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SHORT COMMUNICATION

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Temperature-induced range expansion of a subtropical crab along the California coast

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Abstract

We describe the range expansion and first occurrence of the subtropical crab *Portunus xantusii* (Stimpson, 1860) in northern California during 2016 and link the range expansion to the regional extreme water temperature event during this time. We collected *P. xantusii* occurrence data from crab trapping surveys conducted along the California coast as well as incidental observations by fishermen and SCUBA divers. We then analyzed 10 years of regional offshore temperature patterns using National Data Buoy Center data around the trapping region. We also examined evidence of northern California warm water refugia using sensors monitoring Tomales Bay, Elkhorn Slough, and San Francisco Bay. We found that *P. xantusii* was present in every major estuary north of Monterey Bay and as far north as Tomales Bay and that the documented range expansion was likely due to the unusual oceanographic event that occurred northern California during this time period. Mean offshore temperatures and mean nearshore temperatures during 2014–2016 were about 2°C (one standard deviation) higher than the 2006–2013 mean, with extreme temperatures reaching three standard deviations above the 2006–2013 mean. We suggest that this unusual warm water event permitted survival of dispersing larvae of *P. xantusii* larvae northward via coastal currents, and that the extended warm water period allowed *P. xantusii* to complete its development. Long-term crab trapping programs in place since 1994 within this region provide robust support for the absence of *P. xantusii* prior to 2016. Temperature data indicate that the estuaries in which adult *P. xantusii* was found could allow persistence of adult *P. xantusii* in northern California.

KEYWORDS
California, climate change, extreme events, *Portunus xantusii*, range expansion, temperature

1 | INTRODUCTION

Along the west coast of North America, climate change is projected to increase sea surface temperatures (SST; Rykaczewski & Dunne, 2010; Somero et al., 2016), which could in turn lead to northward expansions in species ranges (Burrows et al., 2014). El Niño Southern Oscillation (ENSO) events and the Pacific Decadal Oscillation (PDO) facilitate temporary northward range extensions of warm water species following these anomalously warm years (Goddard et al., 2016; Lonhart & Tupen, 2001; McGowan, Cayan, & Dorman, 1998; Williams, West, & Zedler, 2001). Furthermore, extreme climate events (ECEs) can cause even more dramatic range expansions than what would typically be witnessed during cyclical climate events (Diez et al., 2012). In this paper, we propose that the Xantus Swimming Crab, *Portunus xantusii* (Stimpson, 1860), has experienced a dramatic 370 km northward range expansion in response to a combination of

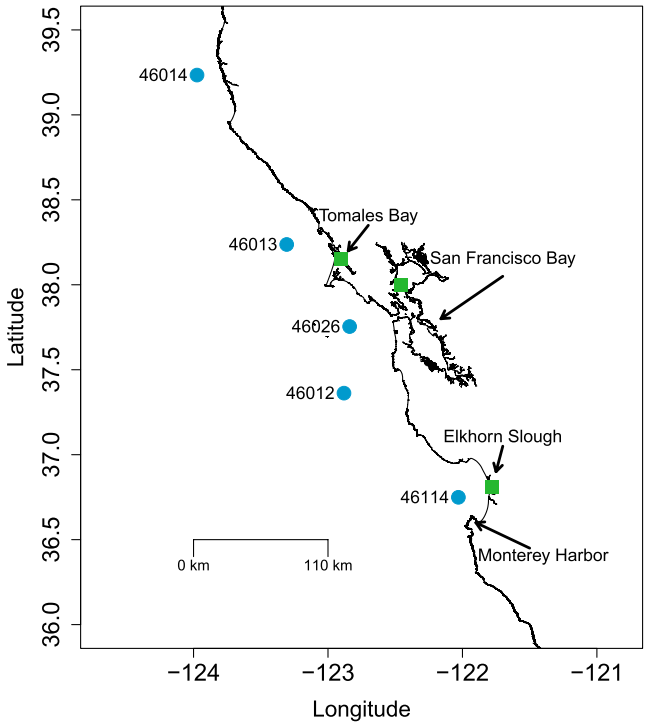

FIGURE 1 Map of study area showing the location of bays and estuaries sampled (black arrows), and the NOAA offshore buoys (blue dots) and estuarine temperature sensors (green squares) used as sources of data in the temperature analysis. Each bay and estuary is labeled, and the NOAA buoys are labeled with their ID numbers

ENSO and ECE events during 2014 and 2015. During this period of time, the combination of a warm water anomaly followed by a strong ENSO event led to sea surface temperatures in the Northern Pacific more than three standard deviations above the long-term mean (Bond, Cronin, Freeland, & Mantua, 2015; Levine & McPhaden, 2016).

