

Anomalous poleward advection facilitates episodic range expansions of pelagic red crabs in the eastern North Pacific

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Abstract

The episodic stranding of millions of pelagic red crabs (*Pleuroncodes planipes*) along California beaches is a striking and puzzling phenomenon. *Pleuroncodes planipes* are usually abundant off Baja California, Mexico, and their appearance in central California is thought to coincide with anomalously warm waters and northward advection related to El Niño. This anecdotal association has stimulated many hypotheses, but no hypothesis has gained clear and convincing support. Motivated by an unprecedented number of *P. planipes* strandings and at-sea observations in 2015–2019, we compiled 10 *P. planipes* datasets spanning 1950–2019, tested the anomalous advection hypothesis using a transport analysis from 1981 to 2010, and explored other compelling hypotheses. We found *P. planipes* presence off central California was related to anomalous advection of waters from Mexico, sometimes but not always associated with El Niño events, with *P. planipes* likely remaining residents of northern waters for several years without additional anomalous transport but potentially facilitated by warm waters. By identifying a mechanism behind episodic *P. planipes* range expansions, we show that a source water index could provide an early indicator for anomalous events in the future.

Oceans are undergoing unprecedented changes as a result of anthropogenic warming, leading to shifts in species distributions, new ecological interactions, and fundamental changes to

ecosystem structure and function (Poloczanska et al. 2013). Indicator species that are easy to sample and exhibit a strong response to environmental variation can provide a means of tracking changes in marine systems that are otherwise difficult to observe (Zacharias and Roff 2001; Hazen et al. 2019). Yet, identifying species that are reliable indicators of anomalous conditions, and resolving mechanistic links between such species and underlying bio-physical processes, are challenging but important goals in contemporary ecology.

Extreme anomalous warm water events, also known as marine heatwaves, have been associated with species in the California Current sighted well outside of their typical home range (Cavole et al. 2016; Lonhart et al. 2019). In particular, the 2014–2016 period in the northeast Pacific saw a prolonged marine heatwave that included the “Blob” (Bond et al. 2015), its evolution to a coastwide warming pattern (Amaya et al. 2016), and the effects of the strong 2015–2016 El Niño (Jacox et al. 2016). Species distribution or abundance shifts reported during this period include

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Additional Supporting Information may be found in the online version of this article.

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67 southern species with 37 unprecedented northern range extensions (Sanford et al. 2019), including unusual occurrences of 36 fish species in Southern California waters from 2014 to 2018 (Walker et al. 2020).

The pelagic red crab (*Pleuroncodes planipes*) is notable because of its importance as forage in the marine food web and conspicuous nature when mass stranding on beaches (Fig. S1; Stimpson 1860). *Pleuroncodes planipes* are typically sub-tropical with a home range off the southwest coast of the Baja California peninsula, yet were sighted as far north as Oregon, U.S.A in 2017 (Sanford et al. 2019). While mass strandings occur regularly in Baja California, strandings in California are historically infrequent events (Boyd 1967; Aurióles-Gamboa et al. 1994). Even with stranding reports increasing after 2014 (Sanford et al. 2019), we still lack a complete understanding of how these events are triggered and how the frequency of such events will change as oceans warm. Furthermore, a general understanding of larval and adult transport, dispersal patterns, and connectivity is needed (e.g., White et al. 2019).

While the life cycle and habitat requirements of *P. planipes* are not fully understood, their ecological importance and ability to serve as a sentinel of anomalous conditions are clear. *Pleuroncodes planipes* have been observed to be both pelagic and benthic at 1–2 yr old and are presumed benthic at 3 yr, though diel vertical migration has been observed (Boyd 1962; Robinson and Gómez-Gutiérrez 1998; Nickels et al. 2019). In the benthic phase, *P. planipes* are abundant along the Baja California continental shelf and undergo an across-shore spawning migration to breed inshore in the winter/spring, returning to cooler slope waters afterward (Boyd 1967; Aurióles-Gamboa 1992; Gómez-Gutiérrez et al. 2000). Planktonic larvae are believed to be swept offshore, returning to the shelf via an opposing undercurrent at depth that is attributed to the conveyor belt of coastal upwelling. During this time, they undergo five morphologically discrete phases, with the duration of each phase shortened by warmer water temperatures (Boyd and Johnson 1963; Longhurst 1967). The highest densities of adult *P. planipes* have been documented at temperatures between 13°C and 16°C, but they can withstand a wide temperature range (at least 9–28°C) and tolerate low oxygen environments (Longhurst 1967; Aurióles-Gamboa 1992; Seibel et al. 2018). *Pleuroncodes planipes* play important trophic roles, being phytoplanktivorous and omnivorous (Longhurst et al. 1967; Aurióles-Gamboa and Pérez-Flores 1997) and serving as an abundant, high-quality food source for many species, including commercially important fish, squid, birds, and whales (Mathews 1932; Alverson 1963; Bazzino et al. 2010).

In California, the mechanisms driving *P. planipes* mass strandings and episodic range expansions remain unclear, but the classic hypothesis explaining the phenomenon is poleward advection or a “system of northerly-moving counter-currents” (Boyd 1967; Longhurst 1967). In general, the California Undercurrent flows northward at depth along the continental

slope, with seasonal and interannual variations in strength (Lynn and Simpson 1987; Lynn and Bograd 2002). At the surface, the seasonally varying Davidson Current flows northward along the coast and is strongest in winter (Lynn and Simpson 1987). Additionally, poleward flow off southern California can be stronger during El Niño (Lynn and Bograd 2002; Bograd et al. 2019) and has been hypothesized to transport southern species into northern waters during these events. Thus, *P. planipes* sightings in California have historically been viewed as an indicator of El Niño impacts, and poleward flow driven by El Niño is the contemporary presumed mechanism behind *P. planipes* range expansions (Longhurst 1967; Stewart et al. 1984; Longhurst et al. 2004). While a preliminary examination of the mean anomalies in alongshore currents did not indicate anomalous transport during 2014–2016 (Zaba and Rudnick 2016), the poleward advection hypothesis remains plausible as alongshore current anomalies could be too simplistic to detect a signal (Rudnick et al. 2017). Furthermore, the poleward advection mechanism has not been adequately tested, and other reasonable hypotheses such as changes in *P. planipes* vital rates driving *P. planipes* range expansions also exist.

Here, we aggregate all available data on *P. planipes* distributions from Baja California, Mexico, to the northwestern U.S. and present a 70-yr time series of *P. planipes* occurrence, revealing the episodic nature of *P. planipes* appearance along the U.S. West Coast. Using these observations, we test the anomalous poleward advection hypothesis using a transport analysis from 1981 to 2010, then summarize other compelling hypotheses that could also explain why *P. planipes* episodically appear up to a thousand kilometers north of their usual range. We show that *P. planipes* presence in central California is an indicator of anomalous oceanic currents and suggest that *P. planipes* distribution may be a useful way of tracking changes in the distribution and ecology of other species, including *P. planipes* predators that follow their prey. Our results have implications for understanding mechanisms of species range expansion via transport and dispersal in boundary current systems related to both anomalous events and secular climate change.

