



# Climate-driven range expansion via long-distance larval dispersal

Cataixa López<sup>1\*</sup>, Benjamin N. Daniels<sup>2</sup>, Evan B. Freel<sup>1</sup>, Andy Lee<sup>3</sup>,  
Jean M. Davidson<sup>2</sup>, Crow White<sup>2</sup>, Mark R. Christie<sup>3,4</sup>, Robert J. Toonen<sup>1</sup>

<sup>1</sup>Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Moku o Lo'e, Kāne'ohe, HI 96744, USA

<sup>2</sup>Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407, USA

<sup>3</sup>Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA

<sup>4</sup>Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA

**ABSTRACT:** Climate-driven warming and changes in major ocean currents enable poleward larval transport and range expansions of many marine species. Here, we report the population genetic structure of the gastropod *Kelletia kelletii*, a commercial fisheries species and subtidal predator with top-down food web effects, whose populations have recently undergone climate-driven northward range expansion. We used reduced representation genomic sequencing (RAD-seq) to genotype 598 adults from 13 locations spanning approximately 800 km across the historical and expanded range of this species. Analyses of 40 747 single nucleotide polymorphisms (SNPs) showed evidence for long-distance dispersal of *K. kelletii* larvae from a central historical range site (Point Loma, CA, USA) hundreds of km into the expanded northern range (Big Creek, CA), which seems most likely to result from transport during an El Niño–Southern Oscillation (ENSO) event rather than consistent on-going gene flow. Furthermore, the high genetic differentiation among some sampled expanded-range populations and their close genetic proximity with distinct populations from the historical range suggested multiple origins of the expanded-range populations. Given that the frequency and magnitude of ENSO events are predicted to increase with climate change, understanding the factors driving changes in population connectivity is crucial for establishing effective management strategies to ensure the persistence of this and other economically and ecologically important species.

**KEY WORDS:** *Kelletia kelletii* · El Niño–Southern Oscillation · ENSO · RADseq · Larval dispersal · Colonization event

## 1. INTRODUCTION

Human-induced ocean warming is causing alterations in species distributions according to their thermal tolerance and ability to adapt (Harley et al. 2006, Poloczanska et al. 2013, Bernardi et al. 2024). More suitable conditions created by ocean warming have enabled many species to successfully disperse poleward and establish populations beyond their historical range limits (Vergés et al. 2014, Spies et al. 2020). Coupled with ocean warming, changes in major

ocean currents and increased frequency of extreme oceanographic events, such as marine heatwaves and El Niño–Southern Oscillation (ENSO) events (Yeh et al. 2009, Cai et al. 2015), are increasing the frequency and magnitude of poleward transport of larvae of many marine organisms. A range expansion occurs when larvae are able to settle, proliferate, and establish a new population outside the historical species distribution range (Poloczanska et al. 2013, Pinsky et al. 2020). This phenomenon is causing a reorganization of marine biota (Bindoff et al. 2007, Lonhart et al.

\*Corresponding author: [cataixalopez@gmail.com](mailto:cataixalopez@gmail.com)

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2019, Sanford et al. 2019), altering the structure and dynamics of community interactions among resident species (Gilman et al. 2010, Gehrels et al. 2016, Marzloff et al. 2016, Wainright et al. 2021). As global temperatures continue to warm and natural communities change, understanding when and how range expansions of marine populations occur is crucial to help in future management and conservation of natural resources.

By the end of the 20th century, the temperature of the northeast Pacific Ocean had risen 0.8°C above pre-1950 historical levels (Roemmich 1992). In the past 2 decades, this region has experienced the combined effects of increasing temperatures and frequencies of anomalous oceanographic events, with 2022 being the warmest year on record (Chao et al. 2017, Harvey et al. 2023). Consequently, many species across different taxa are undergoing shifts in their population distribution and abundance, with a general trend of poleward displacement (Cavole et al. 2016, Molinos et al. 2018, Osland et al. 2021). Some of these population expansions are associated with episodic anomalously warm oceanographic events (Sorte 2001, Lluch-Belda et al. 2005, Yamada et al. 2021). One example is the subtropical red crab *Pleuroncodes planipes*, where adults are sporadically found in central locations of California due to anomalous advection but without evidence of reproduction (Cimino et al. 2021). In contrast, several species have been able to establish stable populations that are reproducing beyond their historical distribution range (Goddard et al. 2016, Spies et al. 2020), which could then act as a source of larvae for future expansions. Such alterations in population dynamics are leading to widespread concern about the future of ecosystem structure and function, and the indirect impacts on regional economies when these variations involve commercially fished species (Gilman et al. 2010, Pinsky et al. 2018, Young et al. 2019, Spies et al. 2020).

Kellet's whelk *Kelletia kelletii* (Buccinoidea) is a subtidal gastropod whose populations have undergone a considerable poleward range expansion along the west coast of North America (Herrlinger 1981, Zacherl et al. 2003). The historical northern range limit of Kellet's whelk was Point Conception, a widely recognized oceanographic and biogeographic border between warm-temperate and cool-temperate species (Ricketts et al. 1985, Hohenlohe 2004, Broitman et al. 2008, Pelc et al. 2009). However, in 1980, 5 adult Kellet's whelks ( $\geq 60$  mm shell length) were found in central California, USA (3 in Monterey Bay and 2 in Big Creek), far north of their historical range, presumably due to ocean warming (Herrlinger 1981).

