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Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*

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Abstract

A long-standing issue in marine biology is identifying spatial scales at which populations of sessile adults are connected by planktonic offspring. We examined the genetic continuity of the acorn barnacle *Balanus glandula*, an abundant member of rocky intertidal communities of the northeastern Pacific Ocean, and compared these genetic patterns to the nearshore oceanography described by trajectories of surface drifters. Consistent with its broad dispersal potential, barnacle populations are genetically similar at both mitochondrial (cytochrome oxidase I) and nuclear (elongation factor 1-alpha) loci across broad swaths of the species' range. In central California, however, there is a striking genetic cline across 475 km of coastline between northern and southern populations. These patterns indicate that gene flow within central California is far more restricted spatially than among other populations. Possible reasons for the steep cline include the slow secondary introgression of historically separated populations, a balance between diversifying selection and dispersal, or some mix of both. Geographic trajectories of oceanic drifters closely parallel geographical patterns of gene flow. Drifters placed to the north (Oregon; ~44°N) and south (Santa Barbara, California; ~34° N) of the cline disperse hundreds of kilometres within 40 days, yet over the long-term their trajectories never overlapped. The lack of communication between waters originating in Oregon and southern California probably helps to maintain strong genetic differentiation between these regions. More broadly, the geographical variation in gene flow implies that focusing on species-level averages of gene flow can mask biologically important variance within species which reflects local environmental conditions and historical events.

Keywords: California Current, cline, dispersal, marine invertebrate, mtDNA sequences, nuclear sequences, selection

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Introduction

Virtually all species of bottom-dwelling marine organisms are distributed in patches that are linked by the dispersal of planktonic larvae (Thorson 1950). As such, larval dispersal plays a fundamental role in the ecology and evolution of marine organisms and their biotic interactions (see reviews in Caley *et al*. 1996; Botsford *et al*. 2001; Grosberg & Cunningham 2001; Strathmann *et al*. 2002). Genetic estimates of the spatial extent of larval dispersal generally support a positive correlation between a species' ability to disperse — as measured by larval lifespan — and the actual distances they travelled (Bohonak 1999). However, a number of more recent studies on fish and invertebrates with long-lived planktonic larvae indicate that planktonic larvae can be locally retained (e.g. Jones *et al*. 1999; Swearer *et al*. 1999; Barber *et al*. 2000; Taylor & Hellberg 2003), suggesting that the realized dispersal of marine organisms is probably less extensive in distance than estimates based on life-history alone predict.

More importantly, there is growing recognition that realized dispersal is probably more complicated than can be estimated from limited sampling from a small portion

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of a species' range. For example, when oceanographic circulation patterns, reproductive timing, larval duration and the availability of suitable habitat geographically vary — a likely scenario for many widely distributed, coastal species — actual dispersal distances may reflect this variation (Shanks 1995; Sponaugle *et al*. 2002). Thus, to the extent that dispersal is more restricted and more geographically variable than is currently acknowledged, the scales over which marine populations are ecologically and evolutionarily connected may be greatly oversimplified.

Here, we explore spatial patterns of gene flow and dispersal in a widespread, invertebrate across rocky intertidal coastlines along the west coast of North America. Such organisms are exposed to a dynamic oceanography that should promote long-distance planktonic dispersal across contiguous habitats. The acorn barnacle *Balanus glandula* (Darwin 1854) — which ranges from Baja California to Alaska — is one of the most intensively studied and abundant members of wave-exposed, upper intertidal communities of the northeast Pacific Ocean (e.g. Paine 1966; Connell 1970; Dayton 1971; Menge 2000). The attached hermaphroditic adults become reproductive within a year of settlement. The released naupliar larvae must feed in the water column for at least 2 weeks before their transformation into cyprid larvae that are competent to settle on the hard substrata (Brown & Roughgarden 1985).

The dynamics of cross-shelf (i.e. east–west) transport of *B. glandula* larvae are well understood. Recruitment onto the shoreline of central California is strongest when there is local or regional relaxation of upwelling events. This is because larvae accumulate at the frontal boundary between upwelled and offshore waters and move ashore when upwelling ceases (Roughgarden *et al*. 1988; Farrell *et al*. 1991). In contrast, the along-shore (i.e. north–south) component has received less attention, in part because it is difficult to track individual cohorts of barnacle larvae. The most obvious currents that run parallel to the shoreline are the poleward Davidson Current, which flows primarily in the late autumn to winter and during a period of low *B. glandula* settlement, and the equatorward California Current, which predominates in the spring and summer months during a period of maximal *B. glandula* settlement (Gaines & Roughgarden 1987; Menge 2000; Strub & James 2000). At flow rates of 10 cm/s, larvae entrained within these currents might travel several hundred kilometres before settlement. However, these are maximal dispersal estimates, and if the majority of larvae that settle remained nearshore during the pelagic stage, then alongshore dispersal and gene flow might be more limited.

To complicate matters, there is also profound regional variation in the oceanographic conditions that different *Balanus glandula* populations encounter which may alter patterns of along-shelf larval dispersal. In Oregon and Washington, the California and Davidson currents are physically closer to the shore than in California (Roughgarden *et al*. 1988; Strub & James 2000), in part because the continental shelf is narrower. Thus, all else being equal, larvae originating in Oregon and Washington are more likely to become entrained within these streaming currents and travel farther before settlement. In California, the along-shore transport of *B. glandula* may be more affected by the complexity of nearshore oceanography, rather than streaming offshore currents.

We sequenced a mitochondrial DNA (mtDNA) and single-copy nuclear (scnDNA) locus from among 12 barnacle populations collected across ~1500 km of North American rocky-intertidal shoreline to test the hypothesis that regional variation in oceanography correlates with regional variation in gene flow. Previous genetic work with *Balanus glandula* indicates potentially conflicting results. Hedgecock (1994) discovered few allozyme differences among populations from southern California to Alaska. Wares *et al*. (2001) suggested a phylogeographical break in mtDNA sequences between populations south of and north of Monterey Bay. The present study uses a broader sampling of populations and two loci to show that the break described by Wares *et al*. (2001) is actually a surprisingly steep cline between northern and southern populations, and that *B. glandula* gene flow varies substantially with geographical location in a manner predicted by local oceanographic conditions.

