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Population genetic analysis of a recent range expansion: mechanisms regulating the poleward range limit in the volcano barnacle *Tetraclita rubescens*

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Abstract

As range shifts coincident with climate change have become increasingly well documented, efforts to describe the causes of range boundaries have increased. Three mechanisms—genetic impoverishment, migration load, or a physical barrier to dispersal—are well described theoretically, but the data needed to distinguish among them have rarely been collected. We describe the distribution, abundance, genetic variation, and environment of *Tetraclita rubescens*, an intertidal barnacle that expanded its northern range limit by several hundreds of kilometres from San Francisco, CA, USA, since the 1970s. We compare geographic variation in abundance with abiotic and biotic patterns, including sea surface temperatures and the distributions of 387 co-occurring species, and describe genetic variation in cytochrome *c* oxidase subunit I, mitochondrial noncoding region, and nine microsatellite loci from 27 locations between Bahia Magdalena (California Baja Sur, Mexico) and Cape Mendocino (CA, USA). We find very high gene flow, high genetic diversity, and a gradient in physical environmental variation coincident with the range limit. We infer that the primary cause of the northern range boundary in *T. rubescens* is migration load arising from flow of maladapted alleles into peripheral locations and that environmental change, which could have reduced selection against genotypes immigrating into the newly colonized portion of the range, is the most likely cause of the observed range expansion. Because environmental change could similarly affect all taxa in a region whose distributional limits are established by migration load, these mechanisms may be common causes of range boundaries and largely synchronous multi-species range expansions.

Keywords: barnacles, dispersal, geographic range limits, intertidal species, migration load, range shifts

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Introduction

The coincidence of anthropogenically driven climate change and shifts in the latitudinal and altitudinal distribution of many species (e.g. Parmesan & Yohe 2003; Perry *et al.* 2005; Parmesan 2006) has fuelled a resurgence of interest in the question of what ecological (e.g. Parmesan & Yohe 2003; Helmuth *et al.* 2005a) and evolutionary (e.g. Hoffmann & Blows 1993; Kirkpatrick & Barton 1997) processes govern geographic range limits. Three mechanisms have been proposed to explain range limits: genetic impoverishment, migration load, or a physical barrier to dispersal (Holt 2003;

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Table 1A). The first two mechanisms depend critically on the level of dispersal into peripheral populations. If immigration is low, then a population at the range border must be demographically sustained largely by self-recruitment, and adaptation to novel conditions may be limited by the availability of heritable genetic variance (i.e. the genetic impoverishment hypothesis; Holt 2003; Hoffmann *et al.* 2003; Blows & Hoffmann 2005; Kellermann *et al.* 2009). If immigration is high, then peripheral populations may be subsidized demographically through immigration; however, the influx of locally maladaptive alleles may constrain the response to selection at the range edge and limit expansion (Haldane 1956; Mayr 1963; Antonovics 1968, 1976; Hoffmann & Blows 1994; García-Ramos & Kirkpatrick 1997; Kirkpatrick & Barton 1997; Lenormand 2002), a constraint typically referred to as 'migration load' (e.g. Hu & Li 2003; Hare *et al.* 2005; Bridle & Vines 2006; Bolnick & Nosil 2007; Lopez *et al.* 2008). Between these two extremes, intermediate levels of dispersal may increase both effective population size and genetic diversity in peripheral populations, facilitating both local adaptation and population expansion (Antonovics 1976; Gomulkiewicz *et al.* 1999; Holt 2003; Holt *et al.* 2005; Bridle & Vines 2006; Garant *et al.* 2007) and enabling 'secular migration', that is, gradual evolution of the species ranges with no long-term range limit (Lomolino *et al.* 2005: p. 154; Table 1B). The third explanation for the maintenance of range boundaries is that limits are set by impenetrable physical barriers to dispersal (Holt 2003; Table 1A).

Distinguishing among these mechanisms depends on documenting patterns of geographic variation in population sizes, genetic diversity, and levels of gene flow in relation to patterns of environmental variation. In principle, each mechanism should produce a specific combination of these patterns (Table 1). Genetic impoverishment, for example, is implicated when circumstances limit the introduction of new alleles by mutation and gene flow, producing small peripheral populations of low genetic diversity that are strongly genetically differentiated. In contrast, migration load is implicated when peripheral populations are genetically very diverse and weakly differentiated (Table 1A: H_1 vs. H_2; reviewed in Hoffmann & Blows 1994; Bridle & Vines 2006; Eckert *et al.* 2008). These genetically driven mechanisms may be distinguishable from a physical barrier that prevents dispersal beyond the present boundary by comparisons of population sizes. Ranges constrained by lack of relevant genetic variation should be characterized by small census and effective population sizes at the boundary due to increasing selection against the resident or immigrant phenotypes; those constrained by high gene flow should have 'soft' range boundaries (Kirkpatrick & Barton 1997), with numerous waif individuals beyond the boundary point at which there is a genetically diverse but small sustained population (Mayr 1963: p. 523–524; Bridle & Vines 2006). In contrast, range limits set by a persistent impenetrable barrier should exhibit an abrupt decline in abundance at the boundary (Table 1: H_1 and H_2 vs. H_3).

The responses of peripheral populations following alteration of the environment by large-scale processes such as climate change provide another perspective from which to infer the causes of range boundaries. If, for example, a species expands its range, then it must disperse beyond a geographic range limit which, therefore, was not an impenetrable physical barrier (falsifying H_3). Moreover, if colonization is rapid and populations within the newly colonized range are genetically diverse, then gene flow is relatively high, implicating migration load as a cause of the original range limit (H_2). In contrast, if colonization is slow and newly established populations are genetically depauperate, then genetic impoverishment probably contributes to the range limit (H_1). Notably, in these latter two cases, the newly colonized range became habitable because of one or more environmental changes, but not because of reduced migration or adaptation.

Here we use a population genetic framework to characterize patterns of mitochondrial sequence and nuclear microsatellite variation in the context of a recent range expansion in the volcano barnacle, *Tetraclita rubescens*. We couple our analyses with descriptions of the abundance and distribution of *T. rubescens*, and changes in its abiotic and biotic environment (see section 'Description of the study species and range'). By considering multiple lines of evidence, we aim to find a consensus for or against the various hypotheses outlined above (Table 1). Our primary goal is to identify the ecological and genetic factors that most likely regulate the northern range limit and the recent changes in distribution (Connolly & Roughgarden 1998) of this locally abundant, widespread barnacle.

Materials and methods

Description of the study species and range

Tetraclita rubescens, the volcano barnacle, is conspicuous and easily identifiable; its basal diameter is 20–50 mm and it is the only mid-intertidal barnacle in California with either reddish coloration and/or a shell composed of four lateral wall plates (Pilsbry 1916; Newman & Abbott 1980; Connolly & Roughgarden 1998). *T. rubescens* is a sessile hermaphrodite that copulates, so an individual can reproduce only if it settles within a penis length of a conspecific (≤11 cm, as indicated by microsatellite

Table 1 (A) Predicted characteristics of populations at the border of a species' range, and in a recently expanded range, under three hypothesized causes of range limits. (B) The predicted characteristics of 'secular migration' (Lomolino *et al.* 2005: p. 154), which results when moderate gene flow introduces intermediate levels of genetic variance thus increasing evolutionary potential (Ellstrand & Elam 1993; Gomulkiewicz *et al.* 1999) and enabling gradual evolution of the species range with no long-term range limit (Mayr 1963), are shown for comparison; although secular migration suggests no long-term range limit, such species will appear to have a range limit when observed for a 'snap shot' in time

A	H_1: Genetic impoverishment	H_2: Migration load	H_3: Physical barrier to dispersal
Characteristics of environment (biotic or abiotic)			
1 Environmental change at margin	Gradual change	Gradual change	Dispersal route blocked/broken
Size of marginal population			
2 Marginal population size	Small	Declining toward border	Large
Border populations			
3 Gene flow	Low	High	Low /medium/high
4 Genetic diversity	Low, decreasing toward margin	High	medium/high
5 Unique alleles	Prevalent	Few	Few/some
Recently expanded range			
6 Timing	Not necessarily coincident with environmental change	Contemporaneous with change in environment	No expansion
7 Gene flow	Low, with old marginal population	High, with populations far within old range	No expansion
8 Genetic diversity	Low	High	No expansion

B	H_{SM}: Secular migration
Characteristics of environment	
1 Environmental change at margin	Gradual, stepped, or abrupt change
Size of marginal population	
2 Marginal population size	Moderate – large
Border populations	
3 Gene flow	Medium
4 Genetic diversity	Moderate
5 Unique alleles	Some
Recently expanded range	
6 Timing	Not necessarily coincident with environmental change
7 Gene flow	Reduced relative to old margin
8 Genetic diversity	Reduced relative to old margin

We do not consider directional flow as a potential cause of range limits (see Byers & Pringle 2006, 2008; Pringle *et al.* 2009) in the case of *T. rubescens* because its high reproductive output and several-weeks pelagic larval duration should cause its dispersal pattern to reflect the probabilistic motion of regional oceanography (Byers & Pringle 2008) which includes current relaxation and reversals on timescales of days to years, including predominant inshore northward flow during fall (Kaplan & Largier 2006; Lynn & Simpson 1987; McLain & Thomas 1983; Pullen & Allen 2001) when *T. rubescens* is reproductive (Hines 1978).

analyses of paternity; M. Kelly, unpublished data). Thus, increasing population density greatly enhances potential reproductive output. *T. rubescens* produces two to three broods per season (June–November), each brood containing hundreds of nauplius larvae. Pelagic larval duration is ~3–4 weeks (ES, unpublished data). Metamorphosed barnacles reach sexual maturity at 2 years and may live 10–15 years (Hines 1978; Newman & Abbott 1980; Ford & Mitton 1993).