Kellet's whelk is an ideal candidate for exploring the mechanism of poleward range expansion because it has high dispersal potential, with pelagic larval durations of up to 60 d (Romero et al. 2012). The first detections of range expansions were ~300 km beyond the historical northern range limit of the species (Herrlinger 1981), and subsequent population surveys found irregular size-frequency distributions that suggest only occasionally successful recruitment (Zacherl et al. 2003, Palmer 2016). These observations beg the question of whether the range expansion was the result of periodic long-distance dispersal events rather than a consistent march northward by an expanding population. Additionally, are these marginal populations maintained by long-distance larval recruitment, perhaps during unusual or periodic (ENSO) oceanographic events, or are they maintained by local recruitment of larvae spawned from within the species' expanded range (Zacherl et al. 2003, Lluch-Belda et al. 2005, Cimino et al. 2021)? However, genetic analyses revealed minimal population structure within the species' historical range using microsatellite loci (White et al. 2010, Selkoe et al. 2010), challenging population genetic inference to address those questions.

Examining the range expansion in Kellet's whelk not only presents an intriguing scientific question on the origin of novel populations but also carries broader ecological and economic implications. Kellet's whelk is a subtidal predator and scavenger with top-down food web effects in kelp forests and also supports the second-largest commercial molluscan fishery in California (Rosenthal 1971, Schmitt 1987, Aseltine-Neilson et al. 2006, Halpern et al. 2006, CDFW 2024). Kellet's whelk is also prey to numerous species (Limbaugh 1955, Rosenthal 1971, Rosenthal et al. 1974), such as sea otters (Lonhart 2001), which are more abundant in central California than in its historical range to the south. Recently, fisheries harvest rates of Kellet's whelk have started to rise in the species' expanded range in central California (CDFW 2024). These studies suggest that the species plays a functional role in kelp forest ecosystems and that its range expansion affects ecological and socio-economic community dynamics in central California. For all of these reasons, understanding how the newly expanded and historical populations are structured is essential for establishing effective and sustainable management strategies for Kellet's whelk and associated communities in the face of climate change. Furthermore, because Kellet's whelk shares habitat and several key life history traits with many other coastal marine species in California (Allen et al. 2006, Froese

& Pauly 2011), the results of this study may help predict future expansion by other ecologically and economically important species in the region.

Previous population genetic studies of Kellet's whelk have been focused primarily on populations within the Southern California Bight (SCB), within the species' historical range (Selkoe et al. 2010, White et al. 2010). The SCB presents a unique marine environment shaped by complex oceanographic conditions, including fluctuating currents, seasonal upwelling, and temperature gradients, which create a dynamic marine environment that influences larval dispersal and population connectivity (Hyde & Vetter 2009, Mitarai et al. 2009, Alberto et al. 2011). These oceanographic conditions provided a better explanation for the low levels of population structure observed using a handful of microsatellite markers, than the geographic distance between populations (Selkoe et al. 2010, White et al. 2010). Here, we enhanced the resolution and coverage by adopting a genomic approach and expanded the study area to include locations from both within the SCB, south of the SCB (historical range), as well as locations north of the SCB (newly expanded range). By analyzing reduced-representation genomic sequencing libraries (ezRAD; Toonen et al. 2013) with an equimolar pooled approach (Pool-seq; Schlötterer et al. 2014), we were able to assess thousands of variable nucleotides (single-nucleotide polymorphism [SNP] loci) from 598 individuals sampled across 13 sites spanning approximately 800 km. This population genomic approach provides a much higher-resolution assessment to quantify population genetic structure and relationships among geographic sites to test hypotheses regarding the poleward dispersal of *K. kelletii* into the newly expanded regions.

## 2. MATERIALS AND METHODS

### 2.1. Sample collection, DNA extraction, and pooling

Foot tissue from 46 *Kelletia kelletii* adults (>60 mm shell length; Rosenthal 1970) – 23 individuals in 2015 and 23 individuals in 2016 – were sampled non-lethally from each of 13 subtidal

locations (~15 m depth) across the species' historical and expanded range (Fig. 1). By only including adults, we aimed to represent the local, established population and avoid the bias in population structure that could arise from recent recruitment if juveniles were included. Collected tissue samples were then frozen on dry ice or liquid nitrogen for transport to the California Polytechnic State University (San Luis Obispo, CA) and stored at  $-80^{\circ}\text{C}$  until processed for DNA extraction.

DNA extraction was performed using an optimized version of the 'salting-out' protocol developed by Li et al. (2011) and modified by Daniels et al. (2023a); the full extraction protocol is detailed in the latter study. Briefly, 30 mg of tissue were lysed with Proteinase K and RNase A in a warm water bath. Subsequently, DNA was separated from proteins, which precipitated in the presence of ammonium acetate by centrifugation, and was then purified from the supernatant via ethanol washes. Finally, precipitated DNA was re-suspended in Tris-EDTA ( $1\times\text{TE}$ ) buffer and stored at  $-20^{\circ}\text{C}$  until further analyses.

