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Dispersal potential and population genetic structure in the marine intertidal of the eastern North Pacific

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Abstract. Population genetic theory and empirical comparisons of sister and sympatric marine species show that life history traits related to dispersal, such as pelagic duration (PD), should affect the frequency and spatial scale of migration, and thus influence population genetic structure. However, recent global analyses have concluded that PD is poorly correlated with marine population genetic structure. Here, we identify and compare genetic structure between four pairs of synchronously diverging co-distributed (SDC) species, drawn from standardized analyses of eight eastern North Pacific rocky intertidal invertebrates and one macrophyte. We test two hypotheses: H_0, that species with similar dispersal potential have similar population genetic structure, and H_1, that species with higher dispersal potential have lower population genetic differentiation. We find that differences in census population size (N_c), fecundity (F), and PD are sufficient to explain measured differences in population genetic structure (ϕ_{ST}, D_{EST}) between SDC species. However, theoretical differences in migration potential, calculated as a function of N_c, F, and PD, exceed empirical differences in migration, suggesting important roles for genetic drift and natural selection in structuring marine populations in the eastern North Pacific. A quantitatively similar relationship between PD and F_{ST} has been calculated for co-distributed species from the Great Barrier Reef, suggesting that meta-analyses of SDC species may reveal general patterns in how species' traits and geographical variation interact to structure populations.

Key words: comparative phylogeography; connectivity; cytochrome c oxidase subunit I (COI); dispersal syndromes; gene flow; genetic drift; migration; pelagic larval duration; selection; synchronously diverging co-distributed taxa.

Introduction

The actual conditions in nature are everywhere not products of single and simple forces, but resultants of many causative influences, often operative through the long course of the ages . . . an observed relation of cause and effect is not invalidated by the presence of other effects due to other causes.

—D. S. Jordan (1908); see also Ghiselin (1997: chapter 14).

Migration is one of five major processes that influence evolution (Wright 1931, Wade and Goodnight 1998, Conner and Hartl 2004) and, until recently, was overwhelmingly considered the dominant influence on marine population genetic structure (Sanford and Kelly 2011; see also Caley et al. 1996). Migration gained prominence in large part because most marine species have planktonic larvae or spores (e.g., Thorson 1950) that demographically and genetically link populations of sessile or sedentary adults inhabiting different locations. The dispersal potential of these larvae and spores was recognized early in the history of marine population genetics as a correlate of gene flow and a possible predictor of population genetic structure (Gooch 1975, Crisp 1978). In the absence of direct measures of dispersal, the time in the plankton stage, most commonly referred to as the pelagic duration (PD), became a commonly used proxy for the expected or realized dispersal distance (e.g., Scheltema 1971, Jablonski 1986).

Comparisons of PD and population genetic structure dominated efforts to understand the role of migration in the evolution of marine populations for the next two to three decades (Riddle et al. 2008). Typically, PD was estimated from growth rates in laboratory cultures, anatomical features, developmental series, and/or field collections (e.g., Scheltema 1971, Brothers et al. 1983), while population genetic structure was usually represented in terms of the fixation index, F_{ST}, and its analogues (e.g., Doherty et al. 1995). Multiple studies on a particular taxon or a particular geographic region often found the expected positive correlation between

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PD and population genetic structure, consistent with the perceived importance of migration in determining marine population genetic structure (Waples 1987, Doherty et al. 1995, Hellberg 1996, Collin 2001, Dawson et al. 2002, Shanks et al. 2003, Paulay and Meyer 2006, Hoffman et al. 2010). However, the relationship was weaker and sometimes nonexistent in aggregate global analyses (e.g., Bohonak 1999). Indeed, several recent analyses of new data sets (Selkoe et al. 2010) and syntheses of hundreds of prior results (Weersing and Toonen 2009, Riginos et al. 2011) conclude that PD is generally a poor predictor of gene flow.

The inconsistent empirical relationship between PD and population genetic structure has renewed interest in the broader suite of interacting factors that govern dispersal and gene flow in marine taxa, and thus cause deviations from the genetic signature predicted on the basis of PD alone. For example, a larger population size or higher per capita fecundity (F) yields a greater number of emigrant offspring, which, all other things being equal, would proportionally increase the number of immigrants into other populations (e.g., Scheltema 1971). Both larger population size and higher per capita F also would increase the probable maximum distance dispersed, because the number of individuals would increase in the long tail of the dispersal kernel. The geographic scale of migration also may be influenced by variation in PD among individuals, species, and temperatures (e.g., Knight 1976, O'Connor et al. 2007), by spatial and temporal variation in the velocities of ocean currents in which plankton drift (Siegel et al. 2003), by larval behavior that may enhance or reduce dispersal relative to passively drifting plankton (Queiroga et al. 1997, Leis 2007), by selection in the plankton (Johnson and Black 1984), and by the distribution of suitable habitat (Alberto et al. 2011). In turn, whether successful dispersal leads to gene flow will be affected by processes including post-settlement selection (Johnson and Black 1984, Sanford and Kelly 2011) and "sweepstakes" variance in individual reproductive success (Hedgecock 1994; e.g., Hellberg 2009, Selkoe et al. 2010, Riginos et al. 2011; also see Whitlock and McCauley 1999). Variation in the relative contributions of these factors, and interactions among them, can produce patterns of genetic variation that are inconsistent and seemingly unpredictable in space and time, termed chaotic genetic patchiness by Johnson and Black (1982; also see Edmands et al. 1996, Selkoe et al. 2010, Toonen and Grosberg 2011).

In principle, global syntheses have the numerical power to discern the relative influence of the many factors affecting migration, and to detect general patterns not apparent in smaller-scale studies. However, by aggregating diverse data sets in treat-as-one-trial analyses (Altman and Deeks 2002), as opposed to meta-analyses of effect sizes (Glass 1976, Hedges et al. 1999), such syntheses may conceal the impacts of PD on the spatial distribution of genetic variation in marine populations. For example, in multi-study comparisons, the type of molecular marker used to characterize genetic structure (e.g., microsatellite, allozyme, mtDNA sequence, or restriction fragment length polymorphism) overall has the greatest influence on estimates of F_{ST} (Weersing and Toonen 2009; see also Riginos et al. 2011). These analyses also reveal significant interactions between geographic location and F_{ST} (Riginos et al. 2011, Selkoe and Toonen 2011), but so far say little about the relative contributions of other, often unmeasured factors known to affect population genetic structure (Marko and Hart 2011).

In the absence of multivariate, multispecies data sets sufficient for thorough global meta-analyses, another approach is needed to infer the mechanisms influencing marine population genetic structure. Studies of synchronously diverging co-distributed (SDC) species may offer a robust and flexible approach. SDC species are taxa that (1) arose from cladogenetic events or have coalescents that are statistically the same age, and (2) since that time have likely occupied the same geographic region (Dawson 2012). The analysis of SDC species reaps many of the benefits of comparisons of sympatric sister species: the taxa are of comparable age and evolutionarily independent, rather than phylogenetically nested, and confounding variables and noise are reduced (Lynch 1989, Barraclough et al. 1998). Comparisons of synchronously diverging species, which include but are not necessarily sister species, should also ameliorate the key drawback of sister-taxon comparisons, reduced sample size (Rosenzweig 1996), and acknowledge that sometimes putative sister comparisons have probably been compromised by extinction of the most closely related species (Marko 2002). Studying synchronously diverging species that also are co-distributed has the added benefits of standardizing the environment in which evolution has taken place, increasing confidence in inferences about extrinsic influences on phylogeographic structure (Kuo and Avise 2005).

In this study, we identify and use SDC species to explore the relationship between dispersal potential and population genetic structure in marine intertidal species of the eastern North Pacific. By controlling for variation in time, environment, and study design (see *Methods*; Dawson 2014) we aim to clarify how multiple attributes of organisms and species, such as F, PD, and population size, influence migration and population genetic structure in this region. We first test the null hypothesis (H_0), that co-distributed species with similar dispersal potential have similar phylogeographic structure. This null expectation arises from the predicted links between dispersal potential, migration, and gene flow, and from phylogeographic simulations when geographic barriers are present (Kuo and Avise 2005). H_0 is an often unwritten assumption of studies that estimate the effect size of dispersal on gene flow by comparing species that differ in PD (Dawson 2012; but see Bird et al. 2007, Pelc et al. 2009). Second, we test the classical hypothesis (H_1),

that greater dispersal potential increases gene flow and decreases population genetic differentiation among locations. Finding support for both hypotheses in this region, we reason that meta-analyses of SDC species may improve understanding of population genetic structure from regional to global scales.

Methods

Study system and species

We focused this analysis on the northeastern Pacific intertidal zone, because it is one of the best-studied maritime systems in the world in terms of its population and community ecology (e.g., Paine 1966, Connell 1970, Barry et al. 1995, Broitman et al. 2008), biogeography (e.g., Valentine 1966, Murray and Littler 1980, Blanchette et al. 2008), and phylogeography (e.g., Burton 1998, Dawson 2001, Wares et al. 2001, Pelc et al. 2009, Kelly and Palumbi 2010). This region includes a major biogeographic transition from the Oregonian Province to the Californian Province (the California Transition Zone; Briggs and Bowen 2011), multiple phylogeographic and/or biogeographic filters of differing intensity (e.g., Dawson 2001, Dawson et al. 2006, Blanchette et al. 2008, Pelc et al. 2009), and a mainland-island array (the Channel Islands in southern California; Fig. 1, Table 1). In addition, a 10-yr biodiversity initiative, the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO), now provides a wealth of information on species distributions and abundances across the region (e.g., Blanchette et al. 2008). Based on this initiative, we chose eight species that occur throughout the northeastern Pacific mainland and island array, and that represent a suite of life history characteristics putatively conferring low, medium, or high dispersal potential (Table 2). The species include the snails *Nucella emarginata* and *Nucella ostrina*, the fucoid alga *Silvetia compressa*, the limpets *Lottia austrodigitalis*, *Lottia digitalis*, and *Lottia scabra*, and the barnacles *Pollicipes polymerus* and *Tetraclita rubescens*. To minimize potentially confounding effects of sample design (Weersing and Toonen 2009, Riginos et al. 2011, Selkoe and Toonen 2011), we surveyed the same geographic region with the same intensity of sampling at each location and used the same locus (mtDNA) for all taxa.

Estimating species dispersal potential

Life history, including F and PD.—We reviewed the published scientific literature describing habitat, abundance, longevity, maturation, reproductive season, *F*, developmental mode, PD, and potential for long-distance dispersal for each of the target species (Table 2). *L. austrodigitalis*, *L. scabra*, *N. emarginata*, *L. digitalis*, *N. ostrina*, *S. compressa*, *P. polymerus*, and *T. rubescens* are broadly co-distributed with at least one other of these species in the middle and/or high intertidal zone(s) from 31–40° N (Tables 1, 2). Age of maturation is similar across species (1–2 yr), except for *P. polymerus*, which may be on the order of 2–4 yr.