Circa 1970, the historical range of *T. rubescens* spanned from Cabo San Lucas in Baja California, Mexico (22°30′N) northward to San Francisco Bay in CA, USA (37°30′N; Newman & Abbott 1980). Although this limit was known at the time to be 'soft'—*T. rubescens* was 'rare north of San Francisco' (Newman 1975), with single *T. rubescens* collected at Shell Beach (38°25′N) in 1957 (Merwin 1957) and 1970 [Bodega Marine Laboratory (BML) collection], Point Reyes (Tomales Point, 38°14′N) in June 1948 [California Academy of Sciences (CAS) collection], and two *T. rubescens* collected at Fort Ross (38°30′N) no later than the early- to mid-1970s (R. Van Syoc, personal communication)—subsequent surveys corroborate northward range expansion. In 1984, *T. rubescens* occurred at Sea Ranch (38°43′N) and Saunder's Reef, CA, USA (38°52′N; Kinnetic Laboratories, Inc., 1985, J. Pearse, personal communication), and in 1995–1996 a single individual was recorded at Cape Mendocino, CA, USA (40°24′N; Connolly & Roughgarden 1998). A single *T. rubescens* was found circa 2007 at Burnt Hill, OR, USA (42° 23′N), but is no longer present (P. Raimondi, personal communication).

Tetraclita rubescens also increased in abundance north of San Francisco Bay. A single *T. rubescens* was collected from Shell Beach by Merwin (1957), and this same cave contained 81 individuals in spring 2007 (ES, personal observations). The North Jetty of Bodega Harbor (38°18′N) yielded only one *T. rubescens* from multiple surveys in 1957 (Merwin 1957); in 2007 a single 1-h search by one person revealed 478 *T. rubescens* (E.S. personal observation). A 1971 survey of the South Jetty recorded no *T. rubescens* (McKnight 1971), but the same area yielded 2376 *T. rubescens* in a single one-hour search (E.S. personal observation). At the nearby Bodega Marine Reserve (38°19′N), approximately 40 intertidal surveys during minus tides between June 1975 and March 1978 recorded *T. rubescens* as 'rare—seen only once or twice' (Ristau *et al.* 1978), but in spring 2006 E.S. recorded 105 *T. rubescens* in a three-hour search. At Cape Mendocino, E.S. recorded six specimens in spring 2005. Recent comprehensive surveys detail the distribution and abundance of *T. rubescens* throughout its range (Sagarin & Gaines 2002a; Blanchette *et al.* 2008).

The range expansion occurred through a region that is largely uninterrupted rocky shore, excepting the sandy beaches interspersed with several rocky headlands within Point Reyes National Seashore (38°00′ N). More sizeable interruptions in the rocky shore habitat of *T. rubescens* occur within the historical range, the most notable being (i) Monterey Bay, (ii) the predominantly sandy mainland coastline delimiting the Santa Barbara Channel and the Southern California Bight from Point Conception to San Diego, and (iii) the region of Guerrero Negro in Baja California. These large discontinuities (including tens of kilometres of uninterrupted sandy beach) in rocky shore evidently have not proved a range barrier to *T. rubescens* and so the species' spatial distribution is essentially linear north–south, encompassing substantial latitudinal changes in abiotic and biotic environments (see section 'Environmental measurements').

A prior allozyme-based analysis of *T. rubescens* collected in 1990 provided mixed evidence of population structure. Ford & Mitton (1993) reported high gene flow (12–85 migrants per generation), but also elevated self-recruitment (coefficient of relatedness = 0.19, $P < 0.05$) at Moss Landing, CA, an isolated rocky jetty along the Monterey Bay shore, located toward the historical northern range limit.

Environmental measurements

Biological. We plotted *T. rubescens* abundances (Sagarin & Gaines 2002a; Blanchette *et al.* 2008) against latitude. We used data from Blanchette *et al.* (2008), reporting the abundances of 387 invertebrate and algal species at 67 intertidal sites between Baja California, Mexico and Alaska, USA, in up to three surveys between January 2001 and January 2006, to identify taxa whose distributions correlated with the northern range limit of *T. rubescens*. These species potentially represent a biological cause of the modern range limit of the volcano barnacle. Because the abundances of *T. rubescens*, and many other species, were not normally distributed (before or after log, square-root, or arctangent transformations), we used Spearman's rank correlation in STATISTICA v. 7 for Windows. We deleted samples 'case-wise' (i.e. when one or both species were absent from a sample) from each species-pair comparison prior to correlation analyses, because the processes causing presence–absence may differ from the processes causing changes in abundance and therefore should not be conflated in analyses. For species whose abundance was significantly positively or negatively correlated with the abundance of *T. rubescens*, we assessed whether their abundances increased or decreased from the historical range (SoSF), through the expanded range (SF-CM), into the region

north of the range of *T. rubescens* (NoCM); we used a sequential Bonferroni procedure to adjust the critical value for significance. A negative correlation, coupled with increased abundance across the volcano barnacle's modern range limit, would be consistent with competitive exclusion or predatory depletion of *T. rubescens*. A positive correlation, coupled with decreased abundance across the volcano barnacle's modern range limit, would be consistent with loss of a positive interaction (facilitation) with *T. rubescens*. If an ecological interaction (e.g. competition, predation, facilitation, symbiosis) linking the population dynamics of correlated species was plausible (e.g. the diet of the species and *T. rubescens* overlap, the species preys on *T. rubescens*, or the species cooccurs with *T. rubescens* in the mid-intertidal zone), we identified the species as a possible biological cause of the range limit of this barnacle. We inferred whether this modern relationship might, however, be a transient coincidence rather than a long-term ecological interaction by asking whether the same changes coincided across the San Francisco region, the historical range limit of *T. rubescens*, in the 1970s (e.g. Abbott & Hollenberg 1976; Newman & Abbott 1980).

Physical. To document latitudinal variation in temperature, we calculated long-term monthly mean sea surface temperatures (SSTs) from data measured by coastal buoys and pier- and quay-mounted stations downloaded from the National Oceanographic Data Center (NODC; http://www.nodc.noaa.gov/dsdt/cwtg/), and identified the coldest, mean, median, and warmest months of the year at each site. We interpolated temperatures between oceanographic stations for comparison with *T. rubescens* abundance data (Blanchette *et al.* 2008). Also, satellite-derived May mean SSTs at all locations surveyed by Sagarin & Gaines (2002a) were downloaded from http://coastwatch.pfel.noaa.gov/sst_comp_high.html for every year from 1999 to 2004. Additionally, monthly mean composites for June and December in every year from 1999 to 2004 downloaded from http://coastwatch.pfel.noaa.gov/sst_comp_high.html were used to calculate minimum, median, mean, and maximum temperatures at each site surveyed by Blanchette *et al.* (2008) for each month across all years. All temperature series were correlated (Spearman's rank correlation) against latitude to assess latitudinal trends and against each other to assess consistency between months. Additional details are provided in the Supporting Information.

Specimen collection, selection and DNA extraction

We collected *T. rubescens* between April 2005 and April 2007 from 29 locations spanning the species' entire present-day range (Table 2). In addition, E.S. sampled transects at several northern sites to estimate the relative numbers of, and measure distances between, individual *T. rubescens.* We haphazardly collected specimens, located primarily in the mid-intertidal zone on rocky substrate, across 50–100 m of shoreline. In the field, we immediately stored the barnacles in ethanol chilled on dry-ice, and returned the samples to UC Davis within 1–5 days, where they were stored at −80 °C.

We selected 15 individuals for mtDNA and microsatellite analyses, plus 15 additional individuals for microsatellite analyses only, per location, except at two sites (CPM, ISM) where low abundances limited sample sizes. We purified DNA from a few-mm^3 piece of adductor muscle using a modified chloroform–phenol extraction protocol (e.g. Dawson *et al.* 1998) or the Puregene® DNA Purification Kit for marine invertebrates, following the recommended protocol (Gentra Systems, MN, USA), in both cases redissolving or eluting DNA in 100 μL 10 mM Tris–HCl pH 8.3. For microsatellite analyses, subsamples of DNA were adjusted to 5 μM.

Mitochondrial DNA

PCR and sequencing. We amplified and sequenced two mitochondrial regions, cytochrome *c* oxidase subunit I (mtCOI) and a noncoding region (mtNCR), using primers described in Table 3. We used 50 μL PCRs that contained 1 μL of template DNA, 5 μL 10× buffer, 5 μL Mg^{2+}, 4 μL of 2.5 mM dNTP, 1.39 μL of 18 μM forward primer, 1.39 μL of 18 μM reverse primer, 32.12 μL ddH_2O, and 0.1 μL 5 U Taq polymerase. PCR conditions were 94 °C for 8 min, 52–54 °C for 1–2 min, 72 °C for 3–4 min, 94 °C for 4 min, 53 °C for 1 min, 72 °C for 2.5–3 min, and then 35 cycles of 94 °C for 45 s, 54 °C for 45 s, 72 °C for 1.5–2 min, followed by a 10-min extension at 72 °C depending on marker and amplicon size. PCR products were cleaned for sequencing using ExoSAP (USB Corporation, Cleveland, OH, USA), adjusted to DNA concentration to 16–26 ng/μL, and sequenced by the UC Davis DNA sequencing facility.

We assembled sequences into contigs (at least one forward and reverse sequence for all specimens) in SEQUENCHER v4.7 (Gene Codes Corporation, Ann Arbor, MI, USA), edited by eye, then exported in FASTA-concatenated format and aligned using CLUSTALX (gap-opening penalty 5 or 10; gap-extension penalty 1, 2, or 5; Jeanmougin *et al.* 1998).