Materials and methods

Data sources for *P. planipes* observations

There is no dedicated observation program aimed at monitoring the distribution and abundance of *P. planipes* along the west coast of North America, but many studies record *P. planipes* observations. Therefore, to understand the distribution of *P. planipes* and possible explanations for episodic northward range expansions, we combined data from many different sources including historic literature, multiple oceanographic research surveys, remotely operated vehicles (ROVs), citizen science programs, and online media. Research surveys include California Cooperative Oceanic Fisheries

Investigations (CalCOFI), Investigaciones MEXicanas de la COrriente de CALifornia (IMECOCAL), Rockfish Recruitment and Ecosystem Assessment Survey (RREAS), West Coast Groundfish Bottom Trawl Survey, and Coastal Pelagic Species surveys (CPS). Citizen science data were harvested from the Global Biodiversity Information Facility (GBIF). Some data sources provided true presence and absence information (i.e., if *P. planipes* were not documented then they were not present), while for other sources, it is unclear if *P. planipes* were truly absent or simply undocumented, as they may not have been included in original protocols. The lack of abundance and absence data is a caveat that we acknowledge. Each data source is described below and summarized in Table S1.

Historic literature

We compiled *P. planipes* observations from published reports (Table S2). Many reports contained anecdotal information with general locations or time periods of observations, while others were more precise. When necessary, we estimated the approximate time period (e.g., corresponding months from seasons) and location (e.g., city latitude).

California cooperative oceanic fisheries investigations

Densities ($\log_{10}(\text{number}) \cdot \text{m}^{-2}$) of *P. planipes* larval stages (zoea 1–5) and megalopa were obtained from CalCOFI, which sampled zooplankton and ichthyoplankton during quarterly cruises from 1951 to present. Due to funding limitations, sampling was done every third year from 1966 to 1984 until quarterly cruises began again in 1984. The sampling domain encompasses southern California but extends from San Diego to San Francisco for most spring cruises. A 1-m diameter ring net with a silk 550 μm mesh was towed obliquely (45°) from 140 m to the surface from 1951 to 1968. The tow depth was extended to 210 m and a 505 μm nylon mesh net was used beginning in 1969. In 1978, the ring net was replaced with a 0.71 m diameter double bongo net (Ohman and Smith 1995).

Data on the abundances of *P. planipes* early life history stages were downloaded from the CalCOFI Zooplankton Database (<http://oceaninformatics.ucsd.edu/zoodb/>). We used all available unpooled data (i.e., individual samples; Lavaniegos and Ohman 2003) from 1951 to 2015. No net correction factors were used, since previous studies only documented different catchabilities for euphausiids and salps (Ohman and Smith 1995; Ohman and Lavaniegos 2002). However, there may be differences in *P. planipes* early life stage catchability if their depth range exceeds 140 m. It should be noted that most sorted samples are from springtime cruises, and only select years have been enumerated; therefore, our coverage is not complete but represents the best available data in California. However, a more complete, “pooled” time series in which aliquots of station-specific samples were combined into a standardized volume of water have been enumerated from 1951 to 2015. This pooled time series offers a more complete record, albeit with a loss of spatial resolution.

Investigaciones MEXicanas de la COrriente de CALifornia

Quarterly IMECOCAL surveys were conducted between 1997 and 2012 off Baja California (24–32°N), and more sporadically between 2013 and 2016 due to funding limitations. A bongo net was obliquely towed in the upper 200 m and all adult *P. planipes* were counted. Larval stages were counted for select stations, including four surveys in 2005, summer surveys from 2003 to 2008, and two in 2016.

Remotely operated vehicle video observations

The Monterey Bay Aquarium Research Institute (MBARI) conducts periodic ROV surveys that record high-resolution video. Using MBARI's Video Annotation and Reference System database (VARS, Schlining and Stout 2006), we queried for observations of “*Pleuroncodes planipes*” and obtained ~700 *P. planipes* observations spanning 1992–2017. VARS observations are largely nonquantitative, thus were used to infer presence only. We confirmed *P. planipes* presence for isolated observations when no other data source had records during that time (e.g., multiple records in the summer of 2010 and 2011, see Fig. S2). It should be noted that all species are manually identified so cases of misidentification are plausible especially as the range of *P. planipes* and the similarly sized squat lobster (*Munida quadrispina*) can overlap. However, the two species can often be easily distinguished by the much longer chelipeds of *M. quadrispina*. It is possible that the angle and clarity of an image could pose a challenge to verify species solely by cheliped length. As *P. planipes* is known to vertically migrate this further sets them apart but with benthic images that are not clear, it could be necessary to look at additional characteristics of physical specimens for positive identification.

Rockfish recruitment and ecosystem assessment survey

The RREAS conducted annual midwater trawls of epipelagic micronekton along central California in May/June since 1983 (<https://upwell.pfeg.noaa.gov/erddap/index.html>; Ralston et al. 2015), from San Diego to Point Delgada since 2004 (Sakuma et al. 2006), and the entire California coast since 2013 (Sakuma et al. 2016). *Pleuroncodes planipes* have been enumerated throughout the RREAS record, though we were only able to obtain presence–absence records from 1990 to 2018 and presence-only records prior to 1990. The first observations in central California occurred in 1985 ($n = 1$ individual) and 1993 ($n = 1$ individual) but larger catches were more common after the survey expanded to the south in 2004. At night, a modified-Cobb midwater trawl with a 26 m headrope, 144 m² theoretical mouth opening, and 9.5 mm cod-end mesh liner was fished at 30 m for 15 min at sampling locations. For stations with large catches of gelatinous zooplankton, trawl times were reduced to 5 min to avoid net damage. We did not implement a scaling factor as we consider only presence/absence. At shallow stations, the net was fished at 10 m to avoid bottom contact.

Benthic trawls

From 2003 to 2018, West Coast Groundfish Bottom Trawl Survey data from May to October were obtained from the NOAA Fishery Resource Analysis & Monitoring division (<https://www.nwfsc.noaa.gov/data/map>). The survey extends from the U.S.–Canada to the U.S.–Mexico border, and the depth range is 55–1280 m (Keller et al. 2017). While the survey is focused on groundfish stock assessments, it provides presence-only information on adult *P. planipes* in bottom trawls.

Coastal pelagic species surveys

As part of CPS stock-assessments, the NOAA Southwest Fisheries Science Center has conducted epipelagic trawls in spring and summer since 2003 in coastal waters of southern and central California (<https://swfsc.noaa.gov/textblock.aspx?Division=FRD&id=1113&ParentMenuId=39>). *P. planipes* were only documented in net hauls from 2015 to 2017, thus absences prior to 2015 are not absolute.

Opportunistic data from Global Biodiversity Information Facility

Pleuroncodes planipes data were downloaded from GBIF 2019, (<https://www.gbif.org>; accessed 11-03-2018) using the search term “*Pleuroncodes planipes*.” Data without date or location information or not considered “research quality” were removed. This search contained 314 observations from nine sources, including iNaturalist.

Stranding media reports

Stranding events were identified using Twitter and the search terms “pelagic red crab” and “tuna crab.” Strandings were confirmed when photographs accompanied sightings. Latitudes and longitudes were estimated where a city or beach was recorded, and the stranding date was the earliest observation when multiple records existed.