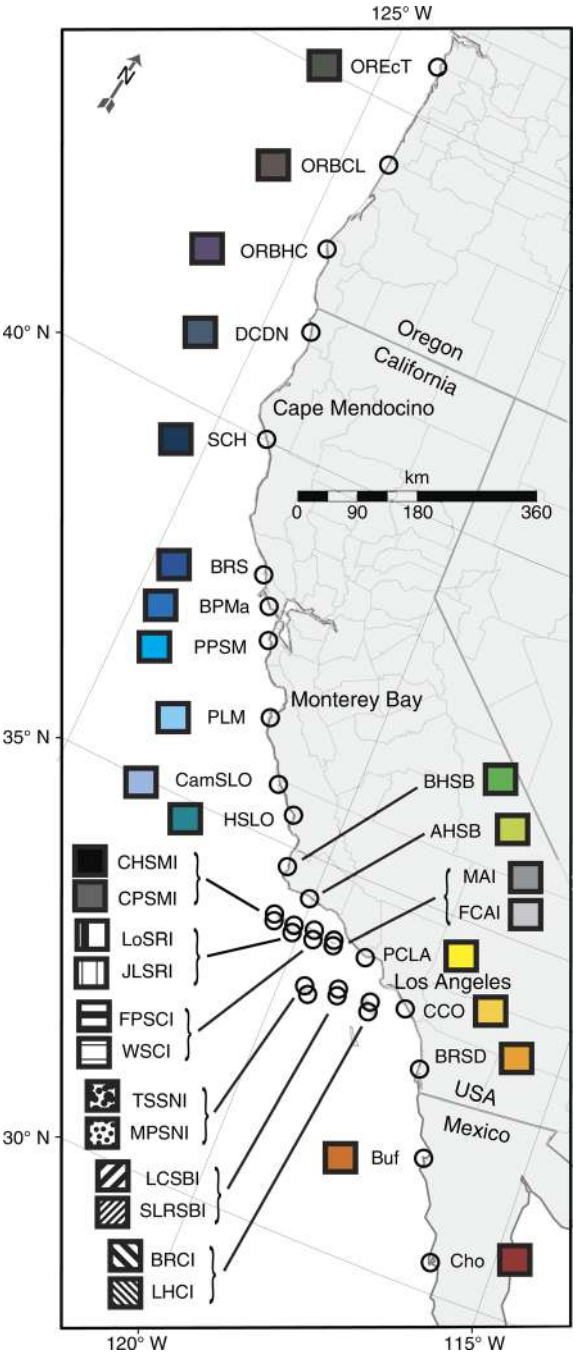

FIG. 1. Sample locations within and principal biogeographic classification of the eastern North Pacific study area. The site names, coordinates, and sample sizes are provided in Table 1. The study area was sampled across two biogeographic provinces, the Oregonian Province and the Californian Province, and 10 subregions (Blanchette et al. 2008). The Californian biota replaces the Oregonian biota across the California Transition Zone from Monterey Bay to Los Angeles (Dawson 2001, Briggs and Bowen 2011). Previously reported phylogeographic discontinuities cluster around Cape Mendocino, Monterey Bay, Point Conception (located between sites AHSB and BHSB), and Los Angeles (Dawson 2001, Cope 2004, Pelc et al. 2009, Kelly and Palumbi 2010).

TABLE 1. Sample sites and sample sizes for COI analysis of the seven invertebrates, and NaD5 of the alga included in this study.

Site	Acronym	Latitude (°N)	Longitude (°W)	County/province on mainland, or island
Individual sites				
Ecola	OREcT	45.750	123.967	Tillamook County
Bob Creek	ORBCL	44.233	124.100	Lane County
Burnt Hill	ORBHC	42.717	124.300	Curry County
Damnation Creek	DCDN	41.653	124.130	Del Norte County
Shelter Cove	SCH	40.031	124.079	Humbolt County
Bodega Reserve	BRS	38.318	123.073	Sonoma County
Bolinas Point	BPM	37.905	122.727	Marin County
Pigeon Point	PPSM	37.185	122.397	San Mateo County
Point Lobos	PLM	36.513	121.944	Monterey County
Cambria	CamSLO	35.540	121.093	San Luis Obispo County
Hazards	HSLO	35.290	120.883	San Luis Obispo County
Boat House	BHSB	34.554	120.611	Santa Barbara County
Arroyo Hondo	AHSB	34.474	120.144	Santa Barbara County
Fraser Point	FPSCI	34.063	119.919	Santa Cruz Island
Cuyler Harbor	CHSMI	34.048	120.336	San Miguel Island
Crook Point	CPSMI	34.022	120.379	San Miguel Island
Paradise Cove	PCLA	34.012	118.793	Los Angeles County
Lobo Canyon	LoSRI	34.019	120.097	Santa Rosa Island
Frenchy's Cove	FCAI	34.007	119.411	Anacapa Island
Middle	MAI	34.006	119.396	Anacapa Island
Willows	WSCI	33.962	119.755	Santa Cruz Island
Johnson's Lee	JLSRI	33.909	120.087	Santa Rosa Island
Crystal Cove	CCO	33.571	117.838	Orange County
Landing Cove	LCSBI	33.482	119.029	Santa Barbara Island
Sea Lion Rookery	SLRSBI	33.472	119.031	Santa Barbara Island
Bird Rock	BRCI	33.452	118.488	Santa Catalina Island
Little Harbor	LHCI	33.385	118.475	Santa Catalina Island
Thousand Springs	TSSNI	33.285	119.530	San Nicolas Island
Marker Poles	MPSNI	33.219	119.496	San Nicolas Island
Bird Rock/Scripps	BRSD	32.871	117.253	San Diego County
la Bufadora	Buf	31.724	116.714	Baja California Norte
la Chorera	Cho	30.470	116.047	Baja California Norte
All sites combined				

Notes: The species shown are the snails *Nucella emarginata* and *Nucella ostrina*, the fucoid alga *Silvetia compressa*, the limpets *Lottia austrodigitalis*, *Lottia digitalis*, and *Lottia scabra*, and the barnacles *Pollicipes polymerus* and *Tetraclita rubescens*. Locations are arranged northernmost (top) to southernmost (bottom). An empty cell indicates the species was not found at that location. Additional information is provided in Fig. 1. COI stands for cytochrome *c* oxidase subunit I, NaD5 stands for NADH dehydrogenase subunit 5. The samples of *S. compressa* reported under SCH were collected at Stornetta Ranch (38.938° N, 123.729° W), and those reported under FPSCI were collected at Forney (34.056° N, 119.922° W) at a distance of several hundred meters on the same headland. NWTSRI has a proxy of Lobo Canyon SRI.

Longevity also is similar across species, roughly 5–10 yr, again excepting *P. polymerus*, which may be on the order of 10–20 yr.

Reproductive patterns (e.g. season, fertilization mode, and larval type) show some consistent differences. Although the reproductive seasons of most species overlap, at least sporadically through the year, and may vary latitudinally and interannually, the alga and mollusks are biased toward reproduction during winter and possibly spring, whereas the barnacles reproduce principally during summer. Reproduction during the summer months (when upwelling occurs) thus distinguishes the internally fertilized barnacles with planktotrophic larvae from the alga, the free-spawning lecithotrophic lottiid molluscs, and the internally fertilized, lecithotrophic *Nucella* species with crawl-away larvae. PD of the planktotrophs is two to four times longer than that of the free-spawning lecithotrophic lottiid limpets, which, in turn, have PDs an order of magnitude greater than the alga *S. compressa*; the PD of *Nucella* spp. is zero. The low dispersal potential implied by the extremely short PD of *S. compressa* and the zero PD of *Nucella* spp. contrasts with their potential for long-distance dispersal.

Census population size (N_c).—We estimated the abundances of attached invertebrates (i.e., *P. polymerus*, *T. rubescens*) and macroalgae (*S. compressa*) using a point-contact method following Murray et al. (2006). A 30-m section of shoreline was designated as the site, and a baseline tape was laid out parallel to the shore immediately above the upper limit of intertidal species; 11 transects were then established at 3-m intervals perpendicular to the baseline (i.e., across shore), extending to approximately 0-m mean lower low water tidal datum (MLLW). The density of sample points in this design is in proportion to the local spatial structure of variance in northeastern Pacific intertidal communities (P. Raimondi, *unpublished data*). The sampling

TABLE 1. Extended.

Sample sizes							
N. emarginata	*N. ostrina*	*S. compressa*	*L. austrodigitalis*	*L. digitalis*	*L. scabra*	*T. rubescens*	*P. polymerus*
	14			15			14
	14			15			15
	14			14			15
	15			13	10		15
	14	14		14	15	14	15
	15	15		13	15	15	15
	15	15		15	15		15
	14	15	1	14	15	15	15
15		16	9	7	15	15	15
15		16	2	12	15	15	14
15		15	13	2	14	14	15
15		15	13	2	15	15	15
15			15		14	15	15
15		13	15		15	15	15
15		16	16		15	15	15
14		15	15		15	15	15
15		13	15		15	17	15
15		16	14		15	15	15
15		15	16		15	15	14
15		13	16		15	14	15
15		15	15		15	15	15
15			16		15	15	15
15		15	15		12	15	15
			15		14	14	15
		14			14	14	14
		15	15		15	15	15
		15	15		14	15	15
15		15	15		15	15	15
14			15		15	15	15
		16	14	1	14	15	15
			15		13	15	15
		14	16		13	15	15
253	115	355	342	137	430	417	491

interval along transects at each site thus varied depending on size and slope of the bench, always providing ~10 times more sample points across shore (n = 100–120) than along shore (n = 11), and the same number of sample points per unit of elevation. Thus, relative abundances of attached invertebrates and macroalgae were estimated as percentages of their occurrence at 1100 sampling points.

We collected data on the mobile invertebrate assemblage (i.e., *Nucella* spp., *Lottia* spp.) using a stratified quadrat design. Three quadrats, 50 × 50 cm, were distributed along each of the 11 transects with one quadrat placed randomly within each of three intertidal zones (high, mid, and low; i.e., 33 quadrats per site). All macroscopic mobile invertebrates within each quadrat were counted and identified to species, or to the lowest taxonomic category possible in the field, i.e., *Nucella* spp., *L. austrodigitalis*/*L. digitalis*, and *L. scabra*/*L. conus*. *Lottia conus* was not sampled for this study, but can be a confounding species for *L. scabra* in the southern portion of its range. Preliminary genetic analyses indicate that *L. scabra* and *L. conus* rarely co-occurred (or co-occurred at levels inconsequential to our analysis), and that *N. emarginata* and *N. ostrina* never co-occurred at sites we surveyed; thus, the surveys reliably estimate N_c for these species. In the case of *L. austrodigitalis*/*L. digitalis*, which our genetic data indicate gradually replace each other in central California, we divided the measured abundance in the range of overlap evenly between the two conflated species to approximate actual abundances across the entire range surveyed.

To compare the abundances of sessile and mobile taxa, we converted counts of mobile invertebrates to percent cover. We measured shell length (l) and width (w) of a subsample of specimens with vernier calipers, converted this to mean individual circular planar-area ($a = \pi[(l/2 + w/2)2]^2$ m^2), and used this number to convert observed mean abundance per site, $^\circ n$, to estimated percent cover ($^e c = {}^\circ n \times a/0.25 \times 100$). We also converted observed percent cover ($^\circ c$) of sessile organisms to an estimate of mean abundance per quadrat ($^e n = {}^\circ c/100a \times 0.25$). For conversions of $^\circ c$ to $^e n$, we additionally measured the planar area of *S. compressa* that was prostrate on the shore during low tide at Davenport Landing, in Santa Cruz, California, USA (July 2011), and confirmed that our *S. compressa* length measure-

TABLE 2. Ranges and life history characteristics of the taxa in this study.