We assessed genetic variation within mtNCR and mtCOI markers and within the mtDNA locus (i.e. concatenated mtNCR + mtCOI) at nucleotide, haplotype, location, and sample levels using 'standard' and 'molec-

Table 2 Sample locations (site, county), site acronym, GPS (°N, °W), and sample sizes for mitochondrial cytochrome *c* oxidase subunit I (mtCOI), mitochondrial noncoding region (mtNCR), and microsatellite loci (STR)

		°N	°W	mtCOI	mtNCR	STR
Mainland California, expanded range						
Cape Mendocino, Humboldt	CMH	40° 24.42′	124° 23.42′	1	1	
Shelter Cove, Humboldt	SCH	40° 02′	124° 04′	15	15	30
Kibesillah Hill, Mendocino	KHM	39° 36.19′	123° 47.36′	15	15	
Van Damme, Mendocino	VDM	39° 16.72′	123° 48.18′	14	14	30
Sea Ranch, Sonoma	SRS	38° 44.46′	123° 30.73′	15	15	
Bodega Reserve, Sonoma	BRS	38° 19.076′	123° 04.290′	15	15	30
Bodega Jetty, Sonoma	BJS	38° 18.291′	123° 03.174′	15	15	
Central California Islands						
Farallon Islands	FAR	37° 40.2′	123° 0.12′	15	15	
Mainland California, established range						
Bean Creek, San Mateo	BCSM	37° 13.59′	122° 24.68′	15	15	30
Scott Creek, Santa Cruz	SCSC	37° 02.53′	122° 14.01′	15	15	
Malpaso Creek, Monterey	MPM	36° 28.92′	121° 56.41′	15	15	
Soberanes Point, Monterey	SPM	36° 26.86′	121° 55.73′	15	15	
Mill Creek, Monterey	MCM	35° 59.00′	121° 29.54′	15	15	
Rancho Marino, San Luis Obispo	RMSLO	35° 32.44′	121° 05.58′	15	15	
Shell Beach, San Luis Obispo	SBSLO	35° 09.56′	120° 41.19′	15	15	30
Refugio Beach, Santa Barbara	RSB	34° 27.63′	120° 04.39′	15	15	
Mussel Shoals, Ventura	MSV	34° 21.32′	119° 26.39′	15	15	
California Channel Islands (Northern)						
Prisoners Harbor, Santa Cruz Island	PHSCI	34° 01.23′	119° 41.20′	15	15	
Coches Prietos, Santa Cruz Island	CPSCI	33° 58.05′	119° 42.47′	14	14	
Mainland California, established range						
Point Mugu, Ventura	PMV	34° 05.07′	119° 03.16′	15	15	
Cabrillo Aquarium, Los Angeles	CAL	33° 42.30′	118° 17.38′	15	15	30
Dana Point, Orange	DPO	33° 27.62′	117° 42.56′	15	15	
Scripps Pier, San Diego	SPSD	32° 51.99′	117° 15.33′	15	15	
California Channel Islands (Southern)						
Isthmus Cove, Catalina Island	ICCI	33° 26.52′	118° 29.55′	15	15	
Pin Rock, Catalina Island	PRCI	33° 25.63′	118° 30.40′	15	15	
Baja California, established range						
Punta Baja, Baja California Norte	PBBCN	29° 57.69′	115° 48.59′	14	14	30
Santa Rosalita, Baja California Norte	SRBCN	28° 41.79′	114° 16.73′	15	15	
San Roque, Baja California Sur	SRBCS	27° 10.69′	114° 23.86′	15	15	30
Isla Santa Margarita	ISM	24° 25′	111° 50′	3	3	

Locations are arranged predominantly north (top) to south (bottom) excepting some channel islands.

ular' diversity indices in Arlequin v.3.11. In Arlequin, we inferred haplotypes from unweighted pairwise sequence difference when all missing positions were excluded. Additional details are provided in the Supporting Information.

Phylogeographic analyses. Tree-based analyses included estimation of the mtDNA gene tree of *T. rubescens* by maximum likelihood (ML) analyses of a concatenated mtNCR+COI dataset, excluding all ambiguous/missing positions. ML analyses used the GARLI (Zwickl 2006) and RAxML (Stamatakis *et al.* 2005) tools provided online by Cyberinfrastructure for Phylogenetic Research (CIPRES; http://www.phylo.org). The maximum likelihood tree was found using GARLI under the GTR + G model. Bootstrap analyses (100 replicates) were completed in RAxML; default options were used in all cases. Additional details are provided in the Supporting Information.

We used nontree-based analyses to describe and compare genetic diversity within and between populations and regions. We compared all pairs of populations, except CMH and ISM (both with <14 individuals), with respect to allelic diversity, nucleotide diversity, estimated population subdivision (ϕ_{ST}), exact tests of population differentiation, mean pairwise sequence differences, and frequencies of shared haplotypes. We also calculated a mismatch distribution for the entire

Table 3 Summary of (A) mitochondrial cytochrome *c* oxidase subunit I and noncoding region and (B) nuclear microsatellite loci used in analyses of *Tetraclita rubescens* population structure

A. mtDNA locus	Forward primer (short name) sequence	Reverse primer (short name) sequence	Amplicon length (nt)
COI	TeRub_COI_01225f (TC5f) CCACWAAYCATAAAGATATTGGAAC	TeRub_COI_02250r (TC0r) CTACTCCTGTMACTCCTCC	~1000
		TeRub_COI_02617r (TC7r) CGYTGKGMTACTATAGCYTCTC	~1500
NCR	TeRub_12S_14526f (TS6f) GCTTGAGGCTGAAGTATAACC	TeRub_Met_00090r (TM9r) CGTTGGGGTATGAACCCAAAAGC	~800

B. Microsatellite locus	Primer 1	Primer 2	Repeat type	Colour (multiplex)	Range in number of alleles per population	Mean (±SD) number of alleles per population
Tetraclita 02	CCGTAATAGCCACACATGCT	CTGAGTAGACATACCACTCACACC	$(TAC)_{31}$	Yellow (1)	17–23	20.5 ± 2.1
Tetraclita 06	TCAAGCGAAGTTAAACAGGAAG	TGACGATGTGAACGGTTGTT	$(TAC)_3$ CAC$(TAC)_8$ TGC $(TAC)_7$	Blue (1)	13–18	16.4 ± 1.6
Tetraclita 09	GATCTCCTTTATCGCCTTTGAG	GATTGCACGTTTCTGATGC	$(TAC)_{13}$ TAT $(TAC)_6$	Red (1)	4–23	15.9 ± 5.6
Tetraclita 11	AAAACAGCGAGGGAGGTTG	ACGAGCGACATAGGGAAGAG	$(TAG)_{16}$	Yellow (2)	15–22	19.1 ± 2.3
Tetraclita 12	CGGTATTGGTGTCAGTGTGG	CCATTGCGAGTCCATTGTAAG	$(TAC)_{23}$ CAC TAT $(TAC)_5$ TAT $(TAC)_5$ $(TAA)_8$	Blue (1)	18–23	20.1 ± 2.0
Tetraclita 14	TGTGTGTGGAAATAAAAAGAACACT	CAGTTTGATAGAAAGGTGCTATTCG	$(TGA)_9$… $(TAC)_{11}$ TTC $(TAC)_4$ TAT $(TAC)_{16}$	Green (2)	—	—
Tetraclita 19	GCGAGGGTCTGAGTAGTACG	CAGGCGCTGAGAGATATACG	$(TAG)_3$ TG $(TAG)_6$ TAA $(TAG)_{11}$ TG $(TAG)_7$	Red (2)	11–18	14.4 ± 2.3
Tetraclita 20	CCCAATTGAAAGAAGTGACG	TGTCCTGTGTATACCATTGTTCATC	$(ACAG)_{13}$	Blue (2)	24–29	26.3 ± 1.7
Tetraclita 21	CAGTCAAATACGCACGCAAC	TCGTATGACAGCTTAGGGTAAAC	$(GCGT)_{12}(GT)_2$	Green (1)	12–16	13.4 ± 1.4
Tetraclita 22	GAGCGGTGGCTAATATTTCG	CCACGACCTGTACTGCACTG	$(GTGC)_6(GT)_5(GC)_2$ $(GT)_2(GCGT)_6$	Yellow (2)	16–20	17.9 ± 1.2

All primers written in 5′ to 3′ orientation.

dataset. We then aggregated populations into two regions defined *a priori*: the set of sites south of San Francisco (SoSF; the historical range) vs. the set of sites north of San Francisco (NoSF; the expanded range). We used AMOVA (Excoffier *et al.* 1992) to compare regions. All nontree-based analyses were completed in Arlequin v3.11 (Excoffier *et al.* 2005). Finally, we conducted two chi-squared tests to determine whether (i) shared haplotypes were distributed uniformly across the range of *T. rubescens* and (ii) shared haplotypes were equally likely to come from any distance as opposed to being under- or over-dispersed. In the first case, the observed regional distribution of sites sharing haplotypes was compared with a null model based on the proportion of pairwise comparisons between locations within or among arbitrarily chosen regions: NoSF, San Francisco to Point Conception, Point Conception to Baja California Sur. In the second case, we compared the distribution of great circle distances (calculated using the Vincenty formula) between pairs of sites sharing haplotypes, in which at least one site was in the NoSF recently expanded range, to the null distribution of distances from all NoSF to all other NoSF or SoSF sites.