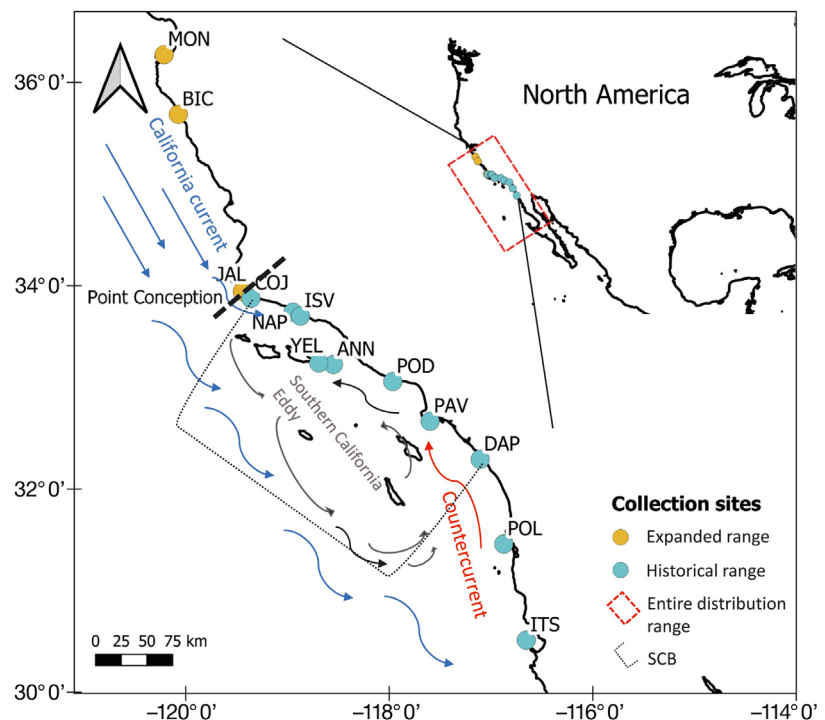


Fig. 1. Locations in California, USA, where tissue samples of *Kelletia kelletii* were collected in 2015 and 2016. Expanded range populations: Monterey (MON), Big Creek (BIC), and Jalama (JAL). Historical range populations within the Southern California Bight (SCB): Cojo (COJ), Naples (NAP), Isla Vista (ISV), Yellow Banks (YEL), Anacapa (ANN), Point Dume (POD), Palos Verdes (PAV), and Dana Point (DAP). Historical range populations south of the SCB: Point Loma (POL) and Isla de Todos Santos (ITS). Main ocean currents within the SCB are also shown

DNA quality was assessed visually using a 1% agarose gel in Tris–acetic acid–EDTA buffer, Gel Red (Biotium) gel stain, and referenced to the 200–10 000 bp Hyperladder I (Bioline, Meridian Bioscience). Because 91.3% of all extractions produced high molecular weight bands (>10 kb) with faint smears from degraded DNA, all specimens were included in the study. Extractions were quantified using the AccuClear Ultra High Sensitivity dsDNA quantification kit (Biotium) with 3 standards and measured using a SpectraMax M2 microplate reader (Molecular Devices). Finally, an equimolar amount of DNA from each of the 46 individuals collected at each location was pooled by collection site (population), ensuring that each library had the same number of individuals. In total, 598 individuals belonging to 13 populations spanning approximately 800 km were included in the analysis.

## 2.2. Library preparation and sequencing

Equimolar pooled ezRAD (Toonen et al. 2013) libraries were generated following the detailed protocol of Knapp et al. (2016) for all 13 sites. Briefly, genomic DNA was digested using the isoschizomer restriction enzymes *Mbo*I and *Sau*3AI (New England Biolabs). Digestions were performed in a total volume of 50  $\mu$ l, containing 25  $\mu$ l of dsDNA (~1  $\mu$ g), 5  $\mu$ l of NEB Cutsmart Buffer (provided with restriction enzymes), 18  $\mu$ l of HPLC-grade water, 1  $\mu$ l *Mbo*I (10 units), and 1  $\mu$ l *Sau*3AI (10 units) under the following thermocycler profile: 37°C for 18 h, then deactivation at 65°C for 20 min. After digestion, samples were cleaned using Mag-Bind TotalPure NGS (Omega Bio-Tek) beads at a ratio of 1:1.18 (DNA:beads) to remove fragments <200 bp (Norcross). Libraries were prepared for sequencing using the KAPA Hyper Prep DNA kit (Roche Sequencing and Life Science) following a modified version of the manufacturer's protocol (see Knapp et al. 2016). Quality control by a Bioanalyzer and sequencing of the libraries on one lane of an Illumina HiSeq2500 were performed in the DNA Technologies and Expression Analysis Core Laboratory at the University of California (Davis, CA).