Materials and methods

Collection, amplification and sequencing of DNA

Approximately 50–100 adults were collected per population from the upper edge of the *Mytilus* mussel zone on exposed, rocky-intertidal shorelines. All adults were collected in summer 2001 and spring 2002, with the exception of Vancouver Island, Point San Luis and some Pacific Grove adults that were collected in summer 2003. Adults were placed into 70–95% ethanol. DNA was extracted with 10% Chelex-100 resin (Bio-Rad Laboratories) from a haphazardly chosen subset of individuals using ~1 mm^3 pieces of cirral tissue. Polymerase chain reaction (PCR) amplification (40 cycles, 52.2 °C annealing) was performed on 386 base pairs (bp) of the 3′ end of cytochrome *c* oxidase I (COI) using the custom-made primers BF2 (5′-TGTAATTGTTACTGCTCATGC-3′) and BR2 (5′-ACCAAARAAYCAGAATAAGTGTTG-3′). Amplifications were sequenced in one direction using a Prism 3100 Genetic Analyser (Applied Biosystems). PCR amplification of 156 bp of an elongation factor 1α (EF1α) exon was performed (40 cycles, 64 °C annealing) using the custom-made primers Ef1_for (5′-ACGGCGACAACATGCTGGAGA-3′) and Ef1_rev (5′-CGGGGTGGTTCAGGACGATGA-3′) and directly sequenced in forward and reverse directions to confirm heterozygotes. Because of the cost and time

involved with sequencing and analysing a scnDNA locus, a relatively small subset of animals was chosen at random to sequence from only nine of the 12 populations that were collected.

Analysis of DNA sequences

The phase of EF1α alleles was determined with a Bayesian analysis of all sequences implemented by PHASE 1.0 (no indels were present: Stephens *et al*. 2001). Genotypes that could not be resolved with greater than 60% confidence were not used in any analysis. All but nine of the 155 bp sequenced from 114 adults (i.e. 0.05%) were assigned a phase with 98% confidence or greater. We are confident that our estimates of population differentiation are not compromised by the possible misassignment of phase of these nine SNPs because of their rarity and because none were utilized to define haplotype groups (see Results). We then used PAUP 4.0 to generate neighbour-joining and maximum parsimony trees using models of substitution suggested by MODELTEST (TrN + Γ, where Γ = 1.64, for COI and F81 for EF1α: Posada & Crandall 1998). Bootstrap values were generated from a resampling of 1000 neighbour-joining trees in MEGA (Kumar *et al*. 2001). The parsimony trees were generated from a heuristic search (random stepwise addition, followed by TBR branch-swapping; 1000 replicates and one tree saved per replicate).

Levels of genetic differentiation (Φ_{ST}, as estimated by Weir & Cockerham 1984) between pairs of populations were generated by the software ARLEQUIN 2.0 (Schneider *et al*. 2000). Statistical significance of Φ_{ST} values was based on distributions of 1000 permutation replicates for each pairwise comparison and an alpha of 0.05. Statistical assessments of population differentiation were also tested using an exact test of the frequencies of the three major haplotype groups A, B and C. Linkage disequilibrium was estimated by the methods described in Asmussen & Basten (1994), as implemented in the software CNDm (see http://statgen.ncsu.edu/brcwebsite/software_BRC.php). Statistical significance of linkage disequilibrium was generated from 1000 Monte Carlo bootstrap replicates and an alpha of 0.05.

Oceanographic drifters

From August 1994 until September 1999, a total of 75 surface drifters was released within 120 km of the coast off Newport (44.6 N) and Coos Bay (43.4 N), Oregon, primarily from spring to early autumn (Barth *et al*. 2000). The WOCE-standard, holey-sock drifters were drogued at 15 m and tracked via satellite over their nominal 2-year lifetimes (Niiler *et al*. 1995). A total of 541 surface drifters were released in the Santa Barbara Channel (SBC) (34.25 N) during all months of the year from 1992 to 1999 (Winant *et al*. 1999). These drifters were of the Davis design with approximately 1-m high cloth vanes (Davis 1985) and were also tracked via satellite for a target period of 40 days. The SBC drifter trajectories occasionally exceeded 40 days but were never longer than 90 days. The drifters are not released on the shoreline — instead they were placed in waters of 15 m depth at locations tens of kilometres offshore.

Simulation of clinal collapse

A computer simulation of stepping stone dispersal was implemented and the rate of the collapse of an analogous cline was estimated. Populations of constant size N in a one-dimensional stepping stone array exchange larvae with the nearest neighbour as a function of the distance between them. Each population is initially started with the same frequency of one allele in a single locus, two allele system. In every generation, genetic drift occurs through the random selection of alleles to be combined into progeny. The probability of dispersal of a propagule from deme y to deme x is estimated as $k(x,y) = \alpha/2\ \exp(-\alpha|x-y|)$, where $1/\alpha$ is the mean distance that larvae disperse from their parents (adapted from Botsford *et al*. 2001 and Palumbi 2003). A conservative assumption was made that gene flow resumed among differentiated populations approximately 10^4 generations ago, after the most recent Pleistocene glacial maximum (~10^4 years). The simulation encompassed 1000 populations of 1000 individuals each distributed along a 1000 km cline.

Results

Phylogeny of mtDNA and nuclear alleles of Balanus glandula

The mitochondrial COI locus of 433 adult barnacles, collected from 12 populations from California to Vancouver Island Canada (Table 1a; GenBank Accession nos AY62954–AY630026), was sequenced. As expected given the enormous population sizes and wide geographic distribution of *Balanus glandula*, there were highly divergent polymorphisms within the COI locus [average pairwise divergence between individuals (± SE) was 2.2% (± 0.4%); variance based on 1000 bootstrap replicates generated by MEGA] that fell into three distinguishable haplotype groups (labelled A_{COI}, B_{COI} and C_{COI}; Fig. 1a). Sixty-five of the 386 bp sequenced of COI were parsimony-informative. Two nucleotide transitions distinguished groups A_{COI} and B_{COI} (sites 90, 177 both third positions) and a single transition separated groups A_{COI} and C_{COI} (site 315, third position). The $A_{COI} : B_{COI}$ and $A_{COI} : C_{COI}$ splits had 21% and 23% neighbour–joining bootstrap support and 100% consensus support (maximum parsimony). The average pairwise divergences between individuals within each of the clades (± SE) were 0.9%

