

Genetic structure of the polychaete *Nereis grubei* in the context of current patterns and life history

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ABSTRACT: Pelagic larval duration and other life history features have been shown to affect the gene flow of marine species. Inter simple sequence repeats (ISSRs) were used to study the genetic structure of 13 putative populations of a polychaete species (Nereididae: *Nereis grubei*) in the Southern California Bight over a short geographic distance (300 km maximum). This species has a short 5 d larval duration and dies following mating (semelparous). Isolation by distance was not identified, with genetic distance high even among populations separated by short distances. Assignment tests using STRUCTURE indicated few recent immigrants within samples. Self-recruitment appears to be the norm for *N. grubei* populations within the Southern California Bight, consistent with a semelparous reproductive strategy.

KEY WORDS: Polychaete · Population genetics · Life history · Southern California Bight

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INTRODUCTION

Gene flow and genetic structuring among sessile marine invertebrates possessing pelagic larvae are dependent on several factors including habitat type, distance among available habitats, prevailing currents, and life history features. Current direction, strength, and variability are particularly important determinants of the migration potential of passively dispersed larvae (Strathmann 1985, Dawson et al. 2001). For a species and its populations to be maintained over time, mechanisms must exist to provide a balance between self-recruitment and dispersal potential among populations (see review by Byers & Pringle 2006). The stability of a population requires the ongoing settling of local progeny (Robertson 2001, Irisson et al. 2004); in contrast, the dispersing of larvae enhances the genetic diversity of populations, enables recolonization of sites following perturbations, and extends the range of a species (Slatkin 1985, Hedgecock 1986).

The length of the pelagic larval period and the timing of reproduction interact with current patterns in

dictating gene flow among populations. For example, species having short larval pelagic periods (Waples 1987, Dawson et al. 2002) or direct development (Knowlton & Jackson 1993, Kyle & Boulding 2000) or that brood their offspring (Hellberg 1996, Burton 1998, Bernardi 2000) tend to show low gene flow and higher genetic structuring relative to taxa having prolonged pelagic larval development. Likewise, if species reproduce during periods of sustained current flow, there will be a continued downstream movement of that species and eventual loss of upstream populations (Byers & Pringle 2006). Therefore, the reproductive cycle of several species has been associated with current structure favorable to enhancing self-recruitment and counter migration of dominant currents (Parrish et al. 1981, Hohenlohe 2004, Watson et al. 2010). For example, along the southern west coast of the United States, the Southern California Countercurrent has a stronger northward effect for coastal pelagic larvae during the winter months (DiLorenzo 2003, Mitarai et al. 2009). Additionally, episodic reversals of current flow, such as those that occur during El Niño events, have been

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demonstrated as extending species' ranges against the prevailing current flow (e.g. north of Point Conception in central California), modifying both community structure (Newman 1979, Seapy & Littler 1980, Blanchette et al. 2008) and phylogeography (see reviews by Burton 1998, Dawson 2001). Lastly, geographic distance as determined by availability of habitat meeting a species' niche requirements (connectivity) often impacts the genetic structuring of marine fauna (Johnson & Black 1998, Earl et al. 2010). Isolation by distance has been demonstrated for a high number of marine fauna along the west coast of the United States (e.g. Hellberg 1996, Buonaccorsi et al. 2004, Cope 2004), although not in all species studied (Chambers 2004).

The Southern California Bight (SCB) originates south of Point Conception and extends southward to the Baja peninsula. Within the SCB, the California Current carries arctic waters southward and deflects offshore at Point Conception. The Southern California Countercurrent flows poleward, carrying equatorial waters, and deflects offshore at the Palos Verdes Peninsula (Owen 1980). The Southern California Eddy rotates these differing water masses in a largely counterclockwise direction, creating eddies within the SCB (Lynn & Simpson 1987). This current structure is therefore complex and highly variable seasonally and annually and is subject to periodic El Niño and La Niña events (Hickey 1992, Browne 1994).