## 2.3. Data filtering and SNPs calling

Libraries were initially trimmed to remove low-quality bases and adapters using dDocent v.2.9.4 (Puritz et al. 2014), obtaining an average of 16 640 463 reads per sample. All raw data generated for this

project are stored in the NCBI BioProject under project PRJNA1131457 (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1131457>) The population of Monterey had the lowest number of reads, with 4 439 406, while Yellow Banks had the highest number, with 45 795 618 reads. The same pipeline was used to align the reads using BWA (Burrows-Wheeler Alignment Tool, mem algorithm; <https://bio-bwa.sourceforge.net/bwa.shtml>) to the *K. kelletii* reference genome, which contains 2 107 417 620 base pairs (2.1 Gb) in 46 654 contigs and a complete Benchmarking Universal Single-Copy Orthologs (BUSCO) score of 84.1% (Daniels et al. 2023b).

SNPs were identified using FreeBayes (E. Garrison & G. Marth preprint doi:10.48550/arXiv.1207.3907) implemented in dDocent, by calling variants from merged bam files produced by the pipeline. The TotalRawSNPs.vcf file contained 18 327 457 shared SNPs with a mean depth distribution of 5.04 (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m753p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m753p073_supp.pdf)), which was filtered through VCFtools v 0.1.16 (Danecek et al. 2011) using the following parameters: maf 0.05, minQ30, and min-meanDP20. To address the potential effect of missing data in our results, we generated a series of files using the filter `–max-missing` as implemented in vcftools, from the most restrictive option (no missing data, max-missing 1) to a very relaxed one (50% missing data, max-missing 0.50). Further filters were explored in AssessPool (<https://github.com/ToBoDev/assessPool>), a bioinformatic program designed to filter, analyze, and visualize pool-seq data (Freel 2024). Downstream analyses only included loci with max-missing 0.75 and 30 $\times$  coverage, which kept reliable SNPs calling with RADseq data while avoiding overrepresented loci with higher quality scores (Bentley et al. 2008, Li 2014, Rivera-Colón & Catchen 2021).

## 2.4. Population genetic analyses

The final vcf filtered file produced was imported to TASSEL v. 5 (Bradbury et al. 2007) to explore population similarities via principal component analysis (PCA). Population genetic differentiation between sites was calculated based on pairwise estimates of  $F_{ST}$  using PoPoolation2, implemented in AssessPool, which also calculates pairwise significance (p-values) using Fisher's exact test (Kofler et al. 2011). We also compared the matrix of our pairwise estimates of genetic differentiation to those obtained by White et al. (2010), where the authors analyzed between 50 and 92 individuals per population from the SCB

using 9 microsatellite DNA loci. For the collection sites shared between both studies (ANN, COJ, ISV, JAL, and YEL, see Fig. 1), we compared  $F_{ST}$  values using a Mantel test in the 'vegan' R package with 9999 permutations to test for significantly correlated results (v. 2.5–7; Oksanen et al. 2020).

### 3. RESULTS

Our ezRAD libraries captured an average of 19% of the Kellet's whelk reference genome after mapping with BWA, with Yellow Banks (40.13%) and Monterey (8.9%) being the populations with the highest and lowest genomic coverage, respectively. After our conservative filtering approach to focus on loci with high coverage and minimized missing data, a total of 40 747 shared SNPs were retained of the 18 327 457 initial shared SNPs, of which 40 339 were biallelic and 408 were multiallelic SNPs. Due to the low number of multiallelic SNPs (1%) and the insensitivity of these findings to their inclusion or exclusion, they were retained for all analyses.

Genetic structure ( $F_{ST}$ ) between pairwise sampling sites ranged from 0.013 between Anacapa and Isla Vista to 0.028 between Naples and Point Loma

(Fig. 2). The 8 sites from the SCB (Fig. 1) had consistently lower values of  $F_{ST}$  for all comparisons, ranging from 0.013 to 0.017 (Fig. 2), while populations within the expanded range showed higher levels of differentiation (i.e.  $F_{ST}$  MON vs. BIC = 0.020, BIC vs. JAL = 0.014, and MON vs. JAL = 0.017). Despite the moderately low values, all pairwise comparisons of  $F_{ST}$  were significant ( $p < 0.01$ ), showing low but significant population genetic structure in Kellet's whelk. Comparing the population genetic structure recovered here to the same 5 sampling sites from the SCB previously reported by White et al. (2010), we found a positive and significant correlation ( $r = 0.55$ ,  $p = 0.05$ ) between the pool-seq SNP and individual-based microsatellite results, which demonstrated isolation by oceanographic distance.

