

Sources of invasions of a northeastern Pacific acorn barnacle, *Balanus glandula*, in Japan and Argentina

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ABSTRACT: Within years of its introduction, the North American barnacle *Balanus glandula* Darwin, 1854 became an abundant member of rocky intertidal communities in Japan and Argentina. To determine the regional sources of these invasions, we compared mitochondrial cytochrome c oxidase subunit 1 (COI) and nuclear elongation factor 1 alpha (EF1) genotypes of native and introduced populations. Previously described population structure at these loci in North America conferred geographic information to genotypes. *B. glandula* from Argentina and southern to central California shared genotypes not found in other native populations. *B. glandula* from Japan and the northeastern Pacific (Puget Sound and Alaska) were differentiated from other populations by the presence of a nearly fixed nucleotide in EF1 and contained all 3 major haplotype groups of COI. These patterns indicate that sources of *B. glandula* in Japan and Argentina are largely from Alaska/Puget Sound and California, respectively. The broad similarity of mean seawater temperatures among introduced and native regions may have facilitated these invasions. The presence of greater variation in air temperatures in the invaded than native regions raises the possibility that temperature-related selection may play an important role in the evolution of these invasive populations. We found no evidence of multiple geographic sources of *B. glandula* in Japan and Argentina, nor of genetic bottlenecks in either invaded region.

KEY WORDS: Marine biological invasions · Marine introductions · Invasion sources · Invasion genetics · *Balanus glandula* · Barnacles

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INTRODUCTION

Biological invasions cause large-scale changes in marine communities (Carlton 1989, 2000, Ruiz et al. 2000, Sax et al. 2005). Several fundamental issues in invasion ecology and management require knowledge of sources. First, do most invasions have single or multiple sources? Multiple sources might facilitate matching of genotypes and new environments, or generate new genotypes, and increase the likelihood of establishment and persistence of a population (Ellstrand & Schierenbeck 2000, Kolbe et al. 2004, Voisin et al. 2005,

Lavergne & Molofsky 2007). Second, invaders can adapt to new environments (Grosholz & Ruiz 2003), but is the adaptability of invaders over shorter (several generations) and longer (10s to 100s of generations) timescales dependent on evolutionary history within native environments (cf. Wares et al. 2005)? Third, are invasions self-promoting? Each invasion creates a new potential source woven into a network of global commerce (Carlton 1987, Bagley & Geller 2000). Answers to these and other related questions require methods to narrow the range of potential source regions from the entire biogeographic range of the species involved.

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Genetic data have been used to suggest probable sources for some marine invasions (McDonald & Koehn 1988, Geller et al. 1997, Ó Foighil et al. 1998, Bagley & Geller 2000, Roman & Palumbi 2004, Zardus & Hadfield 2005). The inferential power of genetic data depends on specific conditions that include the genetic structure of potential source populations and population genetic processes that cause divergence of introduced populations from their source population(s). We took advantage of recent detailed studies of the genetic structure of a rocky shore barnacle, *Balanus glandula*, on its native northeastern Pacific coast to investigate sources for invasions in Argentina and Japan. Native *B. glandula* populations in North America contain profound genetic structure over regional scales (Wares et al. 2001, Sotka et al. 2004, Wares & Cunningham 2005, E. E. Sotka & S. R. Palumbi unpubl. data). Alleles of 2 genes (i.e. the alleles designated C_{COI} and C_{EF1}) occur at 100% frequency at the southernmost location sampled (Huntington Beach, California). These southern allele types decline in frequency to the north until Cape Mendocino. North of Cape Mendocino, C_{COI} is maintained at a low frequency (~10 to 20%) while C_{EF1} is absent. A recent survey also indicated that native populations within Puget Sound, Washington and Juneau, Alaska are virtually monomorphic for B_{EF1} , a northern allele (E. E. Sotka & S. R. Palumbi unpubl. data). The profound spatial structure of *B. glandula* loci allows for the ready identification of the coastal regions of North America that are sources for introduced *B. glandula* in Argentina and Japan.

