lagged by a year (in this example, 2013, 2014, and 2015) as the predictor. To balance complexity and accuracy, we fitted three models: a linear regression, a quadratic model, and a generalized additive model (GAM), recognizing that nonlinear models often require more data to fit robustly. We fit the models using maximum likelihood and evaluated relative support using Akaike's Information Criterion (AIC).

Third, we tested whether stronger El Niño events (higher ONI values) are associated with geographically further extensions (Figure 3; using the reduced dataset of 76 extension events). For each extension event, our response variable was the maximum observed extension distance. Our predictor variable was the assigned ONI for each extension event. As above, we compared the fit of three models to the data: a linear regression, a quadratic model, and a generalized additive model (GAM) and evaluated relative support using Akaike's Information Criterion (AIC). We also tested whether extension distances differ significantly between high ONI years (≥ 0.5, the El Niño threshold) and low ONI years with a Welch two-sample *t*-test.

Finally, we examined how the 2014-2016 MHW influences extension frequency (Figure 4). 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).

3. Results

The final dataset comprises 63 species from 8 phyla and 143 poleward extension events (25 from CalCOFI documents; 118 from literature search; Supp. Fig. 2) observed from 1903 to 2020. The mean extension frequency is 1.22 extensions per year and the mean extension distance is 776 ± 981 km (range:3-4,514 km). Thirty-five species only had one extension event while 18 species had three or more extension events. *Pleuroncodes planipes* had the most recorded extensions with nine events. The frequency of observations increased significantly between 1903 and 2020 (slope = 0.03±0.01 events/year, $t_{56} = 3.14$, $p = 0.0027$, Supp. Fig. 3).

The subset requiring 3+ extension events and Oceanic Niño Index data (used in all El Niño analyses below; see Section 2.5; NOAA 2024) comprises 18 species from 4 phyla and 76 extension events from 1950-2000, averaging 676 ± 720 km in distance with a minimum of 14 km and a maximum of 3,442 km (Figure. 1; Supp. Table 1).

From 1950-2020, more than two-thirds of the episodic extension events occur during El Niño years (52 of 76 extension events; 68%), which is over double the expected frequency based on the long-term El Niño baseline (26%; χ-squared = 70.98, df = 1, p-value < 0.001; Fig. 2a and 2b). Four of the 18 species have all of their extension events occur during or just after an El Niño phase: *Emerita analoga, Euphausia eximia, Pleuroncodes planipes,* and *Velella velella*. Extension event frequency increases significantly with ONI (slope = 0.93±0.32 event/ONI, $t_{36} = 2.88$, $p = 0.0066$; Figure 2c), with ONI explaining ~19% of the variance ($R^2 = 0.19$). These results are from the linear model, which provided a significantly better fit than the quadratic model (ΔAIC = 1086; likelihood ratio test $p < 0.001$). The GAM also did not improve fit relative to the linear model (ΔAIC = 1085).

Extension distance also increases significantly with ONI (slope = 383±121 km/ONI, $t_{74} = 6.66$, $p = 0.0023$; Figure 3b), with ONI explaining ~11% of the variance ($R^2 = 0.11$). As before, we modeled the relationship with linear, quadratic, and GAM and found that neither quadratic (ΔAIC = 0.1; likelihood ratio test $p = 0.18$) nor GAM (ΔAIC = 0.5) was a substantially better fit than the linear model and report the linear regression statistics here. In addition, extension distance is significantly greater in high ONI years than in low ONI years ($t_{34.6} = 2.91$, $p = 0.006$; 95% CI of difference = 168 - 939 km; Figure 3a).

Just under a quarter of all extension events occur during the 2014-2016 marine heatwave (32 of 143 extension events; 22%), which is almost eight times the expected frequency based on the duration of the heatwave (2.6%; χ-squared = 224.9, df = 1, p-value < 0.001; Figure 4). In 2015, our dataset recorded 15 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 (30 of 63; 48%), 17 of those species having extensions exclusively during the 2014-2016 marine heatwave (Supp. Table 1).

4. Discussion

Episodic appearances of rare, warm-water species off California's coast are a remarkable part of the region's ecology and history, yet previously an inventory of these range-extending species was lacking. By collating scientific and historical records since 1900, we documented many species exhibiting these episodic extension events (Figure 1). We also found multiple lines of evidence that episodic extensions are significantly associated with El Niño. The number and distance of range extensions were both positively correlated with El Niño strength (Figure 2c, 3b); range extensions were more likely to coincide with El Niño than expected by chance (Figure 2b); and although some range extensions occurred outside of El Niño events, they traveled shorter distances (Figure 3a). Adding to the large literature on extreme ecological effects of the 2014-2016 large marine heatwave in the eastern North Pacific (Suryan *et al*., 2021, Freedman *et al*., 2020), we reported 32 distinct range extension events during this interval—almost a quarter of our entire dataset, which spans more than a century.

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). Yet, despite centuries of interest, we still know relatively little about how much species' range edges fluctuate from year to year, and what environmental forces drive those short-term shifts (Holt and Keitt 2000, Brown et al. 1996). Recent studies have highlighted that range edges are often more permeable and dynamic than previously thought, responding rapidly to variability in temperature, currents, and habitat availability (Parmesan & Yohe, 2003; Hickling *et al.,* 2006; Burrows *et al.,* 2014; Fredston *et al.,* 2021). This question is especially complex to study in marine systems where ranges are three-dimensional, highly variable across seasons and years, and driven at least in part by ocean currents and where large-scale, long-term data remain scarce. By combining historical records and modern observations, this study expands the temporal scope and taxonomic breadth of our understanding of how far, and how frequently, range edges shift within a dynamic and productive marine ecosystem.

The range extensions that we report here support the hypothesis that El Niño and its associated oceanographic dynamics influence marine biogeography, particularly for species with pelagic life histories. In typical years, poleward transport from southern to northern California is dominant in autumn when winds relax (Melton *et al*., 2009; Hickey, 1979; Lynn & Simpson, 1987; Checkley & Barth, 2009). This seasonal window may restrict poleward dispersal for larvae with short pelagic durations or for species that spawn in other seasons. During El Niño, however, poleward and onshore flows both strengthen and persist for longer periods (Zacherl *et al*., 2003; Lynn & Bograd, 2002; Durazo & Baumgartner, 2002; Jacox *et al*., 2016), relaxing the usual transport barrier and exposing northern habitats to warm waters and southern propagules. Particle-tracking studies show that short-duration particles do not propagate poleward as much as long-duration particles (i.e., continuously pelagic species; Drake *et al*., 2011; Strub *et al*., 2024; Strub and James, 2025). Consistent with this, Sanford *et al.* (2019) found that fully pelagic invertebrates extended on average nearly three times the distance of benthic species during the 2014-2016 marine heatwave and El Niño.

Our results reflect these patterns: pelagic species such as *Velella, Dosidicus gigas, Pyrosoma atlanticum, Euphausia eximia, Euphausia recurva, Nyctiphanes simplex,* and *Chrysaora colorata* all exhibited episodic range extensions, and with the exception of *E. eximia*, their average extension distances exceeded the overall mean (776 km; Supp. Table 1). Species whose extensions occurred exclusively during El Niño (*Emerita analoga, Euphasia eximia, Pleuroncodes planipes, Velella*) are all associated with anomalous poleward and onshore transport (Sorte *et al*., 2001; Lilly & Ohman, 2021; Cimino *et al*., 2021; Jones *et al*., 2021; Simpson, 1984). Oceanographic transport is frequently implicated as the driver of these recurrent extensions; the failure 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). In contrast, *Mexacanthina lugubris* extended poleward multiple times independent of El Niño, suggesting a different mechanism. The iterative extensions of this species, which does not have a pelagic phase, likely reflect an ongoing invasion limited by native competitors rather than transport or temperature (Wallingford & Sorte, 2022).

The El Niño Southern Oscillation is a long-term natural climatic phenomenon, but 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 saw 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 can 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). Ecological responses to this MHW included widespread shifts in plankton composition, declines in primary productivity, mass strandings of sea lions and seabirds, and redistribution of numerous marine invertebrates and fishes (Cavole *et al*., 2016; Sanford *et al*., 2019), all consistent with the large-scale biogeographic reorganization observed in our dataset. When these species expand poleward, they may disrupt established ecological networks, altering trophic interactions and potentially reshaping top-down control (Parmesan, 2006; Walther, 2010). The sustained presence of these species and the resulting "tropicalization" of temperate ecosystems could produce cascading and unpredictable ecological consequences (Vergés *et al*., 2019).

The novel dataset that we present here is based on serendipitous reports of species occurring north of their historical range edge. While the CalCOFI documents add rigor by providing near-annual quarterly surveys conducted by regional taxonomic experts who were especially likely to notice and record unusual invertebrate occurrences, the broader literature review introduces more variability. These reports are largely opportunistic, reflecting when and where scientists happened to look for or find unusual species rather than systematic sampling. We did not draw from existing databases of biological observations, because our goal was to augment existing records via synthesis, and because biodiversity databases often have poor coverage of marine invertebrates. Notably, our dataset cannot identify when episodic range extensions become permanent. This has been documented elsewhere for some species in our dataset: for example, recent literature shows pyrosomes have persisted in the eastern North Pacific since its expansion in 2014 (CalCOFI; Miller *et al*., 2019; Schram *et al*., 2020; O'Loughlin *et al*., 2020). In our dataset, this appears as two separate extension events, though it likely reflects a single continuous presence without yearly reporting (Miller *et al*., 2019; Schram *et al*., 2020; O'Loughlin *et al*., 2020). Another source of bias stems from shifting scientific attention. After El Niño became a widely-studied phenomenon, researchers may have been more inclined to search for and report unusual species during El Niño events. This could inflate the apparent frequency of range extensions during El Niño and during recent marine heatwaves simply because more people were actively looking (although specifically for our results from 2014-2016, the number of range extensions observed is far greater than in other recent years). Additional limitations include uneven geographic and taxonomic coverage: as in other biodiversity datasets (Chapman *et al*., 2024), observations are clustered in well-studied regions and taxa, leaving gaps elsewhere. Detection probability also varied over time with unquantifiable changes in sampling technology, taxonomic expertise, and research priorities. Finally, the dataset reflects presence-only records rather than systematic absence data, which constrains the ability to quantify true rates of range extensions, to describe colonization dynamics at species' poleward range edges, or to rule out undetected events in unsurveyed or unreported areas.

Long-term monitoring programs, such as CalCOFI, are the ideal tool to monitor how species' abundances and geographical distributions respond to environmental variability and change at different time scales (Lindenmayer *et al*., 2012; Hughes *et al*., 2017). However, long-term monitoring programs have limited spatial, temporal, and taxonomic coverage. Synthesis of opportunistic studies has become a critical tool to detect patterns, understand processes, and test hypotheses in changing ecosystems (Halpern *et al*., 2020). Our synthesis underscores that across many years and taxa, episodic poleward range extensions are not isolated curiosities but signals of how climate variability and long-term warming can reshape coastal ecosystems. Our finding that marine invertebrates regularly shift their distributions by hundreds or thousands of kilometers from one year to the next challenges natural resource management and conservation, which are often predicated on fixed geographical representations of species' ranges (Melbourne-Thomas *et al*., 2021). Like many others around the world, the eastern North Pacific marine ecosystem is constantly experiencing environmental variability and change. Understanding how these processes shape species' distributions—particularly for species with life histories that are closely connected to ocean currents—is critical for managing and conserving marine ecosystems now and in the future.

5. Figures

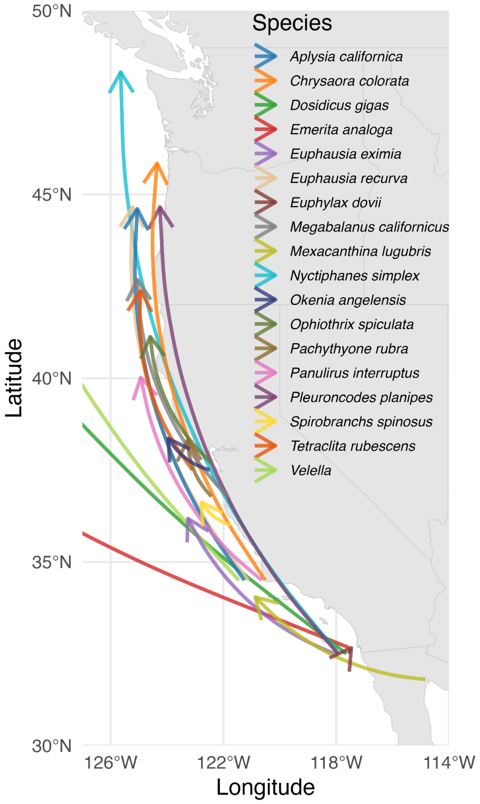


Figure 1. Map of the most northern anomalous observation of marine invertebrates with 3+ extension events (18 species) between 1900 and 2020. Each arrow represents one species. The arrow origin is the historical poleward range edge (see Supplementary Table with the historical range edge data), and the arrow destination is the northernmost point of anomalous observation of the species. The map boundaries cut off three long-range extensions to Alaska and British Columbia (see Supplementary Figure 1). Up to -1 degree of jitter is added to the arrow longitudes to reduce overlap. The 88 episodic extension events of these 18 species have an average distance of 694 ± 783 km with a minimum of 14km and a maximum of 3842 km.