Microsatellites

Genotyping. Ten microsatellite loci, developed by Ecogenics GmbH (Zurich, Switzerland), were amplified in two multiplex PCRs (Table 3). Multiplex 1 used a 10-μL reaction containing 2 μL of 5 μM template DNA, 1.03-μL 1× PCR buffer with 1.5 mM $MgCl_2$, 0.83 μL 2.5 mM DNTP, 0.15 μL of each primer at 10 μM, 0.1 μL HotStarTaq DNA polymerase (Qiagen), and 5.28 μL ddH_2O. PCR conditions for this multiplex were 95 °C for 15 min, followed by 35 cycles of 94 °C for 30 s, 60 °C for 45 s, 72 °C for 1 min, ending with a 30-min extension at 60 °C. PCR products were diluted 1 part with 12 parts ddH_2O. Multiplex 2 used the same reaction mix except 0.75 μL of each primer, 5.66 μL ddH_2O and PCR conditions consisted of 95 °C for 15 min, followed by 10 cycles of 94 °C for 30 s, 58 °C for 90 s, 72 °C for 1 min, then 25 cycles of 94 °C for 30 s, 56 °C for 90 s, 72 °C for 1 min, and concluded with a 30-min extension at 60 °C. PCR products were diluted 1 part with 2 parts ddH_2O. For both Multiplex 1 and 2, 1 μL of product was added to 9 μL formalin containing GeneScan-500 (LIZ) size standard (Applied Biosystems, Foster City, CA, USA) for genotyping on an ABI Prism 3100 Genetic Analyzer in the UC Davis DNA sequencing facility. Additional details are provided in the Supporting Information.

We attempted to genotype 30 individuals from eight sites spanning the range of *T. rubescens*: SCH, VDM, BRS, BCSM, SBSLO, CAL, PBBCN, and SRBCS. If a specimen did not amplify for a particular locus, we conducted at least three additional PCRs in which primer concentrations were diluted to ¼ or ½ original concentration and template DNA diluted to 0.5 μM. If amplification failed in all additional PCRs, we concluded that an individual possessed two null alleles at the locus.

Population genetic analyses. We pooled genotypes of *T. rubescens* in three ways: as a single population across the entire modern range, as one group in the historical range and a second group in the expanded range, and as individual populations at each sampled location across the entire modern range. We used Arlequin v3.11 on each of these pooled data sets to quantify allele size and frequency distributions for each locus and, allowing 20% missing data per locus, to test for Hardy–Weinberg equilibrium (100 000 steps in Markov chain, 1000 dememorization steps), population differentiation (Exact test, 10 000 steps in Markov chain, 1000 dememorization steps), population and regional structure (AMOVA 10 000 permutations), and linkage disequilibrium (pairwise tests, 10 000 permutations).

Results

Environmental measurements

Biological. The abundance of *T. rubescens* showed peaks at *c.* 36–38°N, 33–34°N, and particularly 26–28°N, instead of being normally distributed with respect to latitude (Fig. 1). The abundances of 24 of 387 taxa were significantly correlated with the abundance of *T. rubescens* (Table 4). Of these, 10 co-occurred with *T. rubescens* in the mid-intertidal zone, including one genus of green alga, one brown alga, five red algae, one sponge, and two molluscs. Our knowledge of the natural history of these species does not suggest that any would interact strongly with *T. rubescens*. Nevertheless, the most plausible interaction, if any, between these sessile species and *T. rubescens* would be competition for space, predicting a negative relationship between abundances of these taxa and *T. rubescens* where both occurred, and increased abundance of the potential competitor beyond the present-day range limit of *T. rubescens*. No species exhibited this pattern.

Physical. Sea surface temperatures from NODC buoys are negatively correlated with latitude from southern California to Oregon during each month of the year [-0.952 (for January) $\leq r \leq -0.856$ (for June), $n = 32$, $P < 0.0001$]; correlations between months ranged from 0.833 (January–June, $n = 32$, $P < 0.0001$) to 0.991 (July–August, $n = 32$, $P < 0.0001$). SSTs measured by NOAA

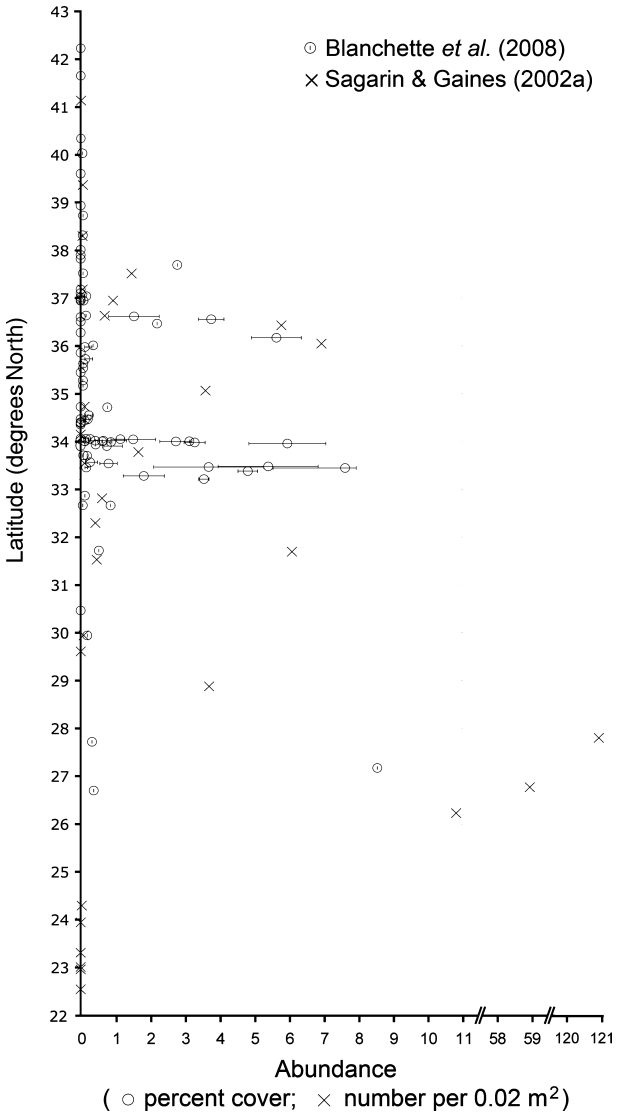

Fig. 1 Latitudinal variation in the abundance of *Tetraclita rubescens* replotted from Sagarin & Gaines (2002a) and Blanchette *et al.* (2008). Note datasets are plotted on different scales of abundance according to the original data. Both datasets illustrate that *T. rubescens* does not have an abundant geographic centre (Sagarin & Gaines 2002b). The many higher abundance observations in the Blanchette *et al.* (2008) dataset at 33–34°N are from the Southern California Channel Islands, which Sagarin & Gaines (2002a) did not sample.

satellites are also negatively correlated with latitude from southern Baja California to Oregon during June ($-0.847 \leq r \leq -0.717$, $n = 121$, $P < 0.0001$) and December ($-0.974 \leq r \leq -0.966$, $n = 121$, $P < 0.0001$), which probably represents upwelling and nonupwelling conditions, respectively; correlations between temperatures in June and December range from $r = 0.758$ (June minimum and December median, $n = 121$, $P < 0.0001$) to $r = 0.889$ (June median and December minimum, $n = 121$, $P < 0.0001$).

Temperatures do not decline linearly with increasing latitude, but occasionally increase with increasing latitude (e.g. in the Southern California Bight and Monterey Bay region), and also increase in variance in particular subregions such as in the Southern California Bight and north of Cape Mendocino (Fig. 2). Given these latitudinal vagaries, *T. rubescens* occur only at locations where June temperatures are between *c.* 9.5–18 °C and December temperatures *c.* 10.7–24.0 °C. The abundance of *T. rubescens*, however, drops precipitously at locations where monthly mean minimum temperatures fall below *c.* 10.5 °C in June and below *c.* 12.2 °C in December, regardless of whether the location is south or north of the historical range limit. The highest abundances occur toward the highest temperatures within the range (*c.* 15–18 °C in June; *c.* 18–20 °C in December).

Barnacle density in expanded range

At the surveyed NoSF locations, many *T. rubescens* were of reproductive size and most were within mating distance of their nearest neighbour (Table 5).

Mitochondrial DNA

PCR and sequencing. Concatenated mtNCR (763 nucleotides) and mtCOI (1344 nucleotides) sequences yielded 1896 positions with no missing data and 394 unique haplotypes from 406 *T. rubescens*. Haplotype frequency ranged from 1 to 4, giving a mean concatenated haplotype diversity = 0.9998 (± 0.0002). The combined haplotypes differed by an average of 17.759 (±7.902 substitutions), with mean nucleotide diversity = 0.009366 (±0.004609) (Table 6). Additional details are provided in the Supporting Information. COI and mtNCR sequences are available in GenBank under accession numbers GU381820–GU382225 and GU382226–GU382631, respectively.