Observer reports

There were individuals who shared their personal observations of *P. planipes* either in the water (diving observations from Tom Laidig, NOAA SWFSC; at-sea observations from the NOAA research vessel Reuben Lasker, Emily Gardner) or on the beach (Jerrold Norton, NOAA SWFSC and Sue Lisin, Monterey Bay Aquarium). We also included records in Sanford et al. (2019) and McClatchie et al. (2016).

Environmental data

Oceanic Niño Index

The Oceanic Niño Index (ONI) was obtained from the NOAA Climate Prediction Center (<https://www.esrl.noaa.gov/psd/data/correlation/oni.data>), and is the 3-month running mean of sea surface temperature (SST) anomalies in the Niño-3.4 region.

Regional ocean model

Oceanographic fields were obtained from a historical reanalysis of the California Current system performed using the Regional Ocean Modeling System (ROMS) with four-dimensional variational data-assimilation (Moore et al. 2013). The model configuration is described in Neveu et al. (2016). The domain spans the U.S. West Coast (30–48°N) and extends from the coast to 134°W (~ 1000 km offshore) with a horizontal resolution of 0.1° (7–11 km) and 42 terrain-following levels resolving the vertical ocean structure. Data assimilated in the model include satellite SST and sea surface height as well as *in situ* temperature and salinity profiles from bathythermographs, ship-based CTD sensors, and Argo profiling floats. For applications where ocean conditions cannot be adequately characterized solely by observations (with limited spatiotemporal coverage) or models (which may not faithfully represent the true ocean state), reanalyses combine the two to offer improved estimates of the ocean state (e.g., Edwards et al. 2015). Atmosphere and ocean reanalyses are often treated as observations when gridded, gap-free environmental information is needed, and the California Current reanalysis employed herein has been used extensively to study the California Current ocean state and its response to interannual-to-decadal climate variability, bottom-up drivers of productivity, and the distribution of marine species (Jacox et al. 2014; Jacox et al. 2016; Becker et al. 2019).

Transport analysis

Source waters to the coastal ocean off central California, a region with episodic *P. planipes* observations, were quantified using back trajectories of passive tracers. The ROMS reanalysis provided the circulation fields for the back trajectories, which were calculated using the adjoint of the ROMS tangent linear model (Moore et al. 2004). Several studies have used the ROMS adjoint in this capacity—elucidating the origins of discrete water parcels by propagating passive tracers from a specified region backward in time to determine their origins. In particular, this method has been used to explore the sensitivity of upwelling source waters in California Current to surface forcing (Song et al. 2011), El Niño (Jacox et al. 2015), and decadal variability (Chhak and Di Lorenzo 2007).

We seeded passive tracers in the surface mixed layer of a coastal region off central California (35–37°N, 0–50 km from shore) and tracked them backward in time to determine the origins of water that ultimately reach central California. We used a historical ROMS reanalysis available from 1981 to 2010 to back-calculate trajectories, which were initialized every month and were run backward in time for three months. To quantify the contribution of southern source waters, for each back trajectory we calculated the fraction of tracer that originated south of the U.S.–Mexico border (32.5°N) 3 months prior to arriving off central California. This cutoff is the northern limit of IMECOCAL surveys and the southern limit of many U.S.–based surveys, which often observe adult *P. planipes*. Thus, we tested

if range expansions could result from the transport of adult *P. planipes* from their usual northern range limit. This calculation provides a monthly “southern source water index” (SSWI) that we used to estimate the potential for anomalous advection from the south to influence *P. planipes* distribution in central California. Due to the change in the model’s wind forcing from the 2.5° ERA 40 product to the higher resolution (0.25°) CCMP product in 1988, the variance of the index prior to 1988 is adjusted for consistency in the magnitude of the seasonal cycle between the pre- and post-1988 periods.

Statistical analyses

We tested whether the occurrence of adult *P. planipes* in central California (35–37°N) in the fall was statistically related to annually averaged SST and SSWI (within 30–37°N and 0–50 km from shore), and mean summer/fall ONI (June–December) from 1981 to 2010. The summer/fall ONI average was used to account for a delayed response to the tropical signal. This analysis focused on adults due to the comparative lack of and inconsistent enumeration of larval data; additionally, larvae are more difficult to detect and are likely affected differently by transport and vital rate mechanisms relative to adult life stages. Generalized additive models (GAMs) were fit using the R “mgcv” package (R Core Team 2019) because they are capable of fitting complex nonlinear relationships, and a smoothness parameter(s) was estimated by generalized cross-validation. Pearson correlation coefficients between the three predictor variables revealed they were not highly related ($R < 0.5$). We ran models with binomial error distributions including all combinations of the predictor variables. Models were ranked using the Akaike information criterion corrected for small sample size (AIC_c) to identify the models that explained the most deviance, had the best balance between bias and precision, and were not overfit (Burnham and Anderson 2002). Models with a $\Delta\text{AIC}_c < 2$ were considered to have substantial support. As an indication of model performance, we reported the percentage of deviance explained and Akaike weight.

We also tested whether SST and SSWI values were significantly different during years when *P. planipes* were not present, when there was a new presence (i.e., no observations in the prior year) and when they were considered to be resident (i.e., observations in the prior year). We recognize the small sample size of presence and residence observations ($n \leq 5$) but by using multiple statistical tests, we aimed to more thoroughly investigate possible drivers of *P. planipes* range expansions. We used an analysis of variance (ANOVA) followed by a multiple comparison test using Tukey’s Honest Significant Difference method to determine if the means differed between groups.

Results

Pleuroncodes planipes distributions

Ten datasets documenting the temporal and latitudinal distribution of larval and adult *P. planipes* were collated from

historical observations, scientific surveys, and media and citizen science platforms, resulting in over 2000 occurrence records (Fig. 1a). Citizen science data played an important role in this research as the public was actively engaged in reporting stranding events. We document the largest latitudinal expansion of *P. planipes* adults (compared to Sanford et al. 2019; Zuercher and Galloway 2019) with southern and northern range limits of 7.33°N (Hannibal Seamount, Panama, Pineda et al. 2016) and 45.92°N (Figs. 1a and S3). The earliest historical records of *P. planipes* occurred in 1859 and 1895 on beaches of Monterey, California (~36.6°N; Stimpson 1860; Boyd 1967) and in 1941 near Los Coronados and Santa Catalina Islands (~32.44°N; Hubbs 1948), highlighting a 46-yr gap in *P. planipes* observations outside of their standard range. The next observations in California waters were in 1957, and the next stranding event in Monterey Bay was in 1960 (Boyd 1967), marking a 16-yr gap between observations off California and a 65-yr gap in reported strandings. Due to these large gaps in observations prior to 1950, we focused on the period from 1950 to 2019.