We found moderately high genetic diversity (Table S1), but comparing the 40 747 SNPs via PCA in TASSEL, which accounted for 27% of the total variance of the data, we found low genetic differentiation among Kellet's whelk populations, with half of the sampling sites clustering within the same group. Although not statistically significant ( $p = 1.0$ ), sites located in the SCB were genetically most similar to each other and distinct from the rest of the range-wide samples (Fig. 3), including the population from

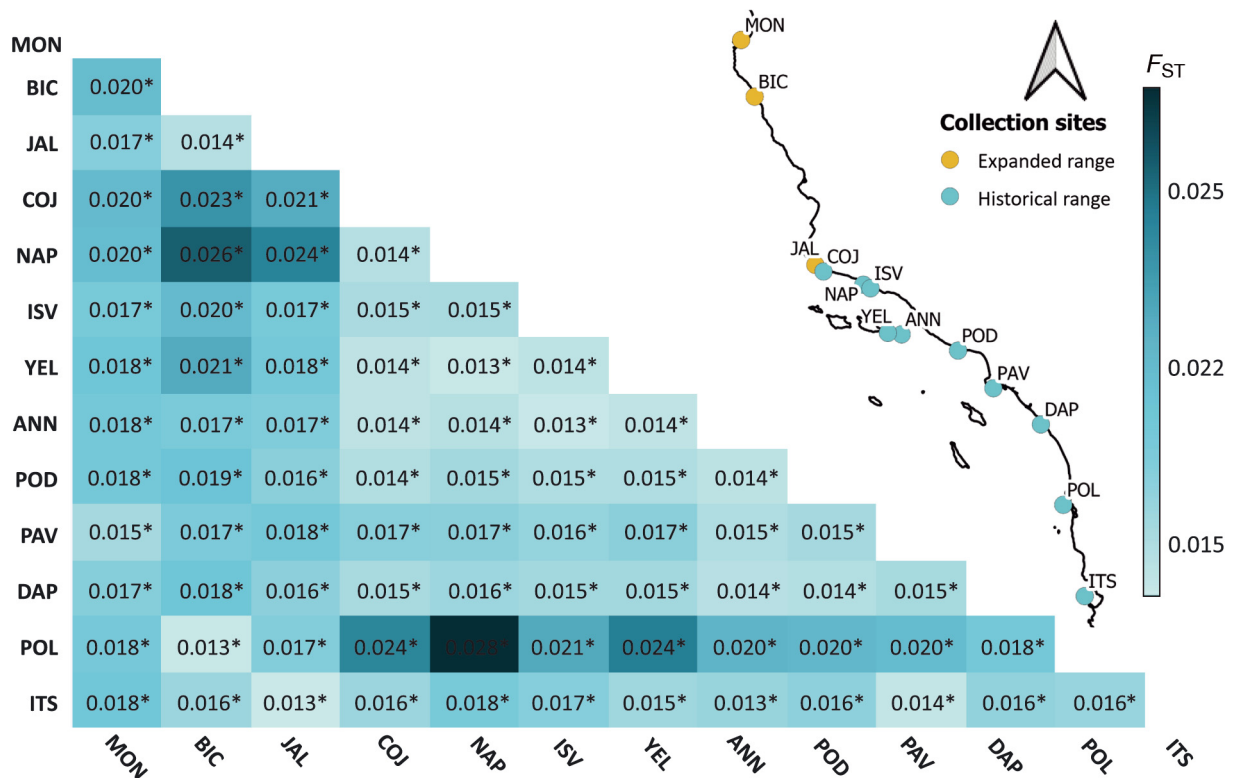


Fig. 2. Heat map representing and including  $F_{ST}$  values generated by PoPoolation2. All pairwise p-values from Fisher's exact test were  $< 0.01$  and thus significant (\*). Site abbreviations as in Fig. 1