In Argentina, early descriptions of the intertidal rocky shores of the southwestern Atlantic (Ringuelet et al. 1962, Olivier et al. 1966, Penchaszadeh 1973) showed a zonation pattern unusual on temperate coasts for the absence of barnacles. Rock surfaces were covered by the small mytilid bivalves *Brachidontes rodriguezii* (d'Orbigny, 1842) and *Perumytilus purpuratus* (Lamarck, 1819). By the end of the 1960s, *Balanus glandula* was detected on experimental plates within the harbor of Mar del Plata (38°S, 57°W; Spivak & L'Hoste 1976, Bastida et al. 1980) and on adjacent rocky shores, where it rapidly became dominant. In contrast, other exotic barnacles in Argentina (*Balanus amphitrite* and *Balanus trigonus*) that were introduced in the early 1960s remain at low levels and are confined to protected bay waters (Spivak 2005). After almost 40 yr in the Southwestern Atlantic, *B. glandula* is now well established along all rocky shores between 37 and 53°S (Orensanz et al. 2002, Schwindt 2007).

In Japan, *Balanus glandula* was found in 2000 for the first time at Sasazaki, Ofunato Bay, on the northeast coast of Japan (Kado 2003). At the time of the discovery, the barnacle had already expanded along the Pacific coast of northern Japan between 38°30' and

42°40' N. The abundance of *B. glandula* varied among harbors and ports, but these barnacles effectively monopolized primary space in 3 commercial harbors and achieved a density of $>10\,000\ m^{-2}$ on intertidal quaysides. From the shell size of the largest individual collected in 2000 and the known growth rate of this species in North America, Kado (2003) speculated that this specimen was more than 8 yr old, implying a date of first arrival no later than 1992. By 2005, gravid barnacles were present at high densities at Kushiro and Katsurakoi on Hokkaido, the northernmost island of Japan, where it was absent in 2000 (R. Kado pers. obs.). Thus, *B. glandula* has reached its present northern and western endpoints at 43°00' N and 144°26' E within 5 yr, expanding as quickly as $25\ km\ yr^{-1}$ (Kado & Nanba, 2006). This is similar to the maximum spread speed estimated for 5 invasive species in Japan (Iwasaki et al. 2004). Southward expansion has not yet been reported.

MATERIALS AND METHODS

Collection and sequencing of *Balanus glandula* in North America were described in Sotka et al. (2004). Adult animals were collected from 2001 to 2004 across ~1600 km of the native range of *B. glandula*. These locations include Juneau, Alaska (58°N, 134°W), Puget Sound (48°N, 124°W), the outer coastlines of Vancouver Island, Washington and Oregon coastlines (latitudes 44° to 48°N: Vancouver Island, Westport Jetty, Cape Mearns and Heceta Head in Sotka et al. 2004), central California (38°N; Bodega Marine Laboratory and Pillar Point in Sotka et al. 2004) and southern California (34°N, 118°W; Huntington Beach). Introduced populations from Argentina were sampled in 2002 at 4 different localities: Mar del Plata (38°S, 57°W), Punta Ameghino (42°S, 65°W), Punta Pardelas (43°S, 64°W) and Cabo dos Bahías (44°S, 65°W). *B. glandula* populations in Japan were collected in 2004 from Ofunato Bay (39°N, 141°E) and Cape Erimo (42°N, 143°E). We amplified, sequenced and analyzed 386 bp of mitochondrial cytochrome c oxidase subunit I (COI) and 155 bp of the nuclear-encoded elongation factor 1 alpha (EF1) using methods described in Sotka et al. (2004). A previous phylogenetic analysis (Sotka et al. 2004) had revealed 3 major haplotype groups in both loci. At COI, 2 nucleotide transitions distinguish haplotypes in clades A_{COI} from B_{COI} (sites 90 and 177, both third codon positions) and a single transition separate haplotypes in clade A_{COI} from those in C_{COI} (site 315, third codon position). At EF1, a couplet of base pair transversions (sites 107 and 108 in Sotka et al. 2004) separate clades A_{EF1} and B_{EF1} while a single transversion separate clades A_{EF1} and C_{EF1} (site 105).

We used these haplotype groupings to characterize barnacles from Argentina and Japan. The native dataset used here was intended for detailed analysis of North American populations beyond the scope of this paper, and has been previously published (Sotka et al. 2004) or will be addressed elsewhere (E. E. Sotka & S. R. Palumbi unpubl. data).