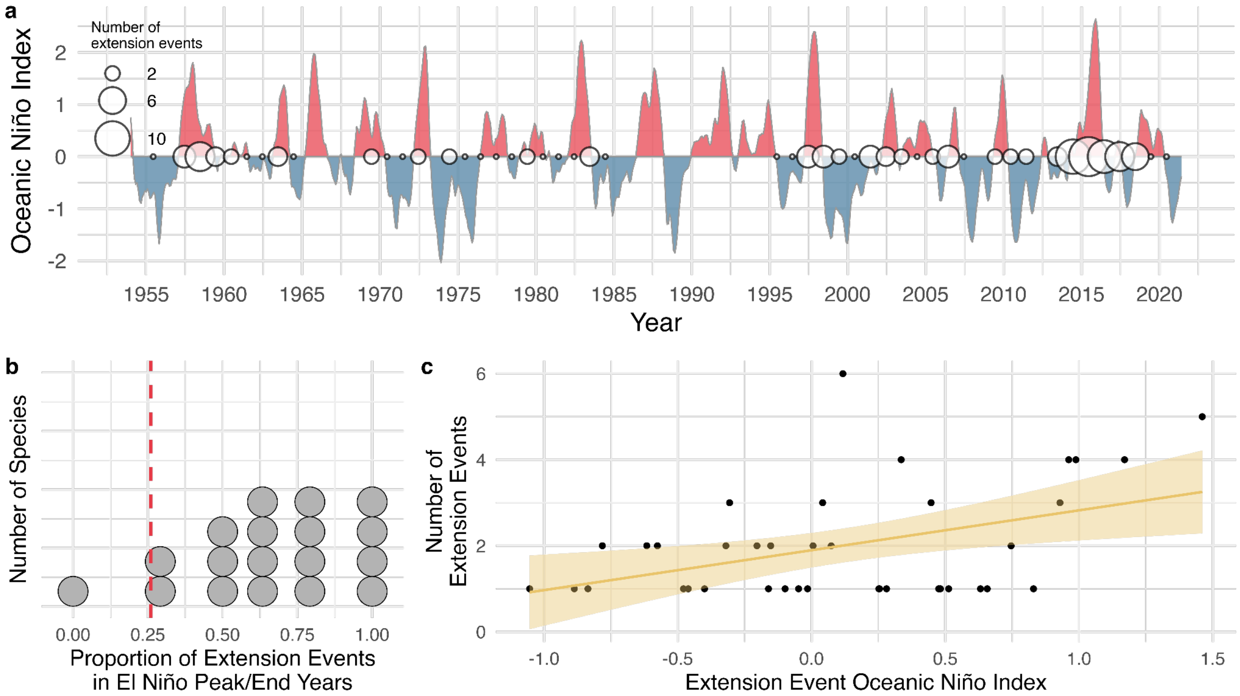


Figure 2. a. Time-series of the Oceanic Niño Index (ONI; National Oceanic and Atmospheric Administration, 2024) where red is positive ONI, or an El Niño event if greater than 0.5, and blue is negative ONI, or a La Niña event if less than -0.5. The number of extension events (when a warm water invertebrate appears north of their historical range edge for a year or set of consecutive years) per year 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 species with 3+ extension events (18 species; one gray circle per species).The red dotted line represents the expected proportion of El Nino events at a monthly resolution. Well over half of all 1950-2020 episodic extension events (52 of 76; 68%) occur during El Niño years, which is over double the expected frequency based on the long-term El Niño baseline (26%; χ-squared = 70.98, df = 1, p-value < 0.001). See supp. Fig. 4 for coloring by the total number of extensions per species. c. Extension event frequency increases significantly with ONI (slope = 0.93±0.32, t_{36} = 2.88, p = 0.0066), with ONI explaining ~19% of the variance (R^2 = 0.19). Each black point represents the number of extension events with a given ONI; the yellow line represents the linear regression and the ribbon indicates the 95% confidence interval for the fitted regression line.

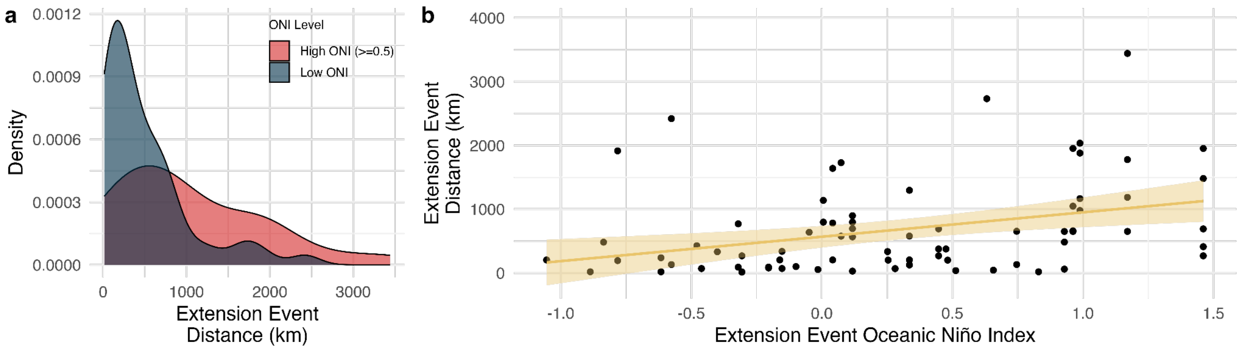


Figure 3. a. The probability density function (y-axis) of the distance of each extension event (x-axis) for extensions occurring during a high Oceanic Niño Index (ONI) period (red, >=0.5) and extensions occurring during a low ONI period (blue, <0.5). Extension event distance is the distance in kilometers from the historical range edge of the marine invertebrate to the furthest poleward point at which they were found during an extension event. The extension distance is significantly higher during high ONI *versus* during low ONI years ($t_{34.6} = 2.91$, $p = 0.006$; 95% CI of difference = 168 - 939 km). b. The extension distance increases significantly with ONI (slope = 383±121, $t_{74} = 6.66$, $p = 0.0023$), with ONI explaining ~11% of the variance seen in extension event distance ($R^2 = 0.11$). 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 linear regression and the ribbon indicates the 95% confidence interval for the fitted regression line.

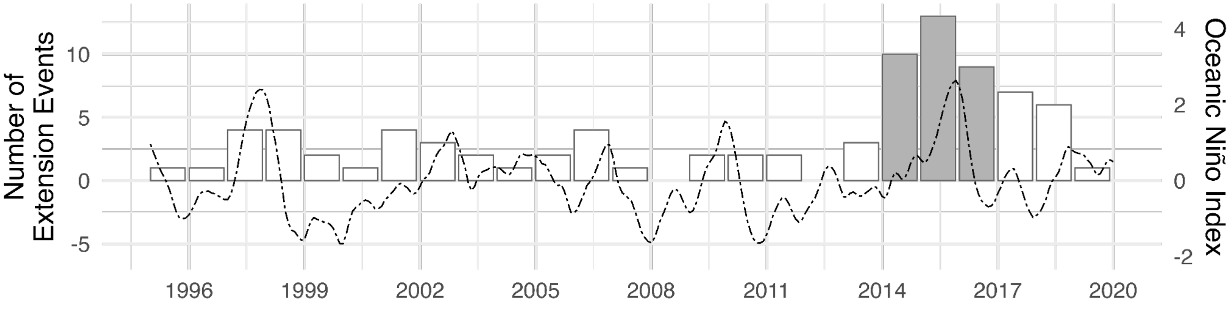


Figure 4. A time-series of the number of extension events (outlined bars), including during the 2014-2016 marine heatwave (shaded bars), and the Oceanic Niño Index (ONI; dotted line) over time (years). Just under a quarter of all extension events (32 of 143; 22%) occur during the 2014-2016 marine heatwave, which is almost eight times the expected frequency based on the proportion of years spanned by the heatwave (2.6%; χ-squared = 224.9, df = 1, p-value < 0.001).

6. References

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

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., 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. (n.d.). *Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific: Winners, Losers, and the Future | Oceanography*. Retrieved October 22, 2025, from https://tos.org/oceanography/article/biological-impacts-of-the-20132015-warm-water-anomaly-in-the-northeast-paci

Chapman, M., Goldstein, B. R., Schell, C. J., Brashares, J. S., Carter, N. H., Ellis-Soto, D., Faxon, H. O., Goldstein, J. E., Halpern, B. S., Longdon, J., Norman, K. E. A., O'Rourke, D., Scoville, C., Xu, L., & Boettiger, C. (2024). Biodiversity monitoring for a just planetary future. *Science*, *383*(6678), 34–36. https://doi.org/10.1126/science.adh8874

Checkley, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, *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*, *54*(1), 7–31. https://doi.org/10.1016/S0079-6611(02)00041-1

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

Gentemann, C. L., Fewings, M. R., & García-Reyes, M. (2017). Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophysical Research Letters*, *44*(1), 312–319. https://doi.org/10.1002/2016GL071039

Glynn, P. W. (1988). EL NIÑO—SOUTHERN OSCILLATION 1982-1983: NEARSHORE POPULATION, COMMUNITY, AND ECOSYSTEM RESPONSES. *Annual Review of Ecology and Systematics*, *19*(1), 309–346. https://doi.org/10.1146/annurev.es.19.110188.001521

Halpern, B. S., Berlow, E., Williams, R., Borer, E. T., Davis, F. W., Dobson, A., Enquist, B. J., Froehlich, H. E., Gerber, L. R., Lortie, C. J., O'connor, M. I., Regan, H., Vázquez, D. P., & Willard, G. (2020). Ecological Synthesis and Its Role in Advancing Knowledge. *BioScience*, *70*(11), 1005–1014. https://doi.org/10.1093/biosci/biaa105

Harari, M. B., Parola, H. R., Hartwell, C. J., & Riegelman, A. (2020). Literature searches in systematic reviews and meta-analyses: A review, evaluation, and recommendations. *Journal of Vocational Behavior*, *118*, 103377. https://doi.org/10.1016/j.jvb.2020.103377

Harvey, B. P., Marshall, K. E., Harley, C. D. G., & Russell, B. D. (2022). Predicting responses to marine heatwaves using functional traits. *Trends in Ecology & Evolution*, *37*(1), 20–29. https://doi.org/10.1016/j.tree.2021.09.003

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

Hickey, B. M. (1979). The California current system—Hypotheses and facts. *Progress in Oceanography*, *8*(4), 191–279. https://doi.org/10.1016/0079-6611(79)90002-8

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, *12*(3), 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Holt, R. d., & Keitt, T. h. (2000). Alternative causes for range limits: A metapopulation perspective. *Ecology Letters*, *3*(1), 41–47. https://doi.org/10.1046/j.1461-0248.2000.00116.x

Hubbs, C. L. (1948). CHANGES IN THE FISH FAUNA OF WESTERN NORTH AMERICA CORRELATED WITH CHANGES IN OCEAN TEMPERATURE. *Journal of Marine Research*.

Hughes, B. B., Beas-Luna, R., Barner, A. K., Brewitt, K., Brumbaugh, D. R., Cerny-Chipman, E. B., Close, S. L., Coblentz, K. E., de Nesnera, K. L., Drobnitch, S. T., Figurski, J. D., Focht, B., Friedman, M., Freiwald, J., Heady, K. K., Heady, W. N., Hettinger, A., Johnson, A., Karr, K. A., … Carr, M. H. (2017). Long-Term Studies Contribute Disproportionately to Ecology and Policy. *BioScience*, *67*(3), 271–281. https://doi.org/10.1093/biosci/biw185

Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal Upwelling Revisited: Ekman, Bakun, and Improved Upwelling Indices for the U.S. West Coast.

Journal of Geophysical Research: Oceans, *123*(10), 7332–7350. https://doi.org/10.1029/2018JC014187

Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., & Bograd, S. J. (2016). Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters*, *43*(13), 7072–7080. https://doi.org/10.1002/2016GL069716

Jones, T., Parrish, J. K., & Burgess, H. K. (2021). Long-term patterns of mass stranding of the colonial cnidarian Velella velella: Influence of environmental forcing. *Marine Ecology Progress Series*, *662*, 69–83. https://doi.org/10.3354/meps13644

Kinlan, B. P., & Gaines, S. D. (2003). Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. *Ecology*, *84*(8), 2007–2020. https://doi.org/10.1890/01-0622

Lenarz, W. H., Ventresca, D. A., Schwing, F. B., Chavez, F., & Graham, W. M. (1995). Explorations of El Niño Events and Associated Biological Population Dynamics off Central California. *CalCOFI Reports*, *36*.

Lilly, L. E., & Ohman, M. D. (2021). Euphausiid spatial displacements and habitat shifts in the southern California Current System in response to El Niño variability. *Progress in Oceanography*, *193*, 102544. https://doi.org/10.1016/j.pocean.2021.102544

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C. R., Hoffmann, A. A., Keith, D. A., Liddell, M. J., Lowe, A. J., Metcalfe, D. J., Phinn, S. R., Russell-Smith, J., Thurgate, N., & Wardle, G. M. (2012). Value of long-term ecological studies. *Austral Ecology*, *37*(7), 745–757. https://doi.org/10.1111/j.1442-9993.2011.02351.x

Lluch-Belda, D., Lluch-Cota, D. B., & Lluch-Cota, S. E. (2005). Changes in marine faunal distributions and ENSO events in the California Current. *Fisheries Oceanography*, *14*(6), 458–467. https://doi.org/10.1111/j.1365-2419.2005.00347.x

Lynn, R. J., & Bograd, S. J. (2002). Dynamic evolution of the 1997–1999 El Niño–La Niña cycle in the southern California Current System. *Progress in Oceanography*, *54*(1), 59–75. https://doi.org/10.1016/S0079-6611(02)00043-5

Lynn, R. J., & Simpson, J. J. (1987). The California Current system: The seasonal variability of its physical characteristics. *Journal of Geophysical Research: Oceans*, *92*(C12), 12947–12966. https://doi.org/10.1029/JC092iC12p12947

MacArthur, R. H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row.