Many species of polychaetes of the family Nereididae, including *Nereis grubei* (Kinberg), possess several qualities that limit gene flow relative to other marine invertebrates. For example, this species has a sexually mature epitokal stage and swarms to the water surface to breed, with both sexes dying following a single mating (Clark 1977). Additionally, the pelagic larval stage is typically brief with a lecithotrophic egg. In contrast, most invertebrate taxa have multiple spawning events during their lifetimes and prolonged pelagic larval periods (weeks to months), providing for greater migration potential (Hedgecock 1986). Specifically, *N. grubei* has a relatively short lifespan of less than 1 yr (Reish 1954, Schroeder 1971) and a pelagic larval duration of 3 to 5 d in the laboratory and has been identified as becoming reproductive throughout the year in the SCB (Reish 1954).

Our goal in this study was to investigate the genetic structuring and genetic diversity of *Nereis grubei*, a wide-ranging rocky intertidal inhabitant of the coasts of North and South America, in the SCB using high-resolution techniques (inter simple sequence repeats, ISSRs). Although several studies have focused on the genetic structuring of intertidal

marine invertebrates of the southern California coastline on a regional scale using DNA sequencing (e.g. Cassone & Boulding 2006, Hurtado et al. 2010, Kelly & Palumbi 2010), little work has been performed among geographically proximal populations using high-resolution techniques (Stoner et al. 2002). With the limitations of gene flow discussed above, we predicted significant genetic structuring even among geographically proximal populations.

MATERIALS AND METHODS

Sampling

Five rocky intertidal sites and 2 Channel Islands were chosen along the southern California coast, ranging from just north of Point Conception (PTCON) to Newport Beach (NEWP) (north to south distance of 298 km; Fig. 1, Table 1). Coastal sites were chosen at immediately north and south of previously identified phylogeographic breakpoints (PTCON and Palos Verdes Peninsula [PVP]; Dawson 2001). Sites intermediate to PTCON and PVP were Ventura (VENT) and Malibu (MALI). Santa Cruz Island (CRUZ) is the largest of the 4 northern Channel Islands (surface area 250 km²) and is 43 km from the California coast;

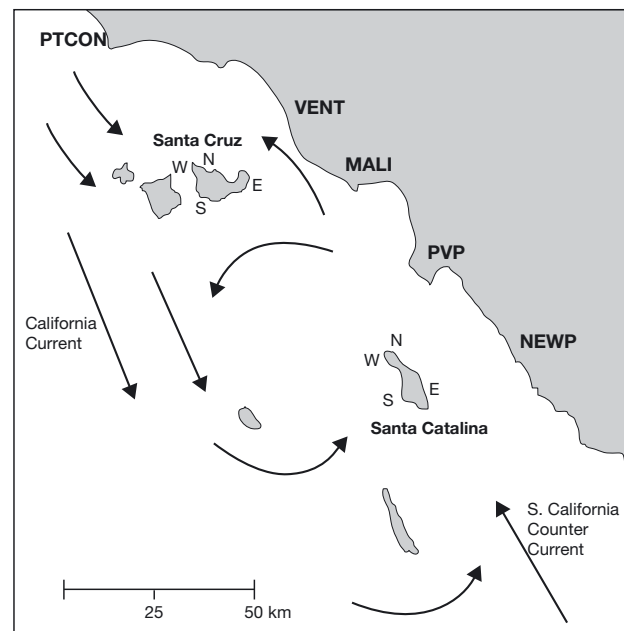


Fig. 1. *Nereis grubei*. Sampling sites in the Southern California Bight (Nuevo Puerto Vallarta, Mexico [MEX] not shown), showing the primary ocean currents (modified from Hickey 1992). MALI = Malibu, NEWP = Newport Beach, PTCON = Point Conception, PVP = Palos Verdes Peninsula, VENT = Ventura

Table 1. *Nereis grubei*. Collection site, abbreviation, number of loci amplified, and proportion of polymorphic loci at the 5% level (PLP) for samples from the Southern California Bight and central Mexico