Nei's Π (or the mean number of differences per base-pair between populations) and its estimated SD and pairwise values of the genetic divergence measurement Φ_{st} were calculated using Arlequin 2.0 on both COI and EF1 sequences (Excoffier et al. 2005). Following Sotka et al. (2004), the model of evolution was TrN + Γ ($\alpha = 1.6$) for COI and F81 for EF1. Statistical significance of Φ_{st} was determined from Monte Carlo sampling of 10 000 bootstrap replicates, and alpha levels of Φ_{st} were adjusted using a Bonferroni correction. Because of low sample size, we treated all Japanese or Argentine barnacles as single populations for Φ_{st} analysis at EF1.

We estimated the relative contribution of the native populations to each introduction using the freeware SPAM 3.7 (Statistics Program for Analyzing Mixtures, available at www.genetics.cf.adfg.state.ak.us/software/spampage.php; Debevec et al. 2000), a program originally developed for mixed stock analysis of fisheries populations. The program employs maximum likelihood and bootstrapping methods to estimate the mixture of baseline populations (i.e. source populations) that has the greatest probability of obtaining the observed genotypic pattern in the target population (i.e. introduced population). The program inputs the haplotype (i.e. A,B,C) frequencies for these analyses. Our native populations were taken to represent the regions where actual source populations may be located. We estimated the relative contribution of native populations and their 95% nonsymmetric confidence intervals (CI) using 10 000 bootstrap replicates. For SPAM 3.7 analysis, non-native samples were pooled to make single Japanese and Argentine populations.

Average monthly seawater temperatures were compiled from the National Oceanographic Data Center (www.nodc.noaa.gov/dsdt/cwtg/npac.html) for North America, the Argentine Oceanographic Data Center (www.hidro.gov.ar/ceado/Ef/Inventar.asp) for Argentina, and the Geological Survey of Hokkaido (www.gsh.pref.hokkaido.jp/download/temperature_data/sea_temp.html) for Japan. Average monthly air temperatures for native regions were compiled from the National Climate Data Center (www.ncdc.noaa.gov) and

for non-native regions from Globalis (<http://globalis.gvu.unu.edu>).

RESULTS

Sequences from non-native populations have been deposited in Genbank (COI: EU004281 to EU004414; EF1: EU495994 to EU496087). Japanese barnacles as a group were nearly monomorphic for B_{EF1} and contained all 3 alleles at COI (Table 1, Fig. 1), a pattern similar to that of northern latitudes in the native range (Puget Sound and Juneau, Alaska). A pairwise Φ_{st} analysis of COI sequences indicates that Japanese populations were statistically indistinguishable from native populations in Alaska, Puget Sound, and the outer coastline of Vancouver Island, Washington and Oregon, while EF1 allele frequencies in Japan were indistinguishable from Alaskan populations. In contrast, there were significantly elevated values of Φ_{st} between Japanese populations and the native populations along central and southern California coastlines at both loci ($\Phi_{st} > 0.20$; Table 1). A mixed stock analysis of Japanese barnacle genotypes (i.e. individuals sequenced at both EF1 and COI; $n = 37$) indicates the majority of the Japanese introduction originated from only Puget Sound, only Alaska or a mix of both locations (mean contribution ~ 0.5 for each population; 95% CI for both populations = 0.0 to 1.0), while a smaller percentage may have originated along the outer coastline of Vancouver Island, Washington and Oregon (mean contribution = 0.05; 95% CI = 0.00 to 0.22).

In contrast with Japanese invaders, Argentine populations contained all 3 major haplotype groups at both loci, a pattern found only in central California (Fig. 1). Pairwise Φ_{st} values at both loci were statistically indistinguishable only between Argentine barnacles and central California populations (Table 2). A mixed stock analysis ($n = 12$ genotypes; Fig. 2) indicates that

Table 1. Locations, allele frequencies and totals, and observed heterozygosity H_O of EF1. COI: mitochondrial cytochrome oxidase I; EF1: nuclear elongation factor 1a

