FISHERIES SCIENCE 2008; **74**: 804–812

Population structure of purple sea urchin *Strongylocentrotus purpuratus* along the Baja California peninsula

NADIA C OLIVARES-BAÑUELOS,[1] LUÍS M ENRÍQUEZ-PAREDES,[2] LYDIA B LADAH[1]* AND JORGE DE LA ROSA-VÉLEZ[2a]

[1]*Department of Biological Oceanography, CICESE, Km 107 Carretera Tijuana-Ensenada, Ensenada, Baja California, and* [2]*Laboratorio de Ecología Molecular, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, México CP 22860*

ABSTRACT: Purple sea urchin *Strongylocentrotus purpuratus* is fished from British Columbia, Canada to Punta Baja, Mexico. The North American population has been divided into northern and southern fishery stocks at the break of Point Conception, but little is known about its southernmost distribution along the Mexican Pacific coast of the Baja California peninsula. In this study purple sea urchin populations in six sites along the Baja California peninsula were analyzed using mitochondrial deoxyribonucleic acid restriction fragment length polymorphism (mtDNA RFLP). A homogeneous distribution of three common haplotypes among all sites was observed. A significant F_{ST} value, however, indicated genetic structure mainly due to the haplotype array in San Miguel, Isla Todos Santos and Punta Baja sites, which were characterized by having high haplotype diversity and several unique haplotypes. Homogeneous distribution of haplotypes along the peninsula could have been influenced by the unidirectional California Current system, flowing north to south. Unique haplotypes in Punta Baja and the structure found could be the result of local oceanographic features specific to this major upwelling zone. It may be necessary to consider the Punta Baja populations individually when managing the purple sea urchin fishery in Baja California, as they show signs of being a unique stock.

KEY WORDS: **Baja California, *COI*, mtDNA, population structure, purple sea urchin, RFLP, *Strongylocentrotus purpuratus*.**

INTRODUCTION

The purple sea urchin *Strongylocentrotus purpuratus* is widely distributed along the western coast of North America, from Alaska to Baja California Sur in Mexico,[1] and is considered an important fishery resource.[2,3] The lack of management policies has provoked a steep harvest decrease in California, Washington and British Columbia at the end of the twentieth century.[3] The same situation applies to the southern part of its distribution, along the Mexican Pacific Coast, where the fishery remains unregulated.[4,5] In general, sea urchin populations are panmictic, showing weak or no genetic structure; larvae are planktotrophic and can spend up to 121 days in the water column,[6] providing these species with a huge dispersal potential. However, urchin larvae, along with the larvae of most benthic invertebrates, require physical advective processes, which vary in space and time, to move onshore to adult habitats;[7–10] this can result in very different recruitment patterns between sites and over years. These mechanisms include wind-induced upwelling and relaxation,[11,12] surface transport generated by direct winds and current forcing,[13] non-linear internal waves[7,14] and internal tidal bores.[9,15] Because many of the above physical processes vary greatly between sites and along coasts at various different scales, differences in recruitment,[16,17] larval retention[18] and population structure may result.[19] The distribution and transport of purple sea urchin larvae has been researched for some time now, and

*Corresponding author: Tel: 52–646–175–0500. Fax: 52–646–175–0545. Email: lladah@cicese.mx
[a]Deceased.
Received 5 February 2007. Accepted 12 February 2008.

doi:10.1111/j.1444-2906.2008.01592.x

while a general association of settlement with relaxation of upwelling has been shown, patterns have been confused by large interannual and between-site differences that are not always explainable.[20,21] Genetic studies also show inconsistencies in population structure, complicating fisheries management decisions. Allozyme analyses of the purple sea urchins from the coast of California[22,23] have shown panmictic populations. However, Edmands *et al.*[24] found population structure using allozymes and cytochrome oxidase I (*COI*) DNA sequencing in purple sea urchins collected between Panther Beach, USA, and Punta Cabras, Mexico. They also observed demographic dissimilarity between sites on a geographic scale, suggesting restricted gene flow in some areas in response to local topography or oceanographic features, which resulted in discrete subpopulations. Flowers *et al.*[25] sequenced *COI* in purple sea urchins from California, but did not find any genetic structure. In Mexico, except in Punta Cabras,[24] the genetic identity and structure of purple sea urchin populations has not been studied and there is no information available to our knowledge on larval distribution or transport.