Site	Abbreviation	# Loci	PLP
Vandenberg Air Force Base	PTCON	38	60.3
Faria Beach	VENT	32	50.8
Sycamore Cove	MALI	28	44.4
White's Point	PVP	32	50.8
Newport Beach	NEWP	31	49.2
Prisoner's Beach	CRUZ-N	30	47.6
Willow Beach	CRUZ-S	20	31.7
China Beach	CRUZ-E	30	47.6
Forney Cove	CRUZ-W	27	42.9
Ripper's Cove	CAT-N	29	46.0
Little Harbor	CAT-S	38	60.3
Hamilton Cove	CAT-E	34	54.0
Parson's Cove	CAT-W	33	52.4
Nuevo Puerto Vallarta	MEX	18	28.6
Mean		32	50.2

Santa Catalina Island (CAT) is the largest of the 4 southern Channel Islands (surface area 197 km²) and is 38 km from the California coast. Geographic distance between islands is 104 km at their closest points. Both islands have predominantly rocky intertidal shorelines (~70%) compared to 15% rocky intertidal habitat along the coast (Dailey et al. 1993). Lastly, a population from Mexico (Nuevo Puerto Vallarta, MEX) was sampled, representing a geographically and potentially genetically distant group (~2000 km), to serve as an outgroup during dendrogram construction.

Eighteen individuals were collected per site during October 2000, which was the second year of a La Niña event (Wingfield & Storlazzi 2007). The CRUZ and CAT sampling was conducted at 4 sites (north, south, east, and west), and samples were labeled as follows: CRUZ-N, CRUZ-S, CRUZ-E, CRUZ-W, CAT-N, CAT-S, CAT-E, and CAT-W, respectively. These 2 groups of 4 intra-island sites were chosen to investigate genetic structuring of these polychaetes along a small geographic scale. Individuals collected were most commonly associated with red algae *Corallina* sp. but were also associated with several other algal species, in colonies of the tubeworm *Phragmatopoma californica* and among the byssal threads of mussels *Mytilus californianus*. Worms were placed in individual vials in 95% ethanol and stored for further analysis.

DNA isolation and analysis

Genomic DNA was extracted from 20 to 25 mg tissue samples of each individual using a modified ver-

sion of the chloroform Tris-acetate borate extraction method (Saghai-Maroo et al. 1984). Proteinase K digestion of proteins was followed by chloroform extraction and isopropanol precipitation of DNA. The resultant pellet was rehydrated with 50 µl of distilled water, and DNA quantity and quality was determined using a NanoDrop-1000™ spectrophotometer (Thermo Scientific). Dilution of the samples was then made for a working solution of 50 ng µl⁻¹ and stored at 4°C for further use. Annealing temperatures and MgCl₂ concentrations were optimized for each primer using a thermal gradient cycler.

The DNA was amplified using each of the 7 ISSR primers individually in 25 µl reaction mixtures: 50 ng DNA, 2.5 mM MgCl₂, 0.50 µl of 10 mM dNTPs, 1.0 µl of an ISSR primer, 2.5 µl of 10× *Taq* buffer, and 1.0 unit of REDTaq® (Sigma) polymerase. Primers used and their annealing temperatures include the following: GA8T, 47.4°C; AC8CA, 56.5°C (Joshi et al. 2000); CAA6, 48.4°C; AC8T, 52.4°C (Raina et al. 2001); GA8C, 48.8°C (Nan et al. 2003); CA8G, 53.0°C (Ikeda et al. 2005); and AG8CC, 53.9°C (Li et al. 2006). Cycling parameters for PCR were as follows: 94°C for 1 min, followed by 35 cycles at 94°C to denature for 1 min, annealing for 1 min, and extension at 72°C for 2 min. Separation of amplified DNA fragments was carried out in 1.4% agarose gels in Tris-acetate-EDTA buffer at 2 V cm⁻¹. The gel was stained with SYBR green™ and documented under UV light (Photodyne™ imaging system) with a 100 bp ladder (HyperLadder II™, Bioline) used for length comparison.