Parameter	Low dispersal	
	N. emarginata/ostrina	*S. compressa*
Reproductive season	mostly November to March, sporadically throughout year,[1,2] ~20% females reproductive[2]	October to May in central California, shorter season farther south
Longevity	6–10 yr[7] (mature at 1–2 yr[8])	8+ yr, (mature for 7+ yr)[9]
Max brood size (no. of larvae)	13.6 ± 3.9 individuals/cap and 5–31 cap/clutch[1,2], several clutches per female per year	~500–5000 individuals/month
Population size/density	≤400 individuals/m^{2} [1]	<10% cover[13]
Habitat	m and h IT[1]	m IT[15]
Geographic range (°N)	31–57, with *N. emarginata* replacing *N. ostrina* at 37.[1,16]	31–40
Reproduction	internal fertilization[17]	free-spawner
Larval type	lecithotrophic in benthic egg capsule, crawl away[1]	zygotes attach to substrate within ~4–6 hr
PD	0 d[1]	<1 d
LDD	yes[20]	possible

Notes: Note that data are provided together for *Nucella* spp. and for *L. austrodigitalis* and *L. digitalis* because these were, until recently, debatably single taxa, and so most data are conflated for the constituent species. PD stands for pelagic duration. LDD stands for long distance dispersal. IT stands for intertidal (w, low; m, middle; and h, high). In the maximum brood size row, cap stands for egg capsule.

Sources: 1, Morris et al. (1980); 2, Spight and Emlen (1976); 3, Fritchmann (1961); 4, Sutherland (1970); 5, Gilman (2006); 6, Dawson et al. (2010); 7, by reference to sister-taxa or closely related congeneric taxa, e.g. Selin (2003), Feare (1970), Crothers (1985); 8, Moran and Emlet (2001); 9, Gunnill (1980); 10, Kay and Emlet (2002) and references therein; 11, by reference to sister-taxa or closely related congeneric taxa, e.g. based on fecundity-size relationship in Kay & Emlet (2002); 12, Gilman (2005); 13, Blanchette et al. (2008); 14, estimated by E. Sanford using basal diameter (2 cm) and percent cover in Sanford and Swezey (2008); 15, Abbott and Hollenberg (1976); 16, Marko (1998); 17, Rawlings (1996), Lloyd and Gosselin (2007); 18, Shanks and Eckert (2005); 19, Lewis (1975); 20, Martel and Chia (1991).

ments were similar to *S. compressa* lengths at other locations (Cho et al. 2001, Whitaker et al. 2010).

Collections for molecular genetic analyses

Between July 2007 and December 2008, we haphazardly collected individual samples of the eight intertidal species at up to 32 sites from La Chorera, Baja California Norte, Mexico (30.470° N, 116.047° W) to Damnation Creek, California, USA (41.653° N, 124.130° W). We collected additional samples at three sites in Oregon, USA (northward to 45.750° N, 123.967° W) in July 2009, and supplemented the *T. rubescens* data set with sequences from five sites sampled between January and May 2006 (Dawson et al. 2010). Samples of *S. compressa* were placed immediately in silica gel and desiccated; collected animals were preserved immediately in 95% ethanol. Fig. 1 and Table 1 show the sites, locations, and sample sizes.

DNA extraction, polymerase chain reactions, sequencing, and genetic diversity

From each invertebrate, we extracted DNA from ~1-mm^{3} subsamples of muscle using a CTAB protocol modified from Dawson et al. (1998). From *S. compressa*, we extracted DNA from 50–80 μg of dried and ground tissue, following McDevit and Saunders (2009). We used 1 μL of purified DNA solution in 50 μL polymerase chain reactions (PCR) with 0.5 units AmpliTaq, a 5 μL 10× buffer (Applied Biosystems, Foster City, California, USA) and final concentrations of 0.5 μmol/L primers (Operon Biotechnologies Inc., Huntsville, Alabama, USA), 2.5–3.0 mmol/L $MgCl_2$ (Applied Biosystems), and 0.2 mmol/L dNTPs (Bioline, Sydney, New South Wales, Australia) to amplify portions of the homologous mitochondrial locus from all species. We sequenced cytochrome *c* oxidase subunit I (COI) from the seven invertebrates and NADH dehydrogenase subunit 5 (NaD5) from *S. compressa*. We chose COI because its range of rates of evolution is reasonably well constrained (Lessios 2008), and it is among the most taxonomically broadly sequenced loci (e.g., Hebert et al. 2003). Like COI, NaD5 is a mitochondrial marker, and in preliminary analyses of macroalgae, showed a similar level of variation as invertebrate COI. Despite the drawbacks of using only one marker per species, these choices standardized to the greatest extent possible

TABLE 2. Extended.

Medium dispersal		High dispersal	
L. digitalis/*austrodigitalis*	*L. scabra*	*T. rubescens*	*P. polymerus*
winter, spring, June, and July [1,3]	winter: mainly January to March; more extended season lower in intertidal zone[1,4,5]	summer: June to November[1,6]	summer[1]
6 yr or more[1]	7–11 yr[1]; 10–20 yr[5]; 10–30 yr[4]	10–15 yr (mature at 2 yr)[1]	up to 20 yr (mature at 5 yr)[1]
~5000–42 000[10] individuals/yr	~5000–50 000[11] individuals/yr (mean 5000–20 000)[11,12], ≤2 broods per year[12]	~3000–150 000 individuals/yr [1]	~0.3–1.7 × 10^6 individuals/yr [1]
no published data	maximum 128–400 individuals/m^2 [12]	240–1120 individuals/m^2 where common [14](up to 5% cover, usually <1%[13])	no published data
h IT[1]	h IT[1,5]	w and m IT[1]	m IT[1]
24–60, with *L. digitalis* replacing *L. austrodigitalis* at 37. [1]	28–43[1]	23–40[1,6]	26–50[1]
free-spawner[10]	free-spawner[11]	internal fertilization[18]	internal fertilization[18]
lecithotrophic[10]	lecithotrophic[11]	brooded to nauplius, then planktotrophic[1]	brooded to nauplius, then planktotrophic[1]
6–14 d[10]	<2 weeks[5,11]	~3–4 weeks[6]	6–7 weeks[19]
no	no	no	yes

the characteristics of the markers we compared (i.e., usually uniparental inheritance, haploid, and clonal) and likely rates of mutation (approximately a twofold rate; Lessios 2008). We amplified COI using the following primer pairs: LCO1490 with HCO2198 for *Nucella* spp. and *P. polymerus* (Folmer et al. 1994), LdigCOI_0112f (5′-taatacacacgggyacrgg) or LdigCOI_00105f (5′-attcacttaatacacacgggyacrgg) with LdigCOI_00669r (5′-ttcagggtcaaagaaggcagt) for *L. austrodigitalis* and *L. digitalis*, Ls_LCO1588e (5′-taatacacacrggwacaggrytcctaa) with Ls_HCO2166 (5′-ggtgttggaataggacagggtctcc) for *L. scabra*, and TC5f with TC7r for *T. rubescens* (Dawson et al. 2010); we amplified NaD5 of *S. compressa* using FvNad5L (5′-tgggggaagatccacattta) and FvNad5R (5′-taccactgagttattgctccc).

Thermal cycling consisted of 35 cycles of 94°C for 30–45 s, 50–57°C for 30–45 s, and 72°C for 60–90 s, followed by 72°C for 10 min and cooling to 4°C. Optionally, the cycle was preceded by one step of 94°C for 4–8 min or by six steps of 94°C for 8 min, 52–58°C for 1–2 min, 72°C for 2–4 min, 94°C for 4 min, 53–57°C for 1 min, and 72°C for 2–3 min (Appendix A).

Amplifications were cleaned using 47 μL PCR product with 4 μL Exonuclease I and 4 μL Shrimp Alkaline Phosphotase (USB Corporation, Cleveland, Ohio, USA), incubated at 37°C for 15 min, 80°C for 15 min, and cooled to 4°C until prepared for sequencing. Sequencing was completed, using PCR primers, on ABI 3730 machines (Applied Biosytems) at the High-Throughput Genomics Unit at the University of Washington (Seattle, Washington, USA) or the UC Berkeley DNA Sequencing Facility (Berkeley, California, USA), following Applied Biosystems protocols.

Electropherograms were checked and base calls confirmed or edited in contigs of forward and reverse reads assembled in Sequencher 4.8 (GeneCodes, Ann Arbor, Michigan, USA). Sequence identities were confirmed by Basic Local Alignment Search Tool (BLAST) searching GenBank (Altschul et al. 1997) and by translation to amino acid sequence to confirm an open reading frame with high similarity to published COI peptide sequences. Sequences were aligned in ClustalX v.2.0 (Larkin et al. 2007), using default settings for both pairwise and multiple alignment steps. Alignments exported in Nexus format were visually inspected in Se-Al v.2.0a11 (A. Rambaut, *unpublished program*), and then reformatted in TextMate v.1.5.8 (MacroMates, Copenhagen, Denmark) for subsequent analyses. Nucleotide substitution models for each locus, excluding missing or ambiguous positions, were estimated using ModelTest v.3.7 (Posada and Buckley 2004). All sequences were deposited in GenBank (accession numbers KJ005125–KJ007519).

Gene tree and network analyses

We reconstructed relationships among COI alleles using either maximum-likelihood analysis in GARLI (Zwickl 2006) run on the CIPRES Portal 2.0 (Miller et al. 2010), or statistical parsimony in TCS (Clement et al. 2000), following the recommendations of Joly et al. (2007). Both methods are suitable for constructing genealogies from sets of closely related DNA sequences

with or without migration (Salzburger et al. 2011). Our choice was determined by the method that yielded the visually most informative figure given the observed geographic distribution of genetic variation in each taxon. In GARLI, we employed the nucleotide substitution model (GTR+I+Γ) that least overparameterized the best-fit model (TrN+I+Γ for *P. polymerus*; TIM+I+Γ for *T. rubescens*), indicated by hLRT and AIC in ModelTest. Maximum likelihood (ML) analyses used estimated base frequencies, estimated proportion invariant sites, four rate categories for the gamma distribution, and random starting trees for eight independent search replicates (all other parameters remained on default values). Bootstrap analyses employed the same parameter values as the initial search for the ML tree, except (due to GARLI configuration) only two (rather than eight) independent search replicates were completed in each of 50 bootstrap repetitions during 10 independent searches, yielding a total of 500 bootstrap repetitions. In TCS, we calculated the 95% connection limits among haplotypes within *N. emarginata*, *N. ostrina*, *S. compressa*, *L. austrodigitalis*, *L. digitalis*, and *L. scabra* networks.