A similar ocean warming event in 2012 in the Gulf of Maine led to range expansions across a range of Crustacean taxa. Termed an "ocean heat wave", the annual mean SST anomaly in the Gulf of Maine during this period was approximately 2°C or 3.5 standard deviations above the long-term mean (Mills et al., 2013), approximately as intense as the event we describe here (Bond et al., 2015). The increases in temperature found similar range expansions across a wide range of Crustacean taxa including American lobsters (Mills et al., 2013), fiddler crabs (Johnson, 2014), blue crabs (Johnson, 2015), and ghost crabs (McDermott & Kraeuter, 2015). Many of these studies from the Gulf of Maine at this time invoked the ocean heat wave as the causative agent for the observed range shift.

Of these Crustaceans, portunid crabs are well adapted to climatic shifts and may represent an indicator species for temperature-induced range expansions. For at least 150 years, swimming portunid crabs such as the eastern Blue Crab (*Callinectes sapidus*) were occasionally found outside of their established range during warm years (Cooke, 1867). Following warm years, *Callinectes sapidus* has been found as north as Nova Scotia, far beyond its typical range limit of Cape Cod (Cooke, 1867; Johnson, 2015; Piers, 1920). Closely related subtropical species of *Callinectes* have also been seen outside of their established ranges. *Callinectes bocorutii*, *C. exasperatus*, and *C. marginatus* individuals were found in North Carolina following warm water conditions (Knott, Wenner, & Thornton, 2003; Perry, 1972), which is well north of their known range limit in southern Florida (Williams, 1974).

On the west coast of North America, native portunid crabs are less common, mainly found south of the United States border (Kuris, Sadeghian, Carlton, & Campos, 2007). Three portunid crabs that are common in Baja California, Mexico have a northern range limit in southern California, notably *Portunus xantussii*, *Callinectes arcuatus*, and *Callinectes bellicosus* (Garth & Stephenson, 1966). These portunid crabs increase in abundance in southern California when water temperatures are particularly warm (Kuris et al., 2007; Williams et al., 2001). *P. xantusii* has rarely been found north of Santa Barbara and has never been found north of Morro Bay (Campos & De Campos, 2012; Garth & Stephenson, 1966; Jensen, 2014). The southern limit of *P. xantusii* has not been well-studied, but surveys have found a subspecies of *P. xantusii* as far south as the equator (Jerde, 1970).

After observing multiple *P. xantusii* individuals, we began compiling observations of this species to determine the extent of this range expansion. We hypothesize that *P. xantusii* expanded its range following the anomalously warm conditions of the northeastern Pacific during the 2014–2016 SST event, analogous to the expansions seen in the western Atlantic and southern California. We present evidence of an expansion front from a series of detections of *Portunus xantusii* in central and northern California and link that expansion to oceanographic conditions in the region.

2 | MATERIAL AND METHODS

2.1 | Study area

We observed *P. xantusii* in several estuaries, including Tomales Bay (Marin County), San Francisco Bay (San Francisco, Alameda and San Mateo Counties), and Elkhorn Slough (Monterey County; see Figure 1). These estuaries vary considerably in their size, hydrology, and physical characteristics. Tomales Bay is a 20-km long drowned river valley with limited human inputs, a steep linear gradient in temperature and salinity, and high residence time in the upper bay. San Francisco Bay is an approximately 85-km long heavily urbanized and biologically invaded estuary with considerable heterogeneity in hydrology, salinity, and other physical features. Elkhorn Slough is an 8-km long estuary with significant agricultural runoff and limited residence time.

2.2 | Crab trapping

We compiled all records for *P. xantusii* during this period (Table 1) from a combination of methods including baited traps and incidental observations by SCUBA divers and fishers. Many of the baited traps were set as part of a long-term investigation of the population dynamics of the non-native European Green Crab (*Carcinus maenas*)