Phylogeographic analyses. Phylogenetic analyses recovered a star-like gene tree with neither strong bootstrap support nor obvious association between position in the gene tree and the geographic location from which a sequence originated (Fig. 3). Similarly, the mismatch distribution constructed using the number of nucleotide differences in all possible pairwise sequence comparisons is unimodal (mean = 17.76, variance 22.03) and not significantly different from that predicted for a single rapidly expanding population (sum of squared deviations = 9.6×10^{-5}, $P = 0.52$; Harpending's raggedness index = 1.79×10^{-3}, $P = 0.75$). Pairwise F_{ST} values ranged from −0.0287 to 0.0438, of which only three (FAR-SPM, FAR-CPSCI, SPM-CPSCI) were significant

Table 4 Species whose abundance was significantly correlated (Spearman's rank correlation, *R*), negatively or positively, with the abundance of *T. rubescens*. Data from Blanchette *et al.* (2008)

	n	*R*	*P*	Median SoSF	Median SF-CM	Median NoCM	Shore zone
Chlorophyta							
Bryopsis spp.	8	0.738	0.0366	0.000	0.000	0.000	LMU
Phaeophyceae							
Halidrys dioica	30	0.616	0.0003	0.000	0.000	0.000	SL
Ralfsiaceae	83	−0.378	0.0004	0.515	0.752	0.643	LMU
Rhodophyta							
Corallina spp	96	0.263	0.0095	5.797	6.020	3.026	SL
Cryptopleura/Hymenena spp.	83	−0.405	0.0001	0.326	0.973	0.254	SL
encrusting coralline	96	0.317	0.0016	1.818	1.527	1.828	
Endocladia muricata	77	−0.247	0.0305	3.446	2.740	1.987	MH
Erythrophyllum delesserioides	12	−0.657	0.0202	0.000	0.000	0.000	L
Halymenia/Schizymenia spp	11	−0.800	0.0031	0.000	0.072	0.620	SL
Mastocarpus jardinii	33	−0.352	0.0448	0.000	0.127	0.000	MH
Mastocarpus papillatus	50	−0.368	0.0085	0.185	3.167	0.805	MH
Mazzaella affinis	73	0.420	0.0002	0.260	0.127	0.000	M
Mazzaella cordata/M. splendens	51	−0.452	0.0009	0.137	3.006	1.348	L
Odonthalia floccosa	13	−0.736	0.0041	0.000	2.928	1.475	L
Petrocelis spp.	73	−0.265	0.0234	0.540	0.878	0.848	LMU
Porifera							
Halichondria spp.	11	0.700	0.0165	0.000	0.000	0.000	SLM
Mollusca							
Mytilus californianus	93	0.210	0.0429	5.901	8.215	7.173	uM
Dendropoma lituella	5	0.900	0.0374	0.000	0.000	0.000	
Littorina keenae	61	0.463	0.0002	0.061	0.000	0.000	UP
Lottia scabra/L. conus	86	0.279	0.0094	0.242	0.107	0.000	UP
Tegula funebralis	44	−0.400	0.0072	0.076	0.144	0.000	M
Annelida							
Spirobranchus spinosus	17	0.517	0.0335	0.000	0.000	0.000	S
Arthropoda							
Megabalanus californicus	12	0.622	0.0307	0.000	0.000	0.000	SL
Bryozoa							
Membranipora spp.	8	0.881	0.0039	0.000	0.000	0.000	SL

n, number of comparisons between *T. rubescens* and the named organism; *P*, *P*-value. Bonferroni correction for 387 tests requires $P < 0.00013$ to satisfy a table-wide significance level of $\alpha_{0.05}$. The median abundance is given in the regions south of San Francisco (SoSF), San Francisco to Cape Mendocino (SF-CM), and north of Cape Mendocino (NoCM), corresponding to the historical and expanded ranges of *T. rubescens*, and regions beyond the current range limit. Distributions in the shore zone from Hewatt (1946), Abbott & Hollenberg (1976), Murray *et al.* (1980), Ruesink (2000), and Lindstrom (2008): S, subtidal; L, lower intertidal; M, middle intertidal; U, upper intertidal; P, supertidal/splash zone. Lower case letters are used as modifiers of the major zone (e.g. uM—upper Middle). A code 'M' would be equivalent to the distribution of *T. rubescens*.

($\alpha = 0.01$; $0.0068 \leq P \leq 0.0088$) before sequential Bonferroni correction for 351 tests (adjusted $\alpha_{0.05} = 0.00014$). An exact test showed no significant differentiation between any pair of populations ($P = 1.000 \pm 0.000$ for all pairwise comparisons; 1023 permutations), evidence of exceedingly high haplotype diversity in all locations; only 16 alleles were shared among locations (Fig. 4).

Of the 16 shared haplotypes, two were shared only among NoSF populations, nine were shared by both NoSF and SoSF populations, and five shared only among SoSF populations. This departs significantly from the predicted frequencies under a null model of haplotypes being shared randomly among locations ($\chi^2 = 6.373$, d.f. 2, $P < 0.05$). Of the nine haplotypes shared by NoSF and SoSF populations, six were shared by NoSF populations and SoSF populations north of Point Conception, which also significantly exceeds the expected frequency if haplotypes were shared randomly among regions ($\chi^2 = 4.50$, d.f. 1, $P < 0.05$). The distribution of distances between pairs of locations sharing a haplotype (of which at least one is NoSF), when binned in 300-km increments to mitigate the small number of possible comparisons ($n = 11$), however, did not statistically differ from the

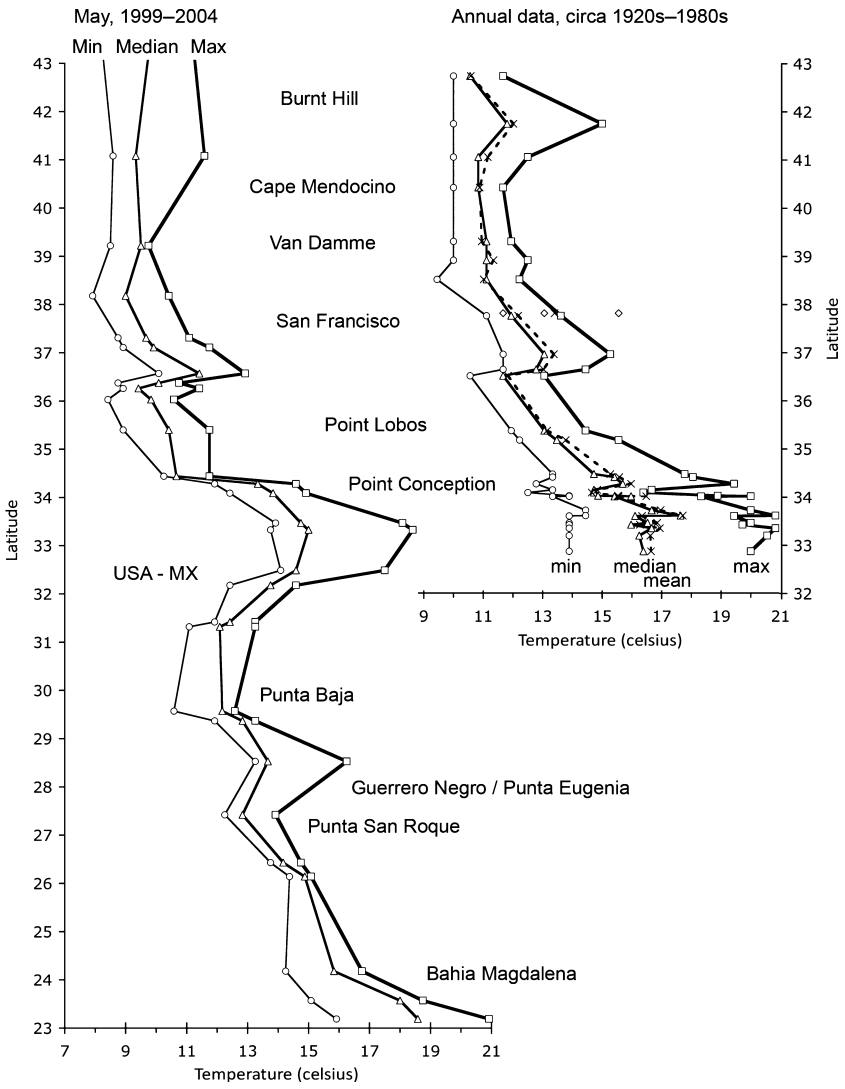

Fig. 2 Temperature variation within and between coastal sites from Oregon to southern Baja California. (A) Median and range of sea surface temperatures recorded in May of each year from 1999 to 2004 calculated [as the mean of three pixels adjacent to each sampling locality (Sagarin & Gaines 2002a)] from 1.1 km resolution AVHRR satellite data using the CoastWatch Data Analysis Tool (see section 'Methods' for details). (B) Moored buoys collected data *in situ* for 7–66 years ending in the mid-1980s (K. Logan, personal communication). Shown are the median, mean, and range of long-term mean monthly temperatures, that is, the coldest month (min), warmest month (max), annual median and mean. Data from buoys and pier-mounted stations are reported by the National Oceanographic Data Center at http://www.nodc.noaa.gov/dsdt/cwtg/all.html for north, central, and south Pacific Coast regions (last updated Tuesday 25 November 2008, 19:02:21 UTC). The sites (and buoy codes) used are, from north to south: Seaside, OR (seasideor), Newport, OR (9435380), Charleston, OR (9432780), Port Orford, OR (9431647), Crescent City, CA (9419750), Trinidad, CA (trinidadca), Mendocino, CA (mendocinoca), Bodega Bay, CA (9416841), Fort Ross, CA (fortrossca), Southeast Farallon Island, CA (46026), Santa Cruz, CA (santacruzca), Pacific Grove, CA (pacificgroveca), Point Lobos, CA (pointlobosca), Morro Bay, CA (morrobayca), Avila Beach, CA (9412110), Gaviota, CA (gaviotaca), Santa Barbara, CA (santabarbaraca), Ventura, CA (venturaca), Port Hueneme, CA (porthuenemeca), Point Mugu, CA (pointmuguca), Zuma Beach, CA (zumabeachca), Santa Monica, CA (9410840), Anacapa Island, CA (anacapaislandca), Los Angeles, CA (9410660), Newport Beach, CA (newportbeachca), Balboa, CA (balboaca), Dana Point, CA (danapointca), San Clemente, CA (sanclementeca), Avalon, CA (avalonca), Oceanside, CA (oceansideca), Scripps Pier, CA (9410230). Buoy locations are plotted here http://www.nodc.noaa.gov/dsdt/cwtg/npac_tmap.html. Several landmarks discussed in the text are shown at their relevant latitude for reference.

predicted distribution based on distances from each NoSF site to all other locations ($\chi^2 = 6.590$, d.f. 5, $P > 0.25$). Nonetheless, the observed distribution was strongly right skewed (mean 533 km, median 436 km) compared with the predicted distribution (mean 586 km, median 566 km).