Genetic diversity, population genetic structure, and historical demography

Using Arlequin v.3.5.1.2 (Excoffier and Lischer 2010), we calculated four population genetic parameters to describe within-group (i.e., taxon or population) genetic variation: haplotype richness (n_a), pairwise sequence distance (psd), haplotype diversity (h), and nucleotide diversity (π). We estimated population genetic structure by calculating global $\phi_{ST,}$ mean and median pairwise ϕ_{ST} (Schneider et al. 2000), and D_{EST} (Jost 2008). We calculated mismatch distributions and compared them with distributions predicted for expanding populations, in part using Harpending's raggedness index. We also compared Ewens-Watterson homozygosity test results for marker neutrality and population equilibrium against Tajima's D and Fu's F, which, if very negative, may indicate population expansion, selection, or admixture. We estimated the magnitude of population expansion using θ, a correlate of effective population size ($\theta = 2N_e\mu$, for a mutation rate μ in a haploid genome), at the beginning (θ_0) and end (θ_1) of the expansion. We calculated all these statistics using Arlequin, except D_{EST}, which we calculated using SPADE (Chao and Shen 2009); analyses in Arlequin assumed a Jukes-Cantor model of nucleotide substitution and employed 10 000 bootstrap replicates for all analyses of significance. We also estimated effective population size N_e (scaled by μ), to provide a long-term indicator of the relative abundances of our target species, by calculating θ_1 using the maximum-likelihood coalescent approach in LAMARC v.2.1.6 (Kuhner 2006); analyses in LAMARC employed the best-fit model for each taxon, as indicated by hLRT and AIC in ModelTest, or as near an approximation as permitted by LAMARC (HKY/F84 for *L. austrodigitalis*, *L. scabra*, and *N. emarginata*, HKY+G for *L. digitalis*, *N. ostrina*, and *S. compressa*, and GTR+I+Γ for *P. polymerus* and *T. rubescens*; with parameter values estimated by LAMARC). Analyses in LAMARC were repeated with five randomly chosen subsets of 25 sequences. We estimated the time to the most recent common ancestor, t_{MRCA}, for each species using Bayesian methods in BEAST v.1.6.1 (Drummond and Rambaut 2007); analyses were repeated with five randomly chosen subsets of 50 sequences. Finally, we also estimated the global migration coefficient, m, in IMa2 (Hey 2010*a*, *b*) using a subset of 10 sample locations spanning each species' range. In the absence of fully bifurcating empirical trees, IMa2 analyses used a random tree generated in Mesquite v.2.75 (Maddison and Maddison 2011) and, for species with structure, trees approximating as best possible (albeit unavoidably imperfectly) the relationships indicated by reconstructed networks. Although preliminary analyses in IMa2 allowed selection of reasonable priors for most species (except *L. scabra* and *L. austrodigitalis*), full analyses completed without error messages and converged reliably only for *Nucella* spp., *P. polymerus*, *S. compressa*, and *T. rubescens*. Command lines are given in Appendix C.

Species comparisons

Using network and phylogenetic analyses to help distinguish species, and τ and t_{MRCA} to estimate divergence times, coupled with information on geographic distributions of clades, we identified pairs of SDC species to test hypotheses H_0 and H_1. For H_1, we estimated the influence of long-term effective population size, modern N_c, F, and PD on F_{ST} by calculating the slope of the line connecting pairs of SDC species. We also explored evidence for general relationships involving all species by regressing each explanatory variable against our empirical estimates of population genetic structure using Statistica v.7.1 (Statsoft, Tulsa, Arizona, USA).

Results

N_c

Published abundances of each species may vary manyfold (e.g., Sanford and Swezey 2008), but maximum density is of similar magnitude across most species, i.e., several hundreds of individuals per square meter (Table 2). The PISCO marine intertidal community surveys show significant heterogeneity among species in both percent cover (median test, $\chi^2 > 87.53$, $df = 7$, $P < 0.0001$) and N_c (median test, $\chi^2 > 67.91$, $df = 7$, $P < 0.0001$), although 43% of post-hoc pairwise comparisons are non-significant ($P > 0.05$; 63% after correction for multiple tests). The significant pairwise differences are attributable to three species: *N. emarginata* and *S. compressa* occur at lower abundances than all other species except *N. ostrina*, whereas *L. scabra* occurs at higher abundance than all other species except *N. ostrina*

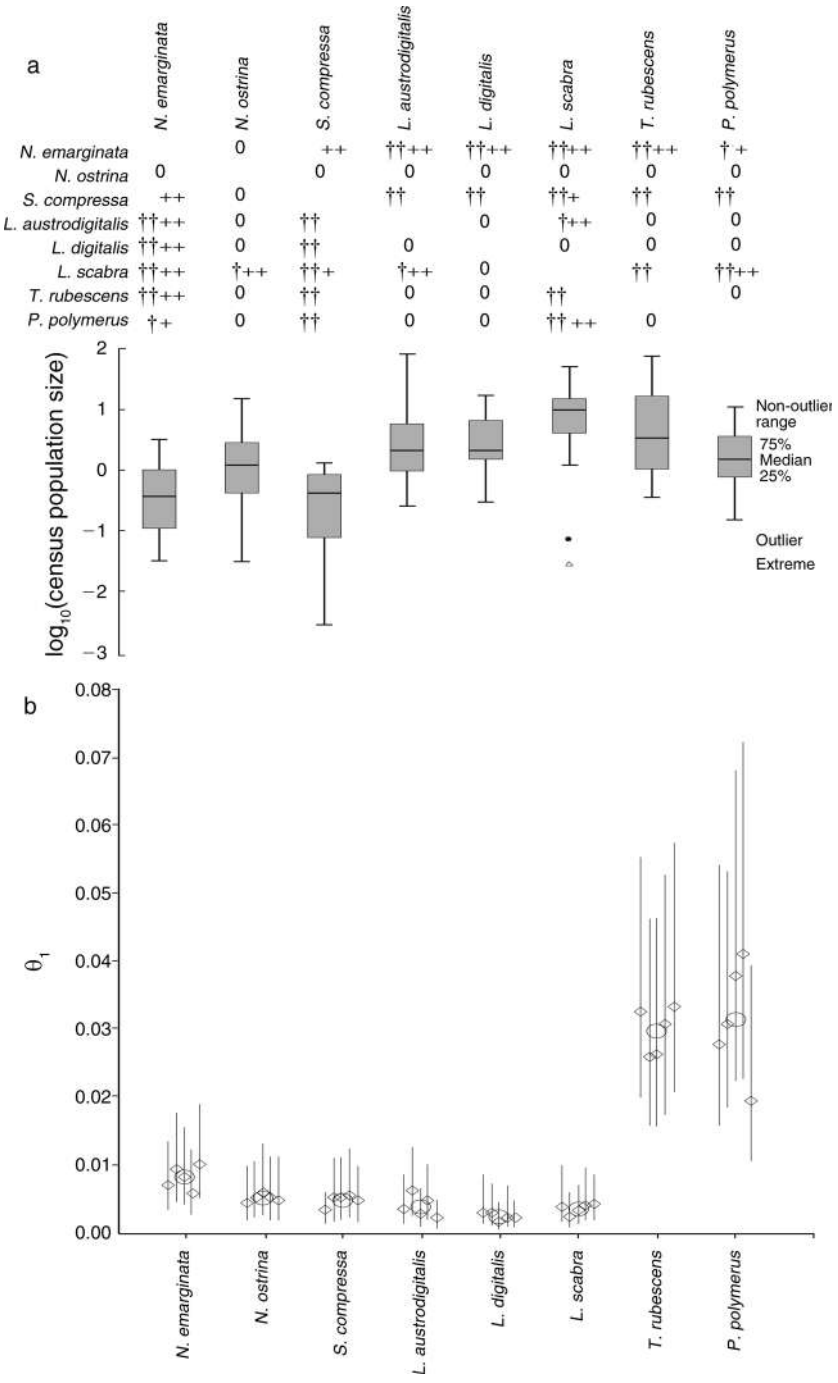

FIG. 2. Estimates of population sizes of *Nucella emarginata*, *N. ostrina*, *Silvetia compressa*, *Lottia austrodigitalis*, *L. digitalis*, *L. scabra*, *Pollicipes polymerus*, and *Tetraclita rubescens*. Box plots in panel a show log-transformed census population sizes of the seven mobile invertebrates measured using a stratified quadrat design, and estimated for *S. compressa* from percent cover data adjusted for mean macrophyte size. Zero abundances are not included in the box plots (data are provided in Appendix B). Statistical significances of pairwise comparisons are indicated above the box plots, as follows: 0 indicates no statistical difference, daggers indicate data including zero abundances (†† $P < 0.05$ after sequential Bonferroni correction for multiple tests, † $P < 0.05$ without correction), pluses indicate data excluding zero abundances (++ $P < 0.05$ after sequential Bonferroni correction for multiple tests, + $P < 0.05$ without correction). Panel b shows mean effective population sizes at the end of expansion, $\theta_1 = 2N_e\mu$, where population size (N_e) is modified by mutation rate μ in a haploid genome. 95% CI were estimated using Lamarc software (Kuhner 2006); replicate estimates were calculated using five randomly chosen subsets of 25 sequences. Proportionality of estimates depends on an even sex ratio in all species; this assumption must be true for the synchronous hermaphroditic barnacles, which are non-selfing (Charnov 1987, Newman and Abbott 1980, Kelly et al. 2012), but may be incorrect for *Nucella* spp. (Spight and Emlen 1976) and *Lottia* spp. (Seapy 1966) in which males may outnumber females by less than 2:1 (see also Niu and Fuji 1989).

and *L. digitalis* (Fig. 2). When zero abundances are excluded, only *N. emarginata* and *L. digitalis* remain statistically distinct.

Gene tree and network analyses

Statistical parsimony haplotype networks and maximum likelihood gene trees revealed distinct patterns of genetic diversity. The lottiid limpets each had two very common haplotypes, whereas *Nucella* spp. and *S. compressa* were characterized by greater genetic evenness; barnacles contained many haplotypes each at low frequency (Fig. 3). The networks and trees also illustrated differences in the geographic distributions of genetic diversity. The common haplotypes in each lottiid species showed partially overlapping parapatric distributions, whereas in *Nucella* spp. and *S. compressa* a high proportion of haplotypes occurred at only one site; in contrast, there was no clear relationship between lineages and geography in the barnacles.

Genetic diversity, population genetic structure, and historical demography

The lottiid limpets were characterized by moderate gene diversity (0.600–0.651), whereas the putatively low- and high-dispersal taxa all had high gene diversity (>0.865; Table 3). Nucleotide diversity was low (0.0027–0.0031) in putatively low and medium dispersers, moderate (0.0042–0.0063) in putatively low, medium, and high dispersers, and high in *P. polymerus* (0.0083). Thus, genetic diversity may vary by PD, albeit non-linearly.

Coalescent analyses recovered two broad categories of effective population size: lower in all gonochoric invertebrates ($\theta_1 < 0.01$) and higher in the simultaneously hermaphroditic non-selfing barnacles ($\theta_1 \approx 0.03$; Fig. 2b). For the monoecious *S. compressa*, $\theta_1 < 0.01$.

Values of ϕ_{ST} and D_{EST} reveal clear and consistent quantitative differences in population genetic structure among species, implicit in the networks and gene trees. The two statistics differ in absolute value, but are highly correlated: mean ϕ_{ST} vs. median ϕ_{ST} has $r = 0.975$ ($P < 0.01$), mean ϕ_{ST} vs. D_{EST} has $r = 0.992$ ($P < 0.01$), and median ϕ_{ST} vs. D_{EST} has $r = 0.955$ ($P < 0.01$). Thus, both ϕ_{ST} and D_{EST} show the same trend: comparatively strong population genetic structure (mean or median ϕ_{ST} and $D_{EST} > 0.7$) in *Nucella* spp. and *S. compressa*, generally moderate population differentiation in the lottiids ($0.5 > \phi_{ST}$ and $D_{EST} > 0.05$), and relatively weak or zero differentiation in the barnacles (ϕ_{ST} and $D_{EST} < 0.1$; Fig. 4). Concomitantly, global coefficients of migration estimated using IMa2 were lower for species with low dispersal potential (*N. emarginata*, $m = 0.074$ [95% CI 0.03–0.14]; *N. ostrina*, $m = 0.080$–0.096 [95% CI 0.030–0.206]; *S. silvetia*, $m = 0.116$–0.136 [95% CI 0.038–0.050]) and higher for species with high dispersal potential (*T. rubescens*, $m = 0.345$–0.460 [95% CI 0.233–0.592]). A table of results is provided in Appendix C.