The Baja California peninsula is dominated by the southern end of the southward flowing California Current (described in detail in Hickey[26]). Inshore of this strong current there is much variability in local oceanographic conditions, upwelling regimes, and alternating localized currents and internal wave regimes (i.e. the Ensenada front[27] and its biophysical implications,[28] the California undercurrent,[29] internal waves and larval transport[30] and general patterns[26,31]). Along this coast there are particular sites, such as Ensenada and Punta Eugenia, where oceanographic features show seasonal patterns such as eddies and upwellings.[32,33] In contrast, there are other areas that are continuously dominated by more persistent strong upwelling (and the resultant upwelling shadows down-current), such as in Campo Kenedy[34] and Punta Baja, where these features are present all year round;[35] these features could affect larval dispersal or retention, and could result in population structure differences at different temporal and spatial scales.[36]

In Mexico, *S. purpuratus* is the second most important resource for the sea urchin fishery (*S. franciscanus* is the first[37]), yet remains unregulated. The maximum harvest of *S. purpuratus* was 815 t in 1996 and was down to 400 t in 2002 (Palleiro-Nayar J, pers. comm., 2003). In order to provide information to managers for fishery regulations, a first approach would be to discriminate genetic differentiation of populations along the coast, a parameter often used for management decisions to approach the fisheries as suggested by Park and Moran[38] and Thorrold *et al.*[39] Here we present a genetic population analysis of *S. purpuratus* collected from San Miguel in northern Baja California to Bahia Tortugas in Baja California Sur. Our main goal with this analysis was to determine if there is a large continuous population or if there are discrete, genetically distinct smaller subpopulations. This is critical management information that should be considered in the light of the increasing interest in this fishery resource.

MATERIALS AND METHODS

Purple sea urchins were collected haphazardly from 1-m^2 intertidal quadrats. Their location was determined using a list of random numbers, and placed parallel to the shoreline[40] in six sites along the west coast of Baja California, Mexico (Fig. 1) in

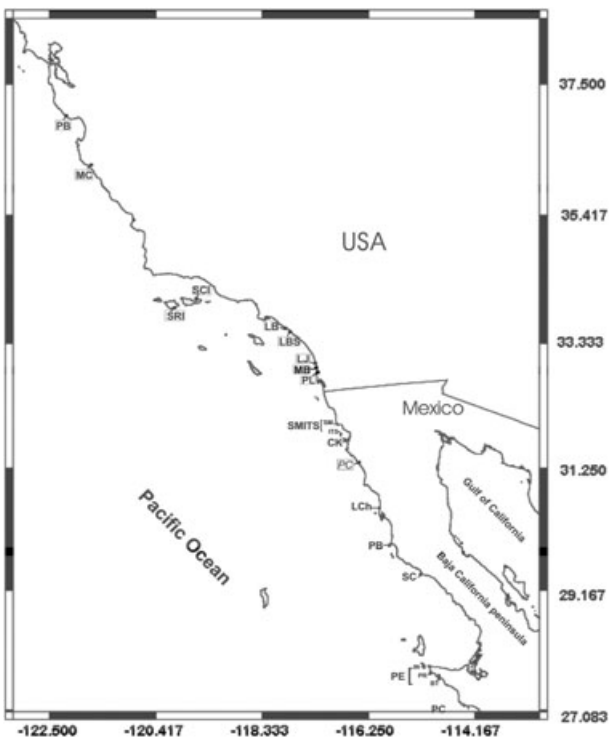

Fig. 1 Sampling sites on the western Baja California coast of this study: SMITS is composed of SM, San Miguel; ITS, Isla Todos Santos (31.8055°N–116.7886°W, 31.9016°N–116.7280°W); CK, Campo Kenedy (31.7022°N–116.6850°W); LCh, La Chorera (30.4706°N–116.0475°W); PB, Punta Baja (29.9486°N–115.8121°W); SC, Punta San Carlos (29.6201°N–115.5089°W). Sampling sites in Baja California Sur: PEL is composed of IN, Isla Natividad (27.8506°N–115.1709°W); PR, Punta Rompiente (27.7255°N–114.9938°W); BT, Bahía Tortugas (27.6627°N–114.8768°W). Boxed sites are those sampled by Edmands *et al.*[24]

2001 and 2002; sampling was done once for each site. The sites are rocky shores with outcropping or rocky points characterized by upwellings, eddies and distinct differences in sea urchin densities (data not shown). In each site at least five quadrats were sampled and a random representative sample of sea urchins was chosen from each quadrat at each site, with a range of 16–27 organisms per site or combined sites. Specimens were transported either alive or preserved in 70% ethanol to the laboratory where either the gonad(s) or the peristomeal membrane of each individual were dissected, labeled and stored at −70°C until further DNA extraction.