Statistical analysis

As ISSRs are dominant markers, individual bands (loci) were converted into a 0/1 matrix (0 for absence, 1 for presence of a specific DNA marker; Nei 1987). Band sizes between the ranges of 300 and 700 base pairs in length were used for analysis. Number of loci and percentage of polymorphic loci (Polymorphism) were determined using AFLP-SURV 1.0 (Vekemans et al. 2002). Dice's coefficient was used to compare the genetic relationships among the sample groups studied using NTSYS 2.2 (Rohlf 2009). Similarity values generated were converted to distance using the formula $1 - [2a/(2a + b + c)]$, where '2a' represents shared loci among samples, and 'b' and 'c' represent loci unique to each sample being compared. To compare genetic diversity and distance values between islands, 2-tailed *t*-tests were used (4 samples per island). The UPGMA (unweighted pair group method with arithmetic mean; Sokal & Sneath 1963)

was used to construct a dendrogram from genetic distance values using NTSYS 2.2.

To test an isolation-by-distance model, pairwise distance values were compared to geographic distances in km using the Mantel test (Mantel 1967) with 1000 randomizations using the software ISOLATION BY DISTANCE (Bohonak 2002). The MEX sample data were not used within this analysis, as the role of this dataset was to serve as an outgroup.

The Bayesian clustering model applied in STRUCTURE v. 2.3 was used to assess genetic structuring among and within populations (Hubisz et al. 2009). The first run of STRUCTURE was to analyze potential genetic structuring among all 14 putative populations studied, in an attempt to determine the 'correct' number of genetic clusters (K). Due to the closeness of the island sample sites and the largely continuous rocky intertidal habitat surrounding these islands (~70%; Dailey et al. 1993), it is plausible that rather than sample sites being discrete populations, the islands may represent metapopulations for *Nereis grubei*. We first conducted STRUCTURE analyses with $K = I$ to XIV, with all individuals included ($n = 252$; 50 000 burn-in steps; 500 000 Markov chain Monte Carlo steps) with 10 iterations. The admixture model was used for each analysis, and default settings were used otherwise. A posterior probability was generated for each K , with ΔK used to indicate the 'correct' value for K (Evanno et al. 2005). Two CRUZ sites (E and W) were assigned to a single population, so K was then set to XIII for a second STRUCTURE analysis to estimate assignment for all individuals. The result of this second analysis was a statistical value for the individual admixture proportion (q) of each individual and for the sample as a whole. A q value of 0.80 was used as the minimum score to assign an individual to a specific population (Falush et al. 2007). This analysis provided insight as to recent gene flow among samples, with migrants assigned as first, second, or previous generation immigrants.

RESULTS

Genetic diversity of populations

For the 14 *Nereis grubei* populations sampled ($n = 252$), 63 loci were amplified with varying frequencies among populations; each of the 7 ISSR primers amplified 9 loci. Genetic diversity, as measured by number of loci amplified and polymorphism, was similar among sites ($\bar{x} = 32$ and 50.2, respectively), except for the PTCON and CAT-S sample sites, which had

higher values of 38 loci amplified ($P = 60.3$), and the MEX site, which had a lower value of 18 loci amplified ($P = 28.6$) (Table 1). Other than the MEX site, there was no observable geographic trend among the coastal sites for genetic diversity. There was no significant difference in genetic diversity for the CAT versus the CRUZ samples as measured by number of loci amplified or polymorphism ($p = 0.065$ for each) or for the island versus the mainland samples ($p = 0.082$ and 0.463, respectively). However, small sample size (4 sites per island) limits the statistical power of these analyses.