The Ewens-Watterson test provided no evidence of deviations from neutrality or population equilibrium, although Tajima's *D* and Fu's *F* are consistent with population expansion, selection, or admixture in *L. austrodigitalis*, *T. rubescens*, and *P. pollicipes* (Table 4). Bayesian Skyride analyses of *L. austrodigitalis*, *L. digitalis*, *T. rubescens*, and *P. polymerus* (the four taxa for which analyses ran reliably, results not shown) support these inferences. Expansion of these taxa was also supported, or at least not strongly refuted, by the mismatch distributions and Harpending's raggedness index, although all lottiids, including *L. austrodigitalis*, had bimodal mismatch distributions (Fig. 5; Table 5). These mismatch distribution analyses provided strong probabilistic refutation of population expansion only for *S. compressa* ($P = 0.0003$), although tests of almost all species were somewhat mixed and marginally significant or non-significant for $\alpha = 0.05$. Comparison of θ_0 and θ_1 under the hypothesis of a demographic expansion were consistent with some increase in population size in all taxa, with expansion initiating approximately $0.30 < \tau < 0.40\%$ (*N. ostrina* and *S. compressa*), $0.50 < \tau < 0.6\%$ (*L. austrodigitalis*, *L. digitalis*, and *T. rubescens*) or $0.80 < \tau < 0.95\%$ (*N. emarginata*, *L. scabra*, and *P. polymerus*; Fig. 6a) before present, although variance often was high. Bayesian estimation of the t_{MRCA} recovered two groups, lower in the barnacles ($t_{MRCA} < \sim 0.005$) and higher in the remaining taxa ($t_{MRCA} \approx 0.010$; Fig. 6b).

Species comparisons

The effects of modern N_c, long-term effective population size, *F*, and PD on the ϕ_{ST} values of SDC species

→

FIG. 3. Cytochrome *c* oxidase subunit I (COI) gene trees for the study taxa. For the putative low- and medium-dispersal taxa, haplotype networks illustrate the allelic diversity (number of circles), frequency (area of circles, range $n = 1$–215; small empty circles represent unsampled haplotypes), source locations (colors and patterns; see key, bottom left), and number of nucleotide differences (branch length; each branch between any two shapes represents a single nucleotide substitution). All networks are drawn to the same scale. For the putative high-dispersal taxa, maximum likelihood trees (one of 16 different trees recovered by 16 searches) illustrate the geographic distribution of alleles according to a simplified color scheme (dark blue represents sites OREcT, ORBCL, ORBHC, DCDN, and SCH; blue represents sites BRS, BPM, PPSM, and PLM; turquoise represents sites CamSLO, HSLO, BHSB, and AHSB; orange represents sites PCLA, CCO, and BRSD; red represents sites Buf and Cho; dark gray represents sites CHSMI, CPSMI, LoSRI, JLSRI, FPSCI, WSCI, MAI, and FCAI; light gray represents BRCI, LHCI, LCSBI, SLRSBI, TSSNI, and MPSNI; black represents internal or shared terminal branches). Bootstrap support was low in the *T. rubescens* tree (only seven branches with ≥80% support included clades of 2–5 taxa) and *P. polymerus* tree (only four branches with ≥80% support included clades of 3–9 taxa; all deep internal branches in the displayed trees received <50% support).

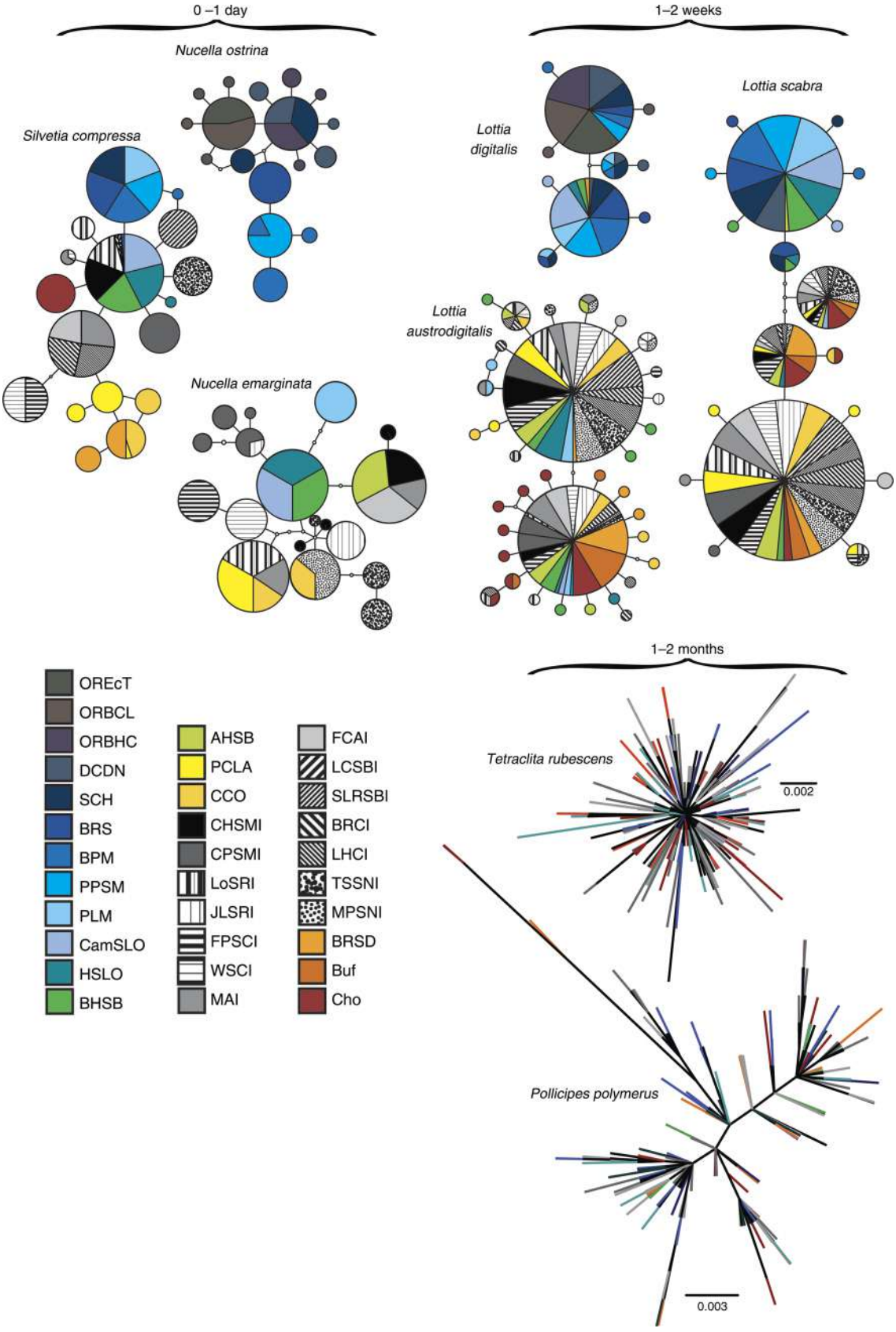
0 –1 day
Nucella ostrina
Silvetia compressa
Nucella emarginata
1–2 weeks
Lottia digitalis
Lottia scabra
Lottia austrodigitalis
1–2 months
Tetraclita rubescens
0.002
Pollicipes polymerus
0.003
OREcT
ORBCL
ORBHC
DCDN
SCH
BRS
BPM
PPSM
PLM
CamSLO
HSLO
BHSB
AHSB
PCLA
CCO
CHSMI
CPSMI
LoSRI
JLSRI
FPSCI
WSCI
MAI
FCAI
LCSBI
SLRSBI
BRCI
LHCI
TSSNI
MPSNI
BRSD
Buf
Cho

TABLE 3. Number of sequences (n_s), haplotype richness (n_a), amplicon length (no. nt), pairwise sequence distance (psd), percentage of psd, and haplotype diversity (h), calculated using the Jukes-Cantor model of nucleotide substitution.

Species	n_s	n_a	no. nt	psd	Percentage of psd ($\pi \times 100$)	h
Nucella emarginata	253	18	655	4.097 ± 2.049	0.63 ± 0.31	0.8805 ± 0.0086
Nucella ostrina	115	17	655	2.043 ± 1.156	0.31 ± 0.18	0.8650 ± 0.0142
Silvetia compressa	343	19	680	2.001 ± 1.131	0.29 ± 0.17	0.8779 ± 0.0084
Lottia austrodigitalis	326	36	462	1.302 ± 0.816	0.28 ± 0.18	0.6167 ± 0.0202
Lottia digitalis	137	10	462	1.225 ± 0.784	0.27 ± 0.17	0.5999 ± 0.0246
Lottia scabra	417	18	524	2.208 ± 1.223	0.42 ± 0.23	0.6510 ± 0.0182
Tetraclita rubescens	402	267	1232	6.366 ± 3.024	0.52 ± 0.25	0.9946 ± 0.0010
Pollicipes polymerus	476	234	658	5.474 ± 2.639	0.83 ± 0.40	0.9769 ± 0.0031

Notes: The variable π represents nucleotide diversity. Values are mean ± SD. Amplicon length is measured in number of nucleotides.

are shown in Fig. 7. Population genetic structure was consistently related to F, $\log_{10}(\phi_{ST}) \propto -0.385F$ to $-1.328F$, and PD, $\log_{10}(\phi_{ST}) \propto -0.025$PD to -0.064PD, whereas the relationship between population genetic structure and N_c was more variable, $\log_{10}(\phi_{ST}) \propto -0.029N_c$ to $-0.435N_c$, and in opposite direction to its relationship with long-term effective population size, $\log_{10}(\phi_{ST}) \propto 163N_e$–$278N_e$. Regressions involving all co-distributed species, of which the majority are synchronously diverging (Fig. 6), generally confirmed patterns seen in comparisons of species pairs. The relationship of ϕ_{ST} to population size was weak or nonsignificant. In contrast, the slope and strength of regressions of ϕ_{ST} against F (e.g., $\log_{10}(\phi_{ST}) = -0.623F - 2.794$, $R^2 = 0.83$, $P < 0.01$ [power to reject the hypothesis of no correlation, one-tailed test, refined Fisher $Z_{r,\alpha,N} = 0.98$, for $r = 0.91$, $\alpha = 0.05$, $N = 8$]) and against PD (e.g., $\log_{10}(\phi_{ST}) = -0.045$ d $- 0.039$, $R^2 = 0.98$, $P < 0.01$ [$Z_{0.99,0.05,8} = 1.00$]) are highly similar to those calculated for each species pair, ($\log_{10}(\phi_{ST}) \propto -0.385F$ to $-1.328F$, $\log_{10}(\phi_{ST}) \propto -0.025$PD to -0.064PD. The covariance structure among the predictor variables is described in Appendix D.

DISCUSSION

Comparisons of sympatric sister species play important roles in biogeography and phylogeography because they ensure that comparisons are made between taxa that are the same age, evolutionarily independent, and affected as little as possible by the dual, and often confounded, histories of lineage and region (Lynch 1989, Dawson et al. 2002). Comparisons of SDC species (i.e., species with statistically similar t_{MRCA} that are broadly sympatric) should yield many of the same benefits of sympatric sister taxon analyses (Dawson 2012), while also reducing the problems of limited sample size and extinction that can limit the power of sister-taxon comparisons (Rosenzweig 1996, Marko 2002).