TABLE 1 Catch data from five bays along the California Coast

Location	Date collected	Latitude	Longitude	Number of individuals	Carapace width (mm)	Sex	Method
Tomales Bay	11/22/2016	38°13'42.1"N	122°58'18.2"W	8	—	—	Fisherman
	8/21/2016	38°9'16.7"N	122°54'26.6"W	1	62	M	Trap
				1	67	M	
	8/22/2016			1	60	M	
				1	63	M	
San Francisco Bay	6/24/2016	37°52'52.3"N	122°30'16.2"W	1	42	F	Trap
				1	46	M	
	12/31/2016	37°47'19.2"N	122°29'49.6"W	1	—	F	
	3/15/2016	37°45'57.0"N	122°16'29.3"W	1	—	—	
	6/4/2016	37°31'21.5"N	122°12'13.1"W	1	—	—	
Elkhorn Slough	6/30/2016	36°48'42.3"N	121°46'18.0"W	1	39	F	Trap
	7/10/2016	36°48'58.4"N	121°46'3.7"W	1	37	F	
	7/15/2016	36°48'37.4"N	121°47'11.8"W	1	54	M	
	8/3/2016	36°48'34.3"N	121°46'58.9"W	1	31	U	
	8/5/2016	36°48'48.2"N	121°46'23.4"W	1	28	F	
	8/7/2016	36°48'38.5"N	121°46'55.5"W	1	47	M	
	8/21/2016	36°48'37.4"N	121°47'11.8"W	1	47	M	
	8/21/2016	36°48'38.5"N	121°46'55.5"W	1	45	M	
	11/10/2016	36°48'42.3"N	121°46'18.0"W	1	53	M	
	7/13/2017	36°48'36.3"N	121°47'8.94"W	1	51	F	
Monterey Harbor	6/3/2016	36°36'15.9"N	121°53'28.4"W	1	—	M	SCUBA

Note. Observations without associated carapace width are labeled unrecorded (—). Sex is coded as male (M), female (F), unknown (U), or unrecorded (—). Methods of observation included baited crab traps (Trap), sport fishermen (Fisherman), and SCUBA observations (SCUBA).

in Northern California. Since 1994, these three bays were part of a larger trapping network set up to document the population dynamics of the European green crab (de Rivera, Grosholz, & Ruiz, 2011; Kelley et al., 2015). Summary statistics and description of the dataset from 2004 to 2010 are available in Kelley et al. (2015), although trapping occurred annually until 2017. This extensive data set provided unequivocal support for the absence of *P. xantusii* in this region and allowed us to investigate the causality of *P. xantusii* expansion.

At all sites, traps were baited with fish (in porous containers) and set at least 10 m apart at approximately +0.0 m mean lower low water (MLLW). Crabs from Tomales Bay were caught using folding crab traps (FT-101, Fukui North America, Eganville, ON, Canada). Crabs from the northern Tomales Bay site were caught by local sport fishermen using subtidal crab pots (model unknown). Crabs from Elkhorn Slough were in either shrimp pots (Model 5555727, Willapa Marine Products Inc., Raymond, WA, USA) or minnow traps (Model 1271, Frabill Inc., Plano, IL, USA). Crabs in San Francisco Bay were caught in minnow traps. All traps were deployed for 24 hr. Following retrieval, we identified all crabs to species, measured carapace width (mm), and determined both sex and reproductive condition. SCUBA divers incidentally observed and photographed the individual in Monterey Bay. A voucher specimen from Tomales Bay was transported to the Bodega Marine Laboratory and frozen (−20°C) for future analysis (Figure 2).

2.3 | Sensor data

To examine regional trends in SST, we examined data from NOAA's National Data Buoy Center (NDBC) offshore buoys bounding the observation region (buoys 46012, 46013, 46014, 46026, and 46092) over a 10-year period (see Figure 1). Averaging across buoys, we calculated the hourly temperature mean and standard deviation for 2006–2013 and determined the 2014–2016 hourly temperature mean and standard deviation. We analyzed these offshore measurements to determine the percent of time above 16°C. Grober (1990) found that 16°C is the temperature at which *P. xantusii* heart rate approaches 75% of its mean value at optimal temperatures.

We examined nearshore temperature trends in Tomales Bay, San Francisco Bay, and Elkhorn Slough. For Tomales Bay, we used temperature data collected with a YSI 6600-V2 sonde since 2010. For San Francisco Bay and Elkhorn Slough, we used temperature data covering 2006–2016 from the National Estuarine Research Reserve (NERR) Centralized Data Office. Because the warmer nearshore temperatures regularly exceeded 16°C, we analyzed these data to determine the percent of time above a 20°C threshold. Physiologically, 20°C is the temperature at which *P. xantusii* heart rate stabilizes (Grober, 1990) and could therefore indicate a less stressful temperature for *P. xantusii* adults. From this data, we calculated the Tomales

Bay 2014–2016 and 2010–2013 hourly mean and standard deviations, and the 2014–2016 and 2006–2013 hourly mean and standard deviations in both Elkhorn Slough and San Francisco Bay.