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

Melbourne-Thomas, J., Audzijonyte, A., Brasier, M. J., Cresswell, K. A., Fogarty, H. E., Haward, M., Hobday, A. J., Hunt, H. L., Ling, S. D., McCormack, P. C., Mustonen, T., Mustonen, K., Nye, J. A., Oellermann, M., Trebilco, R., van Putten, I., Villanueva, C., Watson, R. A., & Pecl, G. T. (2022). Poleward bound: Adapting to climate-driven species redistribution. *Reviews in Fish Biology and Fisheries*, *32*(1), 231–251. https://doi.org/10.1007/s11160-021-09641-3

Miller, R. R., Santora, J. A., Auth, T. D., Sakuma, K. M., Wells, B. K., Field, J. C., & Brodeur, R. D. (2019). Distribution of Pelagic Thaliaceans, Thetys Vagina and

Pyrosoma Atlanticum, During a Period of Mass Occurrence within the California Current. *CalCOFI Reports*, *60*.

National Oceanic and Atmospheric Administration (NOAA). (2024). *Oceanic Niño Index (ONI) and ERSSTv5 data* (No. NOAA National Centers for Environmental Information.) [Dataset]. https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

O'Loughlin, J. H., Bernard, K. S., Daly, E. A., Zeman, S., Fisher, J. L., Brodeur, R. D., & Hurst, T. P. (2020). Implications of *Pyrosoma atlanticum* range expansion on phytoplankton standing stocks in the Northern California Current. *Progress in Oceanography*, *188*, 102424. https://doi.org/10.1016/j.pocean.2020.102424

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(Volume 37, 2006), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pearcy, W. G. (2002). Marine nekton off Oregon and the 1997–98 El Nino. *Progress in Oceanography*, *54*(1), 399–403. https://doi.org/10.1016/S0079-6611(02)00060-5

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Pineda, J., Hare, J. A., & Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. In *OCEANOGRAPHY* (Vol. 20, Issues 3, SI, pp. 22–39). OCEANOGRAPHY SOC. https://doi.org/10.5670/oceanog.2007.27

Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. *Annual Review of Marine Science*, *12*(Volume 12, 2020), 153–179. https://doi.org/10.1146/annurev-marine-010419-010916

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

Schram, J., Sorensen, H., Brodeur, R., Galloway, A., & Sutherland, K. (2020). Abundance, distribution, and feeding ecology of Pyrosoma atlanticum in the Northern California Current. *Marine Ecology Progress Series*, *651*, 97–110. https://doi.org/10.3354/meps13465

Shanks, A. L. (2009). Pelagic Larval Duration and Dispersal Distance Revisited. *The Biological Bulletin*, *216*(3), 373–385. https://doi.org/10.1086/BBLv216n3p373

Simpson, J. J. (1984). El Nino-induced onshore transport in the California Current during 1982-1983. *Geophysical Research Letters*, *11*(3), 233–236. https://doi.org/10.1029/GL011i003p00233

Soifer, L. G., Lockwood, J. L., Lembrechts, J. J., Antão, L. H., Klinges, D. H., Senior, R. A., Ban, N. C., Evengard, B., Fadrique, B., Falkeis, S., Fredston, A. L., Guralnick, R., Lenoir, J., Neate-Clegg, M. H. C., Palacios-Abrantes, J., Pecl, G., Pinsky, M. L., Smith, J. E., Stys, B., … Scheffers, B. R. (2025). Extreme events drive rapid and dynamic range fluctuations. *Trends in Ecology & Evolution*, *40*(9), 862–873. https://doi.org/10.1016/j.tree.2025.06.009

Sorte, C. J., Peterson, W. T., Morgan, C. A., & Emmett, R. L. (2001). Larval dynamics of the sand crab, Emerita analoga, off the central Oregon coast during a strong El Niño period. *Journal of Plankton Research*, *23*(9), 939–944. https://doi.org/10.1093/plankt/23.9.939

Starko, S., Epstein, G., Chalifour, L., Bruce, K., Buzzoni, D., Csordas, M., Dimoff, S., Hansen, R., Maucieri, D. G., McHenry, J., Tietjen, K. L., Timmer, B., & Baum, J. K. (2025). Ecological Responses to Extreme Climatic Events: A Systematic Review of the 2014–2016 Northeast Pacific Marine Heatwave. In B. D. Russell & P. A. Todd, *Oceanography and Marine Biology* (1st ed., pp. 42–96). CRC Press. https://doi.org/10.1201/9781003589600-2

Strub, P. T., & James, C. (2025). Altimeter-Derived poleward Lagrangian pathways in the California Current System: Part 2 – 2-D patterns of parcel transports. *Progress in Oceanography*, *235*, 103495. https://doi.org/10.1016/j.pocean.2025.103495

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, *11*(1), 6235. https://doi.org/10.1038/s41598-021-83818-5

Thompson, A. R., Bjorkstedt, E. P., Bograd, S. J., Fisher, J. L., Hazen, E. L., Leising, A., Santora, J. A., Satterthwaite, E. V., Sydeman, W. J., Alksne, M., Auth, T. D., Baumann-Pickering, S., Bowlin, N. M., Burke, B. J., Daly, E. A., Dewar, H., Field, J. C., Garfield, N. T., Giddings, A., … Weber, E. D. (2022). State of the California Current Ecosystem in 2021: Winter is coming? *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.958727

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

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021

Weber, E. D., Auth, T. D., Baumann-Pickering, S., Baumgartner, T. R., Bjorkstedt, E. P., Bograd, S. J., Burke, B. J., Cadena-Ramírez, J. L., Daly, E. A., De La Cruz, M., Dewar, H., Field, J. C., Fisher, J. L., Giddings, A., Goericke, R., Gomez-Ocampo, E., Gomez-Valdes, J., Hazen, E. L., Hildebrand, J., … Zeman, S. M. (2021). State of the California Current 2019–2020: Back to the Future With Marine Heatwaves? *Frontiers in Marine Science*, *8*, 709454. https://doi.org/10.3389/fmars.2021.709454

Williams, G. D., West, J. M., & Zedler, J. B. (2001). Shifts in Fish and Invertebrate Asseblages of Two Southern California Estuaries during the 1997-98 El Niño. *Southern California Academy of Sciences*, 212–237.

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

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

7. Supplementary

Extended Systematic Review Methods:

In the forward search, we included taxonomic classifications (phylum through order) in our search terms to capture papers that did not use general terms like “invertebrate” but rather referenced specific invertebrate taxa. Taxonomic information (phylum through class, including intermediate ranks such as subphylum and superclass) was downloaded from the World Register of Marine Species (WoRMS) on February 11, 2025 (WoRMS Editorial Board 2025). We included taxa terms that met all of the following criteria: 1) marine (intertidal or deeper), 2) not insects, and 3) not vertebrates. For phyla in which only some classes were relevant (e.g., class Ascidiacea within phylum Chordata), we excluded the phylum name (keeping the class name) from search terms if more than 50% of its classes were excluded to minimize the presence of irrelevant articles. Given the final set of included classes, we obtained the corresponding orders using the R package *taxize* (v0.10.0; Scott Chamberlain and Eduard Szocs, 2013; Chamberlain *et al*., 2020) with the WoRMS database (WoRMS Editorial Board 2025). Taxa terms were restricted to order level and higher to avoid the computational burden of searching exponentially larger numbers of lower-level taxa.

Due to the length of the query, we split it into two groups, A and B, wherein ~half the taxa names were included in A (360 articles returned) and the second half of the taxa terms were included in B (181 articles returned), giving a total of 541 articles from a search in Web of Science’s (WOS) Core Collections on March 6th, 2025. The article titles and associated metadata were exported from WOS. DOIs for all articles were retroactively obtained using R package *rcrossref* (version 1.2.0; Chamberlain *et al*., 2022). Using the DOIs, duplicate articles were removed, leaving 375 unique articles.

R packages used in analyses:

We used R version 4.4.2 (R Core Team, 2024) and the following R packages: cowplot v. 1.2.0 (Wilke, 2025), geosphere v. 1.5.20 (Hijmans, 2024), gganimate v. 1.0.10 (Pedersen and Robinson, 2025), ggh4x v. 0.3.1 (van den Brand, 2025), gt v. 1.1.0 (Iannone *et al*., 2025), here v. 1.0.1 (Müller, 2020), mgcv v. 1.9.1 (S. N. Wood, 2003, 2004, 2011; S. N. Wood *et al*., 2016; S. N. Wood, 2017), moments v. 0.14.1 (Komsta and Novomestky, 2022), openxlsx v. 4.2.8 (Schauberger and Walker, 2025), paletteer v. 1.6.0 (Hvitfeldt, 2021), rcrossref v. 1.2.0 (Chamberlain *et al*., 2022), rnaturalearth v. 1.0.1 (Massicotte and South, 2023), rnaturalearthdata v. 1.0.0 (South, Michael, and Massicotte, 2024), rsoi v. 0.5.6 (Albers, 2023), scales v. 1.3.0 (Wickham, Pedersen, and Seidel, 2023), sf v. 1.0.20 (Pebesma, 2018; Pebesma and Bivand, 2023), taxize v. 0.10.0 (Scott Chamberlain and Eduard Szocs, 2013; Chamberlain *et al*., 2020), tidyverse v. 2.0.0 (Wickham *et al*., 2019), zoo v. 1.8.13 (Zeileis and Grothendieck, 2005).

Supplementary Tables

Supplementary Table 1. Summary table of each marine invertebrate, the only or average poleward extension distance, and the year(s) the species had an extension event. An extension event is recorded for each species in any year when the species appeared north of its historical range edge after not being recorded the previous year.

Summary of Range Extension Events (Part 1)

Mean northward extension distance and extension year per species

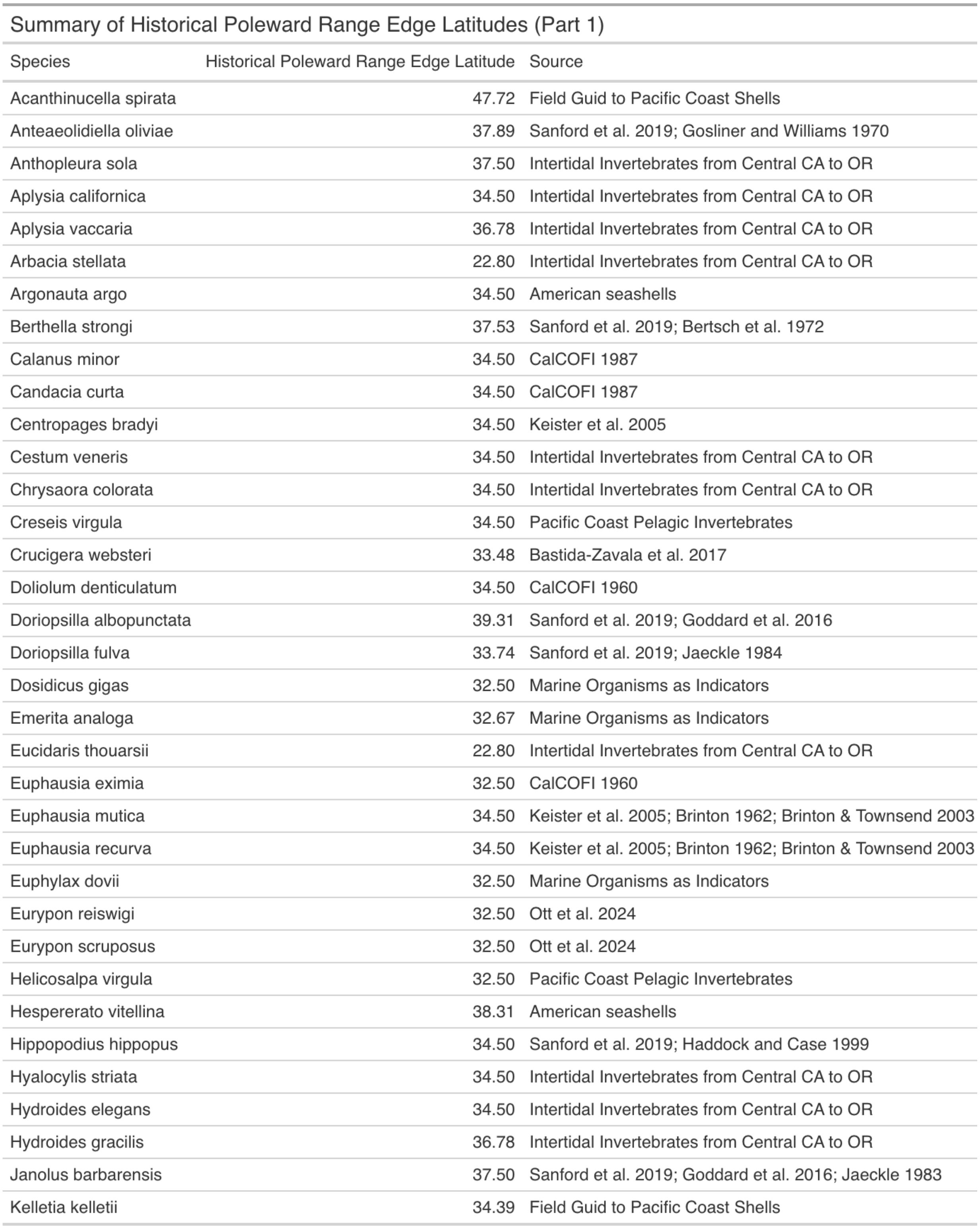
Species	Mean Extension Distance (km)	Extension Years
Anteaeolidiella oliviae	201.7	2015
Anthopleura sola	273.9	2018
Aplysia californica	493.4	1983, 2001, 2004, 2011
Aplysia vaccaria	3.5	2014
Arbacia stellata	4,130.5	2015
Argonauta argo	194.8	2015
Berthella strongi	266.1	2016
Calanus minor	718.1	1958
Candacia curta	746.0	1958
Centropages bradyi	1,374.1	1997
Cestum veneris	1,653.6	2014, 2016
Chrysaora colorata	833.6	1972, 2006, 2014, 2017
Creseis virgula	486.6	2014
Crucigera websteri	949.5	2003
Doliolum denticulatum	364.6	1958, 1969
Doriopsilla albopunctata	327.9	2016
Doriopsilla fulva	1,384.5	2015
Dosidicus gigas	1,506.2	1909, 1934, 1975, 1997, 2002, 2006, 2009
Emerita analoga	2,223.9	1903, 1941, 1957, 1983, 2006, 2015
Eucidaris thouarsii	4,514.0	1958, 1960
Euphausia eximia	421.5	1958, 1978, 2015
Euphausia mutica	1,186.1	1998
Euphausia recurva	926.6	1998, 2014, 2018
Euphylax dovii	18.4	1943, 1959, 1974
Helicosalpa virgula	1,396.0	1963
Hespererato vitellina	12.2	2016
Hippopodius hippopus	484.2	2015
Hyalocylis striata	486.6	2014
Hydroides elegans	767.7	2003
Hydroides gracilis	121.3	2000
Janolus barbarensis	120.7	2015
Kelletia kelletii	331.1	1980