Genetic structuring of populations

No isolation-by-distance was demonstrated using the Mantel test, as no correlation was found between pairwise genetic distance values and geographic distance ($r = 0.0208$, $p = 0.3300$; Table 2). As predicted based on its role as an outgroup (about 2000 km distant from other sites), the MEX sample was the most divergent using Dices coefficient (MEX comparison range of distance values 0.5885 to 0.7137; Table 2). There was high variation in banding patterns among southern California samples. Genetic distance values ranged from 0.3901 (CRUZ-E versus CRUZ-W) to 0.7315 (VENT versus CRUZ-E). The northernmost site, PTCON, was closest in genetic distance to most island samples. Genetic distances were significantly greater among CAT sites relative to CRUZ sites ($p = 0.012$). Genetic distances were large even between close samples (e.g. 10 km between CRUZ-E and CRUZ-N, 0.499). The UPGMA dendrogram is consistent with the distance values stated above (Fig. 2). A high cophenetic correlation ($r = 0.889$) indicates a good fit of the phenogram to the original dataset. The CRUZ sites grouped out with one another and with the PTCON sample. The 2 eastward sites of the CAT sample (CAT-N and CAT-E) were divergent from other island samples, yet CAT-E was most similar to PVP, the most proximal mainland site. The VENT sample was divergent from other southern California samples.

According to our analyses using STRUCTURE, the best model for the population structure is that 13 of the 14 samples represented a unique population (co-assignment of CRUZ-E and CRUZ-W; Fig. 3). q values were high for each sample and overall ($\bar{x} = 0.792$; Table 3). Consistent with high genetic distance values among samples, most individuals (83%) were assigned to their respective populations. The PVP sample had the greatest success of assignment, whereas the MALI sample had the least success of

Table 2. *Nereis grubei*. Pairwise Dice coefficient among 14 populations in the eastern Pacific Ocean above the diagonal and geographic distance in kilometers below the diagonal

	PTCON	VENT	MALI	PVP	NEWP	CRUZ-N	CRUZ-S	CRUZ-E	CRUZ-W	CAT-N	CAT-S	CAT-E	CAT-W	MEX
PTCON	–	0.715	0.543	0.642	0.499	0.496	0.494	0.470	0.476	0.621	0.477	0.559	0.505	0.670
VENT	112	–	0.699	0.656	0.700	0.672	0.619	0.731	0.731	0.704	0.725	0.688	0.697	0.633
MALI	175	72	–	0.490	0.503	0.538	0.485	0.512	0.495	0.671	0.595	0.624	0.492	0.650
PVP	251	147	74	–	0.503	0.481	0.528	0.515	0.613	0.538	0.595	0.475	0.608	0.622
NEWP	298	187	115	40	–	0.490	0.481	0.528	0.515	0.613	0.538	0.595	0.475	0.600
CRUZ-N	135	43	86	135	176	–	0.457	0.499	0.474	0.653	0.528	0.569	0.495	0.611
CRUZ-S	136	61	89	135	176	47	–	0.512	0.436	0.621	0.532	0.579	0.487	0.624
CRUZ-E	135	36	83	125	166	10	36	–	0.390	0.565	0.490	0.557	0.446	0.662
CRUZ-W	136	61	112	163	204	25	23	42	–	0.549	0.464	0.554	0.412	0.638
CAT-N	264	123	69	33	59	134	126	114	139	–	0.554	0.660	0.523	0.702
CAT-S	252	139	89	69	68	146	133	122	154	40	–	0.593	0.508	0.714
CAT-E	276	140	77	33	51	146	140	130	163	13	31	–	0.498	0.687
CAT-W	277	119	62	38	69	122	120	108	141	14	22	36	–	0.589
MEX	2277	2164	2115	2038	1975	2154	2152	2150	2181	2045	2037	2035	2055	–

assignment. Only 5 of 252 individuals were recent immigrants to populations sampled, with 1 individual from VENT most genetically similar to CRUZ-N samples, 2 individuals from CRUZ-W genetically similar to CAT-W and CAT-E samples, and single individuals from CRUZ-E and CAT-S of unknown ancestry. Another 6 individuals were second generation migrants ($q \sim 0.500$), with single individuals from PTCON, VENT, CRUZ-W, and CAT-S most genetically similar to samples from MALI, CRUZ-N, CAT-S, and CAT-E, respectively. Individuals from CAT-N and CAT-E probably had ancestors originating from populations not studied here.