DNA extraction

Total genomic DNA was obtained from 100 mg of frozen tissue homogenized in an extraction buffer containing 10 mM Tris, 1 mM EDTA pH 8.0, 100 mM NaCl, SDS 0.1% and 0.25 mg of proteinase K. Tissue was digested overnight at room temperature, and DNA was purified by a modified phenol–chloroform protocol.[41] Alternatively, we used a salt-modified protocol[42] for which the extraction buffer consisted of 200 mM Tris, 25 mM EDTA, 250 mM NaCl, 0.5% SDS, 2% CTAB, 0.1% PVPP and 0.2% β-mercaptoethanol. Finally, DNA was precipitated in 99% isopropanol, washed in 70% ethanol and resuspended in Tris-EDTA (TE) at pH 8.0.

DNA quantity and quality was evaluated by electrophoresis on 0.7% agarose gels stained with ethidium bromide (0.5 μg/mL) and using a UV-light spectrophotometer (Lambda 40, Perkin Elmer, Waltham, MA, USA).

PCR amplification

Using Primer Select v3.05a software (Winstar, Inc., Madison, WI, USA) and the complete mitochondrial genome sequence of *S. purpuratus*[43] (GenBank accession no. X12631), we designed a pair of primers targeting the *COI* gene for the species: EPCOILf (5′-GTTAAACGGCCGCTGTATC TTG-3′) and EPCOILr (5′-GGTGATTCCTTCCCG TTGAG-3′). With these primers, 126 samples were amplified for a 2093-bp fragment which included the amplified regions recorded by Edmands *et al.*[24] and Flowers *et al.*[25] PCR reactions were performed in a final volume of 50 μL containing 22 mM Tris-HCl pH 8.4, 55 mM KCl, 220 μM dNTPs mix, 4.95 mM $MgCl_2$, 0.05% Tween 20, 10 μM of each primer, 0.22 U of *Taq* polymerase and 30 ng of DNA. We used a 480 thermal-cycler (Perkin Elmer) with the following profile: 5 min at 95°C for initial denaturation then 30 cycles of 1 min at 95°C for denaturation, 1 min at 60°C for annealing and 2 min at 72°C for extension. A final step of 10 min at 72°C was added to be sure of complete extension of the fragments.

Restriction fragment length polymorphism (RFLP) analysis

A theoretical endonuclease digestion analysis was performed by Mapdraw software v3.05a (Winstar Inc.) on the mtDNA *COI* gene sequence reported by Jacobs *et al.*[43] We used a random subsample set of 22 purple sea urchin individuals as well as two red sea urchins *S. franciscanus* for endonuclease selection. As previously reported by Edmands *et al.*,[24] *Acc*II and *Eco*T14I endonucleases were informative, but since we used a longer gene domain, *Rsa*I was also found to show polymorphism. Overnight endonuclease digestions were performed on 600 ng of PCR product, and restriction fragments were separated by electrophoresis on 1.8% agarose gels. The restriction band patterns were visualized by ethidium bromide (0.5 μg/mL), recorded on 667 black-and-white Polaroid film and analyzed through Kodak ID image analysis software v3.6 (Kodak, Rochester, NY, USA) to define fragment size and identify the distinctive haplotypes.

Data analysis

A 2093-bp fragment of mtDNA *COI* gene was analyzed, and it contained the 519-bp fragment of mtDNA *COI* used by Edmands *et al.*[24] All genetic structure and phylogenetic analyses were performed using Arlequin v2.0[44] and Phylip v3.6[45] software, respectively. A preliminary pairwise genetic homogeneity test allowed us to pool together nearby locations (<20 km, Fig. 1), for which no genetic heterogeneity was detected, in order to increase sample size. The two locations SM and ITS were grouped together as SMITS, while IN, PR and BT were grouped as Punta Eugenia (PE), bringing the total number of sites to six in our analysis. The spatial distribution of genetic diversity was analyzed by means of an analysis of molecular variance (AMOVA) based on haplotype frequency, and isolation by distance through Mantel's test (genetic *vs* geographic distances). A bootstrapped distance matrix (100 resamples) was used to construct a neighbor-joining phylogenetic consensus where the red sea urchin *S. franciscanus* was considered as an outgroup.