Our analyses of eight northeastern Pacific intertidal taxa revealed four pairs of SDC species: (1) the snails *N. ostrina* and *L. digitalis*, $t_{MRCA} \approx 0.010$–0.011 mbp (mutations before present), range predominantly >37° N), (2) the alga *S. compressa* and *L. scabra*, $t_{MRCA} \approx 0.010$ mbp, range ~30–41° N, (3) *N. emarginata* and *L. austrodigitalis*, $t_{MRCA} \approx 0.010$–0.013 mbp, range 33–37° N, and (4) the barnacles *T. rubescens* and *P. polymerus*, $t_{MRCA} \approx 0.003$–0.005 mbp, range 26–40° N (see Tables

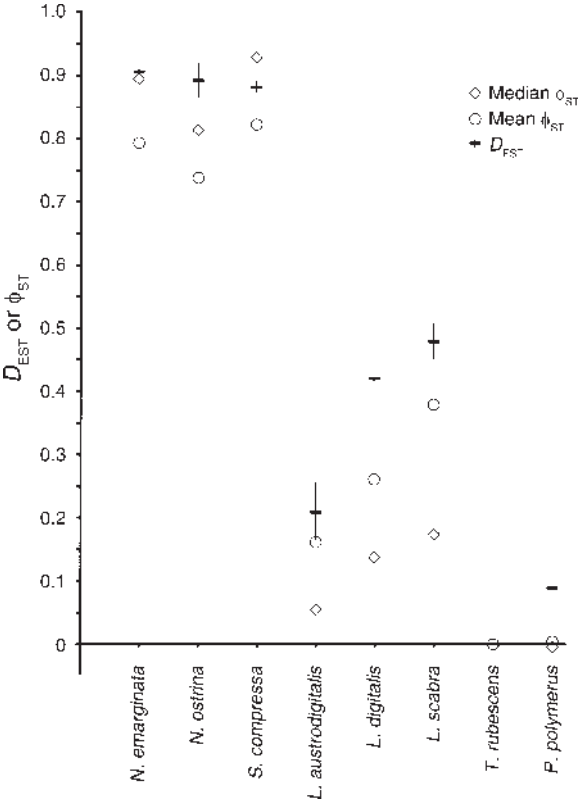

FIG. 4. Genetic estimates of population subdivision. Mean and median ϕ_{ST} (circle and diamond, respectively) and Jost's D_{EST} ± 95% CI (horizontal line with error bars, calculated via percentile method [Jost 2008]). Note that for *T. rubescens*, an adjusted non-negative D_{EST} ± 95% is shown (0.00 ± 0.00). Excluding small samples (*L. austrodigitalis* at sites CamSLO, PPSM, and PLM; *L. digitalis* at sites BRSD, BHSB, HSLO, and PLM) from calculations of ϕ_{ST} generates similar values as those that are plotted: *L. austrodigitalis* mean $\phi_{ST} = 0.16$, median $\phi_{ST} = 0.04$; *L. digitalis* mean $\phi_{ST} = 0.32$, median $\phi_{ST} = 0.33$.

TABLE 4. Tests of neutrality and population equilibrium; Ewens-Watterson homozygosity (EW), Tajima's D, and Fu's F.

Species	EW observed F	EW expected F	P	D	P	Fu's F	P†
N. emarginata	0.12300	0.18499	0.1134	0.00305	0.5759	−0.06478	0.5632
N. ostrina	0.14253	0.15967	0.4474	−0.74904	0.2574	−5.99317	0.0246
S. compressa	0.12463	0.18783	0.1270	−0.48289	0.3742	−4.96302	0.0834
L. austrodigitalis	0.38515	0.09016	1.0000	−2.08002	0.0005	−28.08617	<0.0001
L. digitalis	0.40444	0.29017	0.8686	−0.05855	0.2342	−2.50017	0.1516
L. scabra	0.35060	0.20801	0.9417	−0.57363	0.3238	−3.04422	0.2054
T. rubescens	0.00791	0.00535	1.0000	−2.53056	<0.0001	−24.47782	0.0009
P. polymerus	0.02510	0.00754	1.0000	−2.21503	0.0002	−24.63048	0.0003

† Significant at 5% if $P < 0.02$.
Note: The quantity F in EW observed and expected F is equal to the sum of squared allele frequencies.

2, 5 and Figs. 5, 6). Notably, the third group is synchronous and, throughout its entire range, sympatric with the second group, potentially allowing a wider range of comparisons. By removing variation in time and environment, and also study design (Dawson 2014), we can use these pairs to ask whether species with similar dispersal potential have similar population genetic structure (H_0), and whether species with greater dispersal potential have weaker population genetic structure (H_1).

Comparing SDC taxa of similar dispersal potential (H_0)

Recent empirical results suggest that, like sympatric sister taxa, SDC species should have similar phylogeographic structure if they have similar dispersal potential, i.e., similar habitats, life-histories, and fecundities (Dawson 2012); similar population sizes also are required to meet the expectation of similar population genetic structure (see Marko and Hart 2011). This null hypothesis of phylogeography is supported by our analyses of the barnacles *T. rubescens* and *P. pollicipes*, which have PDs of 1–2 months, habitats that include the mid-intertidal, high per capita fecundities (3000–150 000 per year and 300 000–1 700 000 per year, respectively), statistically similar effective population sizes (and also statistically similar N_c), and very low population genetic structure ($D_{EST} < 0.09$, $\phi_{ST} = 0$). Although these barnacles differ in PD, both species have planktonic developmental periods approximately ≥25 d, which appear to be sufficient to homogenize populations over many hundreds of kilometers (Doherty et al. 1995, Selkoe et al. 2010).

The null hypothesis may also be supported by two comparisons between species in the second and third groups. First, *N. emarginata* and *S. compressa* have PDs of 0–1 d, overlap in the mid-intertidal, F of several hundred (*N. emarginata*) to several thousand (*S. compressa*) offspring, and statistically similar effective population sizes (and N_c when zero abundances are excluded). Both species also show very high population genetic structure ($0.88 < D_{EST} < 0.91$, $0.89 < \phi_{ST} < 0.93$); the slightly lower F in *N. emarginata* is conceptually compatible with fewer migrants and thus slightly higher population differentiation (Fig. 4). Second, *L. austrodigitalis* and *L. scabra* have PDs of 1–2 weeks, overlap in the high intertidal, F of approximately 5000 to 45 000 per year, statistically similar effective population sizes (and also statistically similar N_c), and moderate population genetic structure ($0.21 < D_{EST} < 0.48$, $0.06 < \phi_{ST} < 0.17$).

Of the three species pairs, the comparison of *L. austrodigitalis* with *L. scabra* provides the weakest support for the null expectation due to the observed differences in D_{EST} (or ϕ_{ST}). However, the values of D_{EST} and ϕ_{ST} for *L. austrodigitalis* are probably underestimates of population subdivision, because genetic similarities among locations may be attributable to a high proportion of ancestral alleles due to recent population expansion (Fu's $F = -28.1$, $P < 0.0001$; Table 4) rather than contemporary gene flow.

Thus, two, and possibly all three, pairs of SDC species with similar dispersal potential have quantitatively similar levels of population genetic differentiation. This result supports the null expectation of phylogeography when environmental structure is present (H_0) and provides a rational basis for interpreting dissimilar dispersal potential of SDC species as a cause of observed differences in F_{ST}.

Comparing SDC taxa with different dispersal potential (H_1)

Species sharing a common evolutionary history of time and place, but characterized by different dispersal potentials, should also differ in terms of migration, gene flow, and population genetic structure. The expected effect of differences in migration on population genetic structure can be estimated from the relationship $F_{ST} \approx 1/(4N \times m + 1)$, where N is the population size and m the coefficient of migration (the proportion of a population that is immigrant). Deviations from the expected relationship may reflect selection, mutation, population size differences, nonrandom gene flow, and disequilibrium (Whitlock and McCauley 1999), as well as errors in estimating N and m; however, such estimates are still considered worthwhile in the absence of rigorous demonstration that they are invalid (Karl et al. 2012, Vrijenhoek and Waples 2012). Moreover, of the SDC species that we use to test H_1, all are absent a signature

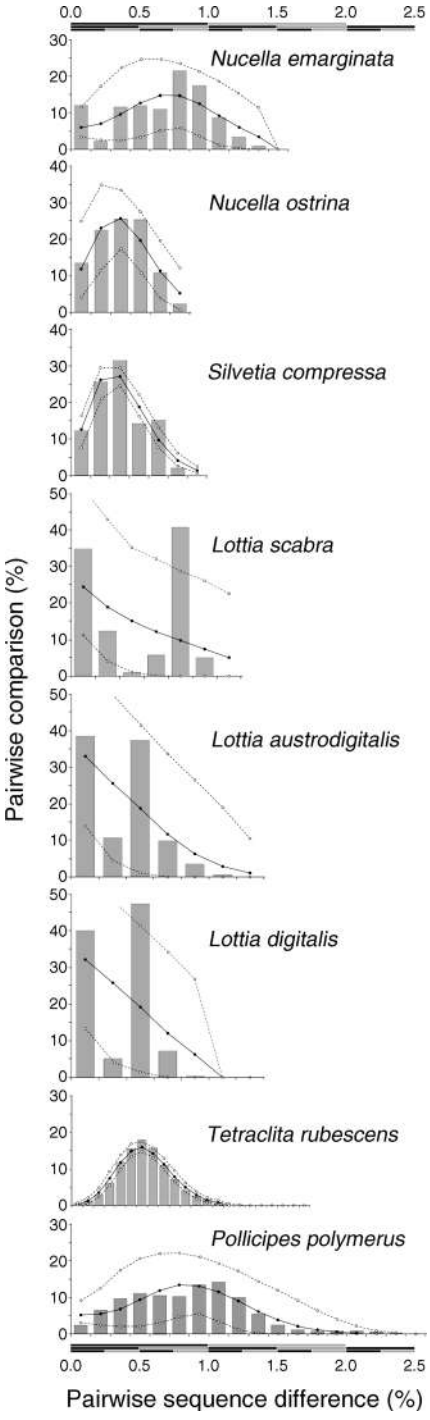

FIG. 5. Mismatch distribution estimates from which demographic histories, including mutational time since most recent expansion (τ), were inferred. The abscissa is scaled as percentage of sequence difference to account for differences in marker size; each interval represents one pairwise nucleotide difference. Points along lines correspond to intervals, dark line shows mean with dashed lines representing 95% CI. Additional details are presented in Table 5.

of selection, five of six show no significant deviation from stable population size, and (notwithstanding intraspecific variation between samples) a majority have statistically similar N_c and N_e. Thus, for these species-level comparisons, we consider F_{ST} a useful first approximation of Nm, the number of migrants per generation, which for marine benthic organisms is potentially affected by the number of reproductive adults and their fecundity in the source population, and the size of the population into which propagules recruit; *m* also is potentially affected by PD.

We can compare the predicted and actual effects of dispersal potential, as a function of *F*, N_c, and PD, on population genetic structure using three pairs of SDC species: (1) *N. ostrina* and *L. digitalis*, (2) *S. compressa* and *L. scabra*, and (3) *N. emarginata* and *L. austrodigitalis*. Although *T. rubescens* and *P. polymerus* also meet the criteria for comparison within our framework, their ubiquitously high inferred gene flow prevents any putative effect of differential migration being resolved using our data set.