Table 1 Φ_{ST} values are below the diagonal; corrected number of differences among sequences within a population are on the diagonal (indicated in italic) and the number of differences per base pair among sequences between populations are above the diagonal. The sample sizes (*n*) are also indicated. EF1α data include sequences inferred as recombinants. Bold numbers indicate significant values ($P < 0.05$)

	n	VI	WA	CM	HH	CB	TH	CMO	FB	BOD	PP	PG	PSL
(a) COI													
VI	29	*0.019*	0.019	0.020	0.019	0.019	0.019	0.019	0.022	0.022	0.025	0.026	0.027
WA	37	−0.003	*0.018*	0.019	0.019	0.018	0.018	0.018	0.021	0.021	0.023	0.025	0.025
CM	37	0.019	−0.002	*0.020*	0.020	0.019	0.020	0.019	0.021	0.022	0.024	0.025	0.025
HH	37	−0.014	0.013	0.025	*0.019*	0.020	0.019	0.019	0.022	0.023	0.025	0.027	0.028
CB	34	0.009	−0.017	−0.015	0.023	*0.019*	0.019	0.019	0.021	0.021	0.023	0.024	0.024
TH	21	−0.012	−0.023	−0.008	−0.013	−0.016	*0.019*	0.018	0.021	0.022	0.024	0.026	0.027
CMO	23	−0.013	−0.014	−0.003	−0.013	−0.010	−0.031	*0.018*	0.021	0.022	0.024	0.026	0.026
FB	34	**0.062**	**0.039**	0.024	**0.069**	0.024	**0.047**	**0.050**	*0.022*	0.021	0.021	0.021	0.021
BOD	37	**0.099**	**0.072**	**0.060**	**0.114**	**0.056**	**0.086**	**0.096**	−0.012	*0.021*	0.020	0.020	0.019
PP	30	**0.238**	**0.209**	**0.179**	**0.250**	**0.183**	**0.230**	**0.240**	**0.056**	0.021	*0.018*	0.016	0.016
PG	67	**0.389**	**0.357**	**0.322**	**0.395**	**0.329**	**0.388**	**0.394**	**0.174**	**0.122**	0.017	*0.014*	0.013
PSL	42	**0.442**	**0.409**	**0.367**	**0.442**	**0.379**	**0.445**	**0.451**	**0.221**	**0.167**	**0.050**	−0.002	*0.011*
(b) EF1α													
VI	7	*0.009*	0.010	0.008	0.008	0.008		0.009		0.011		0.018	0.022
WA	5	−0.010	*0.011*	0.009	0.010	0.008		0.010		0.013		0.022	0.026
CM	5	−0.085	−0.058	*0.009*	0.008	0.008		0.009		0.011		0.019	0.023
HH	5	−0.014	0.062	−0.022	*0.007*	0.008		0.009		0.010		0.017	0.021
CB	6	0.018	−0.058	−0.045	0.083	*0.007*		0.008		0.011		0.021	0.025
CMO	14	−0.038	−0.030	−0.069	0.021	–0.027		*0.009*		0.012		0.019	0.023
BOD	10	0.036	0.100	0.033	0.004	**0.121**		0.072		*0.012*		0.016	0.019
PG	25	**0.399**	**0.466**	**0.418**	**0.408**	**0.499**		**0.440**		**0.246**		*0.012*	0.013
PSL	37	**0.474**	**0.530**	**0.490**	**0.484**	**0.557**		**0.508**		**0.349**		**0.043**	*0.013*

Vancouver Island, Canada (VI, 48°30′N, 124°30′W) Westport Jetty (WA, 46°56′N, 123°51′W), Cape Meares (CM, 45°28′N, 123°58′W), Heceta Head (HH, 44°09′N, 124°08′W), Cape Blanco (CB, 42°50′N, 124°34′W), Trinidad Head (TH, 41°04′N, 124°10′W), Cape Mendocino (CMO, 40°25′N, 124°24′W), Fort Bragg (FB, 39°26′N, 123°48′W), Bodega Marine Laboratory (BOD, 38°19′N, 123°04′W), Pillar Point (PP, 37°30′N, 122°30′W), Pacific Grove (PG, 36°37′N, 121°54′W), and Point Saint Luis (PSL, 35°00′N, 121°00′W).

(± 0.2%), 0.6% (± 0.2%) and 1.1% (± 0.2%) for A_{COI}, B_{COI} and C_{COI} haplotypes, respectively.

There was substantial genetic diversity among 114 adult barnacles at the nuclear, protein-coding gene EF1α [average pairwise divergence between individuals (± SE) was 2.4% (± 0.9%); Table 1b; NCBI Accession nos AY630027–AY630254]. Eight of the 155 bp sequenced of EF1α were parsimony-informative. Out of the 18 unique alleles that were analysed, 10 alleles were confirmed or inferred from homozygotes. The remaining eight alleles, which were the consequence of homoplasy or recombination, were found once or twice within only 25 of 114 adults. These were ignored when generating phylogenies and estimating linkage disequilibrium, but were included in analyses of genetic differentiation (i.e. Φ_{ST}). Two transversions separated groups $A_{EF1\alpha}$ and $B_{EF1\alpha}$ (sites 107 and 108, second and third positions, respectively) while a single transversion separated groups $A_{EF1\alpha}$ and $C_{EF1\alpha}$ (site 105, third position; Fig. 1b). The $A_{EF1\alpha} : B_{EF1\alpha}$ and $A_{EF1\alpha} : C_{EF1\alpha}$ splits had 86% and 63% bootstrap support, respectively, and 100% consensus support.

Geographic variation in mtDNA and nuclear alleles

There were strong geographical differences in allele frequencies at both mitochondrial and nuclear loci. Among COI sequences, A_{COI} and B_{COI} haplotypes dominated northern populations from Vancouver Island, Canada (VI) south to Cape Mendocino, California (CMO) populations, a distance of over 850 km. C_{COI} haplotypes dominated southern populations at Pacific Grove (PG) and Point San Luis (PSL; Figs 1a and 2). A dramatic cline between these northern and southern genetic types occurred along a 475-km section of the central California coast. Ninety-six per cent of individuals from the Pacific Grove population (PG) contained C_{COI} haplotypes. This frequency declined steadily with increasing latitude until the Cape Mendocino population, 13% of which contains C_{COI} haplotypes.

These geographical differences at the COI locus are reflected in pairwise Φ_{ST} values (Table 1a). There were no significant values of Φ_{ST} among pairs of northern populations from VI to CMO ($\Phi_{ST} = -0.031–0.025$), nor between the southern populations PG and PSL ($\Phi_{ST} = -0.002$), but