3 | RESULTS

We caught multiple individuals of *P. xantusii* in Tomales Bay, San Francisco Bay, and Monterey Bay (Elkhorn Slough/Monterey Harbor). Crab carapace width ranged from 28 to 67 mm and included both males and females, though disproportionately more males (see Table 1). The northernmost record in Tomales Bay represents a range expansion of approximately 370 km from previous records (Jensen, 2014), indicating a substantial northward range expansion. All crabs were caught in these sheltered estuaries with no reports from outer coast sites.

Over the past 10 years, the hourly mean of offshore regional temperatures was above 16°C for 2.71% of observations (see Figure 3). Of those observations, 98.8% occurred during the years 2014 and 2015. Non-event years (2006–2013) had an average temperature of 11.74°C ± 1.35°C (mean ± *SD*) whereas event years (2014–2016) had an average temperature of 13.50°C ± 1.78°C. Thus, the average temperature during the event period was at least one standard deviation above the mean and extremes during this period were greater than three standard deviations above the long-term average.

Data from 2010 to 2016 show that temperatures in Tomales Bay were substantially higher than offshore water temperatures due to increased residence time and could indicate a warm water refuge for *P. xantusii* during the summer. Over this time period, hourly temperatures were above 16°C for 39.8% of observations and above 20°C for 4.01% of observations. Of observations above 20°C (mainly in the summer and fall months), 88.9% of records occurred during 2014 and 2015. Non-event years (2010–2013) had an average water temperature of 14.09°C ± 3.04°C whereas event years (2014–2016) had an average water temperature of 15.37°C ± 3.26°C.

Similar to Tomales Bay, Elkhorn Slough temperatures were higher than offshore waters. Hourly observations in Elkhorn Slough were above 16°C for 13.4% of observations and above 20°C for 0.30% of observations. Temperatures in Elkhorn Slough exceeded 16°C each year during summer months, 37.59% of observations above 16°C occurred during 2014 and 2015, and 67.05% of records above 20°C occurred during 2014 and 2015. Non-event years (2006–2013) had an average water temperature of 13.53°C ± 1.86°C whereas event years (2014–2016) had an average water temperature of 14.75°C ± 1.84°C.

San Francisco Bay consistently had the warmest waters with hourly observations above 16°C for 51.79% of observations and above 20°C for 17.47% of observations. Temperatures in San Francisco Bay exceeded 16°C each year during summer months, with only 21.73% of observations above 16°C and 31.05% of observations above 20°C occurring during 2014 and 2015. Non-event years (2006–2013) had an average water temperature of 15.60°C ± 3.99°C, event years (2014–2016) had an average water temperature of 16.91°C ± 3.89°C.

4 | DISCUSSION

Our data strongly suggest that warmer water temperatures likely contributed to a dramatic northward range expansion for *P. xantusii*. Previous trapping in these estuaries found no evidence for *P. xantusii* from 1994 through 2015 (Grosholz *unpublished data*), therefore our

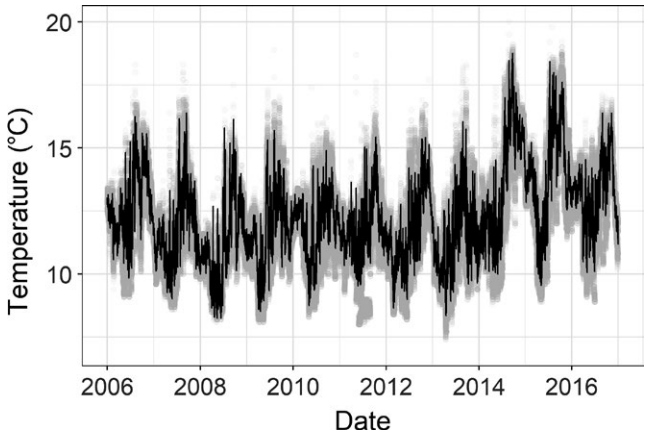

FIGURE 2 Coastal SSTs from 2006 to 2016 along the northern California coast based on data from the NOAA offshore buoys (Figure 1). Shown are the mean (black line) and raw data (gray dots) from all five buoys combined

FIGURE 3 *Portunus xantusii* specimen caught in Tomales Bay on 8/21/2016. Photo credit: Jason Sadowski

observations show an unprecedented range expansion. It is possible that the northern limit for this range expansion is beyond Tomales Bay, but we were unable to find records of *P. xantusii* from any other locations. Of particular, ecological interest is whether the nascent populations of *P. xantusii* will be able to persist over multiple years in their northern California locations. While there is no published relationship between *P. xantusii* carapace size and age, the recorded maximum carapace width of *P. xantusii* is 73 mm (Jensen, 2014). Therefore, the individuals that we collected (some >60 mm) were likely reproductively mature adults possibly greater than 1 year old. Overall, this manuscript indicates that *P. xantusii* has expanded significantly northward and that ocean warming is the driver of that extension.