N. ostrina and L. digitalis.—Census and effective population sizes are statistically indistinguishable between these species (Fig. 2), and thus should not contribute to differences in gene flow. The expected lifetime reproductive output of a *N. ostrina* (mature for ~8 yr, annual $F \sim 700$ larvae) is approximately four to 20 times less than the expected lifetime reproductive output of a *L. digitalis* (mature for perhaps 4–5 yr, annual $F \sim 5000$–$20\,000$ larvae; Table 2). The PD of *N. ostrina* larvae is zero, but pelagic dispersal may occur after dislodgement of post-metamorphic snails (Martel and Chia 1991). If we assume that the median dispersal duration of *N. ostrina* is perhaps several orders of magnitude less than the PD of *L. digitalis*, an error of one or two orders of magnitude has little impact on the calculated value of Nm when the duration for *N. ostrina* is so small (see Doherty et al. 1995). The ratio of migrants calculated from measured ϕ_{ST} for *N. ostrina*:*L. digitalis* is $0.057/1.588 = 0.036$, roughly a 28-fold difference in the number of migrants per generation. Thus, the expected effects of differences in *F* and PD on migration are large enough to explain the observed differences in population genetic structure (Table 6).

S. compressa and L. scabra.—The effective population sizes of these species are statistically indistinguishable, although the N_c of *S. compressa* estimated from percent cover is roughly 1/10 the N_c of *L. scabra*. The expected lifetime reproductive output of a *S. compressa* (mature for up to seven or more years, annual $F \sim 4000$–$40\,000$ zygotes) is approximately the same magnitude as, or up to ~40-fold more than the expected lifetime reproductive output of a *L. scabra* (likely mature for a similar number of years, with annual $F \sim 5000$–$50\,000$ larvae). The PD of *S. compressa* is probably between 1/10 and 1/100 of the PD of *L. scabra*. The ratio of migrants calculated from measured ϕ_{ST} for *S. compressa*:*L. scabra* is $0.019/1.210 = 0.015$, an approximately 63-fold

TABLE 5. Estimates of parameters describing possible demographic expansions estimated from mismatch distributions (Fig. 5).

Species	θ_0	τ	θ_1	Mean	Variance	GoF	*P*	HRI	*P*
N. emarginata	0.002 (0–2.304)	5.328 (2.172–8.049)	16.406 (9.449, inf)	4.097	5.104	0.0161	0.0568	0.04153	0.0517
N. ostrina	0.009 (0–1.085)	2.324 (1.061–3.348)	31.172 (5.635, inf)	2.043	1.661	0.0043	0.1837	0.03784	0.502
S. compressa	0 (0–0.125)	2.072 (1.822–2.43)	inf (19.352, inf)	2.001	1.660	0.0077	0.0050	0.06905	0.0003
L. austrodigitalis	0 (0–0.396)	2.43 (0–5.408)	2.244 (0.859, inf)	1.302	1.421	0.0609	0.1394	0.22538	0.09
L. digitalis	0 (0–0.696)	2.369 (0–4.957)	2.349 (0.969, inf)	1.225	1.134	0.1344	0.0767	0.46601	0.0176
L. scabra	0 (0–2.299)	4.953 (0–54.619)	3.113 (1.368, inf)	2.208	3.647	0.1374	0.0518	0.31632	0.0192
T. rubescens	0.002 (0–0.366)	6.324 (5.76–6.721)	inf (142.906, inf)	6.366	6.425	0.0010	0.0255	0.01191	0.0292
P. polymerus	0.271 (0–2.343)	6.062 (2.93–9.262)	19.213 (11.805, inf)	5.474	9.247	0.0043	0.4094	0.00899	0.7408

Notes: The parameters θ_0 and θ_1 are estimates of the effective population sizes, scaled by the mutation rate ($\theta = N_e\mu$), at the beginning and end (or present day) of the hypothesized demographic expansion, respectively. Demographic expansion, τ, is given in terms of the number of observed mutational differences, i.e., not corrected for length of amplicon (given in Table 3). Values in the first three columns are means with 95% CI in parentheses. For θ_1 column, inf stands for infinite. Observed mean and variance refer to the mean and variance of the mismatch distributions. Goodness of fit test statistic (GoF; sum of squared deviations) is shown with predicted distributions if there had been a single rapid demographic expansion and the associated *P* value. HRI shows Harpending's raggedness index and associated *P* value.

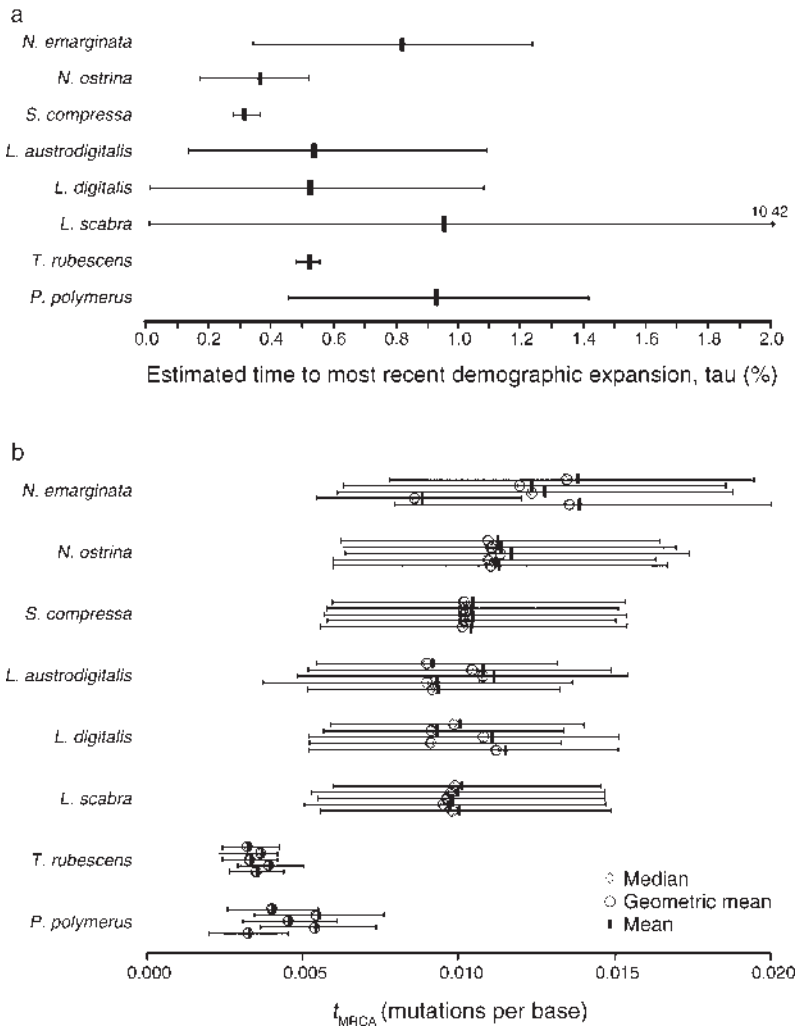

FIG. 6. Durations of evolutionary histories inferred from genetic data. Panel a shows timing of the most recent demographic expansion (τ), represented as the percentage of mutations per base sequenced, with 95% confidence intervals estimated using Arlequin software (Excoffier and Lischer 2010). Panel b shows time to the most recent common ancestor, t_{MRCA}, of each species, with 95% CI estimated using BEAST software (Drummond and Rambaut 2007); replicate estimates were calculated using five randomly chosen subsets of 50 sequences.

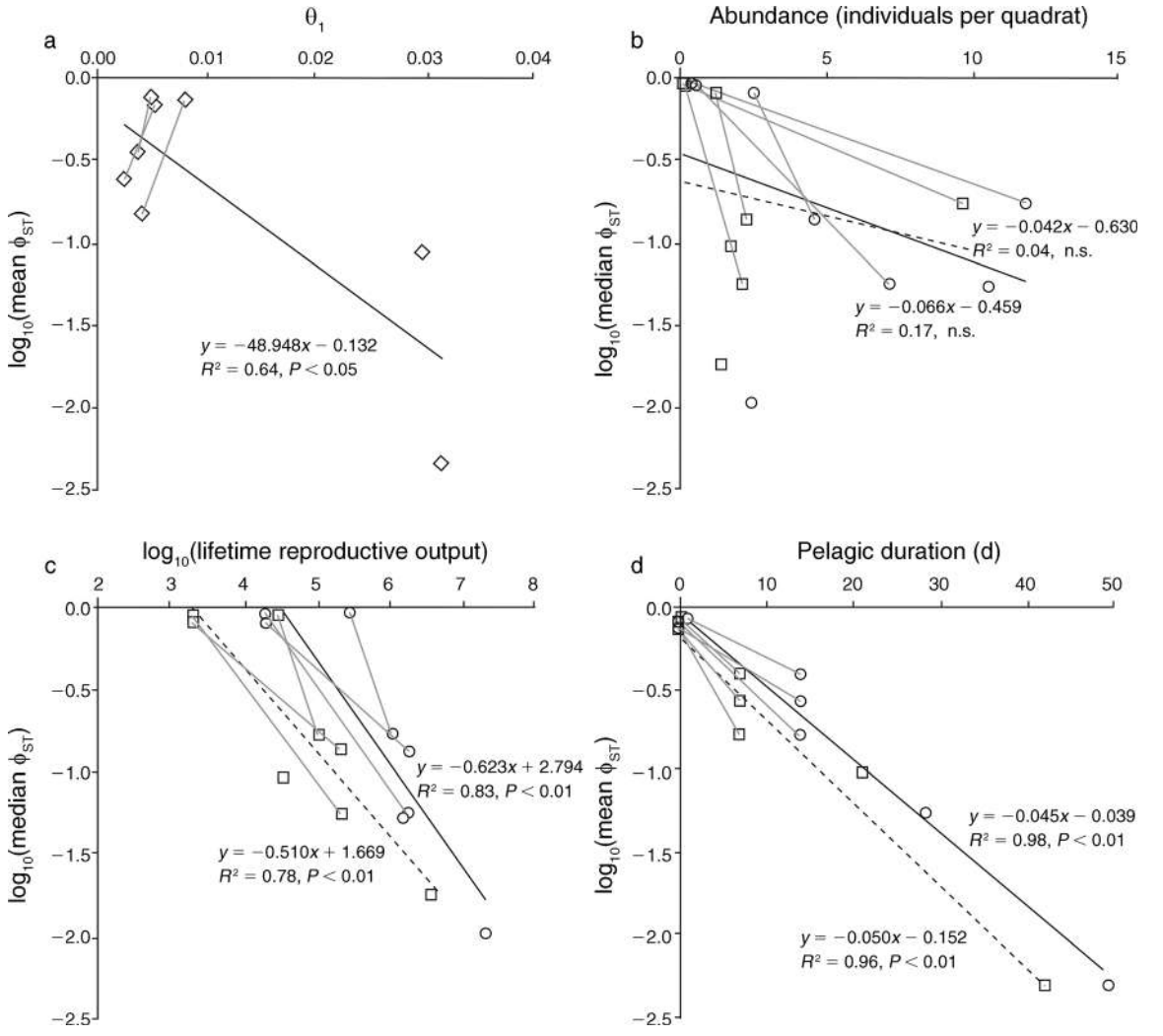

FIG. 7. Effects of population size (effective and census sizes, N_e and N_c, respectively), fecundity (F), and pelagic duration (PD) on population genetic structure (ϕ_{ST}). In all figures, light gray lines join pairs of synchronously diverging co-distributed (SDC) species. The slopes of these lines are (a) $\log_{10}(\phi_{ST}) \propto 163N_e$ to $278N_e$, (b) $\log_{10}(\phi_{ST}) \propto -0.029N_c$ to $-0.435N_c$, (c) $\log_{10}(\phi_{ST}) \propto -0.385F$ to $-1.328F$, and (d) $\log_{10}(\phi_{ST}) \propto -0.025$PD to -0.064PD. In addition, the line of best fit, with associated statistics, is plotted for data sets composed of all eight species for (a) median θ_1, i.e., N_e scaled by μ, (b) N_c including zero abundances, where squares indicate median population size and circles indicate mean, (c) lifetime reproductive output, i.e., years of maturity × annual F, where squares indicate minimum output and circles indicate maximum, and (d) PD, where squares indicate minimum duration and circles indicate maximum. Dashed lines show best fit as calculated using minimum estimates (represented by squares), solid dark lines show best fit as calculated using maximum estimates (represented by circles). The mean or median ϕ_{ST} is shown, according to which gave the better quantitative fit, although both were highly correlated and gave the same qualitative result. Observed $\phi_{ST} < 0$ for *T. rubescens* and *P. pollicipes* were plotted by estimating ϕ_{ST} based on the regression from Doherty et al. (1995), $F_{ST} = -0.043d - 0.315$, where F_{ST} represents the fixation index; alternately plotting these observed values as $\log_{10}(\phi_{ST}) = -2$ or -3 changed the relationships a small degree, ranging from $y = -0.044x - 0.010$, $R^2 = 0.86$, to $y = -0.079x - 0.180$, $R^2 = 0.84$. Power to reject no correlation is shown for (a) refined Fisher $Z_{0.80,0.05,8} = 0.85$ and (b) $Z_{0.41,0.05,8} = 0.28$; details of the power analysis with values for (c) and (d) is given in *Results*. In panel b, n.s. stands for nonsignificant. Covariances among predictor variables are described Appendix C.