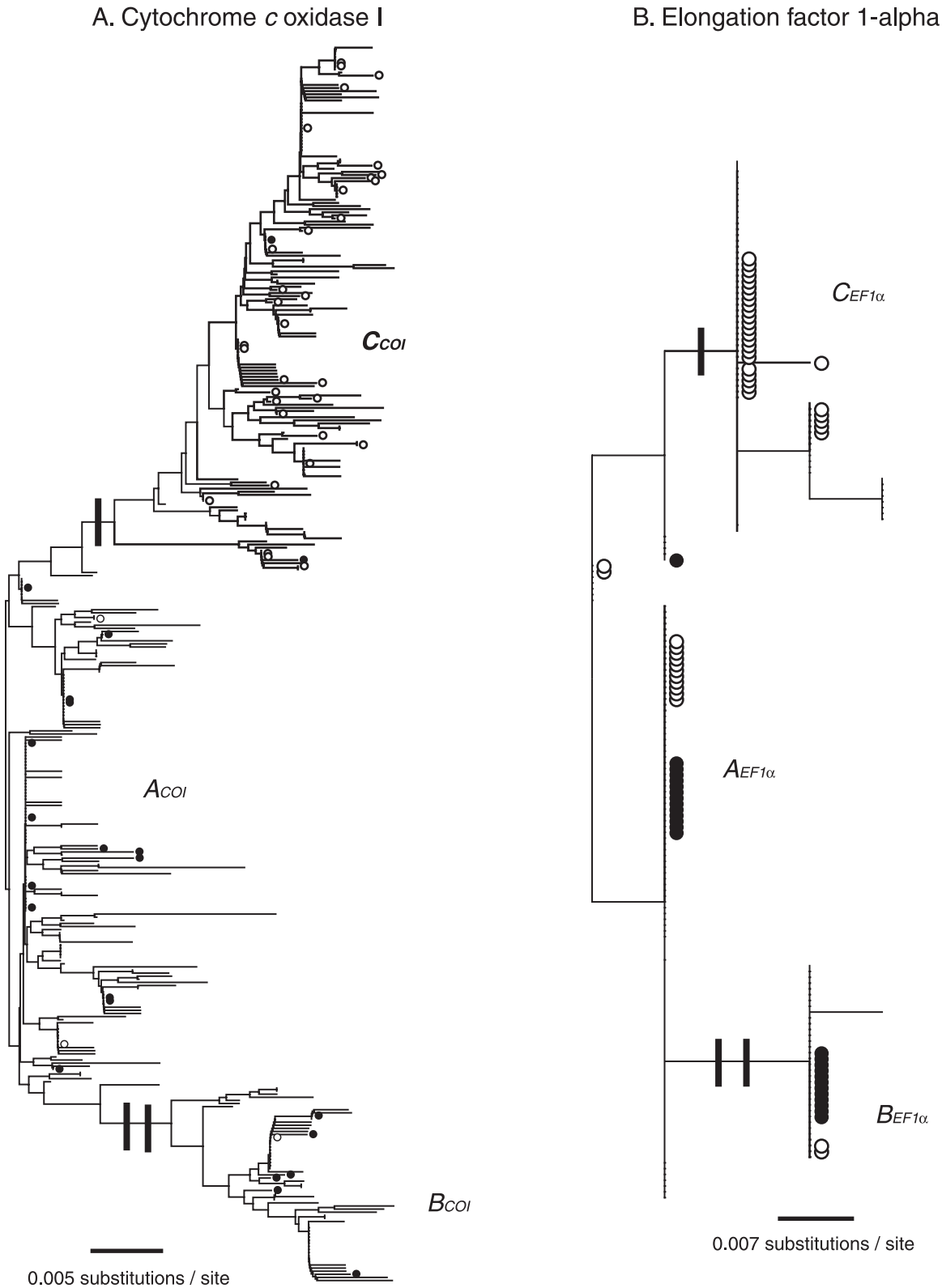

Fig. 1 Neighbour-joining phylogeny of (A) cytochrome *c* oxidase I and (B) elongation factor 1-alpha sequences. Black and open dots indicate individuals from Cape Mendocino and Pacific Grove, respectively. Black rectangles indicate substitutions that describe each node. There are three groups of haplotypes for both COI (labelled A_{COI}, B_{COI} and C_{COI}) and EF1α (labelled $A_{EF1\alpha}$, $B_{EF1\alpha}$ and $C_{EF1\alpha}$). See Results for details.

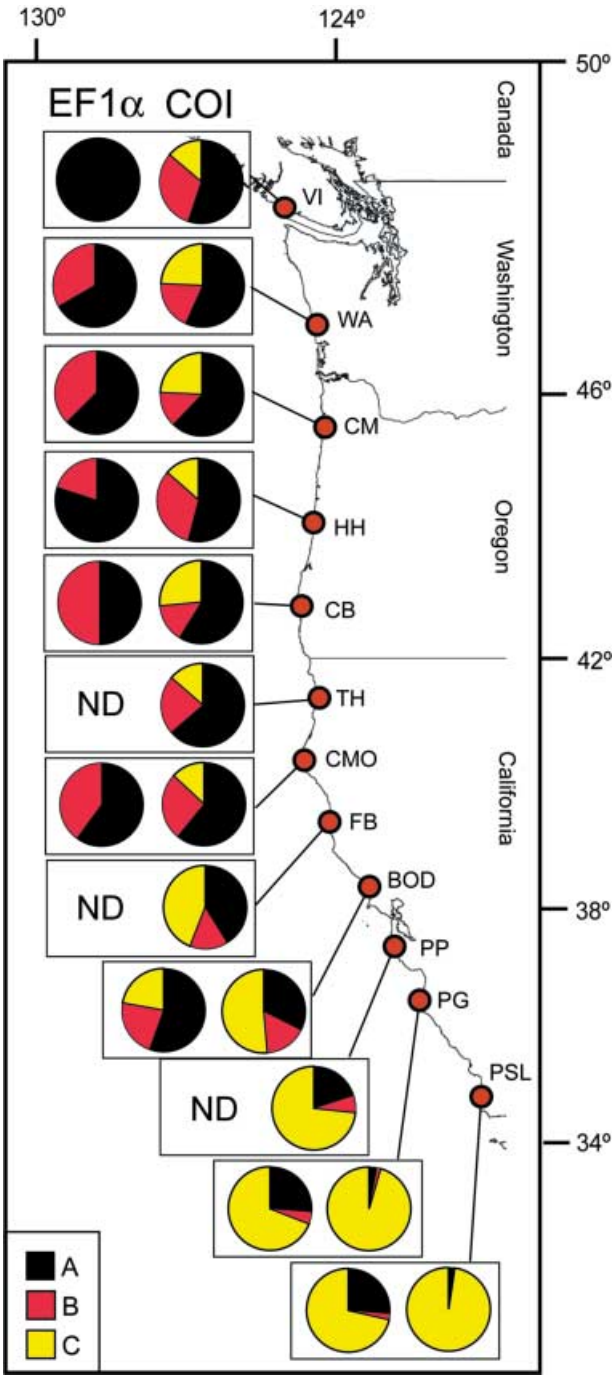

Fig. 2 Frequencies of haplotypes of COI and EF1α for populations from Vancouver Island to central California. Haplotype groups are described in the text and Fig. 1. See Table 1 for key to abbreviations of locations and sample sizes.