DISCUSSION

Direct comparisons of genetic distance values among studies using differing analyses (dominant versus co-dominant loci; microsatellites versus allozymes) are difficult. Nonetheless, genetic structure in *Nereis* is much greater than that typically occurring in marine species (see reviews by Waples 1991, Ward et al. 1994). Self-recruitment appears to be the norm for *Nereis grubei*, as STRUCTURE analysis revealed that ~2% of the 252 individuals sampled were first generation immigrants from unique genetic stocks and another 2% were second generation immigrants. Even with the close geographic distance among island sites, there was little evidence of previous generation migration among those sites, consistent with data demonstrating a lack of isolation by distance.

This high structuring among *Nereis* populations may be related to life history features of this species and is consistent with paired studies of invertebrate species having contrasting life histories (Hellberg 1996, Kyle & Boulding 2000). Further, several studies of invertebrate species that brood their young have also identified similar significant structuring among SCB populations (e.g. solitary coral species *Balanophyllia elegans*, Hellberg 1996; copepod *Tigriopus californicus*, Burton 1998).

The primary opportunity for gene flow among benthic marine invertebrates is during the larval stage. The fate of larvae of *Nereis grubei* following mating in the water column during high tide is subject to several potential outcomes. Several studies have demonstrated that potential dispersal by pelagic larvae is not realized (Burton & Lee 1994, Kyle & Boulding 2000). In drift card surveys, most released drift cards have been shown to be transported immedi-

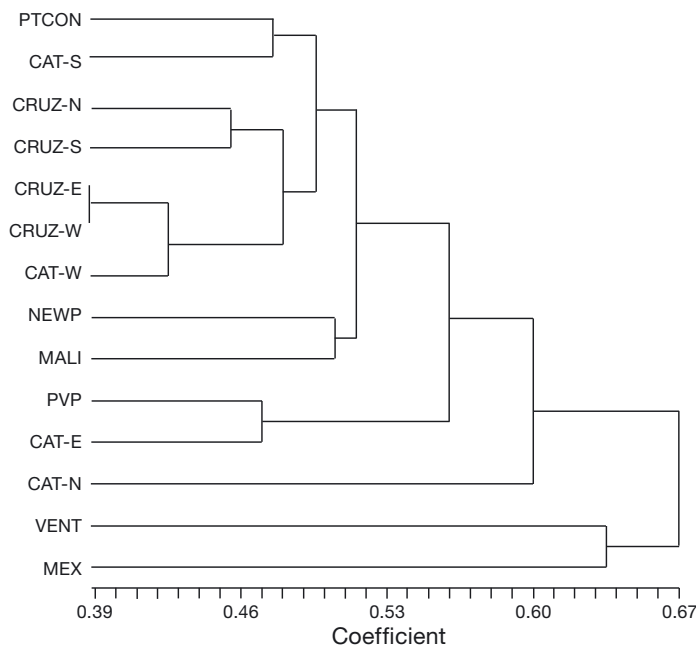


Fig. 2. *Nereis grubei*. UPGMA dendrogram of samples from the Southern California Bight and central Mexico