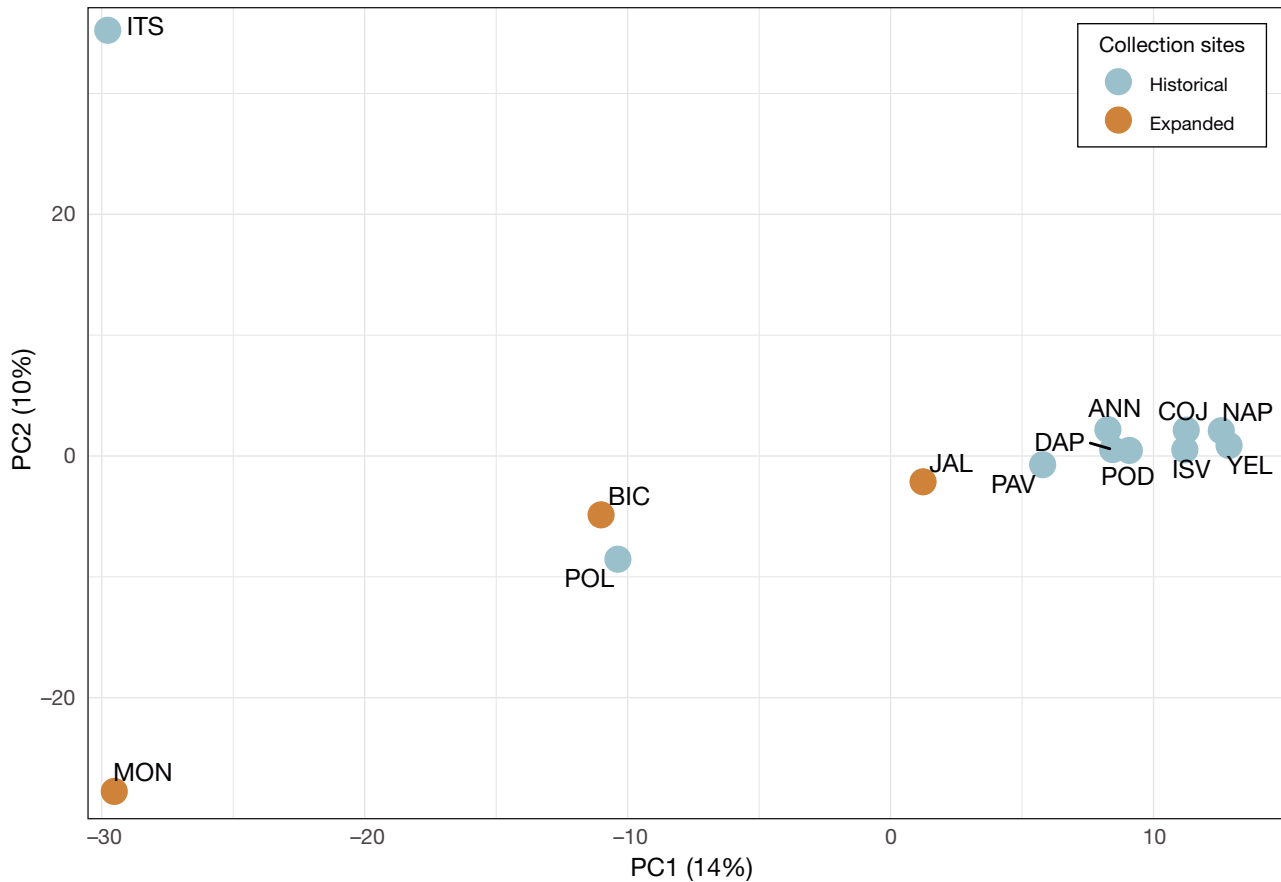


Fig. 3. Principal component analysis (PCA) showing the first 2 axes (explaining 24% of variation) of the genetic differentiation among the Kellet's whelk populations in the expanded and historical distribution range when allowing 25% of missing data and only including SNPs with 30 $\times$ . Total SNPs: 40747. Site abbreviations as in Fig. 1

Jalama (JAL), which is geographically closest to the SCB, but on the other side of Pt. Conception (Fig. 1). Notably, the 2 populations that are geographically highly proximate (~15 km) but on either side of Pt. Conception, namely Jalama (JAL) and Cojo (COJ), were highly differentiated, whereas the 2 most genetically similar populations among all 13 analyzed were Big Creek (BIC), in the expanded range, and Point Loma (POL), located ~550 km apart, in the historical range. Overall, the PCA showed significant population structure throughout the range of Kellet's whelk, with slightly greater differentiation among the populations in the expanded range than among populations within the historical range.

#### 4. DISCUSSION

The results of our study show the low population structure of Kellet's whelks along the geographical distribution range of the species, with genetic divergence among the newly settled populations higher

than among the ones within the historical range. Specifically, sampling sites within the SCB showed the lowest levels of genetic differentiation, clustering together and separated from the 2 other populations within the historical range, POL and ITS. Complicated geography and oceanographic features of the SCB lead to complex current patterns, with internal eddies limiting exchange or promoting high dispersal between distant sites (Hyde & Vetter 2009, Mitarai et al. 2009, Alberto et al. 2011). In fact, there is no correlation between pairwise genetic differentiation or frequency of larval exchange of the Kellet's whelk populations and the Euclidean distances among sites in the SCB (White et al. 2010). For example, the  $F_{ST}$  value between DAP (within the SCB) and POL (outside of the SCB) — only 108 km south of the channel (Figs. 1 & 2,  $F_{ST} = 0.018$ ) — was higher than the  $F_{ST}$  values of more distant locations within the channel (Fig. 2). Instead, nearly 50% of the observed variation in population genetic structure was explained by the frequency of larval exchange predicted by ocean currents (White et al. 2010). Dispersal into and out of the

SCB is limited relative to the open coastline. The open coastline is influenced by an offshore California current towards the south and inshore countercurrent to the north (Fig. 1), with considerable seasonal and inter-annual (ENSO) variability (Hobday 2000, Mitarai et al. 2009, Watson et al. 2010). In addition to oceanographic patterns, coastal pollution was found to be a significant barrier to larval dispersal both within and across the SCB for the bat star *Patiria miniata* (Puritz & Toonen 2011). On the other hand, kelp bed cover, used as a proxy for Kellet's whelk population size, was a significant predictor of genetic diversity and population differentiation of Kellet's whelk (Selkoe et al. 2010), probably because large kelp areas provide more habitat and food for incoming recruits. These studies highlight factors other than geographic distance driving population genetic structure in Kellet's whelk.