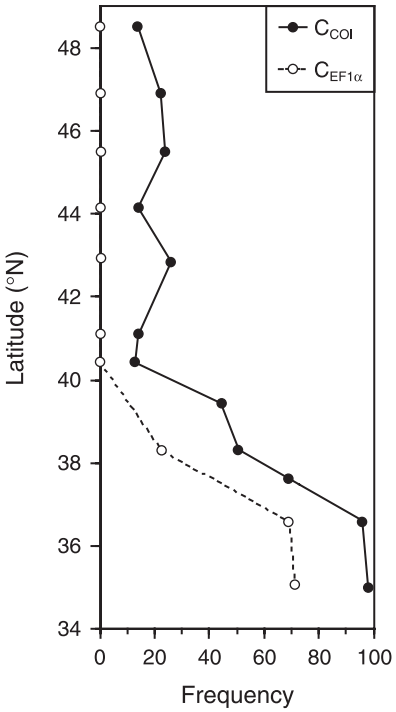

Fig. 3 Frequencies of southern haplotypes for COI and EF1α sequences. Changes in the frequency of southern haplotypes (C_{COI} and $C_{EF1\alpha}$) with latitude are displayed.

the genetic differences between these northern and southern populations were strong (Φ_{ST} = 0.322–0.451) and statistically significant. An examination of the increase of genetic differentiation with geographical distance confirmed that the region between CMO and PG represented the steepest change in genetic differentiation and that there was no isolation by distance among northern populations from VI to CMO (Fig. 3). Furthermore, an exact test of the frequencies of the A, B and C haplotypes (Raymond & Rousset 1995) revealed broadly similar patterns of genetic differentiation to that detected by Φ_{ST} analyses: out of the 66 pairwise comparisons, there was only one pairwise comparison (PP vs. PG) in which the exact test discerned a statistically significant difference that the Φ_{ST} analysis did not.

Sequence data at the nuclear locus (EFIα) revealed concordant geographical patterns of genetic differentiation (Figs 1b, 2 and 3; Table 1b). $A_{EF1\alpha}$ and $B_{EF1\alpha}$ haplotypes dominated northern populations from VI to CMO; in fact, no $C_{EF1\alpha}$ haplotypes were found among these populations. In contrast, $C_{EF1\alpha}$ haplotypes made up ~70% of all alleles from southern populations at PG and PSL (Figs 1b and 2).

There were no significant differences in Φ_{ST} among northern populations from VI to CMO at EF1α (Φ_{ST} = −0.085–0.025; $P > 0.05$; Table 1). Interestingly, there was a small but significant difference between the southern populations at PG and PSL (Φ_{ST} = 0.043; $P < 0.05$). The genetic differences between northern and southern populations were strong (Φ_{ST} = 0.399–0.508) and statistically significant, and the steepest gain in genetic differentiation with geographical distance was found between CMO and PG (Fig. 3). These

patterns were confirmed by an exact test on haplotype frequencies: out of the 36 pairwise comparisons of EF1α data, there was only one comparison (VI vs. WA) in which the exact test discerned a statistically significant difference that the Φ_{ST} did not. We caution that the sample sizes were lower for EF1 α than for COI data, and as such, our statistical power to detect genetic structure among northern populations using EF1 α may be weaker.

Drifter trajectories in the California Current system

There was remarkably little overlap between the trajectories of drifters released off Oregon and those released in the Santa Barbara Channel (or SBC). Ocean-surface drifters released off Oregon enter the California Current and primarily transit southward (Fig. 4), except during winter months when the drifters move northward and near to the coast as part of the Davidson Current. These trajectories indicate the energetic, meandering and eddying flow of the California Current. None of the drifters released off Oregon from 1994 to 1998 returned to the coast south of Point Arena, California (39 N). In contrast, surface drifters released in the Santa Barbara Channel moved northward along the coast almost as far north as Point Arena. The largest northward excursions from the SBC occur during wind relaxation events during the latter half of the year.

Discussion

There is a striking genetic cline between populations of the acorn barnacle *Balanus glandula* across a 475 km region of central California (Figs 1–3; Table 1). Gene frequencies at two loci shift dramatically across the same geographical range. To the north and south of the central California cline, however, there is only weak genetic structure (Figs 2, 3: Table 1: Wares *et al*. 2001), and gene frequencies at COI and EF1α vary little across hundreds of kilometres.

This is an unusual pattern of genetic variation for a species with large dispersal potential. Population genetic studies have documented strong population differentiation in central California but only among species with low potential dispersal (e.g. the cup coral *Balanophyllia elegans*, Hellberg 1994; the snail *Nucella ostrina*, Marko 1998; the copepod *Tigriopus californicus*, Edmands 2001). Because many of these species also display decreasing levels of genetic diversity with increasing latitude, the population-level differentiation of these low dispersers probably reflects a recent northward expansion of populations since the Pleistocene glacial maxima rather than present-day patterns of gene flow. Other species with low dispersal potential also show substantial differences along the coast (Hellberg 1996; Hellberg *et al*. 2001; Hickerson & Ross 2001; Dawson *et al*. 2002).

By contrast, it is uncommon to find significant genetic differentiation between California and more northern populations in invertebrate species with a higher potential for broad dispersal. Studies of high dispersal species along the same region generally document weak genetic structure (Waples 1987; Stepien & Rosenblatt 1991; Sarver & Foltz 1993; Arndt & Smith 1998; Rocha-Olivares & Vetter 1999; Flowers *et al*. 2002). In many cases, populations 1000–1500 km apart show little genetic change and share common alleles at mitochondrial or nuclear loci. There are species of fish with high dispersal potential that display significant genetic differentiation along the California coast (Dawson 2001; Buonaccorsi *et al*. 2002), but none of these differences are as dramatic as those presented here for *Balanus glandula*.

Among barnacles, strong genetic structure has been documented previously but only among populations from distinct oceanic basins, or at allozyme loci that appear to be under selection. There is genetic differentiation among north Atlantic and Mediterranean subpopulations of *Chthamalus montagui* and *C. stallatus* at allozyme loci (Pannacciulli *et al*. 1997) and among Peruvian and Mexican subpopulations of *Pollicipes elegans* in mtDNA sequences (Van Syoc 1994). Allozyme differences in *Semibalanus balanoides* were found among populations separated by tens and hundreds of kilometres (Flowerdew 1983; Holm & Bourget 1994; Dufresne *et al*. 2002). However, Schmidt & Rand (1999) used experimental manipulation and genetic sampling on small spatial and temporal scales to detect selection on the mannose phosphate isomerase, or Mpi, locus, one of the loci that showed population-level differences. A weak ($\Phi_{ST} = 0.0025$) but statistically significant genetic difference was detected among mtDNA control region sequences from *S. balanoides* populations separated by Cape Cod, MA (Brown *et al*. 2001). Other studies have found few to no genetic differences over large swaths of the geographical ranges of barnacles (e.g. *Tetraclita squamosa*, Ford & Mitton 1993; *Chthamalus fissus*, Wares *et al*. 2001).