Summary of Range Extension Events (Part 2)

Mean northward extension distance and extension year per species

Species	Mean Extension Distance (km)	Extension Years
Lissothuria nutriens	216.1	2010, 2017
Loligo opalescens	1,207.3	1941, 1959
Lophogorgia chiliensis	18.4	1960
Lovenia cordiformis	268.9	2016
Lyropectin subnudosus	4,514.0	1959
Malacoplax californiensis	186.4	2016
Megabalanus californicus	331.8	1939, 1981, 1996, 2006, 2009, 2015
Mexacanthina lugubris	364.2	1937, 1955, 1974, 2013, 2017
Neolithodes diomedeae	242.0	1999, 2001
Nyctiphanes simplex	1,174.8	1958, 1977, 1983, 1998, 2015, 2018
Okenia angelensis	66.0	1964, 2015, 2017
Ophiothrix spiculata	127.8	1962, 1979, 2002, 2014, 2016, 2018
Pachythyone rubra	134.6	1971, 1976, 1997, 2017
Panulirus gracilis	18.4	1961
Panulirus interruptus	540.6	1940, 2001, 2005, 2011, 2013
Paraconcavus pacificus	273.1	2016, 2019
Petrolisthes manimaculis	80.8	2017
Phidiana hiltoni	60.3	2014
Physophora hydrostatica	503.2	2015
Pleuroncodes planipes	624.4	1941, 1957, 1969, 1972, 1979, 1982, 1997, 2002, 2014
Portunus xantusii	469.5	1999, 2016
Pyrosoma atlanticum	1,370.5	2014, 2020
Rhincalanus nasutus	718.1	1958
Sagitta pseudoserratodentata	297.3	1998
Spirobranchs spinosus	72.3	1941, 2010, 2013, 2018
Tetraclita rubescens	271.9	1948, 1957, 1970, 1984, 1995, 2005, 2007
Thalia democratica	859.1	1963
Thetys vagina	311.7	1963
Thylacodes squamigerus	501.2	2001, 2017
Uca princeps	4,437.1	2018
Velella velella	1,643.5	1926, 1957, 2015

Supplementary Table 2. Historical poleward range edge latitude for each marine invertebrate and the source for the historical latitude.



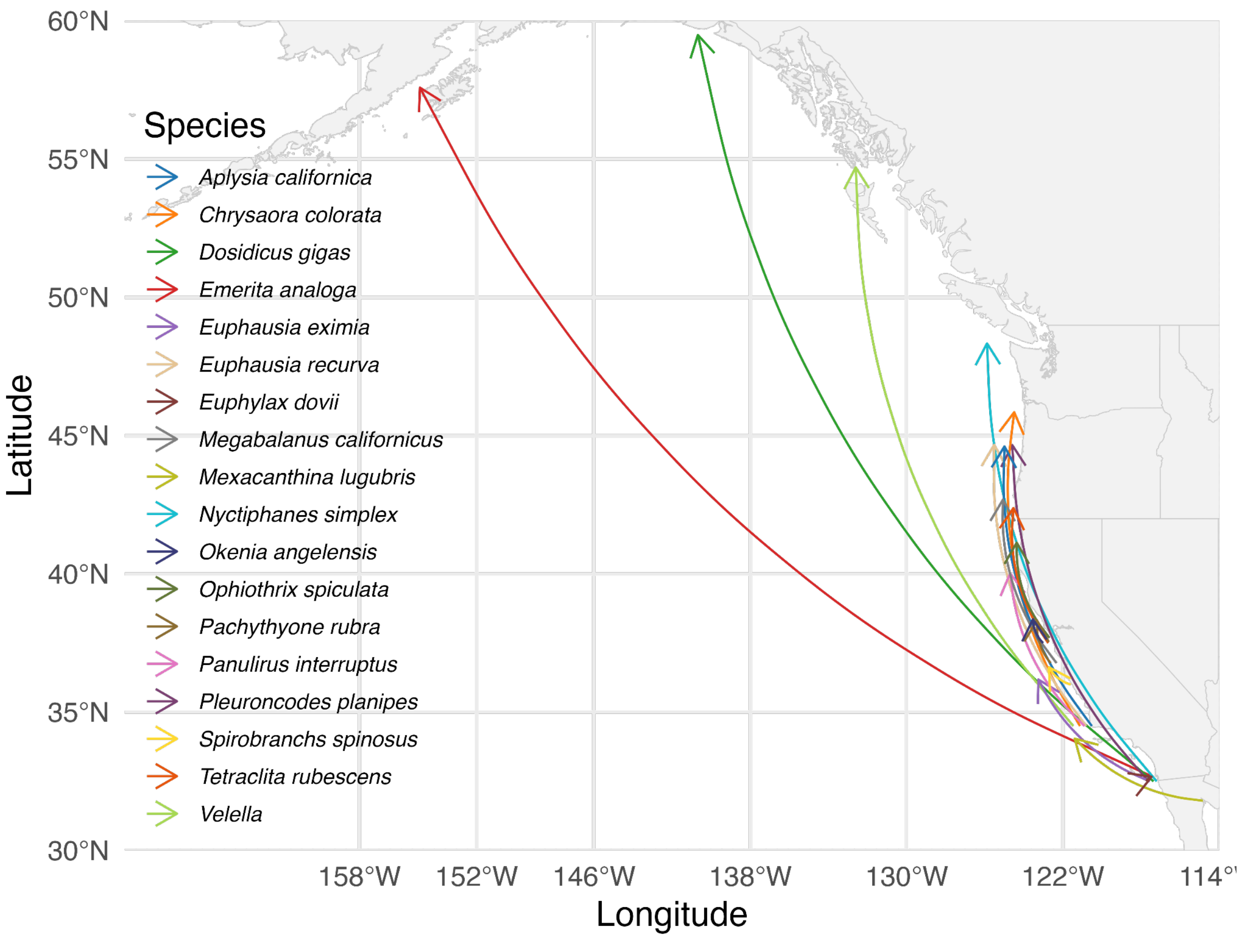
Summary of Historical Poleward Range Edge Latitudes (Part 1)

Species	Historical Poleward Range Edge Latitude	Source
Acanthinucella spirata	47.72	Field Guid to Pacific Coast Shells
Anteaeolidiella oliviae	37.89	Sanford et al. 2019; Gosliner and Williams 1970
Anthopleura sola	37.50	Intertidal Invertebrates from Central CA to OR
Aplysia californica	34.50	Intertidal Invertebrates from Central CA to OR
Aplysia vaccaria	36.78	Intertidal Invertebrates from Central CA to OR
Arbacia stellata	22.80	Intertidal Invertebrates from Central CA to OR
Argonauta argo	34.50	American seashells
Berthella strongi	37.53	Sanford et al. 2019; Bertsch et al. 1972
Calanus minor	34.50	CalCOFI 1987
Candacia curta	34.50	CalCOFI 1987
Centropages bradyi	34.50	Keister et al. 2005
Cestum veneris	34.50	Intertidal Invertebrates from Central CA to OR
Chrysaora colorata	34.50	Intertidal Invertebrates from Central CA to OR
Creseis virgula	34.50	Pacific Coast Pelagic Invertebrates
Crucigera websteri	33.48	Bastida-Zavala et al. 2017
Doliolum denticulatum	34.50	CalCOFI 1960
Doriopsilla albopunctata	39.31	Sanford et al. 2019; Goddard et al. 2016
Doriopsilla fulva	33.74	Sanford et al. 2019; Jaeckle 1984
Dosidicus gigas	32.50	Marine Organisms as Indicators
Emerita analoga	32.67	Marine Organisms as Indicators
Eucidaris thouarsii	22.80	Intertidal Invertebrates from Central CA to OR
Euphausia eximia	32.50	CalCOFI 1960
Euphausia mutica	34.50	Keister et al. 2005; Brinton 1962; Brinton & Townsend 2003
Euphausia recurva	34.50	Keister et al. 2005; Brinton 1962; Brinton & Townsend 2003
Euphylax dovii	32.50	Marine Organisms as Indicators
Eurypon reiswigi	32.50	Ott et al. 2024
Eurypon scruposus	32.50	Ott et al. 2024
Helicosalpa virgula	32.50	Pacific Coast Pelagic Invertebrates
Hespererato vitellina	38.31	American seashells
Hippopodius hippopus	34.50	Sanford et al. 2019; Haddock and Case 1999
Hyalocylis striata	34.50	Intertidal Invertebrates from Central CA to OR
Hydroides elegans	34.50	Intertidal Invertebrates from Central CA to OR
Hydroides gracilis	36.78	Intertidal Invertebrates from Central CA to OR
Janolus barbarensis	37.50	Sanford et al. 2019; Goddard et al. 2016; Jaeckle 1983
Kelletia kelletii	34.39	Field Guid to Pacific Coast Shells

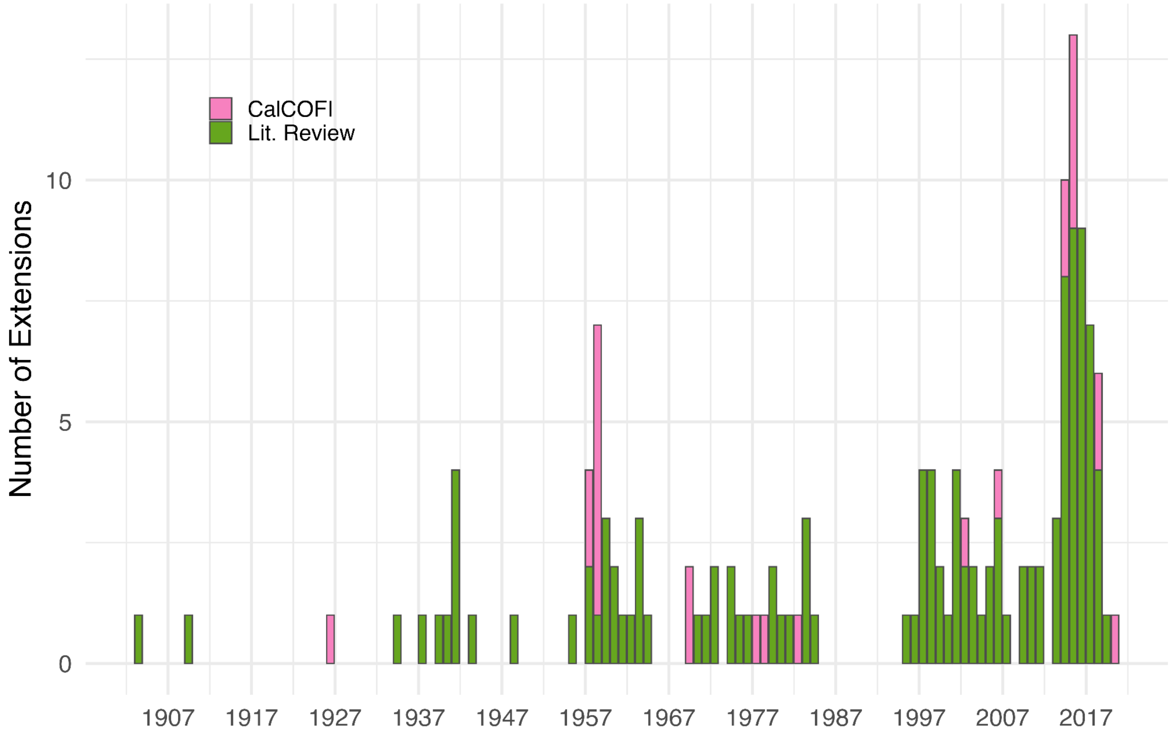
Summary of Historical Poleward Range Edge Latitudes (Part 2)