Analysis of Kellet's whelk population genetic structure across both the historical and expanded range using genomic loci allows us to test hypotheses about the observed range expansion. For example, among the expanded range sampling sites, Jalama (JAL) is located closest to the historical northern range boundary, only ~15 km north of Cojo (COJ) in the SCB. Despite their geographical proximity, these 2 sites straddle the well-known physiological and biogeographic barrier of Point Conception (Broitman et al. 2008, Hyde & Vetter 2009, Selkoe et al. 2010, Alberto et al. 2011), and are among the most genetically divergent of our comparisons ( $F_{ST} = 0.021$ ). Limited gene flow between these sites is also consistent with observed dramatic differences in abundance and size frequency distributions of individuals in the recently expanded population (JAL), compared to individuals from the historical range across Point Conception (COJ) (Zacherl et al. 2003). This study and our data collectively indicate that Kellet's whelk range expansion was not a gradual march northward from the leading edge of the historical range (COJ) into the expanded range, progressively colonizing JAL and stepping northward up to Monterey.

Decreased genetic diversity and increased pairwise differentiation of expanded range populations due to multiple successive founder events are consistent with climate-driven range expansion (Robalo et al. 2020). We saw mixed support for this prediction in terms of increased differentiation among each of the 3 sites in the expanded range relative to the historical range, and no evidence of reduced genetic diversity among samples of 46 adults from each of these sampling sites (Table S1). Instead, we found relatively low population differentiation ( $F_{ST} = 0.013$ ) between Big Creek (BIC, one of the northernmost expanded range

sites) and Point Loma (POL, one of the southernmost historical range sites in our study) compared to the values observed among the rest of the populations, consistent with migration between these geographically distant locations. Furthermore, these 2 geographically isolated populations are genetically most similar in terms of shared SNPs in the PCA analysis, and are highly divergent from other sampled sites (Fig. 3). With thousands of polymorphic SNPs shared by 46 adults per population, it is unlikely that a founder event from the introduction of just a few individuals from POL to BIC, for example by human-mediated transport, could explain the genetic similarity. Given that these locations are ~660 km apart and separated by many other sampled populations, this similarity is most consistent with range expansion through larval transport, possibly associated with an ENSO event (Zacherl et al. 2003). During these ENSO events, reduced thermal barriers to larval dispersal, combined with alterations in the main ocean currents, facilitate dispersal further north beyond the significant biogeographic barrier at Point Conception (Sorte 2001, Lluch-Belda et al. 2005, Yamada et al. 2021, Miller 2023, Ferrera-Rodríguez et al. 2024).

Based on oceanographic models, larval dispersal in the region ranges up to about 400 km, with longer distances occurring during ENSO events (Siegel et al. 2003, 2008, Mitarai et al. 2008). Turbulent near-shore eddies most frequently disperse larvae in this region throughout an area of up to roughly 150 km from the site of release (Mitarai et al. 2009, Berkley et al. 2010, Harrison et al. 2013), which should homogenize nearby sites through time. The fact that Kellet's whelks from POL/BIC are divergent from multiple sites throughout the intervening area suggests that this genetic similarity is more consistent with unusual episodic long-distance dispersal events seen during ENSO than with consistent local exchange among sites in non-ENSO years. In fact, field data identify increased recruitment of whelks in the expanded range following ENSO events (Zacherl et al. 2003, Palmer et al. 2017). The ENSO dispersal hypothesis is also supported by the results of a length–age model for Kellet's whelk, which suggests that the individuals first found in Monterey (Herrlinger 1981) were spawned between 1969 and 1974 (White et al. 2022), coincident with the 1972–73 ENSO event (NOAA 2018). Previous work along the California coast showed evidence of differential larval transport during El Niño years, in which frequent relaxation events transport larvae long distances up the coast from the south (Diehl et al. 2007, Toonen & Grosberg 2011). Although we could not test directionality with these

data, this mechanism provides a plausible hypothesis for the northward range expansion and genetic similarity of distant sites seen here. However, it is also worth noting that strong, consistent upwelling during La Niña years tends to bring larvae down the coast from the north (Diehl et al. 2007, Toonen & Grosberg 2011), so it is possible for the expanded populations to return larvae to the historical range; thus, directionality in this system is worthy of future study.

Both empirical and theoretical studies have shown that PCA plots provide inference about biological processes affecting populations. For example, changes in SNP frequencies caused by migration, isolation, or admixture of populations can be detected and interpreted through visualization in PCA graphs (e.g. Paschou et al. 2007, McVean 2009, Zheng & Weir 2016). Others have used PCA to reveal genetic signatures caused by natural or artificial selection (e.g. Chen et al. 2016, Caldu-Primo et al. 2017), and many have used PCA to understand how geographic separation and genetic differentiation are related, because the distance between points is related to the proportion of shared SNPs among populations (e.g. Novembre et al. 2008, Omberg et al. 2012, Wang et al. 2012, Yang et al. 2017). In our study, MON and ITS populations are not closely positioned together in the PCA plot, indicating genetic differentiation between them. However, their equal divergence from other populations suggests they may have shared historical dispersal patterns, leading to comparable levels of differentiation relative to the other populations. Yet it is noteworthy that these 2 populations also showed the highest amount of missing data (Fig. S2), which may confound RAD-seq results (Arnold et al. 2013, Huang & Knowles 2016, Shafer et al. 2017, Hemstrom et al. 2024). To test whether our results were sensitive to such effects, we looked for a correlation between the amount of missing data per comparison and the corresponding pairwise  $F_{ST}$  value, and did not find any (Fig. S1). Furthermore, performing the analyses with varying cutoffs for missing data ranging from 0 to 50% does change the relative position of these populations in the PCA but does not alter our inferences about the overall population structure (Fig. S3). The only 2 populations greatly affected by the amount of missing data were Monterey (MON) and Isla de Todos Santos (ITS); while the relative amount of divergence between these 2 varies, they generally remain genetically distinct from all other sampled populations (Fig. S1). Thus, our geographically proximate samples from within the expanded range show moderate population differentiation, and are each genetically more similar to some sites within the