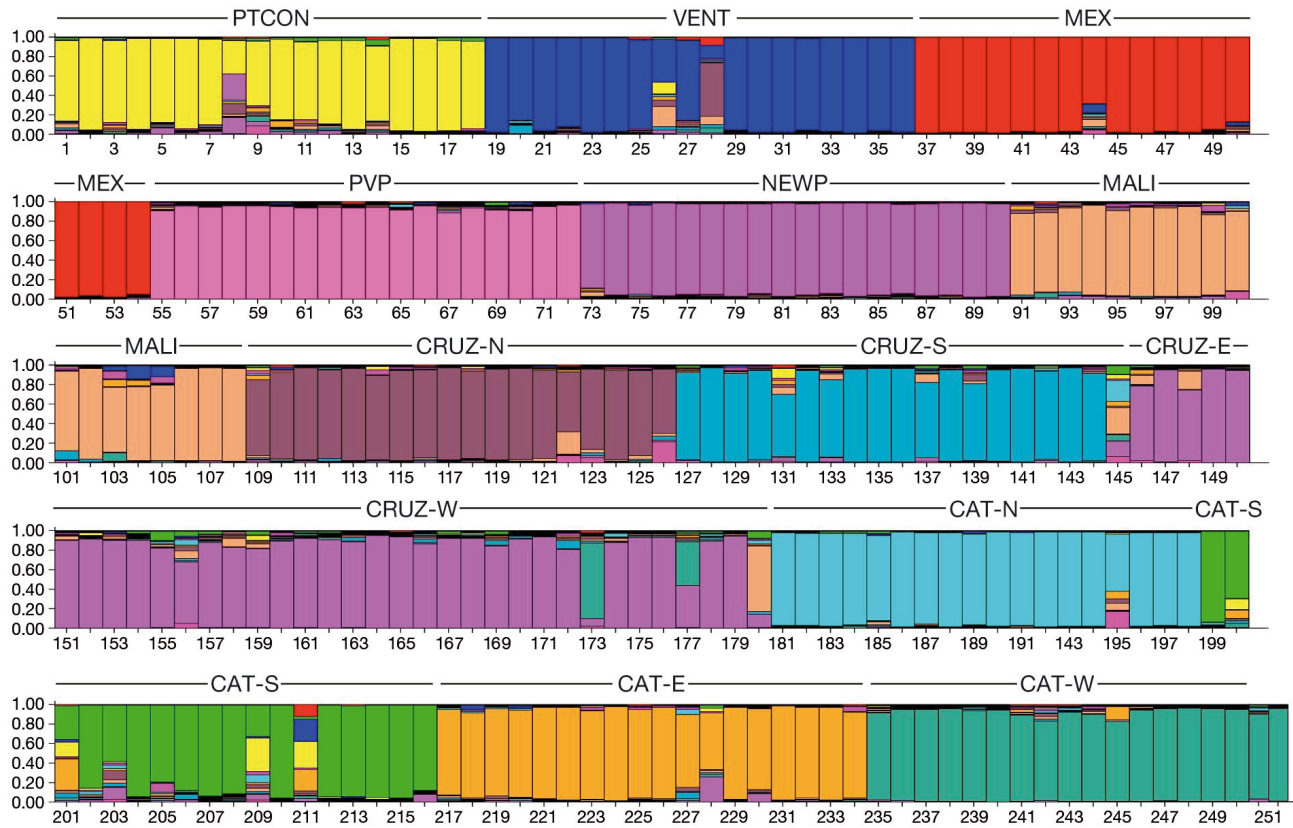


Fig. 3. *Nereis grubei*. Genetic structure among 14 putative populations collected from the Southern California Bight and Mexico using STRUCTURE on a dataset of 252 individuals and $K = XIII$. Each individual is represented by a vertical bar. Note that the CRUZ-E and CRUZ-W samples are categorised as a single larger population

ately shoreward (Schwartzlose 1963, Chambers 2004). In addition to being moved with the prevailing currents, individuals can be trapped in neighboring bays and estuaries (Levin 1986), become entangled in kelp forests (Tegner & Butler 1985, Prince et al.

1987), move with changing tides (Shanks 1983, Pringle & Franks 2001), or be driven offshore by upwelling events (Shanks et al. 2000). Adults could potentially migrate by way of rafting on kelps and other algae that are detached from the rocky intertidal zone during storm activity, normal deterioration due to age, grazing, or disease (Worcester 1994, Edgar 1987, Bushing 2000), although no *N. grubei* have been identified as rafting in published studies. Rafting would greatly enhance the potential dispersal distance of this species.