Species	Historical Poleward Range Edge Latitude	Source
Lissothuria nutriens	36.78	Intertidal Invertebrates from Central CA to OR
Loligo opalescens	32.67	Marine Organisms as Indicators
Lophogorgia chiliensis	32.50	Marine Organisms as Indicators
Lovenia cordiformis	34.50	Intertidal Invertebrates from Central CA to OR
Lyropectin subnudosus	22.80	Field Guid to Pacific Coast Shells
Lytechinus pictus	34.50	Intertidal Invertebrates from Central CA to OR
Malacoplax californiensis	35.30	Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific
Megabalanus californicus	36.78	Intertidal Invertebrates from Central CA to OR
Mexacanthina lugubris	31.80	Fenberg et al. 2017
Neolithodes diomedeae	35.41	Checklist of anomuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific
Nyctiphanes simplex	32.50	Intertidal Invertebrates from Central CA to OR
Oceanapia flava	22.80	Ott et al. 2024
Oceanapia polytuba	22.80	Ott et al. 2024
Okenia angelensis	37.50	Intertidal Invertebrates from Central CA to OR
Ophiothrix spiculata	37.69	Sanford et al. 2019; Morris et al. 1980
Pachythyone rubra	36.78	Intertidal Invertebrates from Central CA to OR
Panulirus gracilis	32.50	Marine Organisms as Indicators
Panulirus interruptus	34.50	Sanford et al. 2019; Ricketts and Calvin 1968
Paraconcavus pacificus	36.78	Intertidal Invertebrates from Central CA to OR
Petrolisthes manimaculis	41.05	Sanford et al. 2019; Jensen 1995; Morris et al. 1980
Phidiana hiltoni	37.89	Sanford et al. 2019; Goddard et al. 2011
Physophora hydrostatica	36.78	Sanford et al. 2019
Pleuroncodes planipes	32.50	Intertidal Invertebrates from Central CA to OR
Portunus xantusii	34.50	Intertidal Invertebrates from Central CA to OR
Pyrosoma atlanticum	40.00	Pacific Coast Pelagic Invertebrates
Rhincalanus nasutus	34.50	CalCOFI 1987
Sagitta pseudoserratodentata	42.00	Keister et al. 2005; Bieri 1959; Alvariño 1965
Scoelcithrix danae	34.50	CalCOFI 1987
Thylacodes squamigerus	34.50	Intertidal Invertebrates from Central CA to OR
Spirobranchs spinosus	36.00	sealifebase
Tetraclita rubescens	37.50	Intertidal Invertebrates from Central CA to OR
Thalia democratica	35.00	Hubbard and Pearcy 1971
Thetys vagina	42.00	Intertidal Invertebrates from Central CA to OR
Uca princeps	22.80	Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific
Velella velella	34.50	Pacific Coast Pelagic Invertebrates

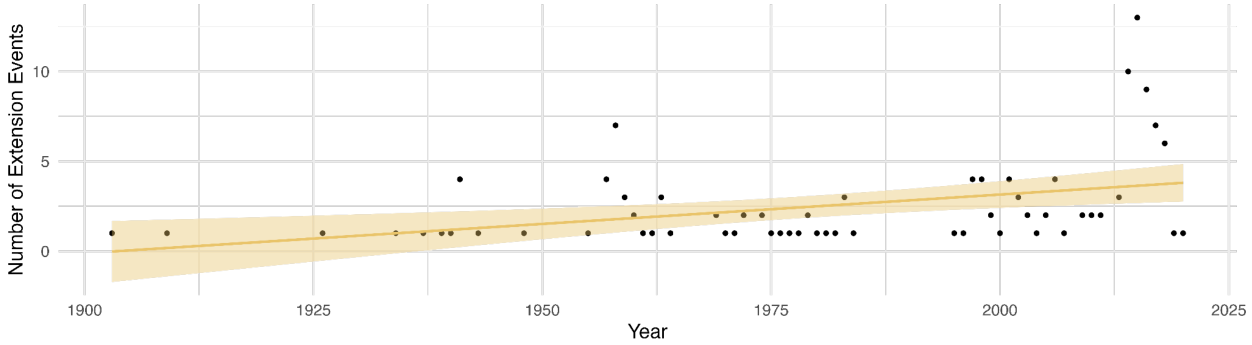
Supplementary Figures



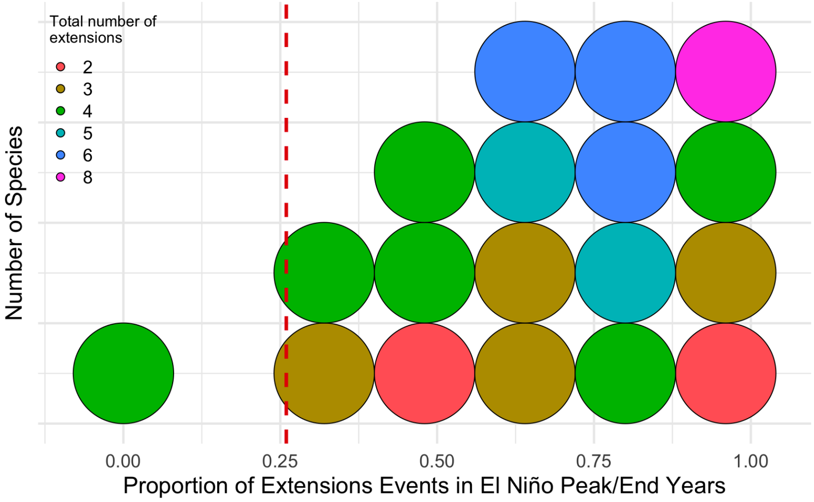
Supplementary Figure 1. This figure is identical to Figure 1 in the main text except that it shows the full extent of the three long-range extensions to Alaska and British Columbia. Map of the most northern anomalous observation of marine invertebrates with 3+ extension events (18 species) between 1900 and 2020. Each arrow represents one species. The arrow origin is the historical poleward range edge (see Supplementary Table 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 88 episodic extension events of these 18 species have an average distance of 694 ± 783 km with a minimum of 14km and a maximum of 3842 km.



Supplementary Figure 2. Annual number of poleward range extension events of marine invertebrates, colored by data source: CalCOFI-derived records in pink and literature-derived records in green. An extension event here is recorded for each species in any year when the species appeared north of its historical range edge after not being recorded the previous year.



Supplementary Figure 3. Linear regression fitted to the number of poleward range extension events of marine invertebrates over time. An extension event here is recorded for each species in any year when the species appeared north of its historical range edge after not being recorded the previous year. The frequency of observations increased significantly between 1903 and 2020 (slope = 0.03±0.01 events/year, t_{56} = 3.14, p = 0.0027).



Supplementary Figure 4. This figure is identical to Figure 2b in the main text except that it colors the circles representing each species by the total number of extension events for that species. The proportion of extension events occurring during the peak or at the end of an El Niño event, for species with 3+ extension events (18 species; one gray circle per species) in the timeseries beginning in 1903. The red dotted line represents the expected proportion of El Nino events at a monthly resolution. Well over half of all 1950-2020 episodic extension events (52 of 76; 68%) occur during El Niño years, which is over double the expected frequency based on the long-term El Niño baseline (26%; χ-squared = 70.98, df = 1, p-value < 0.001).

Supplementary Search Terms for Literature Review

The following terms were used to search the Web of Science Core Collection. The complete list of terms is provided below, along with subsets A and B, each containing half of the taxa. Subsets A and B were queried separately because the full list exceeded the maximum query length allowed by Web of Science.

Full search terms:
TS = **(("east* Pacific" OR "northeast* pacific" OR "Alaska" OR "BC" OR "California" OR "Oregon" OR "Washington") AND ("ocean*" OR "sea*" OR "marine*" OR "*tidal" OR "coast*") AND ("invertebrate*" OR (("*tidal" OR "*benthic" OR "*fouling") NEAR/0 ("species" OR "community")) OR**"*Eoacanthocephal*" OR "*Palaeacanthocephal*" OR "*Clitellat*" OR "*Gephyre*" OR "*Polychaet*" OR "*Branchiopod*" OR "*Cephalocarid*" OR "*Copepod*" OR "*Hexanaupli*" OR "*Ichthyostrac*" OR "*Malacostrac*" OR "*Maxillopod*" OR "*Merostomat*" OR "*Ostracod*" OR "*Pycnogonid*" OR "*Remipedi*" OR "*Tantulocarid*" OR "*Thecostrac*" OR "*Articulat*" OR "*Craniat*" OR "*Lingulat*" OR "*Rhynchonellat*" OR "*Gymnolaemat*" OR "*Stenolaemat*" OR "*Sagittoide*" OR "*Appendiculari*" OR "*Ascidiace*" OR "*Larvace*" OR "*Leptocardi*" OR "*Myxin*" OR "*Sorberace*" OR "*Thaliace*" OR "*Anthozo*" OR "*Cubomedusa*" OR "*Cubozo*" OR "*Hexacoralli*" OR "*Hydrozo*" OR "*Myxozo*" OR "*Octocoralli*" OR "*Scyphomedusa*" OR "*Scyphozo*" OR "*Staurozo*" OR "*Zoanthari*" OR "*Gastroide*" OR "*Nud*" OR "*Tentaculat*" OR "*Eucycliophor*" OR "*Rhombozo*" OR "*Adelostellat*" OR "*Asteroide*" OR "*Asteroide*" OR "*Crinoide*" OR "*Crinoide*" OR "*Echinoide*" OR "*Echinoide*" OR "*Holothurioide*" OR "*Holothuroide*" OR "*Holothuroide*" OR "*Klot*" OR "*Ophiuroide*" OR "*Ophiuroide*" OR "*Stelleroide*" OR "*Enteropneust*" OR "*Graptolithoide*" OR "*Pterobranchi*" OR "*Allomalorhagid*" OR "*Cyclorhagid*" OR "*Homalorhaga*" OR "*Amphineur*" OR "*Bivalvi*" OR "*Caudofoveat*" OR "*Cephalopod*" OR

"*Conchifer*" OR "*Gastropod*" OR "*Lamellibranchiat*" OR "*Loricat*" OR "*Monoplacophor*" OR "*Pelecypod*" OR "*Polyplacophor*" OR "*Polyplaxiphor*" OR "*Scaphopod*" OR "*Solenoconchi*" OR "*Solenogastre*" OR "*Adenophore*" OR "*Chromadore*" OR "*Enople*" OR "*Secernente*" OR "*Gordia*" OR "*Gordioid*" OR "*Gordioide*" OR "*Nectonematoid*" OR "*Anopl*" OR "*Arhynchocoel*" OR "*Enopl*" OR "*Hoplonemerte*" OR "*Palaeonemerte*" OR "*Pilidiophor*" OR "*Polyplacotomi*" OR "*Uniplacotomi*" OR "*Cestod*" OR "*Monogene*" OR "*Monogenoide*" OR "*Monopisthocotyl*" OR "*Polyopisthocotyl*" OR "*Trematod*" OR "*Turbellari*" OR "*Afrenulat*" OR "*Frenulat*" OR "*Calcare*" OR "*Calcispongi*" OR "*Calcispongia*" OR "*Demospongia*" OR "*Hexactinellid*" OR "*Homoscleromorph*" OR "*Hyalospongia*" OR "*Sclerospongia*" OR "*Eurotatori*" OR "*Pararotatori*" OR "*Seisonide*" OR "*Eutardigrad*" OR "*Heterotardigrad*" OR "*Xenoturbellid*" OR "*Acanthocephal*" OR "*Annelid*" OR "*Arthropod*" OR "*Aschelminthe*" OR "*Brachiopod*" OR "*Bryozo*" OR "*Cephalorhynch*" OR "*Chaetognath*" OR "*Cnidari*" OR "*Ctenophor*" OR "*Cycliophor*" OR "*Dicyemid*" OR "*Echinodermat*" OR "*Ectoproct*" OR "*Entoproct*" OR "*Gastrotrich*" OR "*Gnathostomulid*" OR "*Hemichordat*" OR "*Kinorhynch*" OR "*Loricifer*" OR "*Mesozo*" OR "*Mollusc*" OR "*Nematod*" OR "*Nematomorph*" OR "*Nemerte*" OR "*Nemertin*" OR "*Nemertin*" OR "*Orthonectid*" OR "*Pentastomid*" OR "*Phoronid*" OR "*Placozo*" OR "*Platyhelminthe*" OR "*Pogonophor*" OR "*Porifer*" OR "*Priapulid*" OR "*Rotatori*" OR "*Rotifer*" OR "*Sipunculid*" OR "*Tardigrad*" OR "*Xenacoelomorph*" OR "*Chelicerat*" OR "*Crustace*" OR "*Pancrustace*" OR "*Tetraconat*" OR "*Craniiforme*" OR "*Linguliforme*" OR "*Rhynchonelliforme*" OR "*Cephalochordat*" OR "*Tunicat*" OR "*Urochordat*" OR "*Endocnidozo*" OR "*Medusozo*" OR "*Asterozo*" OR "*Crinozo*" OR "*Echinozo*" OR "*Aculifer*" OR "*Placophor*" OR "*Catenulid*" OR "*Rhabditophor*" OR "*Obturat*" OR "*Perviat*" OR "*Silice*" OR "*Acoelomorph*" OR "*Xenacoel*" OR "*Allotriocarid*" OR "*Multicrustace*" OR "*Oligostrac*" OR "*Aplacophor*" OR "*Neonemerte*" OR "*Pronemerte*" OR "*Neodermat*" OR "*Gyracanthocephal*" OR "*Neoechinorhynchid*" OR "*Echinorhynchid*" OR "*Polymorphid*" OR "*Capilloventrid*" OR "*Crassiclitellat*" OR "*Enchytraeid*" OR "*Haplotaxid*" OR "*Lumbriculid*" OR "*Oligochaet*" OR "*Randiellid*" OR "*Tubificid*" OR "*Arhynchobdellid*" OR "*Rhynchobdellid*" OR "*Echiur*" OR "*Echiuroide*" OR "*Amphinomid*" OR "*Eunicid*" OR "*Phyllodocid*" OR "*Archiannelid*" OR "*Psammodrilid*" OR "*Spintherid*" OR "*Sabellid*" OR "*Spionid*" OR "*Terebellid*" OR "*Capitellid*" OR "*Cossurid*" OR "*Opheliid*" OR "*Orbiniid*" OR "*Anomopod*" OR "*Cladocer*" OR "*Ctenopod*" OR "*Gymnomer*" OR "*Haplopod*" OR "*Onychopod*" OR "*Spinicaudat*" OR "*Brachypod*" OR "*Herpyllobioid*" OR "*Platycopioid*" OR "*Calanoid*" OR "*Andreinide*" OR "*Canuelloid*" OR "*Cyclopide*" OR "*Cyclopoid*" OR "*Harpacticoid*" OR "*Lerneopodide*" OR "*Misophrioid*" OR "*Monstrilloid*" OR "*Mormonilloid*" OR "*Philichthyide*" OR "*Sarcotacide*" OR "*Siphonostomatoid*" OR "*Thaumatopsylloid*" OR "*Arguloid*" OR "*Cephalobaenid*" OR "*Porocephalid*" OR "*Raillietiellid*" OR "*Reighardiid*" OR "*Stomatopod*" OR "*Leptostrac*" OR "*Amphionidace*" OR "*Decapod*" OR "*Euphausiace*" OR "*Amphipod*" OR "*Anisopod*" OR "*Bochusace*" OR "*Cumace*" OR "*Ingolfiellid*" OR "*Isopod*" OR "*Lophogastrid*" OR "*Mictace*" OR "*Mysid*" OR "*Mysidace*" OR "*Stygiomysid*" OR "*Tanaidace*" OR "*Thermosbaenace*" OR "*Bathynellace*" OR "*Palaeocaridace*" OR "*Xiphosurid*" OR "*Cladocop*" OR "*Halocyprid*" OR "*Myodocopid*" OR "*Cladocopid*" OR "*Platycopid*" OR "*Podocop*" OR "*Podocopid*" OR "*Punciocopid*" OR "*Beyrichiid*" OR "*Pantopod*" OR "*Nectiopod*" OR "*Dendrogastrid*" OR "*Laurid*" OR "*Apygophor*" OR "*Cryptophialid*" OR "*Lithoglyptid*" OR "*Pygophor*" OR "*Akentrogonid*" OR "*Kentrogonid*" OR "*Lepadiforme*" OR "*Pedunculat*" OR "*Scalpelliforme*" OR "*Sessili*" OR "*Ibliforme*" OR "*Iblomorph*" OR "*Balanomorph*" OR "*Calanticomorph*" OR "*Pollicipedomorph*" OR "*Scalpellomorph*" OR "*Verrucomorph*" OR "*Craniid*" OR "*Lingulid*" OR "*Rhynchonellid*" OR "*Terebratulid*" OR "*Thecideid*" OR "*Cheilostomat*" OR "*Cheilostomatid*" OR "*Ctenostomat*" OR "*Ctenostomatid*" OR "*Cyclostomat*" OR "*Cyclostomatid*" OR "*Esthonioporat*" OR "*Aphragmophor*" OR "*Phragmophor*" OR