Evolution of the central California cline

Though it would be impossible to know with certainty, it is likely that such strong genetic differences were generated when barnacle subpopulations became historically separated and diverged by drift or local selection. This could have occurred at the height of the Pleistocene ice ages when sections of the North American coastline that are currently connected were isolated. An ice-free coastal zone probably persisted near the Queen Charlotte Islands off British Columbia (Pielou 1991) that provided a refugium for a number of nearshore fish and invertebrates (Horn & Allen 1978; Arndt & Smith 1998; Hickerson & Ross 2001). The refuge probably supported *B. glandula* because these barnacles are one of the most common intertidal species on the shores of western North America. When the glaciers

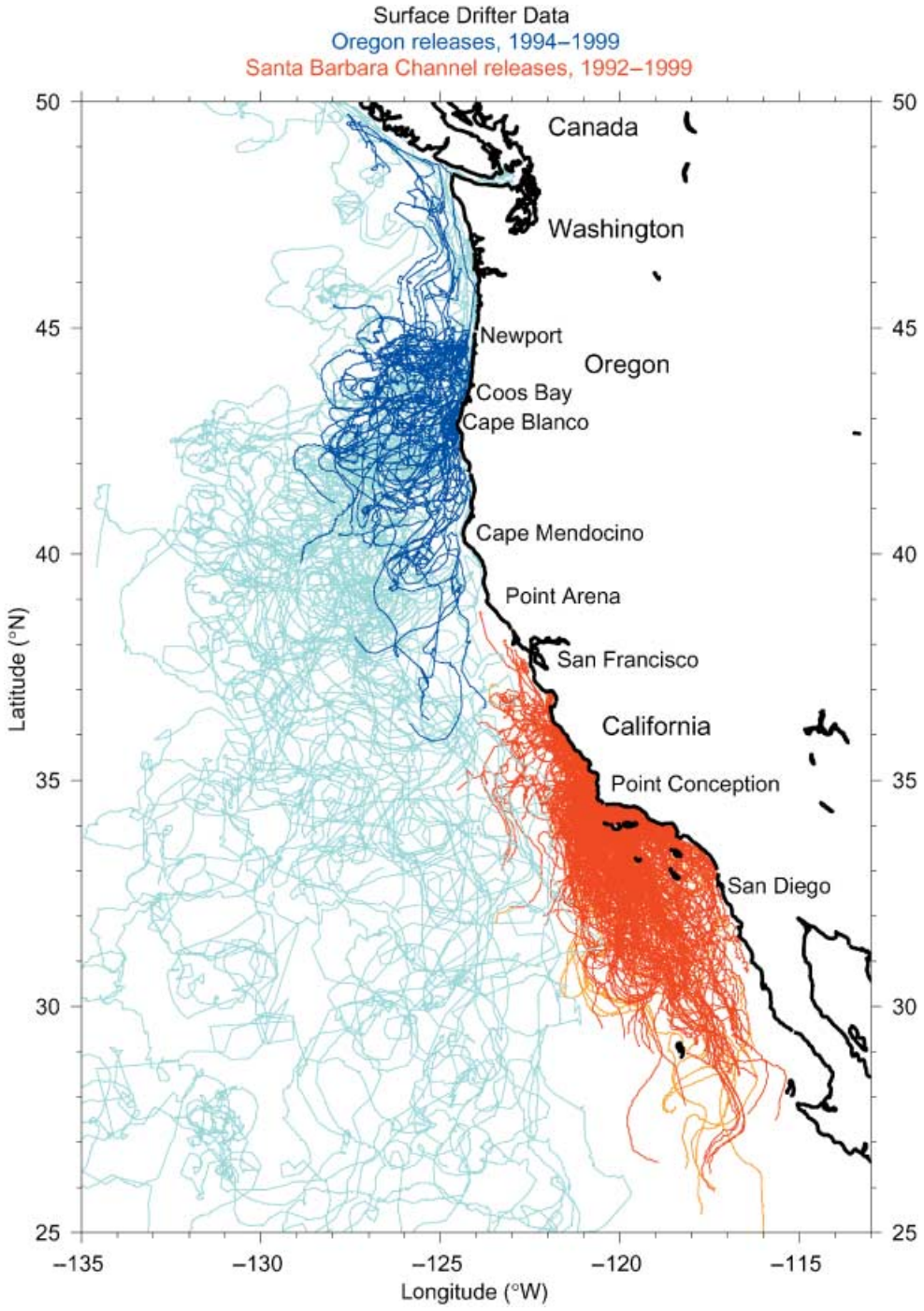

Fig. 4 Surface drifter trajectories in the California Current. Drifters released off Newport and Coos Bay, Oregon, are coloured dark blue (first 40 days) and light blue (up to 2 years). Drifters released in the Santa Barbara Channel are coloured red (first 40 days) and orange (up to 90 days).

receded, this isolated northern population would have expanded along coastlines that were always ice-free (i.e, mid-Washington through northern California) and overlapped with southern populations in central California to produce the cline describe here. Consistent with this hypothesis, a substantial fraction of the southern C_{COI} haplotype occurs within Oregon, Washington and Vancouver Island populations that may indicate the historical presence of 'southern' populations. An analogous scenario has been postulated for the American Oyster *Cassostrea virginica* across the phylogeographical break at Cape Canaveral, FL (Hare & Avise 1996).

The simplest explanation for the persistence of these barnacle clines since the end of the Pleistocene is that the clines are homogenizing extremely slowly because barnacle larvae are dispersing very limited distances in central California. However, a computer simulation of the timing of collapse of a neutrally evolving cline suggests that this scenario is unlikely. When mean dispersal distance was 10 km or more per generation, the cline disappears in far less than 10 000 generations (Fig. 5). A Monte Carlo bootstrap analysis indicates that the measured cline in C_{COI} haplotype frequencies (i.e. 96% at PG declining to 13% at CM) was significantly sharper from that predicted by the simulation after 7500 and 10 000 generations ($P < 0.01$ in both cases; null distributions were generated by bootstrapping the variation found among the five simulation runs using 10 000 iterations). Thus, if the COI and EF1 loci were evolving neutrally, then the persistence of the genetic clines since the last glacial maximum implies that the dispersal distances in the central California region typically average much less than 10 km per generation, perhaps only one to a few kilometres. A dispersal distance of 1 km on average seems highly improbable given that these microscopic larvae must feed in the water column for at least 2 weeks before settlement (Brown & Roughgarden 1985).