Larval observations were recorded by two surveys along the Baja California and California coasts, including CalCOFI (1951–2015, 31.48–37.62°N) and IMECOCAL (2003–2016, 24.32–32.25°N) (Fig. 1a). Though larval samples were collected in most survey years, all years have not yet been enumerated due to the labor intensity of data processing (Fig. 2). Larval observations from spring CalCOFI cruises mark the earliest occurrence records of *P. planipes* from systematic scientific surveys (Figs. 1a and 2). Larval *P. planipes* occupied the Southern California Bight (SCB, ~32–34.5°N) during all years for which station-specific, unpooled samples were enumerated (15 of 60 yr) with only one larval record off central California in the 7 yr of enumeration (36.78°N in 1999; Figs. 1a and 2). Pooled enumerations spanned the entire CalCOFI time series and showed larvae consistently occupied the SCB (88% occurrence in 52 of 60 yr) with absences occurring in 1976, 1977, 1982, 1994, 1996, 2001, 2006, and 2012 (Fig. 3). Observations in central California were sparse (24% occurrence in 10 of 41 yr, Fig. 3). From IMECOCAL, larval occurrences off Baja California were ubiquitous, occurring in all 8 yr of sampling and present in ~61% of stations sampled ($n = 482$ stations, Fig. 2).

Adult *P. planipes* were near ubiquitous off Baja California in years of IMECOCAL’s sampling (1997–2016, 22°N–32.4°N, Figs. 1a and 2). CalCOFI does not record adult crabs, thus, the sampling of southern California waters was opportunistic until the RREAS included the SCB in 2004. In the SCB, RREAS catches of *P. planipes* in net trawls were sporadic, occurring in 2004, 2006, 2012–2013, and 2015–2018. Observations of *P. planipes* in central California were less frequent, with observations in 1985 and 1993, and after the recent marine heatwave from 2015 to 2019 (including pers. obs., Fig. 1a,b). No sightings north of 40°N, the demarcation between the central and northern California Current system (Checkley and Barth 2009), were documented until 2017 with six

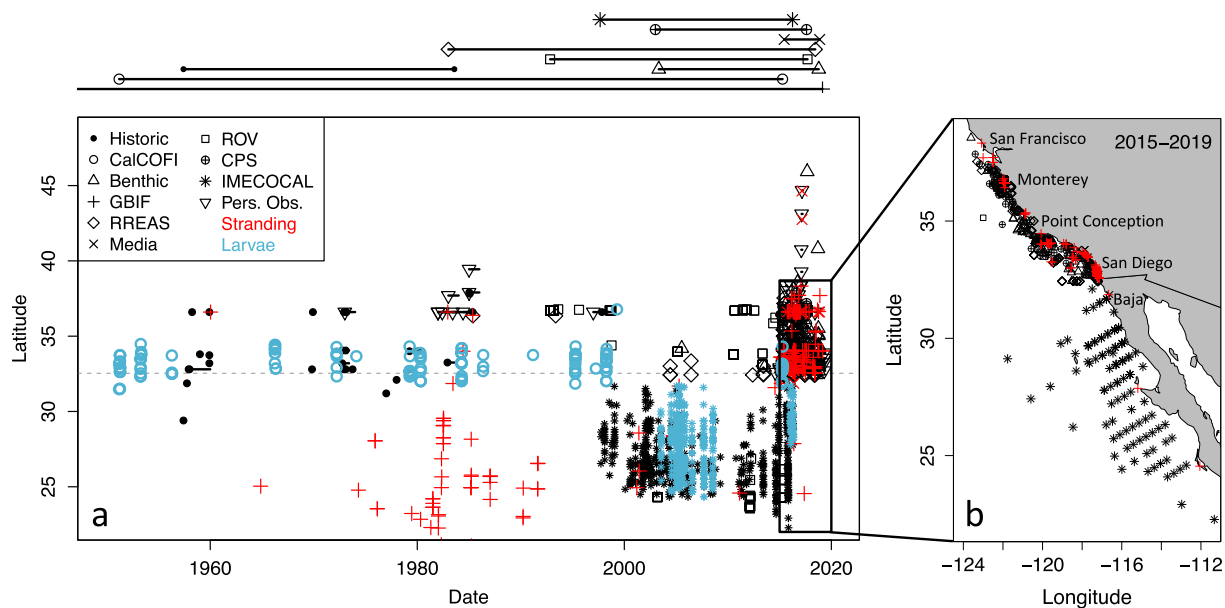


Fig 1. *Pleuroncodes planipes* observations along the west coast of North America from Baja California, Mexico to the Canadian border. **(a)** Time series of *P. planipes* at-sea observations and beach standings (red). CalCOFI and IMECOCAL records include larval stages (blue) while all other records are assumed to be adults. Strandings are generally records from the media and citizen science (GBIF). ROV and benthic trawl data are often seafloor observations. Historic records are from the literature. RREAS and CPS records include adults from trawl surveys. Personal observations were obtained from individuals or observations in reports/publications. Horizontal bars above panel a represent the time range of observations for each data source, though many have gaps and are not continuous. **(b)** The anomalous spatial distribution of adult *P. planipes* from Baja California to San Francisco from 2015 to 2019 (symbols correspond to panel a). Details of the data sources can be found in the Methods section.

observations north of this oceanographic boundary (including two in Oregon), and one in 2018 (Fig. 1a, Sanford et al. 2019). Coinciding with the 2014–2016 marine heatwave, *P. planipes* began washing up on beaches in 2015 and were seen in many at-sea surveys (Fig. 1a), remaining in northern waters at least through 2019. While there were more established surveys in recent decades to document the unprecedented distribution of *P. planipes* from 2015 to 2019 (Fig. 1b), these wide-ranging and numerous observations indicate unusual conditions in the California Current system.

Addressing the poleward advection hypothesis

Using a data-assimilative ROMS, we tested the hypothesis that adult *P. planipes* range expansion to central California was driven by anomalous poleward advection. By tracking passive tracers backwards in time, we were able to discern the origins of waters that arrived off the central California coast from 1981 to 2010, which are not discernable by simply averaging alongshore currents. Based on the tracer experiments, we created an index of the proportion of water originating south of the U.S.–Mexico border. This SSWI exhibited considerable variability across multiple timescales (Fig. 4). The seasonal cycle was characterized, with some exceptions, by low SSWI values (minimal influence of southerly source waters) in the spring/summer and elevated SSWI values through fall/winter. On interannual to decadal timescales, extended periods of higher or lower SSWI were evident and often corresponded with persistent SST

anomalies. For example, anomalously strong northward advection was evident through much of the 1990s, a period of persistent warm SST anomalies, while relatively weak northward advection with coincident cold anomalies occurred from 1999 through the early 2000s. Similarly, high SSWI values corresponded with U.S. West Coast warming during prominent El Niño events (e.g., 1982–1983, 1997–1998). However, there were times when northward transport and SST anomalies diverged (e.g., 1987, 1989, 2004, 2007, and 2010), and similarly, not all El Niño events coincided with warm SST anomalies along the U.S. West Coast (e.g., 1986–1988, 2002–2003, 2009–2010; Fiedler and Mantua 2017).

In our focal study area along central California (35–37°N), *P. planipes* were observed in 11 of the 30 yr for which SSWI was calculated (Fig. 4). Sightings were grouped into a few time periods—the early to mid-1980s, early to late 1990s, and 2010s (while 2010 was the last year for which the SSWI was available, there were sightings in subsequent years; Figs. 1 and 4). Although *P. planipes* presence in this region coincided with El Niño events in some cases (e.g., 1982–1983, 1992, 1995, 1997–1998), *P. planipes* were also absent during other El Niño events (e.g., 1987) and were observed during neutral or cold (La Niña) El Niño Southern Oscillation states (e.g., 1999, 2011–2012). Thus, attributing their presence off central California to El Niño is not an adequate mechanistic explanation.