Location	COI alleles				EF1 alleles				H_O
	A	B	C	Total	A	B	C	Total	
Argentina: Mar del Plata	16	5	30	51	5	3	2	10	0.600
Argentina: Patagonia	7	5	20	32	3	2	15	20	0.400
Japan: Cape Erimo	21	10	3	34	4	44	0	48	0.167
Japan: Ofunato Bay	13	4	0	17	0	24	0	24	0.000
Alaska	26	6	1	33	2	66	0	68	0.059
Puget Sound	193	87	24	304	0	70	0	70	0.000
VI/WA/OR	66	24	20	110	28	16	0	44	0.364
California: central	25	12	56	93	26	6	38	70	0.343
California: south	0	0	40	40	0	0	30	30	0.000
Grand total	367	153	194	714	68	231	85	384	

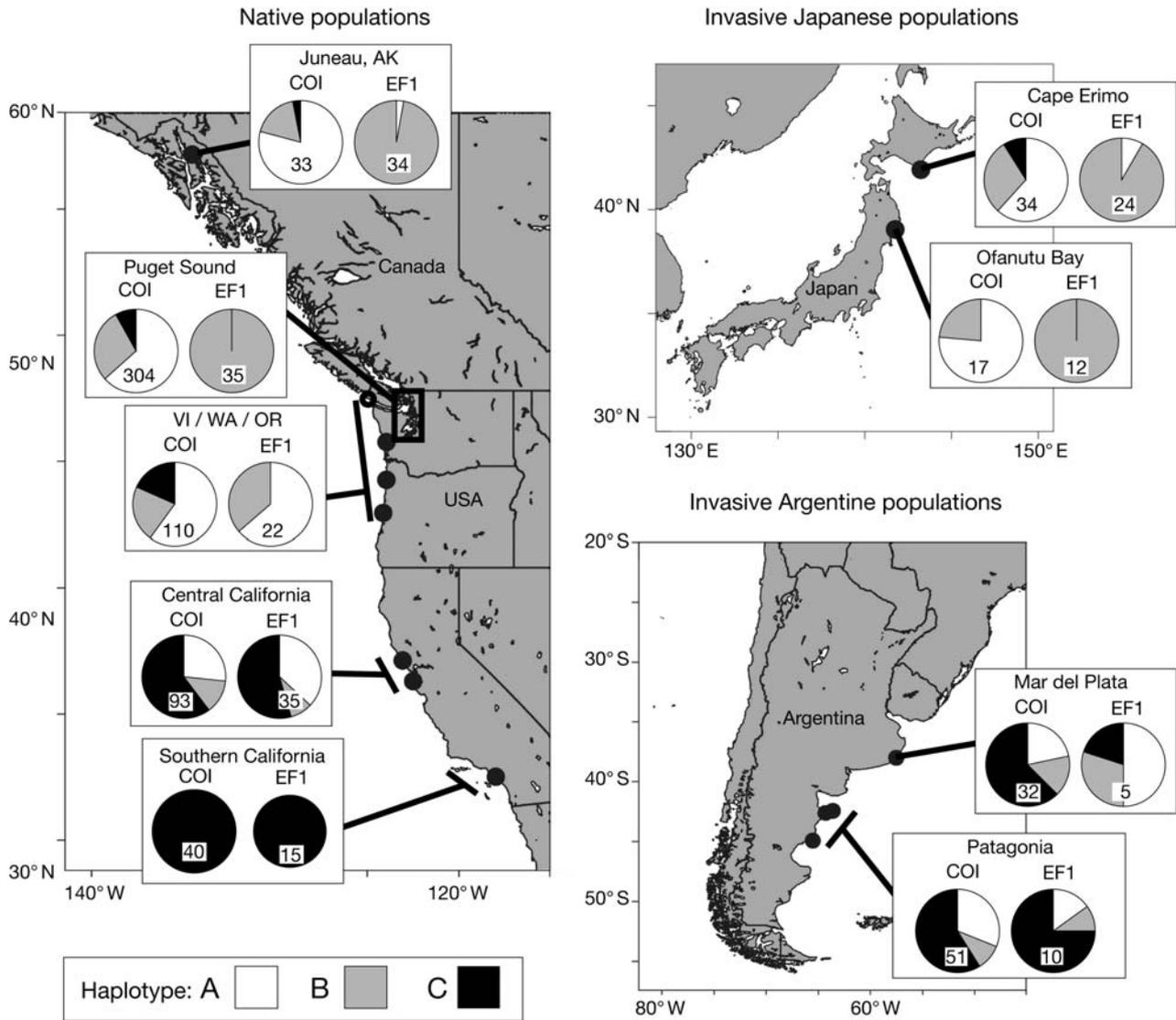


Fig. 1. *Balanus glandula*. Allele frequencies at 2 genetic loci (cytochrome oxidase I [COI], elongation factor 1 alpha [EF1]) from native and introduced populations. Numbers indicate number of individuals genotyped. AK: Alaska; OR: Oregon; VI: Vancouver Island; WA: Washington State