"*Copelat*" OR "*Aplousobranchi*" OR "*Enterogon*" OR "*Phlebobranchi*" OR "*Pleurogon*" OR "*Stolidobranchi*" OR "*Myxiniforme*" OR "*Aspiraculat*" OR "*Cyclomyari*" OR "*Desmomyari*" OR "*Doliolid*" OR "*Pyrosomatid*" OR "*Salpid*" OR "*Carybdeid*" OR "*Chirodropid*" OR "*Actiniari*" OR "*Antipathari*" OR "*Cerianthari*" OR "*Ceriantipathari*" OR "*Corallimorphari*" OR "*Coralliomorphari*" OR "*Ptychodactiari*" OR "*Scleractini*" OR "*Zoanthide*" OR "*Zoanthiniari*" OR "*Hydroid*" OR "*Milleporin*" OR "*Trachylin*" OR "*Anthoathecat*" OR "*Anthoathecata*" OR "*Anthomedusa*" OR "*Athecat*" OR "*Gymnoblaste*" OR "*Laingiomedusa*" OR "*Leptomedusa*" OR "*Leptothecat*" OR "*Siphonophor*" OR "*Siphonophora*" OR "*Thecaphor*" OR "*Thecat*" OR "*Actinulid*" OR "*Limnomedusa*" OR "*Narcomedusa*" OR "*Trachomedusa*" OR "*Trachymedusa*" OR "*Bivalvulid*" OR "*Multivalvulid*" OR "*Alcyonace*" OR "*Gorgonace*" OR "*Helioporace*" OR "*Malacalcyonace*" OR "*Pennatulace*" OR "*Scleralcyonace*" OR "*Coronata*" OR "*Rhizostomea*" OR "*Semaeostomea*" OR "*Stauromedusa*" OR "*Madreporari*" OR "*Beroid*" OR "*Archiplanoide*" OR "*Cambojiid*" OR "*Cestid*" OR "*Cryptolobiferid*" OR "*Cydippid*" OR "*Ganeshid*" OR "*Lobat*" OR "*Platyctenid*" OR "*Platyctenida*" OR "*Thalassocalycid*" OR "*Symbiid*" OR "*Heterocyemid*" OR "*Euclasteroide*" OR "*Platyasterid*" OR "*Peripodid*" OR "*Velatid*" OR "*Brisingid*" OR "*Forcipulatid*" OR "*Spinulosid*" OR "*Notomyotid*" OR "*Paxillosid*" OR "*Valvatid*" OR "*Bourgueticrinid*" OR "*Comatulid*" OR "*Cyrtocrinid*" OR "*Hyocrinid*" OR "*Isocrinid*" OR "*Latistellat*" OR "*Cidaroid*" OR "*Echinothuroid*" OR "*Pourtalesioid*" OR "*Diadematoid*" OR "*Micropygoid*" OR "*Aspidodiadematoid*" OR "*Echinothurioid*" OR "*Pedinoid*" OR "*Arbacioid*" OR "*Camarodont*" OR "*Echinoid*" OR "*Salenioid*" OR "*Stomopneustoid*" OR "*Temnopleuroid*" OR "*Holasteroid*" OR "*Spatangide*" OR "*Spatangoid*" OR "*Echinoneoid*" OR "*Clypeasteroid*" OR "*Echinolampadace*" OR "*Aspidochirot*" OR "*Aspidochirotid*" OR "*Dactylochirotid*" OR "*Dendrochirot*" OR "*Dendrochirotid*" OR "*Elasipodid*" OR "*Holothuriid*" OR "*Molpadid*" OR "*Molpadiid*" OR "*Persiculid*" OR "*Synallactid*" OR "*Apod*" OR "*Apodid*" OR "*Synaptid*" OR "*Euryala*" OR "*Gnathophiurid*" OR "*Ophiura*" OR "*Phrynophiurid*" OR "*Euryalid*" OR "*Ophiurid*" OR "*Amphilepidid*" OR "*Ophiacanthid*" OR "*Ophioleucid*" OR "*Ophioscolecid*" OR "*Cephalodiscoide*" OR "*Rhabdopleuroide*" OR "*Anomoirhag*" OR "*Echinorhagat*" OR "*Kentrorhagat*" OR "*Xenosomat*" OR "*Manzanellid*" OR "*Nuculanid*" OR "*Nuculid*" OR "*Solemyid*" OR "*Arcid*" OR "*Limid*" OR "*Mytilid*" OR "*Ostreid*" OR "*Pectinid*" OR "*Pteriid*" OR "*Carditid*" OR "*Anomalodesmace*" OR "*Euheterodont*" OR "*Pholadomyid*" OR "*Trigoniid*" OR "*Unionid*" OR "*Adapedont*" OR "*Cardiid*" OR "*Galeommatid*" OR "*Gastrochaenid*" OR "*Hiatellid*" OR "*Lucinid*" OR "*Myace*" OR "*Myid*" OR "*Sphaeriid*" OR "*Venerid*" OR "*Chaetodermatid*" OR "*Nautilid*" OR "*Decapodiforme*" OR "*Bathyteuthid*" OR "*Idiosepid*" OR "*Myopsid*" OR "*Oegopsid*" OR "*Sepiid*" OR "*Spirulid*" OR "*Teuthid*" OR "*Octopod*" OR "*Vampyromorph*" OR "*Caenogastropod*" OR "*Littorinimorph*" OR "*Neogastropod*" OR "*Stenogloss*" OR "*Cycloneritid*" OR "*Cycloneritimorph*" OR "*Neritimorph*" OR "*Archaeogastropod*" OR "*Mesogastropod*" OR "*Rhipidogloss*" OR "*Anisobranchi*" OR "*Cocculinid*" OR "*Lepetellid*" OR "*Neomphalid*" OR "*Pleurotomariid*" OR "*Seguenziid*" OR "*Trochid*" OR "*Architectibranchi*" OR "*Pleurobranchomorph*" OR "*Anaspide*" OR "*Aplysiid*" OR "*Aplysiomorph*" OR "*Archaeopulmonat*" OR "*Bullomorph*" OR "*Cephalaspide*" OR "*Heterostroph*" OR "*Pteropod*" OR "*Runcinace*" OR "*Runcinid*" OR "*Tectibranchiat*" OR "*Thecosomat*" OR "*Umbraculid*" OR "*Notaspide*" OR "*Nudibranchi*" OR "*Pleurobranchid*" OR "*Ellobiid*" OR "*Gymnomorph*" OR "*Stylommatophor*" OR "*Systellommatophor*" OR "*Siphonariid*" OR "*Neopilinid*" OR "*Callochitonid*" OR "*Chitonid*" OR "*Lepidopleurid*" OR "*Dentaliid*" OR "*Gadilid*" OR "*Neomeniamorph*" OR "*Pholidoskepi*" OR "*Cavibeloni*" OR "*Sterrofusti*" OR "*Aphelenchid*" OR "*Araeolaimid*" OR "*Ascaridid*" OR "*Benthimermithid*" OR "*Chromadorid*" OR "*Desmodorid*" OR "*Desmoscolecid*" OR "*Monhysterid*" OR "*Plectid*" OR "*Rhabditid*" OR "*Spirurid*" OR "*Strongylid*" OR "*Tylenchid*" OR "*Dioctophymat*" OR

"*Dioctophymatid*" OR "*Dioctophymid*" OR "*Dioctophymoide*" OR "*Dorylaimid*" OR "*Marimermithid*" OR "*Mermithid*" OR "*Trichinellid*" OR "*Enoplid*" OR "*Rhaptothyreid*" OR "*Trefusiid*" OR "*Triplonchid*" OR "*Anguilluloide*" OR "*Nectonematoide*" OR "*Nectonematid*" OR "*Arhynchonemerte*" OR "*Bdellomorph*" OR "*Monostilifer*" OR "*Polystilifer*" OR "*Urichorhynchocoel*" OR "*Archinemerte*" OR "*Carinomiforme*" OR "*Tubulaniforme*" OR "*Heteronemerte*" OR "*Hubrechtiiforme*" OR "*Schizonemertin*" OR "*Polyplacotome*" OR "*Cladhexe*" OR "*Hoilunge*" OR "*Trichoplace*" OR "*Amphilinide*" OR "*Gyrocotylide*" OR "*Bothriocephalide*" OR "*Caryophyllide*" OR "*Cathetocephalide*" OR "*Cyclophyllide*" OR "*Diphyllide*" OR "*Diphyllobothriide*" OR "*Eucestod*" OR "*Lecanicephalide*" OR "*Litobothriide*" OR "*Onchoproteocephalide*" OR "*Phyllobothriide*" OR "*Proteocephalide*" OR "*Pseudophyllide*" OR "*Rhinebothriide*" OR "*Spathebothriide*" OR "*Tetrabothriide*" OR "*Tetraphyllide*" OR "*Trypanorhynch*" OR "*Capsalide*" OR "*Dactylogyrid*" OR "*Dactylogyride*" OR "*Gyrodactylide*" OR "*Monocotylide*" OR "*Montchadskyellide*" OR "*Chimaericolide*" OR "*Diclybothriide*" OR "*Mazocraeide*" OR "*Polystomatide*" OR "*Aspidogastrid*" OR "*Stichocotylid*" OR "*Azygiid*" OR "*Bucephalidid*" OR "*Digene*" OR "*Diplostomid*" OR "*Echinostomid*" OR "*Faustulid*" OR "*Plagiorchiid*" OR "*Strigeid*" OR "*Strigeidid*" OR "*Vestimentifer*" OR "*Athecanephri*" OR "*Thecanephri*" OR "*Heterocoel*" OR "*Homocoel*" OR "*Baeriid*" OR "*Leucosolenid*" OR "*Lithonid*" OR "*Sycettid*" OR "*Syconos*" OR "*Asconos*" OR "*Clathrinid*" OR "*Leucettid*" OR "*Murrayonid*" OR "*Gumminea*" OR "*Halisarcid*" OR "*Lithistid*" OR "*Agelasid*" OR "*Ancorinid*" OR "*Astrophorid*" OR "*Axinellid*" OR "*Biemnid*" OR "*Bubarid*" OR "*Ceratoporellid*" OR "*Choristid*" OR "*Clionaid*" OR "*Craniellid*" OR "*Desmacellid*" OR "*Desmacidonitid*" OR "*Hadromerid*" OR "*Halichondrid*" OR "*Haplosclerid*" OR "*Heteroscleromorph*" OR "*Merliid*" OR "*Nepheliospongid*" OR "*Petrosid*" OR "*Poecillastrid*" OR "*Poecilosclerid*" OR "*Polymastiid*" OR "*Scopalinid*" OR "*Sphaerocladin*" OR "*Spirastrellid*" OR "*Spirophorid*" OR "*Spongillid*" OR "*Suberitid*" OR "*Tethyid*" OR "*Tetractinellid*" OR "*Trachycladid*" OR "*Dendroceratid*" OR "*Dictyoceratid*" OR "*Keratosid*" OR "*Verticillitid*" OR "*Chondrillid*" OR "*Chondrosid*" OR "*Chondrosiid*" OR "*Verongid*" OR "*Verongiid*" OR "*Amphidiscosid*" OR "*Aulocalycoid*" OR "*Fieldingid*" OR "*Hexactinos*" OR "*Hexactinosid*" OR "*Hexasterophor*" OR "*Lychniscos*" OR "*Lychniscosid*" OR "*Lyssacinos*" OR "*Lyssacinosid*" OR "*Sceptrulophor*" OR "*Homosclerophorid*" OR "*Plakinid*" OR "*Collothecacea*" OR "*Flosculariacea*" OR "*Ploim*" OR "*Seisonace*" OR "*Seisonid*" OR "*Apochel*" OR "*Parachel*" OR "*Arthrotardigrad*" OR "*Echiniscoide*" **) AND (("population*" OR "range*" OR "range edge*" OR "geograph*" OR "distribution*" OR "limit*") NEAR/2 ("shift*" OR "extension*" OR "expansion*")))**