Alternatively, the clines may have persisted because diversifying selection acts to impede homogenization as a result of gene flow in each generation, as is commonly the case among naturally occurring clines (Endler 1977; Arnold 1997). In general, selection that maintains clines arises because hybrids of the parental lines are incompatible, or because hybrids or their parents are less fit in non-native environments (termed endogenous and exogenous selection, respectively). It appears likely that a combination of selective modes play important roles in many clines, especially those between hybridizing species, e.g. *Mercenaria* clams (Bert & Arnold 1995) and *Mytilus* mussels (Bierne *et al*. 2002).

Maintaining a steep cline in the face of broad dispersal requires strong diversifying selection. At equilibrium, this balance can be represented by $w^2 = \sigma^2 s^{-1}$, where w is the cline width (defined as the inverse of the slope of the steepest portion of the cline, or ~550 km in the case of *B. glandula*: Barton & Gale 1993), σ is the standard deviation in dispersal distance of offspring from their parent, and s is the selection coefficient (Barton & Hewitt 1985). For instance, if dispersal were high enough that larvae travelled 100–200 km on average, then diversifying selection in the order of $s = 0.04–0.14$ at both loci would be needed to maintain the dual clines observed here. If dispersal were in the order of 10 km on average, a far lower selection coefficient ($s < 0.001$) would be required to maintain the cline.

There are several *a priori* reasons to believe that the *B. glandula* cline is maintained in part by environmentally based selection. In particular, there is strong concordance between the hybrid zone and several transitions in biotic and abiotic conditions. First, densities of *B. glandula* are far greater in Oregon and Washington than in central and southern California (Connolly & Roughgarden 1999; Connolly *et al*. 2001). Second, central California represents a broad transition between northern and southern flora

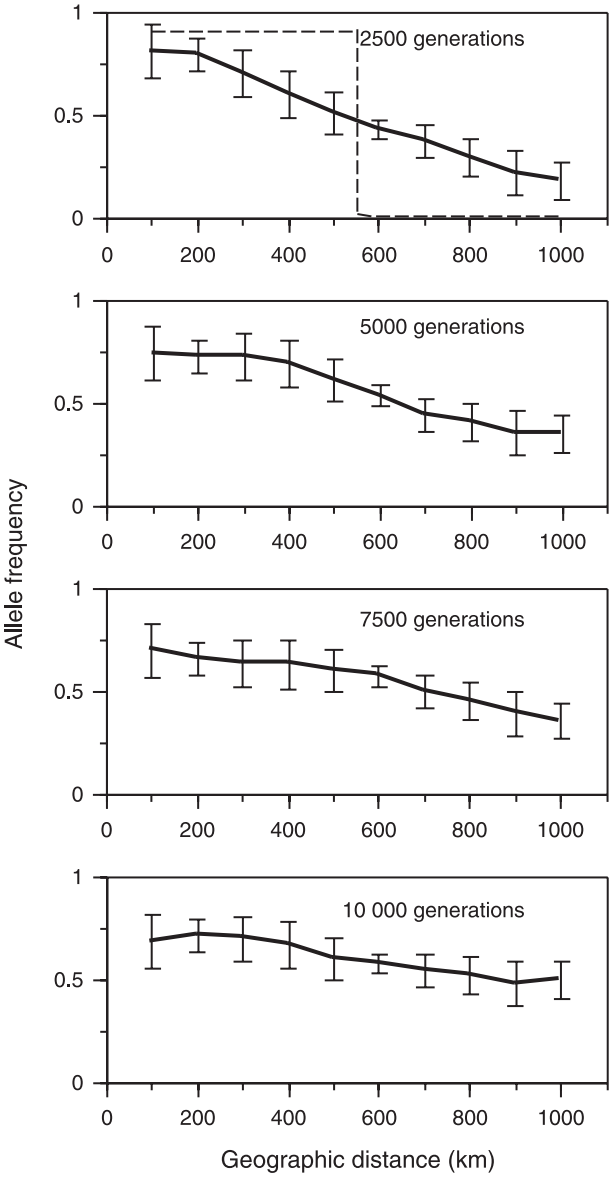

Fig. 5 The average (± SD) allele frequency of demes during collapse of a neutral step cline. The simulations ($n = 5$) estimated allele frequency across 1000 demes, each separated by 1 km. Demes in the first and second halves of the 1000 km transect started with an initial allele frequency of 0.9 and 0.0, respectively, and were allowed to degrade by drift and migration (mean dispersal distance = 10 km). The dotted line indicates allele frequency at time 0.

and fauna (e.g. Valentine 1966; Hayden & Dolan 1976; Horn & Allen 1978), and many species' endpoints occur at Monterey Bay. Third, air temperatures in southern California exceed temperatures in Oregon and Washington by 6–12 °C in the winter and 3–11 °C in the summer (data taken from the National Climate Data Center http://rredc.nrel.gov/solar/old_data/). The latitudinal gradient in air temperature is particularly noteworthy, given that air temperature tightly correlates with *B. glandula* body temperatures (Harley & Lopez 2003) and the mortality of temperate barnacles on rocky shorelines is largely the consequence of exposure to air (e.g. Schmidt & Rand 1999; Harley & Helmuth 2003). Fourth, average monthly sea surface temperatures in central and southern California coastlines exceed temperatures in Washington and Oregon by 4–6 °C in the winter and 2–4 °C in the summer (absolute temperature ranges from 8 to 18 °C: see LaJeunesse & Trench 2000). The effects of these latitudinal shifts in water temperature on the local fitness of settled and larval *B. glandula* is not known, but development is known to be highly temperature dependent (Strathmann 1987). Finally, the absolute breadth of intertidal habitat increases with latitude. The average tidal range in Oregon and Washington averages 8.4 feet (2.5 m) while the range in southern California (Pacific Grove to San Diego) averages 5.4 feet (1.6 m; NOAA tidal observations; http://co-ops.nos.noaa.gov). The implications of this tidal compression for the evolutionary ecology of marine invertebrates are unexplored, but in theory it could alter rates of feeding, consumption, and predation across the intertidal community. We do not know which, if any, of these transitions across central California exerts selection on the barnacle cline, but are currently pursuing transplantation experiments to quantify its strength.

Another method that is commonly used to detect selection within genetic clines is to quantify linkage disequilibrium. Linkage disequilibrium, or the nonrandom association of alleles at two or more loci, indicates an excess of parental genotypes and a reduction of hybrids relative to that predicted by the allele frequencies under Hardy–Weinberg equilibrium (Barton & Gale 1993). This genetic signature arises when strong selection impedes rampant hybridization within a cline, and parental types broadly disperse into the clinal region from their native habitats. The power of this approach is that the degree of linkage disequilibrium between unlinked loci approximates the strength of selection when selection is relatively weak ($s < 0.10$: Barton & Gale 1993).