By classifying *P. planipes* sightings (or lack thereof) as a function of the annual mean in regional SST and southern

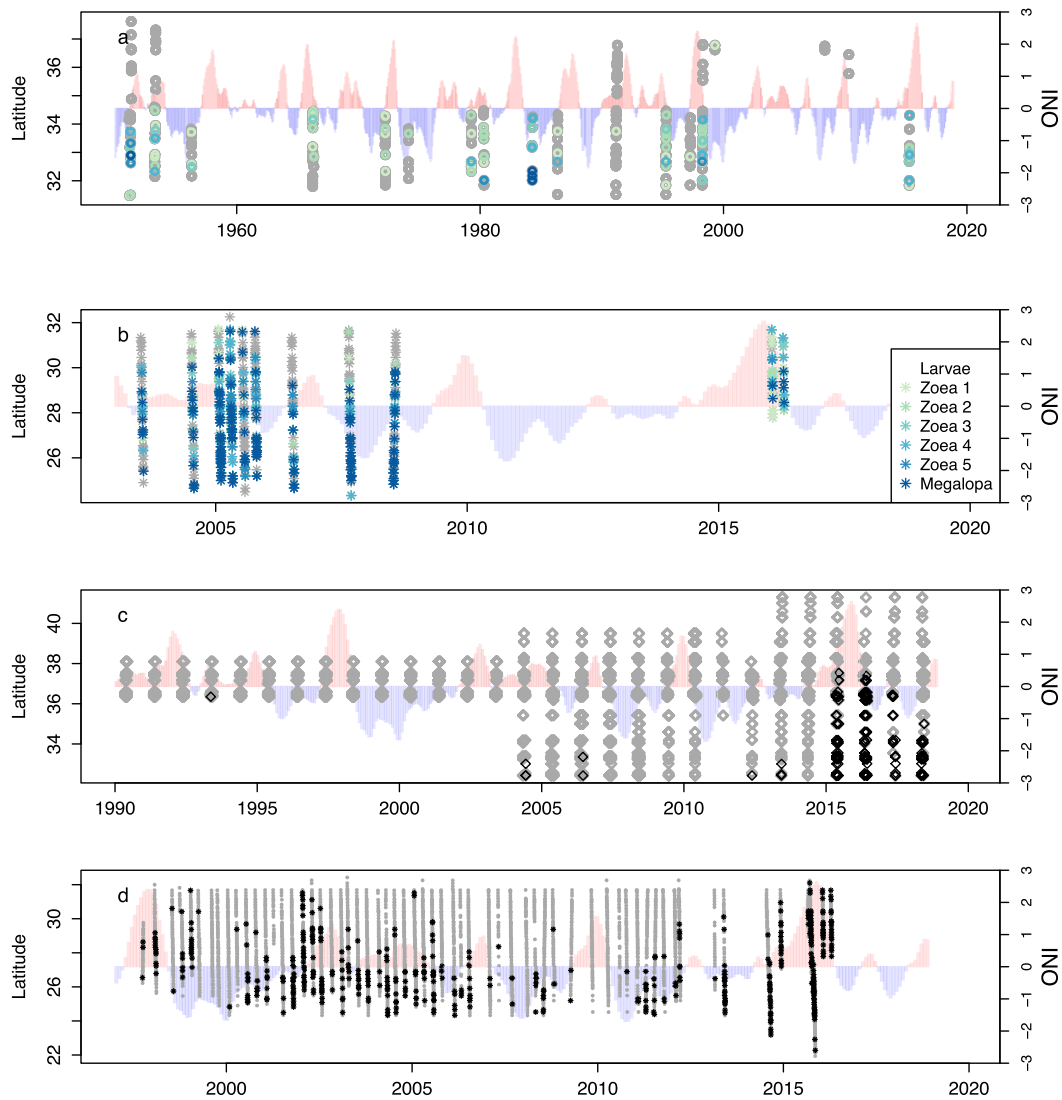


Fig 2. The presence (colored or black) and absence (gray) of *P. planipes* over time for data sources with presence/absence information, including data from (a) CalCOFI surveys with the colored points corresponding to larval life history stage shown in panel b, (b) IMECOAL larvae, (c) RREAS adults, and (d) IMECOAL adults. The Oceanic Niño Index (ONI) is shown in the background. Note the differences in time periods displayed.

source water influence, we found support for anomalous poleward advection as a driver of *P. planipes* presence off central California. The 6 years that had the highest SSWI and SST (i. e., those above the 80th percentile) all had *P. planipes* sightings (Fig. 5a). Furthermore, *P. planipes* sightings during years of low SSWI (1984–1985, 1998–1999) followed years of high SSWI, indicating that these may be “carryover” periods when *P. planipes* are resident following an advection event. Statistical models also showed warmer SST and higher SSWI were predictive of *P. planipes* presence (deviance explained ~77%, Table 1, Fig. S4), but correlation does not indicate causation. Further statistical tests revealed the SSWI was significantly higher in years when *P. planipes* were newly present than when they were not present ($p = 0.002$, Fig. 5b). Similarly, the SSWI was higher when *P. planipes* were resident than

when they were not present ($p = 0.04$), but the standard deviation in the SSWI for residence was large and may indicate a high SSWI was not required for residency in central California (Fig. 5b). In contrast, SST was not significantly different at the 95% confidence interval between years when *P. planipes* were newly present and were not present ($p = 0.07$), but SST was significantly warmer in years when *P. planipes* were resident than when they were not present ($p = 0.002$) (Fig. 5c). There were no significant differences in SSWI ($p = 0.7$) or SST ($p = 0.4$) when *P. planipes* were present or resident. Thus, new *P. planipes* presence was more strongly associated with the SSWI and residence was more strongly associated with SST (Fig. 5b,c).

These results support the hypothesis that adult *P. planipes* were brought to central California by anomalous poleward