historical range than they are to one another. These results are more consistent with multiple long-distance colonization events of these newly range-expanded populations than a slow poleward march of an expanding population.

Alternatively, selection could drive population differentiation irrespective of dispersal, similar to patterns identified for the intertidal crab *Petrolisthes cinctipes* along the northern California coastline (Toonen & Grosberg 2011). Previous work showed that Kellet's whelk may be capable of adapting to the colder environment by altering its metabolic rates (Vasquez et al. 2019, Lee et al. 2024) and increasing the concentration of proteins involved in energy metabolism and oxidative stress (Vasquez et al. 2019, Daniels et al. 2023b, Lee et al. 2024). Adaptation to cold temperatures may help explain the persistence of individuals in the extended range, but the mechanism by which whelks colonized these northern range expanded sites remains unknown. One hypothesis is that MON is divergent from all other locations in the PCA as a result of long-distance dispersal, followed by selection among recruits to survive in colder environments, which results in a unique population signal. In support of this hypothesis, Lee et al. (2024) found Kellet's whelk in the expanded range to be upregulating triosephosphate isomerase (TPI), an essential enzyme for cold stress response. Nevertheless, whether these divergence patterns are driven by a response to selection, genetic drift, or a combination of both mechanisms requires additional studies.

## 5. CONCLUSIONS AND IMPLICATIONS

Most marine animal species have a biphasic life cycle in which dispersal occurs primarily through the pelagic larval phase (Thorson 1950, Kinlan & Gaines 2003, Weersing & Toonen 2009, Burgess et al. 2016). Larval dispersal kernels are generally leptokurtic, in which most successful recruits remain relatively close (10s to ~100 km) to the spawning site but with a long tail of some individuals that can be transported much longer distances (Kot et al. 1996, Strathmann et al. 2002, Siegel et al. 2008, D'Aloia et al. 2015). Poleward range expansions have been studied for decades in terrestrial organisms, with many following a stepping-stone pattern, in which most dispersal occurs relatively near the parents to form reproductive populations that seed further expansions (Ibrahim et al. 1996, Morales 2002, Thomas 2010, Saura et al. 2014, Robalo et al. 2020). This process would result in a continuous slow-and-steady population range expansion through mul-



multiple successive founder events, because long-distance dispersers are unlikely to find mates, even if they survive and grow to reproductive maturity. The predictable consequences of such a process include reduced genetic diversity and high differentiation of populations in the expanded portions of the range relative to those in the historical range (Robalo et al. 2020).

Contrary to such predictions, the first observations of Kellet's whelk in the species' expanded range was ~300 km beyond its historical northern range limit (Herrlinger 1981). Further, observations of irregular size-frequency distributions in the expanded range suggest that recruitment has been episodic (Zacherl et al. 2003, Palmer et al. 2017). In support of these early observations, our results here show both high genetic diversity and minimal population genetic structure ( $F_{ST} \approx 0.01-0.03$ ) of Kellet's whelk along its entire geographical distribution range. The greatest genetic divergences are seen among the newly expanded populations and some portions of the historical range, but those differences are roughly equivalent to the full range of population differentiation observed among sites within the historical range (Fig. 2). Further, each of these divergent expanded-range samples is more similar to a site within the historical range than to any geographically proximate location. In particular, the genetic similarity of Point Loma (POL), deep in the historical range, to Big Creek (BIC) in the recently expanded range provides compelling evidence of long-distance larval dispersal. Overall, the observed patterns are more consistent with long-distance dispersal from central range origins, likely associated with an ENSO event, than with progressive northward population expansion due to ocean warming.

Our findings have implications not only for Kellet's whelk but likely for many other ecologically and economically co-distributed species in California that share similar dispersal characteristics and life history traits, such as the spiny lobster *Palinurus interruptus* and California sheephead *Semicossyphus pulcher* (Allen et al. 2006, Selkoe et al. 2010, Froese & Pauly 2011). The frequency and amplitude of ENSO events are predicted to increase under climate change (Power et al. 2013, Cai et al. 2015), which will likely result in more frequent northward expansions and changes in biogeographic species ranges similar to Kellet's whelk. Studies such as this one, focused on understanding and identifying the factors altering marine population dynamics, are essential to establishing effective management and conservation measures that ensure the health of marine ecosystems and the services they provide to human populations.

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