A preliminary analysis of cytonuclear disequilibrium among the COI and EF1 loci indicates that if selection acts to maintain the *B. glandula* cline, this selection may not be very strong. Individuals with northern COI alleles and homozygous northern EF1a genotypes (N-NN, representing the mtDNA and nuclear genotypes, respectively) occur in 77% of northern populations (VI-CMO) and about 40% of individuals in Bodega (Table 2). Likewise, individuals with the southern COI and EF1a genotypes (S-SS) represent 50% of the southern populations (PG-PSL; Table 2). In the centre of the cline (i.e, at Bodega), none of the ten animals from Bodega are 'southern-like', while four of the 10 animals are 'northern-like' (Table 2). The absence of some 'southern-like' animals in the centre of the cline generates a weak signal of linkage disequilibrium ($D < 0.001$; $P = 0.44$), suggesting that selection against hybridization within the cline is not strong, and that broad dispersal of southern barnacles into the cline (~200 km) does not occur with regularity.

Table 2 Number of individuals with genotypes dominating northern (N) and southern (S) regions. Northern haplotypes are are A_{COI}, B_{COI}, A_{EF1} and B_{EF1}. Southern haplotypes are C_{COI} and C_{EF1}

	EF1α		
COI	NN	NS	SS
Northern populations (VI to CMO)			
N	30	1	
S	8		
Bodega population			
N	4		1
S	3	2	
Southern populations (PG and PSL)			
N		1	
S	3	21	34

Taken together, our data do not support either of two extreme scenarios along a continuum of the selection/dispersal balance. That is, the clines are not maintained by relatively strong selection ($s > 0.10$) and very broad dispersal (hundreds of km), nor by a nonequilibrial secondary introgression of neutral alleles and extremely restricted dispersal (< 1 km). Rather, the clines are probably maintained by relatively weak selection and somewhat restricted dispersal. Determining the relative strengths of these processes will require more genetic loci and larger sample sizes.

Nearshore oceanography and gene flow

Several aspects of the nearshore oceanography within the northeastern Pacific are strikingly consistent with the geographical patterns in gene flow that are implied by our data. First, the trajectories of drifters released offshore of Oregon and southern California clearly indicate that these waters rarely mix (Fig. 4). Drifters tracked from their origin off central Oregon for 40 days rarely enter shelf waters south of Point Arena. Even after a year, the drifters are

more likely to enter the equatorial currents than central or southern California waters. Another study also found that drifters primarily released off northern California (39–39.5 N) did not enter shelf regions south of Point Reyes (38 N: Brink *et al*. 2000). These patterns imply that barnacle larvae caught in these currents rarely move from Oregon to central or southern California in a single generation, and thus, that the maintenance of strong genetic differences among northern and southern regions is partly the result of the restricted dispersal of pelagic larvae (Figs 2, 3).

The offshore movement of coastal waters originating in Oregon is driven in part by a strong and persistent southward wind and the Ekman transport that arises as a consequence (Halliwell & Allen 1987). In addition, strong, wind-driven, plumes of water can be pushed from the coast at coastal promontories (e.g. Cape Blanco) and form a major portion of the equatorward transport in the California Current (Barth *et al*. 2000). Once offshore, these plumes deepen and extend below the depth of the shelf-break (Haney *et al*. 2001), making it unlikely that the formerly coastal water — containing a mixture of nearshore larvae — will ever return to shallow regions.

Second, although the drifter trajectories show scant connection between California and Oregon, the spread of drifters along the northern and southern coasts suggests that coastal currents might move larvae hundreds of kilometres along the continental shelves of Oregon and southern California (Fig. 4). Broad genetic similarity among barnacle populations to the north and south of the central California cline (Figs 2, 3) is entirely consistent with this broad dispersal potential. The one exception to this trend (i.e. differentiation at EF1α between PG and PSL) may be an artefact of sampling error, because larger sample sizes at the more quickly evolving COI locus displayed no such differences.

Finally, although we have no data for drifters that originated in central California, there is indirect oceanographic evidence that suggests that larval dispersal may be short. Barnacle larvae in California are transported across the continental shelf (i.e. east–west axis) by regional relaxation of upwelling events (Roughgarden *et al*. 1988; Farrell *et al*. 1991) or by large areas of eddy formation (Wing *et al*. 1995). Largier (2003) points out that this movement across the shelf can be time-consuming — perhaps days or weeks to move out to the California Current, and days or weeks for the return — because the movement of water masses nearshore is impeded by the friction of water with bottom topography and onshore promontories. The offshore boundary currents are farther offshore in central California than in Oregon (Strub & James 2000), suggesting that coastal larvae spawned in these areas may be less likely to exit the offshore currents successfully and settle on the intertidal than in other places. Further study of nearshore current patterns could clarify the fate of larvae drifting along the central and northern California coasts, and provide a basis for evaluating the physical constraints on movement patterns of coastal larvae.

Summary

A steep genetic cline in the barnacle *Balanus glandula* across a 475 km region of central California indicates that gene flow in central California is far more restricted spatially than predicted by the potential dispersal of this species. The evolutionary forces that maintain these striking clines are uncertain, but in theory, these genetic patterns could be the consequence of a slow secondary introgression of historically separated populations, a balance between diversifying selection and dispersal, or some mix of both. In one extreme scenario, the slow speed with which allopatric groups of haplotypes introgress indicates that dispersal distances in *B. glandula* are extremely limited in central California (~1 km per generation on average). This appears unlikely because of the highly mixed nature of nearshore oceanography. At the other extreme, strong selection coupled with broad dispersal (~100–200 km) could jointly operate to maintain the cline. Such non-neutral evolution of these loci is suggested by the concordance of geographical shifts in several environmental conditions with the position of the barnacle cline. However, a preliminary analysis of linkage disequilibrium between the two loci revealed that if such selection were present, then it is unlikely to be very strong. Thus, the cline may be maintained by relatively weak selection and restricted dispersal of barnacle larvae relative to their potential dispersal. Because the distinction among these hypotheses largely depends on the neutrality (or lack thereof) of the genetic loci, future efforts will focus on empirical estimates of selection coefficients across the cline and the degree of linkage disequilibrium at the centre of the cline.

In contrast to the restricted gene flow within central California, barnacle populations outside the cline are genetically similar across hundreds of kilometres. Such geographical variation emphasizes that gene flow is not a species-specific trait but is instead a reflection of local environmental conditions and historical events. If such gene flow serves as a direct proxy for dispersal, then our work suggests that the spatial scales over which marine populations are ecologically and evolutionarily connected can be greatly oversimplified without intensive sampling and analysis across a large portion of their geographical ranges.

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