Table 2. *Balanus glandula*. Φ_{st} analysis of sequence data at 2 loci between invasive (shaded) and native (unshaded) populations. P-values were generated from a distribution of 10 000 Monte Carlo replicates and adjusted using a Bonferroni correction (*significantly different from 0 after correction). Invasive populations were grouped at EF1 because of low sample size

	Cytochrome oxidase I				Elongation factor 1 alpha		
	Japan (Ofunato Bay)		Argentina (Cape Erimo) (Mar del Plata) (Patagonia)		Japan	Argentina	
Japan (Cape Erimo)	-0.008						
Argentina (Mar del Plata)	0.235*	0.177*					
Argentina (Patagonia)	0.199*	0.155*	0.006		Argentina	0.673*	
Juneau, Alaska	-0.009	-0.003	0.231*	0.195*	Juneau, Alaska	0.019	0.679*
Puget Sound, Washington	0.002	-0.012	0.211*	0.188*	Puget Sound, Washington	0.078*	0.720*
Vancouver Island, WA, OR	0.023	-0.003	0.132*	0.112*	Vancouver Island, WA, OR	0.423*	0.290*
Central California	0.234*	0.180*	-0.002	0.004	Central California	0.603*	0.007
Southern California	0.624*	0.532*	0.180*	0.194*	Southern California	0.855*	0.263*

Argentine genotypes ($n = 12$) originated only from central California (mean contribution = 0.63; 95% CI = 0.153 to 1.0) or a mix of central and southern California (mean contribution = 0.30; 95% CI = 0 to 0.65). A small proportion may have originated along the outer coastline of Vancouver Island, Washington and Oregon (mean contribution = 0.07; 95% CI = 0 to 0.36).

We found no obvious differences in nucleotide diversity at COI between invasive and native populations (Fig. 3). At EF1, the nucleotide diversity of invasive Argentine populations was 5-fold greater than Japanese, Alaskan and Puget Sound populations, and nearly 2-fold greater than the outer coastlines of Vancouver Island, Washington, Oregon and California. These estimates, however, have substantial variance and population differences in diversity were not assessed statistically.

DISCUSSION

Balanus glandula from the Pacific Northwest and in Japan were differentiated from other native populations by the presence of a fixed nucleotide in EF1 (position 105) and contained all 3 major COI haplotype groups (i.e. A_{COI} , B_{COI} and C_{COI}). In contrast, *B. glandula* from Argentinian and Californian populations contained all haplotypes at both EF1 and COI. These genetic results indicate that the source of Japanese *B. glandula* populations is predominantly Alaska, Puget Sound or both, while Argentine invaders originated within California (Figs. 1 & 2, Table 1).

Many marine invasions have been shown by genetic analyses to have multiple origins (Geller et al. 1997, Zardus & Hadfield 2005, Voisin et al. 2005), which is not unexpected when major shipping ports are spread within the native range of potential invaders. Interbreeding among barnacles from different sources could

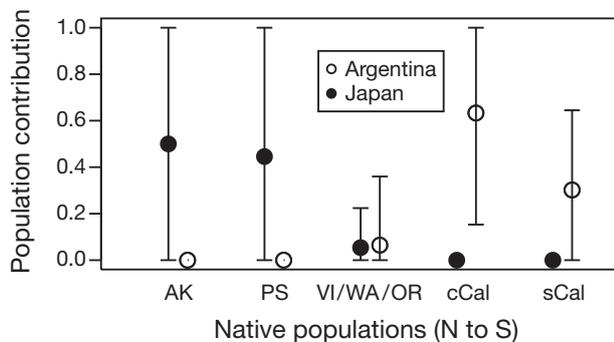


Fig. 2. *Balanus glandula*. Estimates of the contribution by native populations to invasive populations in Argentina and Japan. Mean estimates of contribution of native populations, and their upper and lower 95% CI (vertical bars) from 10 000 bootstrap replicates were calculated using SPAM 3.7. Abbreviations as in Fig. 1; cCal: central California; PS: Puget Sound; sCal: southern California