difference in the number of migrants per generation. Thus, the expected effects of differences in N_c, PD, and F on migration can account for the observed differences in population genetic structure (Table 6).

N. emarginata and L. austrodigitalis.—The estimated effective population size of *N. emarginata* is twice the effective population size of *L. austrodigitalis*, whereas the N_c of *N. emarginata* is 1/10 the N_c of *L. austrodigitalis*. The expected lifetime reproductive output of a *N. emarginata* (mature for ~8 yr, annual F ~700 larvae) is approximately fourfold to 40-fold less than the expected lifetime reproductive output of a *L. austrodigitalis* (as *L. digitalis* above, presumed mature for 4–5 yr, annual F ~5000–42 000 larvae). The PD of *N.*

TABLE 6. Numbers of migrants per generation, Nm, calculated from census population size (N_c), fecundity (F), and PD of pairs of synchronously diverging co-distributed species.

Species pair	Relative N_c	Relative Nm estimated from PD	Relative annual F	Range of cumulative estimated potential differences in Nm	Empirically inferred relative magnitude of Nm, inferred from ϕ_{ST}
N. ostrina–L. digitalis	1	4.2–4.3	4–20	16.8–86	28
S. compressa–L. scabra	1–10	3.6–4.2	3.6–36	13.0–1512	63
N. emarginata–L. austrodigitalis	1–20	4.2–4.3	4–40	16.8–3440	144

Notes: All numbers show Nm for the higher disperser as a factor of the values for the lower disperser. N_c and F are used as direct estimates of Nm (in these calculations, m is considered to be constant). For PD, Nm is calculated from PD using the fixation index, F_{ST}, and the regression of Doherty et al. (1995); $F_{ST} = -0.043d - 0.315$ followed by $Nm = (1/F_{ST} - 1)/4$. Although concerns are frequently voiced regarding the effects of nonequilibrium dynamics on estimation of Nm from F_{ST}, a majority of our SDC species meet a majority of the relevant assumptions, and so we consider F_{ST} a useful first approximation of Nm (see also Karl et al. [2012], Vrijenhoek and Waples [2012]). The cumulative effect on Nm, as the product of the effects of N_c, F, and PD, brackets the empirically inferred difference, calculated from measurements of population genetic structure (ϕ_{ST}).

emarginata larvae is zero, but once again, pelagic dispersal may be greater than zero due to post-metamorphic dispersal (Martel and Chia 1991); for the purposes of this discussion we assume that the median dispersal duration of *N. ostrina* is several orders of magnitude less than the PD of *L. austrodigitalis*. The ratio of migrants calculated from measured ϕ_{ST} for *N. emarginata* : *L. austrodigitalis* is $0.030/4.284 = 0.007$, i.e., a 144-fold difference in the number of migrants per generation. Thus, the expected effects of combined differences in N_c, F, and PD on migration can explain the observed differences in population genetic structure (Table 6).

Taken together, the combined differences in F, N_c, and PD are sufficient to account for the differences in population genetic structure for all pairs of SDC species in this study. The effects of N_e, N_c, F, and PD on population genetic structure, however, are not proportional to their potential effects on migration (Table 6). Long-term effective and modern N_c is an unreliable or poor predictor of differences in population genetic structure (Fig. 7). N_c is positively related to population genetic structure, consistent with the predicted effect of N_c on migration, but the relationship is highly variable among species pairs, possibly reflecting variable recruitment and differing demographics (Fig. 7; Thorson 1950). Thus, our genetic estimates of effective population size, which most strongly reflect historically low abundances, are negatively related to population genetic structure, a relationship that is consistent with the expectation that less vagile species will have more stable local population sizes through time due to more consistent self-recruitment (Thorson 1950). In contrast, plots of ϕ_{ST} against F and PD for each species pair suggest that the production of dispersive propagules and the duration that they spend as plankton or plankto-nekton are reliable predictors of differences in population genetic structure among these species in this region (Fig. 7; see also Treml et al. 2012). Moreover, the strong correlation of ϕ_{ST} with F and PD across all taxa indicates the relationship is robust to any error in pairing SDC species.

The magnitudes of the effects of F, and particularly PD, are strikingly consistent among species pairs, suggesting that comparisons of the effect sizes for many pairs of SDC species may be broadly informative about the causes of marine population genetic structure (Fig. 7). Moreover, all are similar to the relationship between ϕ_{ST} and PD calculated from analyses of eight species of fishes co-distributed on the Great Barrier Reef, $\log_{10}(F_{ST}) = -0.043\ d - 0.315$, $R^2 = 0.85$, by Doherty et al. (1995). Thus, in contrast to the recent inference from treat-as-one-trial analyses that PD is a poor predictor of gene flow, our study suggests that meta-analyses of effect sizes may provide evidence of a strong effect of migration on marine population genetic structure. That traits that affect migration, such as F and PD, are themselves strongly correlated across taxa (Appendix D; see also, e.g., Reaka et al. 2008) suggests that dispersal syndromes, perhaps also including behavioral and biomechanical abilities, may determine the major characteristics of population genetic structure (e.g., Clobert et al. 2009).

The effects of migration are modified by genetic drift and/or selection

The migration rate inferred from ϕ_{ST} is near the lower bound (i.e., in the second, fourth, or 25th percentile) of the range of rates inferred from differences in F, N_c, and PD (Table 6). Although Nm estimated from ϕ_{ST} (i.e., $N_e m$) is expected to underestimate $N_c m$ (Whitlock and McCauley 1999), the sex ratios in our SDC species (1–2 males : 1 female; Seapy 1966, Spight and Emlen 1976, Niu and Fuji 1989) and genetic estimates of N_e do not explain the observed bias. Rather, the consistently low estimates of gene flow, relative to potential migrants, indicate that the effect of migration is regularly attenuated by mechanisms that act more strongly on species with higher dispersal potential (e.g., Thorson 1950), and that losses of propagules may be stochastic, or due to selection in the plankton, or during or after recruitment (e.g., Johnson and Black 1982, 1984). Private alleles in island populations of *N. emarginata*, for example, suggest genetic drift associated with long-

distance dispersal. Geographic concordance of intraspecific phylogeographic structure (in *L. scabra*) with range limits of recent (*N. emarginata–N. ostrina*) and older (*L. austrodigitalis–L. digitalis*) sister species suggests that one or more long-term extrinsic environmental factors limit migration across the northern half of the California Transition Zone. Comparisons of populations throughout the ranges of co-distributed species, including across clines and at range limits shared by multiple species, should provide further insight into interactions among mechanisms of evolution, and how these vary geographically and taxonomically (e.g., García-Ramos and Kirkpatrick 1997, Hare et al. 2005, Sotka and Palumbi 2006). Analyses of SDC species also may clarify how drift, migration, and selection influence range size (Jablonski 1986), a region-specific phenomenon that treat-as-one-trial analyses also suggest is weakly influenced by PD (Lester et al. 2007).

The developing role for comparisons of SDC species

There is a growing consensus that many contemporary and historical factors can affect genetic and phylogeographic patterns in marine organisms (e.g., Marko and Hart 2011). By a priori acknowledging the influences of evolutionary time and the extrinsic environment, sympatric sister species comparisons reduce the number of factors that may confound estimation of the effects of intrinsic organismal characteristics on gene flow. Sympatric sister species comparisons, which appeared as ad hoc components of phylogeographic studies (Taylor et al. 1996, Bernatchez and Wilson 1998, Stepien et al. 2000) before being adopted as the core element of study design (e.g., Dawson et al. 2002, Bernardi 2005), however, remain rare (Steele et al. 2009); their potential to test predictions about the causes of genetic and phylogeographic structure is thus limited by sample size. Comparisons of SDC species provide the benefits of sympatric sister species analyses in a broader diversity of situations, for example, when sympatric species are not sister species, or when the sister taxon is extinct. Furthermore, because SDC species reduce the number of confounding variables, using SDC species should improve estimates of effect sizes by general linear modelling, likelihood, or Bayesian analyses. Indeed, the effects of life history differences on population genetic structure may be estimated most accurately when these techniques are applied in a specific geographic context (Selkoe and Toonen 2011; see e.g., Hare et al. 2005, Sotka and Palumbi 2006, Ilves et al. 2010, Riginos et al. 2011).

The challenge in marine evolutionary biology thus remains how to accurately characterize the varying contributions of many possible factors on genetic structure of different lineages in specific places, and also to identify generalities across taxa and regions. In this context, comparisons of SDC taxa are advantageous for several reasons. In principle, the SDC framework is applicable at a variety of taxonomic levels, for example, comparing SDC infraspecific clades as well as SDC species. To the extent that it is possible, analyses of SDC taxa employ the strengths of the control and comparative methods to estimate effect sizes (response ratios, as in Hedges et al. 1999). Moreover, SDC comparisons can be applied retrospectively to mine existing genetic data sets to better estimate the effects of differences in intrinsic organismal characteristics on gene flow. Finally, by expediting accurate estimation of intrinsic effects, SDC taxa comparisons can yield many diverse data sets with which to explore how environmental differences between regions affect gene flow. SDC species comparisons, which focus on improving knowledge of local systems, therefore pave the way toward global meta-analyses of the many interacting factors that influence marine population genetic structure.

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Supplemental Material

Appendix A

Species-specific polymerase chain reaction conditions (*Ecological Archives* M084-015-A1).

Appendix B

Relative population sizes of study species (*Ecological Archives* M084-015-A2).

Appendix C

IMa2 command lines and summary of results (*Ecological Archives* M084-015-A3).

Appendix D

Covariance structure among the predictor variables (*Ecological Archives* M084-015-A4).

Data Availability

Data associated with this paper have been deposited in GenBank (accession numbers KJ005125–KJ007519). Additional data have been deposited in the PISCO archive: http://data.piscoweb.org/DataCatalogAccess/DataCatalogAccess.html