Table 5 Size and proximity of *Tetraclita rubescens* at three sites north of San Francisco (see Table 2, Fig. 4)

Site	Mean (±SE) size (b.d. mm)	Size range (b.d. mm)	% ≤11 cm to nearest neighbour	Sample size (*n*)
VDM	22.4 ± 0.53	5.2–35.2	90.9	88
SRS	22.5 ± 0.53	5.0–33.3	73.6	87
BRS	21.0 ± 0.57	4.7–35.0	50.5	105

The sizes (basal diameters, b.d.) of the first ~90 individuals encountered were recorded along with distance to nearest neighbour (as an indicator of proximity to reproductive partners). Individuals separated by >11 cm were regarded as unable to copulate because paternity data collected by M. Kelly (personal communication) indicate that this is the maximum distance that an individual can reach a sexual partner with its penis.

Microsatellites

Genotyping. The number of alleles per locus ranged from 12 to 29, except for locus Tetra09 at SRBCS which amplified in few individuals (10 gene copies) yielding only four alleles. The size–frequency distributions of alleles are shown by locus and by location in Fig. 5. Two of nine microsatellite loci (Tetra11 and Tetra12) had >20% missing data and were excluded from all subsequent analyses.

Population genetic analyses. Genotype frequencies at the majority of loci in the majority of samples (exceptions: Tetra11 at SCH, VDM, BRS, CAL, SRBCS; Tetra20 at CAL, SBSLO), and all loci when all samples were pooled across the range, deviated significantly from Hardy–Weinberg equilibrium (HWE; $P \leq 0.05$). The large multilocus deviation is due to a high proportion of inferred null alleles at most loci (Table 7). The high allelic richness and gene diversity also indicate that at least some of the observed deviation from HWE may be due to sampling error. With these caveats, we compared the distributions of alleles (Fig. 5) to generate rule-of-thumb estimates of genetic diversity and population structure. Pairwise F_{ST} values calculated between all populations ranged from 0.0000 to 0.0095 ($P > 0.134$). The exact test indicates no population differentiation ($P = 1.00$ for all pairwise population comparisons). Global AMOVA partitioned 100% of variance over all useable loci (Tetra02, Tetra06, Tetra09, Tetra19, Tetra20, Tetra21, Tetra22) within populations, providing no statistical support ($F_{ct} = 0.0026$, $P = 0.190 \pm 0.004$) for the hypothesis of two geographic groupings—an historical range south of San Francisco and an expanded range north of San Francisco—of *T. rubescens*.

Table 6 Genetic diversity in concatenated COI-NCR mitochondrial locus

Site	mtDNA (NCR+COI)	
	h ± SD	π ± SD
Mainland California, expanded range		
SCH	1.000 ± 0.024	0.0085 ± 0.0045
KHM	1.000 ± 0.024	0.0103 ± 0.0054
VDM	1.000 ± 0.027	0.0090 ± 0.0048
SRS	1.000 ± 0.024	0.0092 ± 0.0049
BRS	1.000 ± 0.024	0.0096 ± 0.0050
BJS	1.000 ± 0.024	0.0100 ± 0.0053
Central California Islands		
FAR	1.000 ± 0.024	0.0096 ± 0.0051
Mainland California, established range		
BCSM	1.000 ± 0.024	0.0089 ± 0.0047
SCSC	1.000 ± 0.024	0.0085 ± 0.0045
MPM	1.000 ± 0.024	0.0091 ± 0.0048
SPM	1.000 ± 0.024	0.0080 ± 0.0043
MCM	1.000 ± 0.024	0.0097 ± 0.0050
RMSLO	1.000 ± 0.024	0.0091 ± 0.0048
SBSLO	1.000 ± 0.024	0.0091 ± 0.0048
RSB	1.000 ± 0.024	0.0093 ± 0.0049
MSV	1.000 ± 0.024	0.0092 ± 0.0049
(Northern) California Channel Islands		
PHSCI	1.000 ± 0.024	0.0110 ± 0.0058
CPSCI	1.000 ± 0.027	0.0086 ± 0.0046
Mainland California, established range		
PMV	1.000 ± 0.024	0.0097 ± 0.0051
CAL	1.000 ± 0.024	0.0092 ± 0.0048
DPO	1.000 ± 0.024	0.0094 ± 0.0050
SPSD	1.000 ± 0.024	0.0104 ± 0.0055
(Southern) California Channel Islands		
ICCI	1.000 ± 0.024	0.0086 ± 0.0046
PRCI	1.000 ± 0.024	0.0091 ± 0.0048
Baja California, established range		
PBBCN	1.000 ± 0.027	0.0108 ± 0.0057
SRBCN	1.000 ± 0.024	0.0093 ± 0.0049
SRBCS	1.000 ± 0.024	0.0101 ± 0.0053
Global	*0.9998 ± 0.0002*	*0.0094 ± 0.0046*

CMH and ISM not included due to very small sample sizes.
h, haplotype diversity; π, nucleotide diversity.

AMOVA also revealed no significant between-population ($0.059 \leq P \leq 0.630$; Bonferroni corrected $\alpha_{0.05}$ for seven tests is 0.007) or between-region ($0.090 \leq P \leq 0.982$; Bonferroni corrected $\alpha_{0.05} = 0.007$) structure at any locus. Locus-by-locus AMOVA confirmed that >98% of variance in six of the seven loci occurred within populations; variance between populations or regions was consistently nonsignificant ($0.08 \leq P \leq 0.63$). However, allelic frequencies at Tetra02 may differ slightly north vs. south of San Francisco ($F_{SC} = 0.0130$, $P = 0.044$). Analyses of pairwise linkage disequilibrium among loci with <20% missing data showed significant ($\alpha = 0.010$) linkage among alleles in 8–17 out of 21 possible

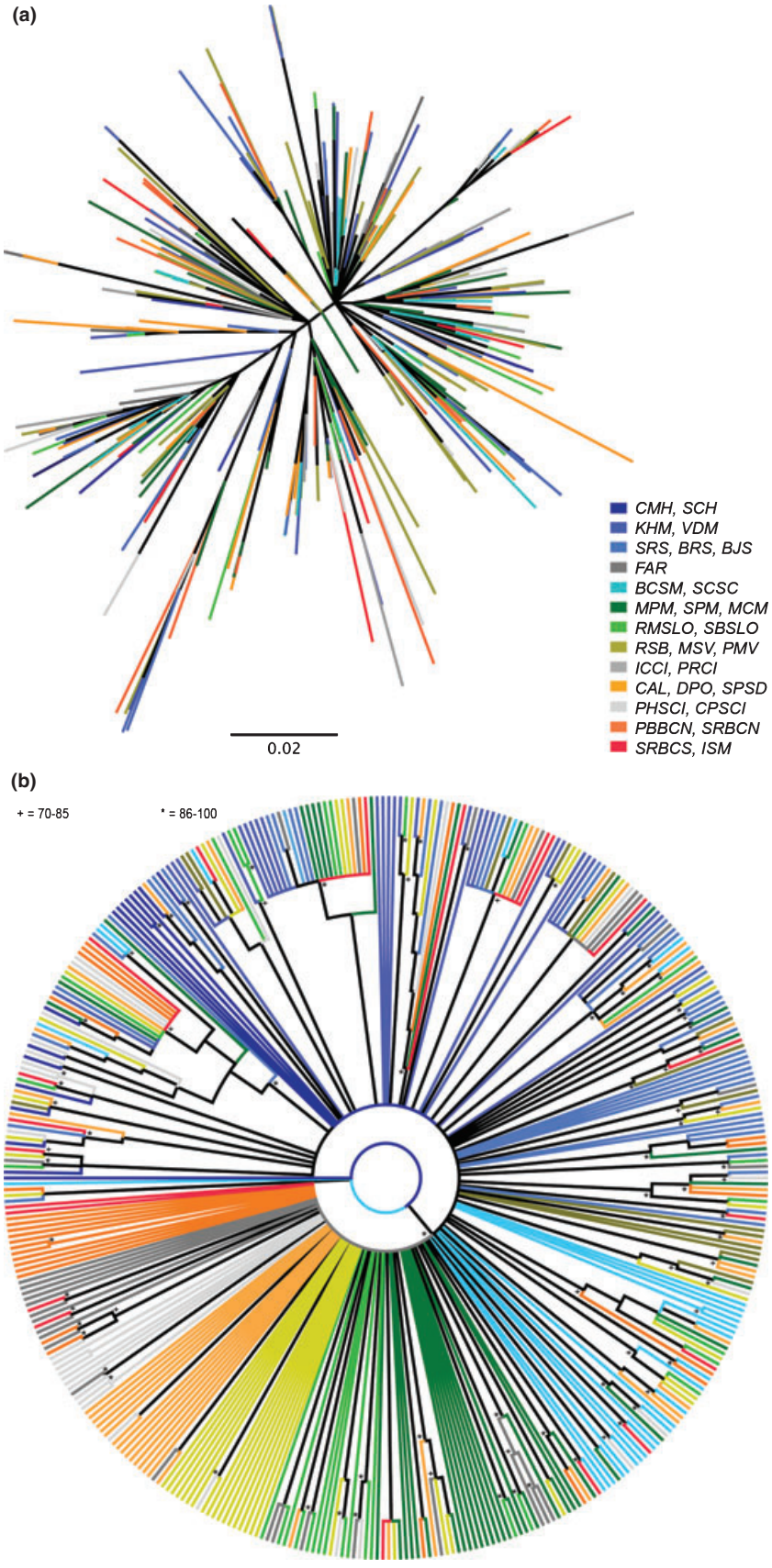

Fig. 3 Mitochondrial gene tree constructed using maximum likelihood analyses of combined cytochrome *c* oxidase subunit I and noncoding region. (A) The single maximum likelihood tree constructed using GARLI. (B) The 50% bootstrap consensus constructed using RaxML. Branches marked + were recovered from 70% to 85% of bootstrap datasets. Branches marked * were recovered from 86% to 100% of bootstrap datasets. Colours represent the general geographic region from which samples were collected. Sample location codes are given in Table 2.