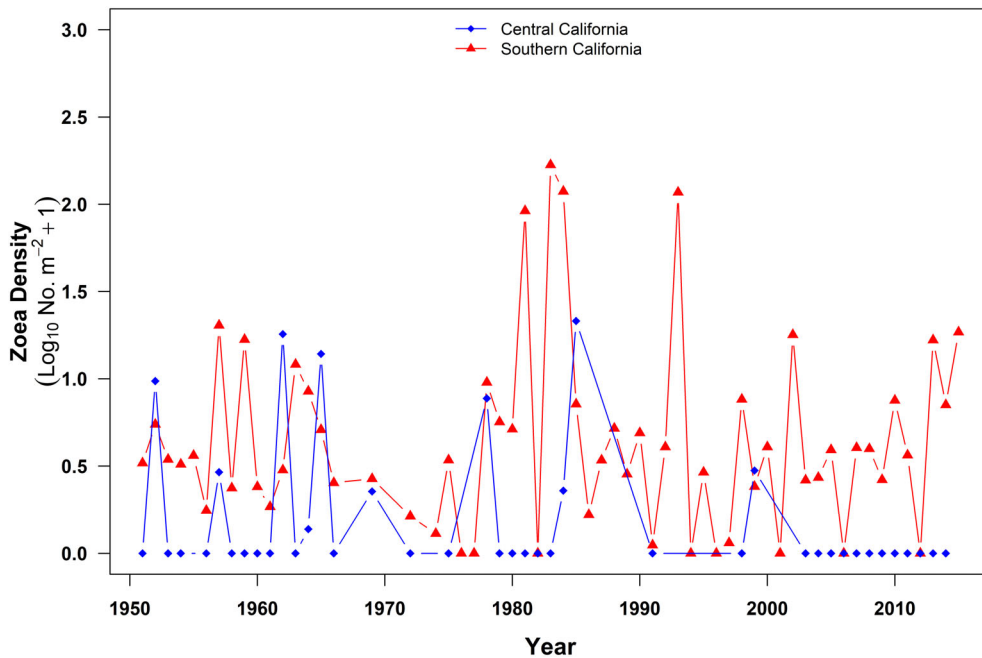


Fig 3. Time series of *P. planipes* zoea density from pooled, spring nighttime CalCOFI bongo net tows. Red denotes southern California stations along standard CalCOFI lines 80–93 (31.5–34.58°N) and blue denotes central California stations along CalCOFI lines 60–70 (34.66–37.62°N). Data are missing for southern California in 1967, 1968, 1970, 1971, and 1973. Data are missing for central California in 1955, 1967–1968, 1970–1971, 1973–1974, 1976–1977, 1986–1990, 1992–1997, 2000–2002, and 2015.

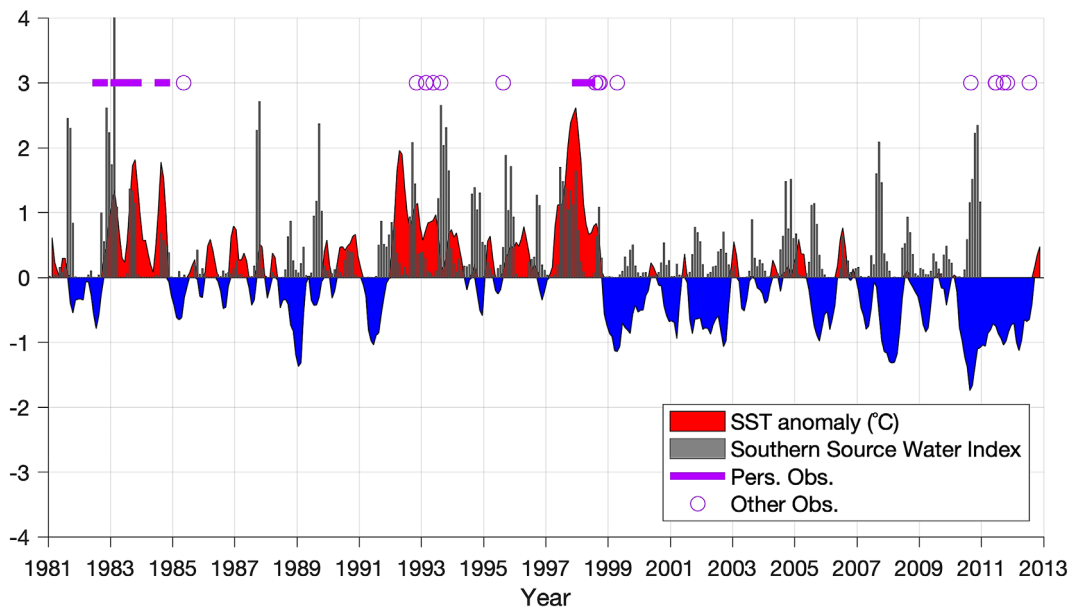


Fig 4. Time series of monthly SST anomalies, averaged from the coast to 50 km offshore and from 30 to 37°N to capture anomalies along the path from Baja California to central California (warm anomalies denoted in red and cold anomalies in blue), a scaled southern source water index from 1981 to 2010 (dark gray; % of water originating south of 32.5°N scaled by a factor of 25 so maximum percentages were ~60%), and *P. planipes* adult observations (purple, as shown in Fig. 1) within the central California study region (35–37°N).

advection and were able to persist locally for one to two additional years (i.e., through the spring of 1985 and 1999, Fig. 5a). This period of local residency may have been facilitated by warm waters (i.e., in 1984 and 1998, Fig. 5a,c) and is

consistent with the lifespan of *P. planipes* that initially arrive as ~2-yr-old adults. It could be argued that the influence of temperature on *P. planipes* presence was similar to that of poleward transport, as *P. planipes* were also associated with the

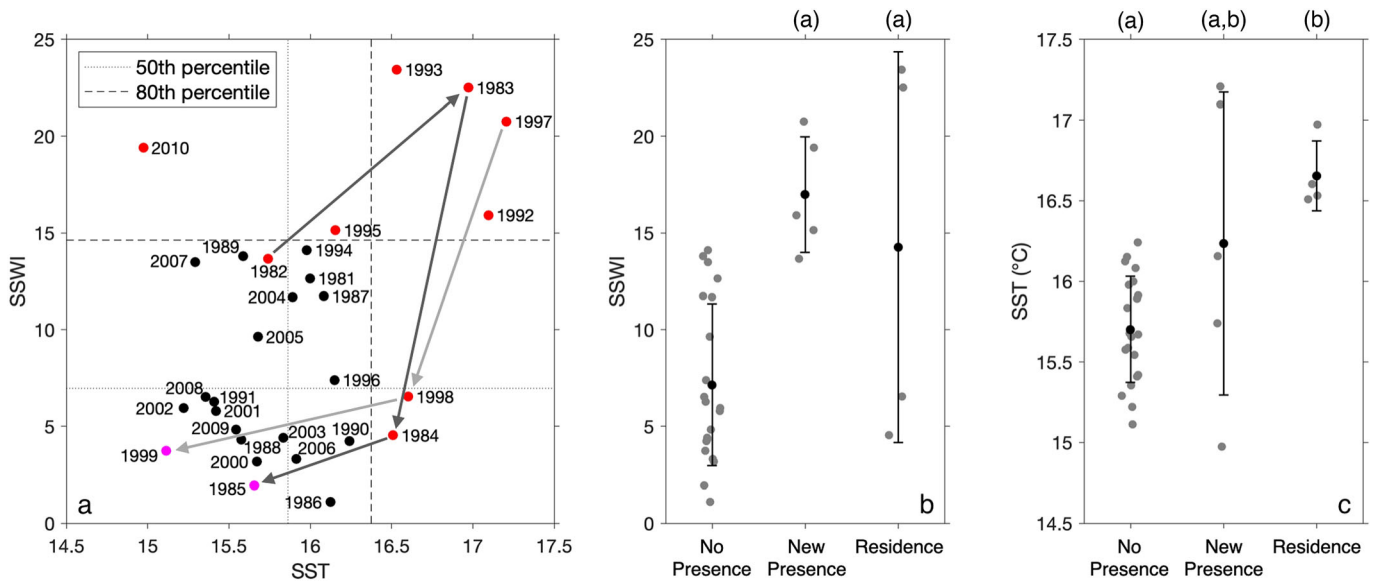


Fig 5. Annual averages of sea surface temperature (SST) and the southern source water index (SSWI) from our central California study region in relation to *P. planipes* adult presence. **(a)** SST and the SSWI with red points indicating *P. planipes* presence at sea and/or on shore in central California in fall and magenta points indicate *P. planipes* presence only in spring. Black points are years with no *P. planipes* observations. Dotted and dashed lines show the 50th and 80th percentiles, respectively, of SST and southern source water contribution. Arrows indicate evolution of transport and SST for consecutive years of *P. planipes* sightings. The mean and standard deviation (black) in **(b)** the SSWI, and **(c)** SST in years with no *P. planipes* presence ($n = 21$), new *P. planipes* presence (i.e., when there were no observations in the previous year, $n = 5$), and *P. planipes* residence (i.e., when there were observations the previous year, $n = 4$) during the fall. Gray points are individual annual observations. **(b,c)** Common letters indicate nonsignificant differences between means at the 0.05 level (Tukey's test).