Table 3. *Nereis grubei*. Admixture proportion (q) and assignment of samples as determined by STRUCTURE

Sample	q	Proportion of correct assignment
PTCON	0.850	15/18
VENT	0.865	16/18
MALI	0.692	11/18
PVP	0.930	18/18
NEWP	0.926	18/18
CRUZ-N	0.837	14/18
CRUZ-S	0.885	14/18
CRUZ-E-W	0.795	28/36
CAT-N	0.862	14/18
CAT-S	0.754	11/18
CAT-E	0.880	16/18
CAT-W	0.909	17/18
MEX	0.909	16/18
Overall	0.792	208/252

In spite of the limitations discussed above, predictions of a potential dispersal distance for a species based on velocities of prevailing currents often have the underlying assumption of a linear flow for the larvae of that species (Bushing 2000, Sotka et al. 2004). Additionally, this linear assumption is particularly problematic due to the complex and variable currents of the SCB. Velocities of the 2 primary currents of the SCB differ, with the California Current having a more variable speed of 4 to 50 cm s^{-1} (Lynn & Simpson 1987, Poulain & Niiler 1989) and the Southern California Countercurrent having a velocity ranging

from 10 to 20 cm s⁻¹ (Reid & Schwartzlose 1962, Hickey 1992). Using mean current velocities of 25 and 15 cm s⁻¹, respectively, provides estimated potential dispersal distances of 108 km southward (estimate of 216 km at maximal current velocity) and 65 km northward (estimate of 87 km at maximal velocity) for *Nereis grubei*, which has a larval period of up to 5 d (Reish 1954). With this dispersal window, gene flow could potentially occur between most adjacent coastal populations, within island populations, among island populations solely in a north to south direction by way of the California Current (geographic distance of 104 km), or from the mainland to island populations (minimum distance of 43 km from the coastline for Santa Cruz Island and 38 km from the coastline for Santa Catalina Island).

Several seasonal current changes that typically occur within the SCB impact the direction of larval transport and include a strengthening of the southward California Current during the summer, potentially drawing larval migrants from more northern populations (Bray et al. 1999, Winant et al. 1999); a strengthening of the Southern California Countercurrent during the winter months, drawing migrants northward from southerly populations (DiLorenzo 2003, Mitarai et al. 2009); and a strengthening of the Southern California Eddy during the summer months (Hickey 1992, DiLorenzo 2003). Epitokal *Nereis grubei* individuals originating from the SCB have been identified during spring, summer, and fall months (Reish 1952); this breadth of reproductive effort may be an effective strategy in maximizing reproduction success for individuals having one reproductive opportunity while exposing pelagic larvae to a variety of current patterns, providing both self-recruitment opportunities and enhancing gene flow among populations.

Additionally, interannual variability in these current patterns is high (Lynn & Simpson 1987, DiLorenzo et al. 2004). Further disruptions of typical current patterns occur during El Niño and La Niña events, which strengthen the effects of the Southern California Countercurrent and California Currents, respectively, on larval transport (Dever & Winant 2002, Lynn & Bograd 2002, Watson et al. 2010). As *Nereis grubei* is a short-lived semelparous species, episodic current patterns such as the La Niña event of the present study could impact the genetic structure of this species more so than for iteroparous species.

The grouping of the CRUZ sites with PTCO is consistent with biogeographic and larval recruitment studies of CRUZ marine invertebrates (Seapy &

Little 1980, Broitman et al. 2005, Blanchette et al. 2006), in addition to the primary current impacting this island (California Current; Blanchette et al. 2002, Winant et al. 2003). The western CAT sites (CAT-W and CAT-S) also grouped with PTCO, consistent with flow dynamics of the California Current in the SCB (Broitman et al. 2005, Blanchette et al. 2009). The grouping of the eastern CAT sites (CAT-N and CAT-E) with proximal coastal sites (PVP) is also consistent with biogeographic data (Reish 1964) and may result from larval transport via the Southern California Eddy (Blanchette et al. 2002, Winant et al. 2003). The divergence of the VENT sample is surprising based on its proximity to other samples. There are no contour or current irregularities associated with this site, nor is this site subject to regular perturbations that could promote bottlenecks and allow genetic drift to become a dominant force in the genetics of intertidal organisms present. Lastly, genetic diversity of individuals collected from this site were within the range of other site data (R. Johnson unpubl. data), supporting a lack of genetic drift resulting from bottlenecks for this sample. Further study may provide insight into this divergence.

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