Fig. 4 Map of the west coast of North America, from Baja California (sites ISM-PBBCN) through California (sites SPSD-CMH) and into Oregon (southern state line is approximately 10 km south of Burnt Hill), which encompasses the entire modern range of *Tetraclita rubescens*. Several landmarks mentioned in the text are shown for orientation. Curves link pairs of sites that share a mitochondrial haplotype (no sites shared more than one haplotype). Black lines link pairs in which at least one site is in the recently expanded range north of San Francisco; grey lines link pairs in which neither pair is in the recently expanded range.

comparisons (SCH 17, VDM 10, BRS 14, BCSM 14, SBSLO 10, CAL 8, PBBCN 14, SRBCS 13), but 16/21 when all samples were considered as being from a single population.

Discussion

Our combined study of geographic, population, and genetic variation shows that in the last 30–40 years *T. rubescens* has expanded its distribution northward several hundred kilometres from its prior range limit in the vicinity of San Francisco, *c.* 1970 (Newman & Abbott 1980; Sanford & Swezey 2008). The preponderance of these data suggest the expansion was largely due to a northward shift in the climate envelope in which *T. rubescens* can maintain positive population growth rather than to adaptation to novel environmental conditions more extreme than those in which the species historically persisted.

Range limits and range expansion in T. rubescens

The classic definition of a range limit is the 'line beyond which the selective factors of the environment prevent successful reproduction' (Mayr 1963: p. 523; see Gilman 2006), or in more demographic terms, the peripheral location beyond which 'the birth rate falls below the death rate, and the population is no longer able to sustain itself' (Kirkpatrick & Barton 1997: p. 1). This general description can be applied pragmatically (e.g. Holt *et al.* 2005) to recognize range limits that are attributable not only to the classic latitudinal environmental gradient, but also to physical barriers to dispersal (e.g. Grigg & Hey 1992), increasing distances

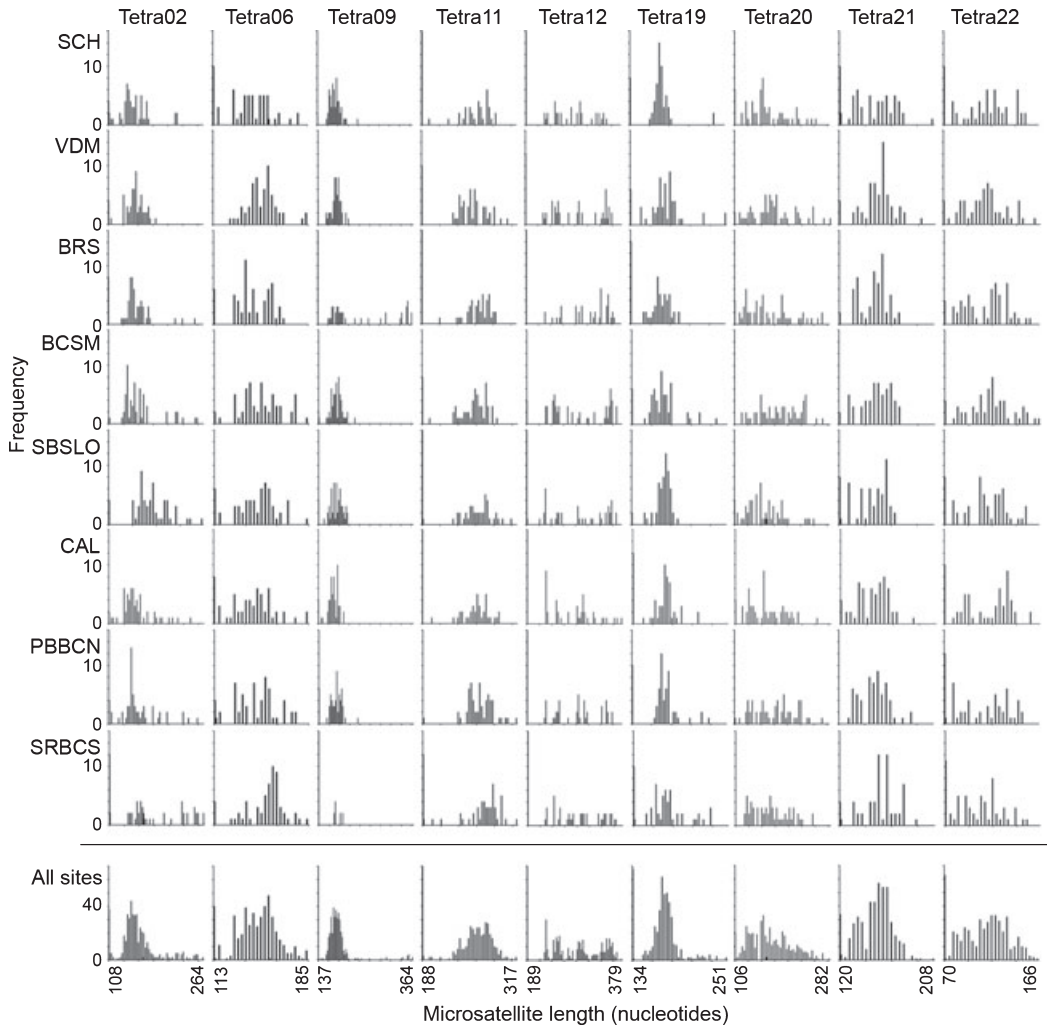

Fig. 5 Size–frequency distributions of alleles, by locus (Tetra02, Tetra06, Tetra09, Tetra11, Tetra12, Tetra19, Tetra20, Tetra21, Tetra22) and by location (SCH, VDM, BRS, BCSM, SBSLO, PBBCN, CAL, SRBCS) and globally for 'all sites' combined.

Table 7 Genetic diversity (mean ± standard deviation) in microsatellite loci at the eight locations surveyed

Site	No of alleles/gene copies	Observed heterozygosity	Expected heterozygosity	Gene diversity
Mainland California, expanded range				
SCH	17.3 ± 4.0/52.9 ± 3.2	0.524 ± 0.140	0.929 ± 0.030	0.77 ± 0.42
VDM	18.0 ± 4.2/56.6 ± 1.9	0.615 ± 0.163	0.929 ± 0.022	0.78 ± 0.41
BRS	18.1 ± 5.4/52.3 ± 5.3	0.520 ± 0.169	0.931 ± 0.029	0.78 ± 0.44
Mainland California, established range				
BCSM	19.0 ± 5.4/57.7 ± 2.1	0.556 ± 0.117	0.939 ± 0.017	0.85 ± 0.44
SBSLO	17.1 ± 4.9/52.0 ± 6.0	0.597 ± 0.136	0.927 ± 0.025	0.77 ± 0.42
CAL	17.9 ± 4.1/53.7 ± 3.7	0.597 ± 0.168	0.929 ± 0.020	0.75 ± 0.41
Baja California, established range				
PBBCN	17.7 ± 5.2/54.9 ± 4.6	0.507 ± 0.153	0.926 ± 0.026	0.80 ± 0.43
SRBCS*	17.3 ± 7.0/47.0 ± 16.9	0.465 ± 0.292	0.916 ± 0.059	0.72 ± 0.39

*Alternative estimates of genetic diversity values if locus Tetra09 is excluded due to extremely small number of gene copies (n = 10): No of alleles/gene copies 19.5 ± 4.3/53.2 ± 4.8, Observed heterozygosity 0.542 ± 0.229, Expected heterozygosity 0.935 ± 0.031, Mean gene diversity 0.97 ± 0.74.

between decreasing amounts of suitable habitat (e.g. Hastings *et al.* 2005; Gilman 2006; Samis & Eckert 2007), or other potential causes (e.g. Magiafoglou *et al.* 2002; Holt *et al.* 2005; Byers & Pringle 2006; Sanford *et al.* 2006).

Based on this definition, the population at the range limit of *T. rubescens*, a sessile nonselfing hermaphrodite that copulates, must consist of at least two mature individuals, one within a penis-length of the other, in a location with a long-term stable or increasing census population size to which they could feasibly contribute progeny. The northern-most location at which stable or increasing numbers (Newman & Abbott 1980; cf. Connolly & Roughgarden 1998; cf. Blanchette *et al.* 2008) of potentially copulating *T. rubescens* (Table 5) have been documented is Van Damme, Mendocino County (VDM). As presently resolved by available molecular data, *T. rubescens* is effectively one genetic population between all sites studied from Baja California Sur to Humboldt County and therefore reproduction at VDM could, in principle, contribute to maintenance of the population in its entirety, including that at VDM. Although additional fieldwork may reveal that more northerly sites also meet these criteria, currently, according to the classic definition, VDM is the best documented, modern, northward range limit of *T. rubescens*. A modern range limit at VDM, approximately 2° of latitude north of the range limit recognized in 1980 (Newman & Abbott 1980) therefore yields a range expansion of at least ~220 km great circle distance.

An alternative range-limit definition, such as the northernmost extent of any individual of the species (e.g. Lomolino *et al.* 2005), would not change the conclusion that a range expansion has occurred, instead altering only the defined geographic location of the modern limit. Using this definition the northern limit would have been Burnt Hill, OR, USA, for the life-time of a single specimen circa 2007, as opposed to Cape Mendocino currently (E.S. personal observation) and in 1995 and 1996 (e.g. Connolly & Roughgarden 1998) or Saunder's Reef in 1984 (Kinnetic Laboratories 1985).