A:

TS = (("east* Pacific" OR "northeast* pacific" OR "Alaska" OR "BC" OR "California" OR "Oregon" OR "Washington") AND ("ocean*" OR "sea*" OR "marine*" OR "*tidal" OR "coast*") AND ("invertebrate*" OR (("*tidal" OR "*benthic" OR "*fouling") NEAR/0 ("species" OR "community")) OR"*Eoacanthocephal*" OR "*Palaeacanthocephal*" OR "*Clitellat*" OR "*Gephyre*" OR "*Polychaet*" OR "*Branchiopod*" OR "*Cephalocarid*" OR "*Copepod*" OR "*Hexanaupli*" OR "*Ichthyostrac*" OR "*Malacostrac*" OR "*Maxillopod*" OR "*Merostomat*" OR "*Ostracod*" OR "*Pycnogonid*" OR "*Remipedi*" OR "*Tantulocarid*" OR "*Thecostrac*" OR "*Articulat*" OR "*Craniat*" OR "*Lingulat*" OR "*Rhynchonellat*" OR "*Gymnolaemat*" OR "*Stenolaemat*" OR "*Sagittoide*" OR "*Appendiculari*" OR "*Ascidiace*" OR "*Larvace*" OR "*Leptocardi*" OR "*Myxin*" OR "*Sorberace*" OR "*Thaliace*" OR "*Anthozo*" OR "*Cubomedusa*" OR "*Cubozo*" OR "*Hexacoralli*" OR "*Hydrozo*" OR "*Myxozo*" OR "*Octocoralli*" OR "*Scyphomedusa*" OR "*Scyphozo*" OR "*Staurozo*" OR "*Zoanthari*" OR

"*Gastroide*" OR "*Nud*" OR "*Tentaculat*" OR "*Eucycliophor*" OR "*Rhombozo*" OR "*Adelostellat*" OR "*Asteroide*" OR "*Asteroide*" OR "*Crinoide*" OR "*Crinoide*" OR "*Echinoide*" OR "*Echinoide*" OR "*Holothurioide*" OR "*Holothuroide*" OR "*Holothuroide*" OR "*Klot*" OR "*Ophiuroide*" OR "*Ophiuroide*" OR "*Stelleroide*" OR "*Enteropneust*" OR "*Graptolithoide*" OR "*Pterobranchi*" OR "*Allomalorhagid*" OR "*Cyclorhagid*" OR "*Homalorhaga*" OR "*Amphineur*" OR "*Bivalvi*" OR "*Caudofoveat*" OR "*Cephalopod*" OR "*Conchifer*" OR "*Gastropod*" OR "*Lamellibranchiat*" OR "*Loricat*" OR "*Monoplacophor*" OR "*Pelecypod*" OR "*Polyplacophor*" OR "*Polyplaxiphor*" OR "*Scaphopod*" OR "*Solenoconchi*" OR "*Solenogastre*" OR "*Adenophore*" OR "*Chromadore*" OR "*Enople*" OR "*Secernente*" OR "*Gordia*" OR "*Gordioid*" OR "*Gordioide*" OR "*Nectonematoid*" OR "*Anopl*" OR "*Arhynchocoel*" OR "*Enopl*" OR "*Hoplonemerte*" OR "*Palaeonemerte*" OR "*Pilidiophor*" OR "*Polyplacotomi*" OR "*Uniplacotomi*" OR "*Cestod*" OR "*Monogene*" OR "*Monogenoide*" OR "*Monopisthocotyl*" OR "*Polyopisthocotyl*" OR "*Trematod*" OR "*Turbellari*" OR "*Afrenulat*" OR "*Frenulat*" OR "*Calcare*" OR "*Calcispongi*" OR "*Calcispongia*" OR "*Demospongia*" OR "*Hexactinellid*" OR "*Homoscleromorph*" OR "*Hyalospongia*" OR "*Sclerospongia*" OR "*Eurotatori*" OR "*Pararotatori*" OR "*Seisonide*" OR "*Eutardigrad*" OR "*Heterotardigrad*" OR "*Xenoturbellid*" OR "*Acanthocephal*" OR "*Annelid*" OR "*Arthropod*" OR "*Aschelminthe*" OR "*Brachiopod*" OR "*Bryozo*" OR "*Cephalorhynch*" OR "*Chaetognath*" OR "*Cnidari*" OR "*Ctenophor*" OR "*Cycliophor*" OR "*Dicyemid*" OR "*Echinodermat*" OR "*Ectoproct*" OR "*Entoproct*" OR "*Gastrotrich*" OR "*Gnathostomulid*" OR "*Hemichordat*" OR "*Kinorhynch*" OR "*Loricifer*" OR "*Mesozo*" OR "*Mollusc*" OR "*Nematod*" OR "*Nematomorph*" OR "*Nemerte*" OR "*Nemertin*" OR "*Nemertin*" OR "*Orthonectid*" OR "*Pentastomid*" OR "*Phoronid*" OR "*Placozo*" OR "*Platyhelminthe*" OR "*Pogonophor*" OR "*Porifer*" OR "*Priapulid*" OR "*Rotatori*" OR "*Rotifer*" OR "*Sipunculid*" OR "*Tardigrad*" OR "*Xenacoelomorph*" OR "*Chelicerat*" OR "*Crustace*" OR "*Pancrustace*" OR "*Tetraconat*" OR "*Craniiforme*" OR "*Linguliforme*" OR "*Rhynchonelliforme*" OR "*Cephalochordat*" OR "*Tunicat*" OR "*Urochordat*" OR "*Endocnidozo*" OR "*Medusozo*" OR "*Asterozo*" OR "*Crinozo*" OR "*Echinozo*" OR "*Aculifer*" OR "*Placophor*" OR "*Catenulid*" OR "*Rhabditophor*" OR "*Obturat*" OR "*Perviat*" OR "*Silice*" OR "*Acoelomorph*" OR "*Xenacoel*" OR "*Allotriocarid*" OR "*Multicrustace*" OR "*Oligostrac*" OR "*Aplacophor*" OR "*Neonemerte*" OR "*Pronemerte*" OR "*Neodermat*" OR "*Gyracanthocephal*" OR "*Neoechinorhynchid*" OR "*Echinorhynchid*" OR "*Polymorphid*" OR "*Capilloventrid*" OR "*Crassiclitellat*" OR "*Enchytraeid*" OR "*Haplotaxid*" OR "*Lumbriculid*" OR "*Oligochaet*" OR "*Randiellid*" OR "*Tubificid*" OR "*Arhynchobdellid*" OR "*Rhynchobdellid*" OR "*Echiur*" OR "*Echiuroide*" OR "*Amphinomid*" OR "*Eunicid*" OR "*Phyllodocid*" OR "*Archiannelid*" OR "*Psammodrilid*" OR "*Spintherid*" OR "*Sabellid*" OR "*Spionid*" OR "*Terebellid*" OR "*Capitellid*" OR "*Cossurid*" OR "*Opheliid*" OR "*Orbiniid*" OR "*Anomopod*" OR "*Cladocer*" OR "*Ctenopod*" OR "*Gymnomer*" OR "*Haplopod*" OR "*Onychopod*" OR "*Spinicaudat*" OR "*Brachypod*" OR "*Herpyllobioid*" OR "*Platycopioid*" OR "*Calanoid*" OR "*Andreinide*" OR "*Canuelloid*" OR "*Cyclopide*" OR "*Cyclopoid*" OR "*Harpacticoid*" OR "*Lerneopodide*" OR "*Misophrioid*" OR "*Monstrilloid*" OR "*Mormonilloid*" OR "*Philichthyide*" OR "*Sarcotacide*" OR "*Siphonostomatoid*" OR "*Thaumatopsylloid*" OR "*Arguloid*" OR "*Cephalobaenid*" OR "*Porocephalid*" OR "*Raillietiellid*" OR "*Reighardiid*" OR "*Stomatopod*" OR "*Leptostrac*" OR "*Amphionidace*" OR "*Decapod*" OR "*Euphausiace*" OR "*Amphipod*" OR "*Anisopod*" OR "*Bochusace*" OR "*Cumace*" OR "*Ingolfiellid*" OR "*Isopod*" OR "*Lophogastrid*" OR "*Mictace*" OR "*Mysid*" OR "*Mysidace*" OR "*Stygiomysid*" OR "*Tanaidace*" OR "*Thermosbaenace*" OR "*Bathynellace*" OR "*Palaeocaridace*" OR "*Xiphosurid*" OR "*Cladocop*" OR "*Halocyprid*" OR "*Myodocopid*" OR "*Cladocopid*" OR "*Platycopid*" OR "*Podocop*" OR "*Podocopid*" OR "*Punciocopid*" OR "*Beyrichiid*" OR "*Pantopod*" OR "*Nectiopod*" OR "*Dendrogastrid*" OR "*Laurid*" OR "*Apygophor*" OR "*Cryptophialid*" OR "*Lithoglyptid*" OR "*Pygophor*" OR "*Akentrogonid*"

OR "*Kentrogonid*" OR "*Lepadiforme*" OR "*Pedunculat*" OR "*Scalpelliforme*" OR "*Sessili*" OR "*Ibliforme*" OR "*Iblomorph*" OR "*Balanomorph*" OR "*Calanticomorph*" OR "*Pollicipedomorph*" OR "*Scalpellomorph*" OR "*Verrucomorph*" OR "*Craniid*" OR "*Lingulid*" OR "*Rhynchonellid*" OR "*Terebratulid*" OR "*Thecideid*" OR "*Cheilostomat*" OR "*Cheilostomatid*" OR "*Ctenostomat*" OR "*Ctenostomatid*" OR "*Cyclostomat*" OR "*Cyclostomatid*" **) AND (("population*" OR "range*" OR "range edge*" OR "geograph*" OR "distribution*" OR "limit*") NEAR/2 ("shift*" OR "extension*" OR "expansion*")))**

B:

TS = (("east* Pacific" OR "northeast* pacific" OR "Alaska" OR "BC" OR "California" OR "Oregon" OR "Washington") AND ("ocean*" OR "sea*" OR "marine*" OR "*tidal" OR "coast*") AND ("invertebrate*" OR (("*tidal" OR "*benthic" OR "*fouling") NEAR/0 ("species" OR "community")) OR "*Esthonioporat*" OR "*Aphragmophor*" OR "*Phragmophor*" OR "*Copelat*" OR "*Aplousobranchi*" OR "*Enterogon*" OR "*Phlebobranchi*" OR "*Pleurogon*" OR "*Stolidobranchi*" OR "*Myxiniforme*" OR "*Aspiraculat*" OR "*Cyclomyari*" OR "*Desmomyari*" OR "*Doliolid*" OR "*Pyrosomatid*" OR "*Salpid*" OR "*Carybdeid*" OR "*Chirodropid*" OR "*Actiniari*" OR "*Antipathari*" OR "*Cerianthari*" OR "*Ceriantipathari*" OR "*Corallimorphari*" OR "*Coralliomorphari*" OR "*Ptychodactiari*" OR "*Scleractini*" OR "*Zoanthide*" OR "*Zoanthiniari*" OR "*Hydroid*" OR "*Milleporin*" OR "*Trachylin*" OR "*Anthoathecat*" OR "*Anthoathecata*" OR "*Anthomedusa*" OR "*Athecat*" OR "*Gymnoblaste*" OR "*Laingiomedusa*" OR "*Leptomedusa*" OR "*Leptothecat*" OR "*Siphonophor*" OR "*Siphonophora*" OR "*Thecaphor*" OR "*Thecat*" OR "*Actinulid*" OR "*Limnomedusa*" OR "*Narcomedusa*" OR "*Trachomedusa*" OR "*Trachymedusa*" OR "*Bivalvulid*" OR "*Multivalvulid*" OR "*Alcyonace*" OR "*Gorgonace*" OR "*Helioporace*" OR "*Malacalcyonace*" OR "*Pennatulace*" OR "*Scleralcyonace*" OR "*Coronata*" OR "*Rhizostomea*" OR "*Semaeostomea*" OR "*Stauromedusa*" OR "*Madreporari*" OR "*Beroid*" OR "*Archiplanoide*" OR "*Cambojiid*" OR "*Cestid*" OR "*Cryptolobiferid*" OR "*Cydippid*" OR "*Ganeshid*" OR "*Lobat*" OR "*Platyctenid*" OR "*Platyctenida*" OR "*Thalassocalycid*" OR "*Symbiid*" OR "*Heterocyemid*" OR "*Euclasteroide*" OR "*Platyasterid*" OR "*Peripodid*" OR "*Velatid*" OR "*Brisingid*" OR "*Forcipulatid*" OR "*Spinulosid*" OR "*Notomyotid*" OR "*Paxillosid*" OR "*Valvatid*" OR "*Bourgueticrinid*" OR "*Comatulid*" OR "*Cyrtocrinid*" OR "*Hyocrinid*" OR "*Isocrinid*" OR "*Latistellat*" OR "*Cidaroid*" OR "*Echinothuroid*" OR "*Pourtalesioid*" OR "*Diadematoid*" OR "*Micropygoid*" OR "*Aspidodiadematoid*" OR "*Echinothurioid*" OR "*Pedinoid*" OR "*Arbacioid*" OR "*Camarodont*" OR "*Echinoid*" OR "*Salenioid*" OR "*Stomopneustoid*" OR "*Temnopleuroid*" OR "*Holasteroid*" OR "*Spatangide*" OR "*Spatangoid*" OR "*Echinoneoid*" OR "*Clypeasteroid*" OR "*Echinolampadace*" OR "*Aspidochirot*" OR "*Aspidochirotid*" OR "*Dactylochirotid*" OR "*Dendrochirot*" OR "*Dendrochirotid*" OR "*Elasipodid*" OR "*Holothuriid*" OR "*Molpadid*" OR "*Molpadiid*" OR "*Persiculid*" OR "*Synallactid*" OR "*Apod*" OR "*Apodid*" OR "*Synaptid*" OR "*Euryala*" OR "*Gnathophiurid*" OR "*Ophiura*" OR "*Phrynophiurid*" OR "*Euryalid*" OR "*Ophiurid*" OR "*Amphilepidid*" OR "*Ophiacanthid*" OR "*Ophioleucid*" OR "*Ophioscolecid*" OR "*Cephalodiscoide*" OR "*Rhabdopleuroide*" OR "*Anomoirhag*" OR "*Echinorhagat*" OR "*Kentrorhagat*" OR "*Xenosomat*" OR "*Manzanellid*" OR "*Nuculanid*" OR "*Nuculid*" OR "*Solemyid*" OR "*Arcid*" OR "*Limid*" OR "*Mytilid*" OR "*Ostreid*" OR "*Pectinid*" OR "*Pteriid*" OR "*Carditid*" OR "*Anomalodesmace*" OR "*Euheterodont*" OR "*Pholadomyid*" OR "*Trigoniid*" OR "*Unionid*" OR "*Adapedont*" OR "*Cardiid*" OR "*Galeommatid*" OR "*Gastrochaenid*" OR "*Hiatellid*" OR "*Lucinid*" OR "*Myace*" OR "*Myid*" OR "*Sphaeriid*" OR "*Venerid*" OR "*Chaetodermatid*" OR "*Nautilid*" OR "*Decapodiforme*" OR "*Bathyteuthid*" OR "*Idiosepid*" OR "*Myopsid*" OR "*Oegopsid*" OR "*Sepiid*" OR "*Spirulid*" OR "*Teuthid*" OR "*Octopod*" OR "*Vampyromorph*" OR "*Caenogastropod*" OR