Northward currents during this extreme period could serve as a mechanism for *P. xantusii*'s northward dispersal. Previous research has indicated that during weak upwelling periods, coastal currents can flow northward up to 100 km (Wing, Botsford, Largier, & Morgan, 1995). The warm waters during this extreme event were also accompanied by anomalously weak upwelling and weak southward currents (Bond et al., 2015); therefore, northward currents could have become more dominant during this period of time. Portunid crabs are poised to take advantage of northward currents as this group has one of the longest pelagic larval durations (PLD, 45 days), second only to Cancrid crabs (60 days; Hines, 1986). While longer PLDs are not necessarily associated with large species range (Hines, 1986), they may increase the probability of long-distance dispersal events (Shanks, 2009). Another portunid crabs, *C. arcuatus*, frequently extends its range northward to southern California via larvae dispersal when conditions permit, although there is little evidence that adult populations have ever become established (Williams et al., 2001).

The SST offshore of Northern California may serve as a dispersal barrier during typical years. Studies of fiddler crab (*Uca pugnax*) larval development found that larvae were unable to metamorphose into the megalope stage when exposed to 14°C or below (Sanford, Holzman, Haney, Rand, & Bertness, 2006), while adult fiddler crabs were able to overwinter in colder climates by capping their burrows (Johnson, 2014). We hypothesize that a similar mechanism occurred here, in which the normal offshore SSTs are too cold for successful dispersal of *P. xantusii* larvae from southern California. Physiologically, the SST of the 2014–2016 event permitted larvae from southern California to fully develop and reach these northern California estuaries. As little is published about the *P. xantusii* reproductive cycle, it is unclear whether the observed adults will sustain local populations or if they will become locally extinct without propagules from southern source populations. Therefore, we are uncertain whether Tomales Bay, San Francisco Bay, and Elkhorn Slough will represent a sufficient thermal refuge to permit long-term establishment of *P. xantusii*.

Although our data indicate that *P. xantusii* has persisted through a northern California winter in at least one estuary (Elkhorn Slough), it remains to be seen if *P. xantusii* will reproduce locally and sustain the northern California populations for multiple generations. Unfortunately, little is known about the thermal and salinity tolerances of *P. xantusii*. Cardiac function, a correlate of activity in crabs (see Leffler, 1972, Burton, Richardson, & Moore, 1980), decreases rapidly in *P. xantusii* as temperatures decline below 20°C (Grober, 1990). A similar experiment in *Callinectes sapidus* found that heart rate declines below 15°C and is quite low by 13°C (Burton et al., 1980), a temperature associated with low metabolic rate and low activity in *C. sapidus* (Leffler, 1972). The large proportion of time above 16°C in Tomales Bay, San Francisco Bay, and Elkhorn Slough during summer months may allow adult population of *P. xantusii* to persist given that thermal tolerance can be physiologically plastic in portunid crabs (Tepolt & Somero, 2014). However, the evidence from subtropical individuals indicates that temperatures well below 15°C could be stressful (Grober, 1990).

Our study builds upon studies of extreme events in the Atlantic Ocean by providing strong evidence linking an extreme climate event to a range expansion. The observations of Crustacean expansion (Johnson, 2014; McDermott & Kraeuter, 2015) into the Gulf of Maine following the "ocean heat wave" (Mills et al., 2013) suggested that the warm water anomaly led to the dispersal of these species. Earlier studies of *Callinectes* species (Cooke, 1867; Perry, 1972) made similar links range expansions and warm water years. Our study combines strong evidence of previous absence with long-term monitoring data to add further support of Crustacean range expansion during warm years.

Although it is also possible that *P. xantusii* was already present at these sites and increased in abundance in response to the unusual warming event, this is highly unlikely. Of the tens of thousands of crabs trapped in this region, not a single example of *P. xantusii* had ever been found prior to 2016 (Grosholz *unpublished data*). Therefore, the likelihood that *P. xantusii* was overlooked in earlier years is extremely remote and dispersal associated with the extraordinarily high SST is the most parsimonious explanation.

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