Comparing empirical patterns with theoretical predictions to infer the cause(s) of a range limit

The extension of the range limit of *T. rubescens*, as defined here from *c.* 37°49′N in the 1970s to at least 39°17′ N in 2008, provides an opportunity to study the causes of range limits and range expansion by comparing empirical patterns with the predictions of theory (e.g. Hoffmann & Blows 1994; Kirkpatrick & Barton 1997; Holt & Keitt 2000; Table 1). Such studies are fundamental (Holt & Keitt 2000) but still rare in the literature (Sagarin *et al.* 2006). We compare empirical data with the patterns predicted to result from three potential causes of range limits—genetic impoverishment (H_1), migration load (H_2), and a physical barrier to dispersal (H_3)—or from secular migration (H_{SM}) (Table 1). We consider the environmental setting and compare the measured and predicted spatial patterns of abundance, gene flow, and genetic diversity across a contemporaneous landscape (i–v; Table 1) and the effects of temporal environmental change (vi–vii; Table 1).

(i) *The abiotic and biotic environment.* Many decades of data describe spatial and temporal patterns in the biotic and abiotic environments of California's coastal marine taxa. Surveys of algae (Murray *et al.* 1980), fishes (Horn & Allen 1978; Horn *et al.* 2006), barnacles (Newman & Abbott 1980), molluscs (Newell 1948; Valentine 1966), and broader surveys of intertidal community structure (Blanchette *et al.* 2008) all show that an area of relatively gradual biotic transition within one bioregion encompasses both the historical and modern range limits of *T. rubescens*. There are neither coincident range limits in species with ecologically important interactions with *T. rubescens* (Table 4), nor any enhanced predation on *T. rubescens* by dogwhelks (*Nucella* spp.) in the northern part of the range (Sanford & Swezey 2008). A largely monotonic, decline in monthly mean minimum, median, mean, and maximum SSTs is a consistent, long-term, feature across the region from ~37°N to ~40°N (Fig. 2) and is probably matched by long-term mean patterns in subaerial temperature although interannual extremes may deviate due to microclimates (Helmuth *et al.* 2006). Thus biotic and abiotic environmental gradients or 'ramps' (*sensu* Hoffmann & Blows 1994) coincide with the historical and modern range limits of *T. rubescens*, rather than areas of major biotic turnover or abrupt physical change (which, for example, occur farther south at Monterey Bay, Point Conception, or Los Angeles (Dawson 2001; Legaard & Thomas 2006, 2007; Blanchette *et al.* 2008; Pelc *et al.* 2009; Fig. 2)). This coincidence of range limits with an environmental gradient, rather than a discontinuity, agrees with the predictions of genetically impoverished isolated marginal populations (H_1), migration load (H_2), and a snapshot of secular migration (H_{SM}). It is inconsistent with an absolute physical barrier to dispersal (H_3).

(ii) *Abundance.* Two published surveys describe the abundance of *T. rubescens* as declining toward and across its northern range limit (Fig. 1). This pattern, consistent with a 'soft' boundary (Mayr

1963; Kirkpatrick & Barton 1997), corresponds to the predictions of H_1 and H_2, but not the predictions of H_3 or H_{SM}.

(iii) *Gene flow*. Previous analyses of allozyme variation (Ford & Mitton 1993), plus our own data on mitochondrial DNA sequence (Fig. 3) and microsatellite variation (Fig. 5), all indicate very high gene flow across the entire range of *T. rubescens*. Estimates of Nm between populations range from 12 to 85 (Ford & Mitton 1993) to Nm » 1000 across the entire distribution of *T. rubescens*, including peripheral populations (this study). Such high gene flow is consistent with H_2, and would also be consistent with H_3 and perhaps H_{SM}, but is contrary to the expectations of genetic impoverishment (H_1).

(iv) *Genetic diversity*. Allozymes (Ford & Mitton 1993), mitochondrial DNA haplotypes, and microsatellite loci (Tables 6 and 7) all exhibit very high genetic diversity, both within and among populations, consistent with H_2 and possibly H_3, but not H_1 or H_{SM}.

(v) *Unique alleles*. It is not possible with the current dataset to assess the frequencies of unique alleles due to the very high genetic diversity in *T. rubescens*.

(vi) *Timing of range extension*. The northward expansion of *T. rubescens* since the 1970s coincided with ≈0.8 °C warming of coastal California waters during the second half of the 20th Century (Enfield & Mestas-Nuñez 1999; Sagarin *et al.* 1999) and ≈0.4°C warming of SST, averaged annually and spatially between 23°N and 60°N, from the 1970s to 2000 (Smith & Reynolds 2003). Range expansion should correspond to environmental change if a range limit is caused by migration load (H_2); environmental change also would permit (but is not required for) range expansion under scenarios H_1 and H_{SM}. Range expansion is inconsistent with a constant physical barrier to dispersal (H_3) and is sustained beyond periodic warm-water intrusions due to El Niño that can result in short-term range extensions (e.g. Hubbs 1948; Lluch-Belda *et al.* 2005). The spatial extent of the northward expansion of *T. rubescens* in relation to the degree of ocean warming since the 1970s is also consistent with H_1 (and also H_2 and H_3 in the absence of mutation or immigration of maladapted alleles in peripheral populations). The monthly mean SST difference between the historical range limit at ≈38°N and the current range limit at or beyond ≈39°N is approximately 0.5–1.0 °C, depending on the SST (minimum, mean, median, or maximum) dataset considered (Fig. 2).

(vii) *Gene flow in the expanded range*. Newly occupied locations within a range expansion offer opportunities to distinguish among genetic causes of range limits. The average distance between locations sharing haplotypes found in the expanded range should indicate, approximately, the distance over which alleles have dispersed within the period of the expansion. Although our sampling of allelic diversity in *T. rubescens* is incomplete, we estimated the median distance between putative source locations and recipient sites of *T. rubescens* haplotypes was 436 km. The modern pattern accrued in no more than 15 generations (assuming a generation time of two years), giving a per generation median dispersal distance >29 km (pelagic larval duration is 18–26 days at 13°C, E.S. unpublished data). This distance is relatively long for marine invertebrates with pelagic larvae (see Kinlan & Gaines 2003 for comparisons), similar to range expansion of hundreds of kilometres in a few decades measured in marine zooplankton (Beaugrand *et al.* 2002) and fish (Perry *et al.* 2005; Sabatés *et al.* 2006) in response to climate change. These high rates of migration are consistent with estimated $F_{ST} = 0$ between locations in the expanded range (NoSF) and those in the established range (SoSF). Thus, genetic analyses of the expanded range, like those of populations within the historical range, support H_2 and argue against H_1, H_3, and H_{SM}.

Despite this high dispersal ability, analyses of allozymes showed a signal of increased self-recruitment toward the historical periphery (Ford & Mitton 1993) and our analyses indicate slightly, but statistically significantly, elevated recruitment into northern peripheral locations from other northern sites (Fig. 4). These suggestions of barely perceptible decrease in gene flow between peripheral populations are consistent with the expectation from H_2 (but not H_1, H_3, or H_{SM}) of reduced gene flow into populations approaching the periphery because their decreasing population size and therefore smaller output of propagules (see '*Abundance*' above). This pattern may indicate the general spatiotemporal scale of gene flow in *T. rubescens*, or more specific geographic patterns of retention and recruitment facilitated by eddies, relaxation of upwelling, or other oceanographic features, with durations of a few days to months, that may occur at multiple locations along eastern boundary currents (e.g. Wash-

burn *et al.* 1993; Pullen & Allen 2001; Kaplan & Largier 2006; Dudas *et al.* 2009).

(viii) *Genetic diversity in the expanded range*. When new habitats are colonized by small numbers of propagules, and dispersal follows a stepping-stone pattern, recently colonized locations typically ought to have reduced genetic diversity compared with the historically established range (Phillips *et al.* 2008; Pujol & Pannell 2008). The high dispersal ability of *T. rubescens* (see *Gene flow in the expanded range*), however, has led to genetic diversity in the expanded range largely comparable with that in the historical range, more consistent with H_2 and largely inconsistent with H_1, H_3, or H_{SM}.

Interpretation, and broader implications

The data available on *T. rubescens* best correspond to the classical descriptions of a range limit that is a 'soft [boundary] declining asymptotically to 0 rather than actually vanishing at a defined point in space' (Kirkpatrick & Barton 1997: p. 19). These data also strongly suggest (in seven of our eight comparisons above, and in Table 1) that migration load is the primary factor setting the northern range limit of *T. rubescens*, although our analysis does not prove the absence of heritable genetic variation in one or more key traits. Furthermore, environmental amelioration, which relaxes the strength of selection against immigrant phenotypes at a particular location, probably because of climate change, appears to be the primary factor that enabled range expansion.

Whether the coupled mechanisms of migration load and environmental change have caused other species to establish then expand their geographic ranges is unclear; the breadth of data describing changes in *T. rubescens* is not currently available for most other northeastern Pacific species. However, it is possible that relaxation of migration load may be a common driver of range expansions because relaxation of selection attributable to climate change is a more probable mechanism than random mutation for observed large-scale, largely synchronous, mostly unidirectional, multi-species changes in distribution of marine taxa (e.g. Perry *et al.* 2005). Environmental change of relevant variables would synchronously relax selection on high-dispersal species subject to migration load and low-dispersal species subject to genetic impoverishment. The speed and extent of range expansion in response to environmental change may reflect the vagility of species (Perry *et al.* 2005), with high dispersal species, such as *T. rubescens*, showing rapid distant range expansion effectively contemporaneously with environmental change.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Materials and methods.

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