"*Littorinimorph*" OR "*Neogastropod*" OR "*Stenogloss*" OR "*Cycloneritid*" OR "*Cycloneritimorph*" OR "*Neritimorph*" OR "*Archaeogastropod*" OR "*Mesogastropod*" OR "*Rhipidogloss*" OR "*Anisobranchi*" OR "*Cocculinid*" OR "*Lepetellid*" OR "*Neomphalid*" OR "*Pleurotomariid*" OR "*Seguenziid*" OR "*Trochid*" OR "*Architectibranchi*" OR "*Pleurobranchomorph*" OR "*Anaspide*" OR "*Aplysiid*" OR "*Aplysiomorph*" OR "*Archaeopulmonat*" OR "*Bullomorph*" OR "*Cephalaspide*" OR "*Heterostroph*" OR "*Pteropod*" OR "*Runcinace*" OR "*Runcinid*" OR "*Tectibranchiat*" OR "*Thecosomat*" OR "*Umbraculid*" OR "*Notaspide*" OR "*Nudibranchi*" OR "*Pleurobranchid*" OR "*Ellobiid*" OR "*Gymnomorph*" OR "*Stylommatophor*" OR "*Systellommatophor*" OR "*Siphonariid*" OR "*Neopilinid*" OR "*Callochitonid*" OR "*Chitonid*" OR "*Lepidopleurid*" OR "*Dentaliid*" OR "*Gadilid*" OR "*Neomeniamorph*" OR "*Pholidoskepi*" OR "*Cavibeloni*" OR "*Sterrofusti*" OR "*Aphelenchid*" OR "*Araeolaimid*" OR "*Ascaridid*" OR "*Benthimermithid*" OR "*Chromadorid*" OR "*Desmodorid*" OR "*Desmoscolecid*" OR "*Monhysterid*" OR "*Plectid*" OR "*Rhabditid*" OR "*Spirurid*" OR "*Strongylid*" OR "*Tylenchid*" OR "*Dioctophymat*" OR "*Dioctophymatid*" OR "*Dioctophymid*" OR "*Dioctophymoide*" OR "*Dorylaimid*" OR "*Marimermithid*" OR "*Mermithid*" OR "*Trichinellid*" OR "*Enoplid*" OR "*Rhaptothyreid*" OR "*Trefusiid*" OR "*Triplonchid*" OR "*Anguilluloide*" OR "*Nectonematoide*" OR "*Nectonematid*" OR "*Arhynchonemerte*" OR "*Bdellomorph*" OR "*Monostilifer*" OR "*Polystilifer*" OR "*Urichorhynchocoel*" OR "*Archinemerte*" OR "*Carinomiforme*" OR "*Tubulaniforme*" OR "*Heteronemerte*" OR "*Hubrechtiiforme*" OR "*Schizonemertin*" OR "*Polyplacotome*" OR "*Cladhexe*" OR "*Hoilunge*" OR "*Trichoplace*" OR "*Amphilinide*" OR "*Gyrocotylide*" OR "*Bothriocephalide*" OR "*Caryophyllide*" OR "*Cathetocephalide*" OR "*Cyclophyllide*" OR "*Diphyllide*" OR "*Diphyllobothriide*" OR "*Eucestod*" OR "*Lecanicephalide*" OR "*Litobothriide*" OR "*Onchoproteocephalide*" OR "*Phyllobothriide*" OR "*Proteocephalide*" OR "*Pseudophyllide*" OR "*Rhinebothriide*" OR "*Spathebothriide*" OR "*Tetrabothriide*" OR "*Tetraphyllide*" OR "*Trypanorhynch*" OR "*Capsalide*" OR "*Dactylogyrid*" OR "*Dactylogyride*" OR "*Gyrodactylide*" OR "*Monocotylide*" OR "*Montchadskyellide*" OR "*Chimaericolide*" OR "*Diclybothriide*" OR "*Mazocraeide*" OR "*Polystomatide*" OR "*Aspidogastrid*" OR "*Stichocotylid*" OR "*Azygiid*" OR "*Bucephalidid*" OR "*Digene*" OR "*Diplostomid*" OR "*Echinostomid*" OR "*Faustulid*" OR "*Plagiorchiid*" OR "*Strigeid*" OR "*Strigeidid*" OR "*Vestimentifer*" OR "*Athecanephri*" OR "*Thecanephri*" OR "*Heterocoel*" OR "*Homocoel*" OR "*Baeriid*" OR "*Leucosolenid*" OR "*Lithonid*" OR "*Sycettid*" OR "*Syconos*" OR "*Asconos*" OR "*Clathrinid*" OR "*Leucettid*" OR "*Murrayonid*" OR "*Gumminea*" OR "*Halisarcid*" OR "*Lithistid*" OR "*Agelasid*" OR "*Ancorinid*" OR "*Astrophorid*" OR "*Axinellid*" OR "*Biemnid*" OR "*Bubarid*" OR "*Ceratoporellid*" OR "*Choristid*" OR "*Clionaid*" OR "*Craniellid*" OR "*Desmacellid*" OR "*Desmacidonitid*" OR "*Hadromerid*" OR "*Halichondrid*" OR "*Haplosclerid*" OR "*Heteroscleromorph*" OR "*Merliid*" OR "*Nepheliospongid*" OR "*Petrosid*" OR "*Poecillastrid*" OR "*Poecilosclerid*" OR "*Polymastiid*" OR "*Scopalinid*" OR "*Sphaerocladin*" OR "*Spirastrellid*" OR "*Spirophorid*" OR "*Spongillid*" OR "*Suberitid*" OR "*Tethyid*" OR "*Tetractinellid*" OR "*Trachycladid*" OR "*Dendroceratid*" OR "*Dictyoceratid*" OR "*Keratosid*" OR "*Verticillitid*" OR "*Chondrillid*" OR "*Chondrosid*" OR "*Chondrosiid*" OR "*Verongid*" OR "*Verongiid*" OR "*Amphidiscosid*" OR "*Aulocalycoid*" OR "*Fieldingid*" OR "*Hexactinos*" OR "*Hexactinosid*" OR "*Hexasterophor*" OR "*Lychniscos*" OR "*Lychniscosid*" OR "*Lyssacinos*" OR "*Lyssacinosid*" OR "*Sceptrulophor*" OR "*Homosclerophorid*" OR "*Plakinid*" OR "*Collothecacea*" OR "*Flosculariacea*" OR "*Ploim*" OR "*Seisonace*" OR "*Seisonid*" OR "*Apochel*" OR "*Parachel*" OR "*Arthrotardigrad*" OR "*Echiniscoide*" **) AND (("population*" OR "range*" OR "range edge*" OR "geograph*" OR "distribution*" OR "limit*") NEAR/2 ("shift*" OR "extension*" OR "expansion*")))**

Supplementary References

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

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*.

Braid, H. E., Deeds, J., DeGrasse, S. L., Wilson, J. J., Osborne, J., & Hanner, R. H. (2012a). 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

Braid, H. E., Deeds, J., DeGrasse, S. L., Wilson, J. J., Osborne, J., & Hanner, R. H. (2012b). 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

Brand, T. van den. (2025). *ggh4x: Hacks for `ggplot2'*. https://CRAN.R-project.org/package=ggh4x

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*.

Chamberlain, S., Szoecs, E., Foster, Z., Arendsee, Z., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner, J., O'Donnell, J., Oksanen, J., Tzovaras, B. G., Marchand, P., Tran, V., Salmon, M., Li, G., & Grenié, M. (2020). *taxize: Taxonomic information from around the web*. https://github.com/ropensci/taxize

Chamberlain, S., Zhu, H., Jahn, N., Boettiger, C., & Ram, K. (2022). *rcrossref: Client for Various `CrossRef' `APIs'*. https://CRAN.R-project.org/package=rcrossref

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

Commercial use of the jumbo squid, Dosidicus gigas. (1936). *California Fish and Game*, *22*, 143–144.

Cosgrove, J. (2005). The first specimens of Humboldt squid in Briish 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

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*.

Hijmans, R. J. (2024). *geosphere: Spherical Trigonometry*. https://CRAN.R-project.org/package=geosphere

Hvitfeldt, E. (2021). *paletteer: Comprehensive Collection of Color Palettes*. https://github.com/EmilHvitfeldt/paletteer

Iannone, R., Cheng, J., Schloerke, B., Hughes, E., Lauer, A., Seo, J., Brevoort, K., & Roy, O. (2025). *gt: Easily Create Presentation-Ready Display Tables*. https://CRAN.R-project.org/package=gt

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

Komsta, L., & Novomestky, F. (2022). *moments: Moments, Cumulants, Skewness, Kurtosis and Related Tests*. https://CRAN.R-project.org/package=moments

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

Massicotte, P., & South, A. (2023). *rnaturalearth: World Map Data from Natural Earth*. https://CRAN.R-project.org/package=rnaturalearth

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

Müller, K. (2020). *here: A Simpler Way to Find Your Files*. https://CRAN.R-project.org/package=here

O'Loughlin, J. H., Bernard, K. S., Daly, E. A., Zeman, S., Fisher, J. L., Brodeur, R. D., & Hurst, T. P. (2020). Implications of Pyrosoma atlanticum range expansion on phytoplankton standing stocks in the Northern California Current. *Progress in Oceanography*, *188*, 102424. https://doi.org/10.1016/j.pocean.2020.102424

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

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439–446. https://doi.org/10.32614/RJ-2018-009

Pebesma, E., & Bivand, R. (2023). *Spatial Data Science: With applications in R*. Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016

Pedersen, T. L., & Robinson, D. (2025). *gganimate: A Grammar of Animated Graphics*. https://CRAN.R-project.org/package=gganimate

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

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

Schauberger, P., & Walker, A. (2025). *openxlsx: Read, Write and Edit xlsx Files*. https://CRAN.R-project.org/package=openxlsx

Scott Chamberlain & Eduard Szocs. (2013). taxize—Taxonomic search and retrieval in R. *F1000Research*. https://f1000research.com/articles/2-191/v2

South, A., Michael, S., & Massicotte, P. (2024). *rnaturalearthdata: World Vector Map Data from Natural Earth Used in `rnaturalearth'*. https://CRAN.R-project.org/package=rnaturalearthdata

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

Weber, E. D., Auth, T. D., Baumann-Pickering, S., Baumgartner, T. R., Bjorkstedt, E. P., Bograd, S. J., Burke, B. J., Cadena-Ramírez, J. L., Daly, E. A., de la Cruz, M., Dewar, H., Field, J. C., Fisher, J. L., Giddings, A., Goericke, R., Gomez-Ocampo, E., Gomez-Valdes, J., Hazen, E. L., Hildebrand, J., … Zeman, S. M. (2021). State of the California Current 2019–2020: Back to the Future With Marine Heatwaves? *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.709454

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*.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wickham, H., Pedersen, T. L., & Seidel, D. (2023). *scales: Scale Functions for Visualization*. https://CRAN.R-project.org/package=scales

Wilke, C. O. (2025). *cowplot: Streamlined Plot Theme and Plot Annotations for `ggplot2'*. https://CRAN.R-project.org/package=cowplot

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

Wood, S. N. (2003). Thin-plate regression splines. *Journal of the Royal Statistical Society (B)*, *65*(1), 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

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