Table 1. Generalized additive models relating adult *P. planipes* presence or absence in the fall to annual mean sea surface temperature (SST) and the southern source water index (SSWI), and summer/fall Oceanic Niño Index (ONI) from 1981 to 2010. The models are described by the deviance explained, AIC_c for small sample size, the amount of information lost or ΔAIC_c (difference from the lowest AIC_c), and Akaike weight revealing relative model support. Models are sorted by ascending ΔAIC_c and the only model with $\Delta AIC_c < 2$ or substantial support is bolded.

Model	Deviance explained (%)	AIC_c	ΔAIC_c	Akaike weight
<i>P. planipes</i> presence/absence in fall~				
$s(SST) + SSWI$	77.49	19.5	0.0	0.70
$s(SST) + SSWI + ONI$	82.40	21.5	2.0	0.25
$s(SST)$	54.63	25.4	5.9	0.036
$s(SST) + ONI$	53.36	28.1	8.6	0.0094
SSWI	35.48	28.3	8.8	0.0085
ONI + SSWI	36.91	30.0	10.5	0.0035
ONI	0.06	41.1	21.6	<0.001

warmest years in the 30-yr record (Fig. 5). However, we point to 2010, and to a lesser degree 1982, as evidence that anomalous transport was the dominant mechanism. *Pleuroncodes planipes* presences during those years were associated with high SSWI but colder than average temperatures; indeed, SST in 2010 was the coldest in the record. *Pleuroncodes planipes* were also reported off central California in 2011 and 2012, a cold La Niña period (Figs. 1 and 4), further supporting the hypothesis that episodic range expansions (e.g., in 2010) can be followed by several years of local residency.

It is also possible that *P. planipes* life history can impact the presence of adults and larvae in central California. Larval detections in central California corresponded to periods of adult sightings in the mid-1980s (1984 and 1985) and late 1990s (1999; Fig. 3). No larval data were collected in 1992–97, but larvae were absent in central California in 1982–83, 1998, and 2010–2012 when adults were present. Therefore, larvae were present 1–2 yr after adults were already observed. Larval and adult presence in these years (1984, 1985, and 1999) corresponded to low SSWI and intermediate to low SST but

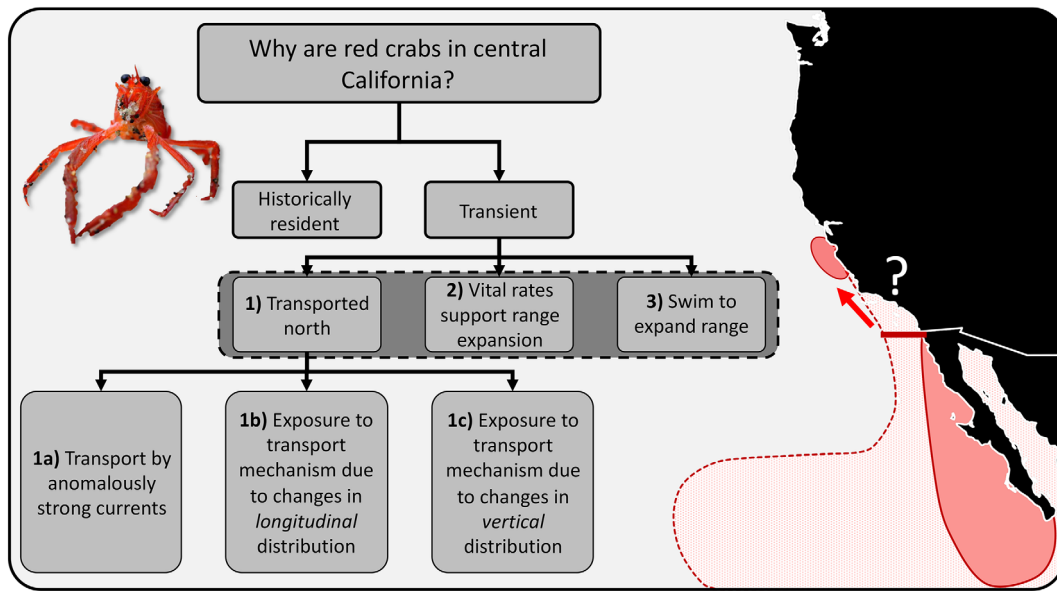


Fig 6. Proposed hypotheses explaining why *P. planipes* are occasionally seen in central California (small red oval on map) in comparison to their home range south of U.S.-Mexico border (red horizontal line) off of Baja California, Mexico (larger red area on map, i.e., the region of greatest abundance from Boyd (1967) and includes IMECOCAL data). The pink shaded region shows the outlying occurrences from Boyd (1967). The dark gray, dashed box represents three processes that may not be mutually exclusive. Figure 1a–c describes different mechanisms related to the northward transport of *P. planipes*.

occurred during the 2 years when *P. planipes* adults were present in the spring (Fig. 5a), possibly suggesting local reproduction rather than an advection-driven presence. Furthermore, larval stage identifications showed zoea stages 1–4 present in 1984, zoea 4–5 in 1985, and zoea 1 in 1999; unfortunately, no larval data were collected in 1986–1990 or 2000–2002 to track any subsequent growth but the lack of adult presence beyond these years indicates that local recruitment did not occur. The absence of larvae during years when adults were present could be related to colder water temperatures in some cases (e.g., 2010–2012, Fig. 4), where colder temperatures increase larval stage duration and thus, susceptibility to predation or advection away from suitable post-larval habitat (Boyd 1962).

Our results suggest there may be a threshold in the SSWI or a period of time required to transport *P. planipes* northward. It appears that multiple months of a high SSWI were necessary to transport *P. planipes* to central California. For example, there were a few years in the record without *P. planipes* sightings in which the SSWI peaked to levels that were similar to years with *P. planipes* sightings (i.e., SSWI > 2 in 1981, 1987, 1989, 2007, Fig. 4), yet the SSWI annual averages during those years were below the 80th percentile (Fig. 5). Similarly, SSWI values in years when *P. planipes* were newly present compared to when they were not present revealed a possible threshold in SSWI at ~15 (Fig. 5b), indicating the annual SSWI average must exceed this strength for *P. planipes* to be transported to central California. The presence of an advective pathway without *P. planipes* observations in central California could indicate a lack of observational data; however, we find

this unlikely given the number of datasets that were interrogated and the clear pattern detected in the data (Fig. 1). We acknowledge that it is possible that adults were present in 1994 given the high SSWI in 1992–1993 and presence of *P. planipes* in 1992, 1993, and 1995 (Fig. 5a).