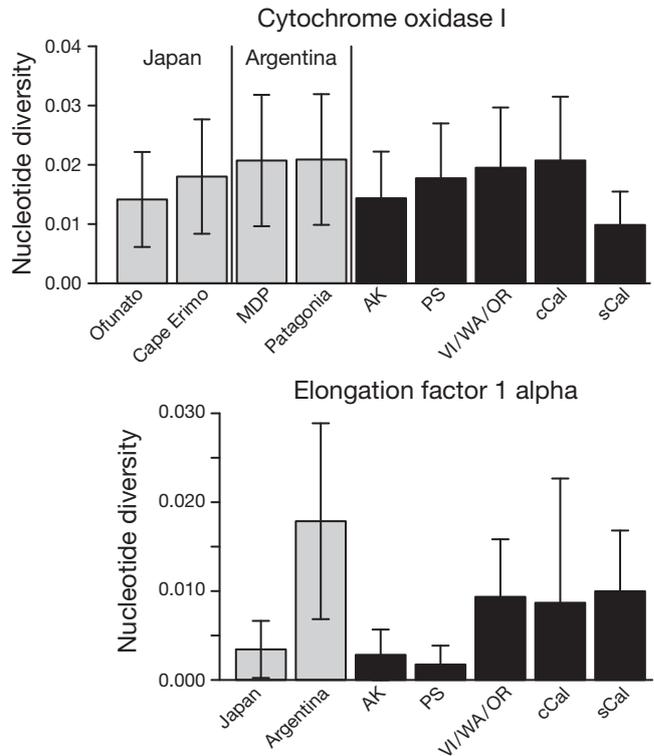


Fig. 3. *Balanus glandula*. Genetic diversity (\pm SD) at COI and EF1 within native and introduced populations. Note that we grouped Japanese and Argentine populations because of low sample size at Argentina. Abbreviations as in Figs. 1 & 2; MDP: Mar del Plata

result in novel genotypes that have higher genetic fitness in new environments than native genotypes (Ellstrand & Schierenbeck 2000, Voisin et al. 2005). However, although we can distinguish regional sources for *Balanus glandula* invasions, we do not have the ability to distinguish whether it invaded from a single or multiple sources within regions (Fig. 2). This is because of the relatively weak population differentiation within regions (e.g. Puget Sound and Alaska).

The invasions of *Balanus glandula* in Argentina and Japan have independent sources on the northeastern Pacific shore, and do not indicate perpetuation of invasions at the global level in which established invasions serve as sources for others (Bagley & Geller 2000). In general, not all invasions will have the same opportunity to found new invasions. Rather, ports in countries with the greatest number of trading partners and volume of shipping will become servers of ballast water (containing propagules of potential invaders) or fouled ships' hulls to the greatest number of non-native sites. Argentina's major export partners are Brazil, the USA, Chile and Germany, while most imports are from Brazil, the USA, China and Germany (www.cia.gov/library/publications/the-world-factbook/index.html). These countries are the most probable recipients of

invasive species from Argentina. On a global scale, however, Argentina is not a major trader, with a total of US \$78 billion (2006) combined imports and exports. Japan, on the other hand, has a larger economy and more trading partners, with US \$1.1 trillion (2005) combined import and exports. Of the 3 countries hosting *B. glandula*, the USA has the largest combined trade of US \$2.9 trillion (2005) and many trading partners. Argentina, then, is not likely to be a major stepping-stone for marine invasions, while North America and Japan are more likely to contribute their own biota and pass on invaders to many other regions. We predict that Japan will be a source for new invasions of *B. glandula*.

The Japanese result confirms the prediction of Kado (2003) that populations in Klawak, Alaska or the Puget Sound ports of Vancouver, Seattle and Tacoma were likely sources for the initial invasion of *Balanus glandula* because it was initially abundant only in commercial ports such as Ofunato, Hachinohe and Muroran. These ports receive ships laden with timber that embark from those North American ports. An alternative hypothesis, that we now reject, was a central California source, as the Ofunato port also receives oil cokes from San Francisco, Benicia, and Pittsburg (all in San Francisco Bay); our data demonstrate that central California is an improbable source for the genotypes of *B. glandula* in our Japanese samples.