Discussion

This study presents a comprehensive, 70-yr time series of *P. planipes* observations from Baja California, Mexico, to the northwestern U.S. and reveals the transient nature of *P. planipes* distributions off central California. Using this rich dataset, we found support for the hypothesis that anomalous poleward advection of adult *P. planipes* (~2 yr old) facilitates episodic northern range expansions. Once transported, *P. planipes* likely remain in northern waters for the remainder of their 5-yr lifespan, potentially facilitated by or coinciding with anomalously warm conditions. These data suggest that they can maintain their adult population but cannot successfully recruit in their new range as illustrated by the episodic nature of adult presence (Fig. 1) and infrequent larval observations in central California (Figs. 2 and 3). Specifically, in 1999, the presence of zoea 1 (larval stage duration of ~12 d, Boyd and Johnson 1963) in central California provides possible evidence of local reproduction but the absence of subsequent adult observations indicates no survival. While statistical analyses showed SST and the SSWI were correlated with *P. planipes* occurrence, only the SSWI provided a mechanistic explanation for how *P. planipes* first appear in central California waters. These findings suggest the potential for *P. planipes* arrival off central California as an indicator of anomalous

transport, with or without concomitant occurrence of El Niño, and highlight a potential pathway for the range expansion of other species under future climate change scenarios. Other processes may simultaneously be facilitating range expansions (e.g., changes in population size, or vertical or longitudinal distributional shifts, see Fig. 6), though evidence to support these alternative hypotheses is lacking, and there is currently insufficient empirical data with which to test them.

Possible additional mechanisms driving range expansions

Although the results from the passive tracer simulation indicate that anomalous advection of *P. planipes* adults is sufficient to explain their northward range expansion from Baja California to the U.S. West Coast, there are other plausible mechanisms that could affect their distribution and abundance (Fig. 6). While we found no evidence for larval transport and subsequent recruitment, it remains plausible. The appearance of adults in northern waters could be facilitated by changes in the distribution of key predators, their vital rates (e.g., growth and mortality, hypothesis 2, Fig. 6) or their spatial distribution within their core Baja California habitat (hypothesis 1bc, Fig. 6). For instance, shifts in the distribution or population size of predators have long been associated with anomalously warm water (Hubbs 1929; Lluch-Belda et al. 2005; Cavole et al. 2016) and if such changes reduce the mortality rates of *P. planipes*, an increased number of *P. planipes* may be subject to northerly transport. Alternatively, mortality rates of *P. planipes* could be related to increased rates of development associated with warmer temperatures (Boyd and Johnson 1963). Faster growth rates and decreased stage duration could reduce *P. planipes* mortality, as early life history stages and small body size are typically associated with high mortality (Boyd and Johnson 1963; Lavaniego 1992; Diez et al. 2016).

Changes in either the longitudinal or vertical distribution or the timing of spawning of *P. planipes* in their core habitat could alter their susceptibility to poleward flowing currents (hypothesis 1bc, Fig. 6). For example, a shoreward contraction of *P. planipes* may expose a substantially larger portion of the population to poleward flow near the coast of Baja California, resulting in a greater portion of the population transported north. This increased exposure to northward currents, combined with increased vital rates, could increase the proportion of the surviving population advected north. Additionally, an abundance increase due to changes in vital rates may require *P. planipes* to inhabit a larger range, perhaps also leading to increased exposure to advection.

While *P. planipes* are strong swimmers (Robinson and Gómez-Gutiérrez 1998; Robinson et al. 2004) capable of seasonal onshore-offshore movements and perhaps routine diel vertical migration, there is little evidence of *P. planipes* actively swimming ~1000 km to expand their range (hypothesis

3, Fig. 6). However, this is a hypothesis we cannot dismiss using present data. *P. planipes* could swim to shift or expand their range under favorable or unfavorable habitat conditions, and this active behavior may interact with physical processes to facilitate expansion.

Importance of methods using tracers instead of ocean currents

The SSWI represents a powerful method for quantifying changing influences of advection on regional water properties and biological communities. While the California Current system is characterized by mean surface and subsurface currents (e.g., the California Current, California Undercurrent, and Davidson Current), their strong spatial and temporal variability preclude simple measures of poleward or equatorward advection such as area averages of alongshore velocity (Zaba and Rudnick 2016). For example, in underwater glider data from the SCB, Rudnick et al. (2017) found evidence of anomalous poleward transport in salinity observations even though no clear signal emerged in alongshore velocity fields. Similarly, our preliminary investigations showed that averaging alongshore velocity over the depths and cross-shore bounds associated with the California Undercurrent cannot reproduce variability captured by backward tracer trajectories which unambiguously identify the source of water originating in a specified region, accounting for the meandering path it travels along the way. The SSWI or similar indices are broadly applicable to questions of anomalous transport in the California Current, and by using the backward tracer trajectories, similar indices could be constructed to quantify variability in source water contributions from the north or west or from other depths (Chhak and Di Lorenzo 2007; Jacox et al. 2015).

Conclusions

As originally hypothesized by Boyd (1967) and Longhurst et al. (1967), episodic *P. planipes* range expansions appear to be driven by anomalous poleward transport of adults. Our results strongly support northward transport and temporary residency as the primary drivers of *P. planipes* presence and, thus, mass strandings off central California. Residency may be facilitated by warm waters related to physiological requirements, food availability, predation, or may simply be a result of concomitant advection and climate processes. High connectivity in the marine environment supports at least episodic transport of larvae and adults but there is currently no evidence for self-recruitment in central California. We did not rule out other plausible, but more nuanced hypotheses associated with changes in vital rates or *P. planipes* distribution/abundance in relation to life history traits and larval dispersal, or behavior that might alter their exposure to northward flowing currents. Testing these remaining questions and hypotheses outlined in Fig. 6 likely requires targeted studies to elucidate *P. planipes* life cycle events and habitat preferences, including data on stage-dependent dispersal, cross/along-shelf

distribution, vertical distribution, and the responses of these characteristics to environmental variation.

Our results suggest *P. planipes* are a sentinel species for climate-driven range expansions, and given the numerous observational opportunities from research surveys, this species could serve as a case study for understanding the complex biophysical processes underlying larval vs. adult transport, dispersal, recruitment, and connectivity in dynamic coastal environments (e.g., Cowen and Sponaugle 2009). Future work will include extending our SSWI to investigate the unprecedented number of *P. planipes* observations preceding, during and following the marine heatwave of 2014–2016, which requires developing a broader reanalysis product. Potentially, this SSWI index could serve more broadly as an indicator of ocean circulation anomalies that lead to changing species distributions (e.g., Sanford et al. 2019). For endangered or commercially important species that may follow their preferred prey, such a leading indicator could provide actionable information to fishers or to resource managers who use time-area closures to moderate negative interactions with species of concern (Welch et al. 2019). Understanding climate drivers of range expansion is a fundamental building block to projecting ecological interactions into the future. Early indicators of anomalous conditions can help improve the resilience of marine-dependent human communities, and support climate-ready resource management.

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Conflict of interest

None declared.

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