It is possible that the broad similarity of seawater temperatures in source and target regions may have facilitated these invasion events. (Fig. 4). Warmer sites in southern (average monthly sea surface temperature [SST] of 13.9 to 21.1°C) or central California (10 to 15.6°C; 18.9°C in some sites in San Francisco Bay) were source to warmer sites of invasion in Argentina (southernmost Argentine sites of our study: 8.8 to 13.5°C; northernmost: 11.0 to 19.0°C). Colder sources in Puget Sound (Seattle: 7.7 to 13.3°C) and/or Alaska (2.2 to 11.1°C) seeded invasions of the colder waters of Japan (present northern limits to *Balanus glandula*: -0.3 to 19.1°C; southern limits: 7.7 to 22°C).

At the same time, seasonal variation in air and seawater temperatures along these invaded shores tends to be greater than that experienced by their source populations (Fig. 4). In Japan, there is greater seasonal variation in mean monthly seawater temperatures than is found for any other location along the northeastern Pacific or Argentina. Japanese waters get as warm as Californian waters in the summer, and as cold as Puget Sound and Alaskan waters in the winter. Similarly, Japanese islands experience tremendous seasonal variation in mean monthly air temperatures (north: -10 to 20°C; south: 0 to 25°C). In Argentina, seawater temperatures are similar to those of central and southern California, while air temperatures tend to be colder in Argentina during the winter (north: 10 to 25°C; south: 0 to 10°C).

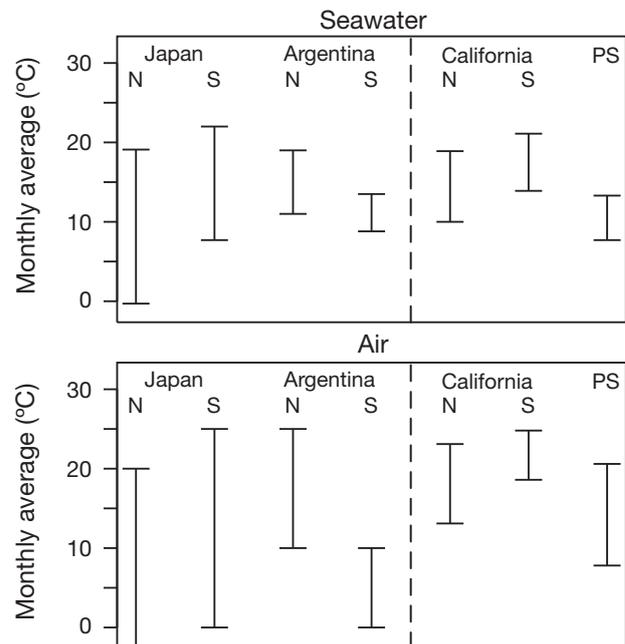


Fig. 4. Average monthly temperatures (max. and min.) of seawater and air for regions in Japan, Argentina, and the native range of *Balanus glandula* (California and Puget Sound). N and S: data taken from the northern and southern ends of each region, PS: Puget Sound

These temperature profiles should be interpreted cautiously, given the coarse temporal resolution of the data and the complex of factors that regulate the temperatures experienced by intertidal organisms (Helmuth et al. 2002). However, if ambient conditions are a proxy for the abiotic environment of barnacles, then it appears that both sets of introduced barnacle populations tend to experience greater seasonal variation in temperature than barnacles in their native range. Because of its intertidal habitat, *Balanus glandula* body temperatures are closely tied to air temperatures during low tides (Harley & Lopez 2003), and the mortality of these and other temperate barnacles is largely the consequence of this exposure to air (Gosselin & Qian 1996, Schmidt & Rand 1999). Thus, these climate data suggest the possibility of air temperature-related selection regimes in Argentina and Japan that appear to differ from native habitats.

There was no obvious decline in genetic diversity of COI and EF1 among nonnative introductions relative to their native sources (Fig. 3). This suggests that a substantial number of invaders (i.e. effective population sizes of 10s to 100s of individuals at the least) were able to successfully colonize and reproduce in novel habitats. This result agrees with the conclusions of recent reviews (Wares et al. 2005, Roman & Darling 2007) that many invading populations have no or very slight reduction in genetic diversity relative to native populations.

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