RESULTS

The largest number and greatest density of sea urchins was found in the northern sampling sites. In order to perform a better comparison we chose to combine the southern sampling sites because of the low number of sea urchins found in those sites. In total 13 haplotypes were found along the studied distribution of 126 purple sea urchin individuals. Three of them were common across the sites (*SpCOI*-3, *SpCOI*-8 and *SpCOI*-11), while the other 10 were only present in some sites, with some as rare or unique haplotypes (Fig. 2). Punta Baja (PB) displayed the highest number of haplotypes and unique haplotypes (*SpCOI*-1, *SpCOI*-6 and *SpCOI*-7).

The overall mean haplotype diversity was 0.7331 ± 0.072, ranging from 0.6638 ± 0.0876 at Punta Baja (PB) to 0.8162 ± 0.0607 at La Chorera (LCh), with no statistical differences found between sampling sites because standard errors were large (Table 1). In contrast, overall *F*-statistics showed significant differences among sites ($F_{ST} = 0.023$, $P < 0.0010$), which could be interpreted as a structured population. Pairwise F_{ST} values shown with this result was significantly influenced by PB and SMITS as shown in Table 1. No significant correlation between genetic and geographic distance was detected (Mantel's Test $r^2 = 0.004$, $P = 0.054$, 1000 permutations).

Although bootstrap support was low, the neighbor-joining tree seems to discriminate at least three groups of haplotypes. The first group comprised a single haplotype (*SpCOI*-4), which was represented by only one individual found at La Chorera (LCh), and seems to be closely related to *S. franciscanus*. A second group comprised another two haplotypes (*SpCOI*-12 and *SpCOI*-13), again represented by only one individual each, found at LCh, but also at the southernmost sites (PE). Finally, the other 10 haplotypes formed a third group, widely distributed along the study area (Figs 2 and 3).

DISCUSSION

Panmictic populations are common for coastal invertebrates with planktotrophic larvae,[24,25,46] since such a development strategy promotes a continuous gene flow between nearby locations.[47] In the present study we found that *S. purpuratus* exhibited a weak genetic structure along the west coast of Baja California, Mexico (F_{ST} 0.0494). Three haplotypes dominated the study area, representing nearly 70% of the individuals at each site and thus homogenizing genetic diversity, as would be expected from a panmictic metapopulation. A similar pattern of haplotype occurrence was previously reported for California and northern Baja California,[24,25] which was suggested to be due to active transport of larvae favored by the California Current, which runs from north to south. Edmands *et al.*[24] used a 519-bp segment of mtDNA *COI* gene from nine sites in California, USA and one in Baja California, Mexico and Flowers *et al.*[25] used a 358-bp sequence of mtDNA *COI* from seven sites in California, USA for the same species. The main difference between our results and that of other authors is that we used six sites along the Baja California peninsula, Mexico (>500 km between northern- and southernmost sites) that represent the southern distribution of *S. purpuratus*,[1] and our data support the idea that southern populations have higher genetic diversity than northern populations. We suggest this because mutations arising in the south would be less likely to move northward and more likely to move southward, as pointed out by Edmands *et al.*[24] While some haplotypes were common among all sites suggesting homogeneity, significant genetic differentiation was, however, detected between the SMITS and PB sites, according to the pairwise comparisons. SMITS was the northernmost site; it exhibited the lowest number of haplotypes, and *SpCOI-11* was its most common haplotype unlike the other sites. PB had the highest number of haplotypes and the greatest number of unique haplotypes. This result may be due to sample size, as genetic analysis of marine population structures often indicates only slight geographic differentiation in species with high dispersal potential.[19] However, the PB site and the pooled SMITS sites had the largest number of individuals, and still showed significant differences in our data set. Therefore, we assume that our data show true patterns rather than artifacts of sampling error.

Avise[47] mentions that local events of ocean dynamics can disrupt genetic homogeneity, allowing the occurrence of genetic patches even when high gene flow is present through the range of a species. Even in a unidirectional flow such as the California Current, differing patterns of upwelling and relaxation can cause regional retention,[18] as a few haplotypes of LCh, PB, SC and PE sites show. The SMITS sites are within Todos Santos Bay (in front of Ensenada), one on the lee side of the island (ITS) potentially limiting the bay from connectivity with offshore, while the other site is directly west of the island, within the bay, on the mainland (SM); this bay may potentially act as a retention site. Retention has been shown in semi-enclosed environments for the sea urchin *Evechinus chloroticus*

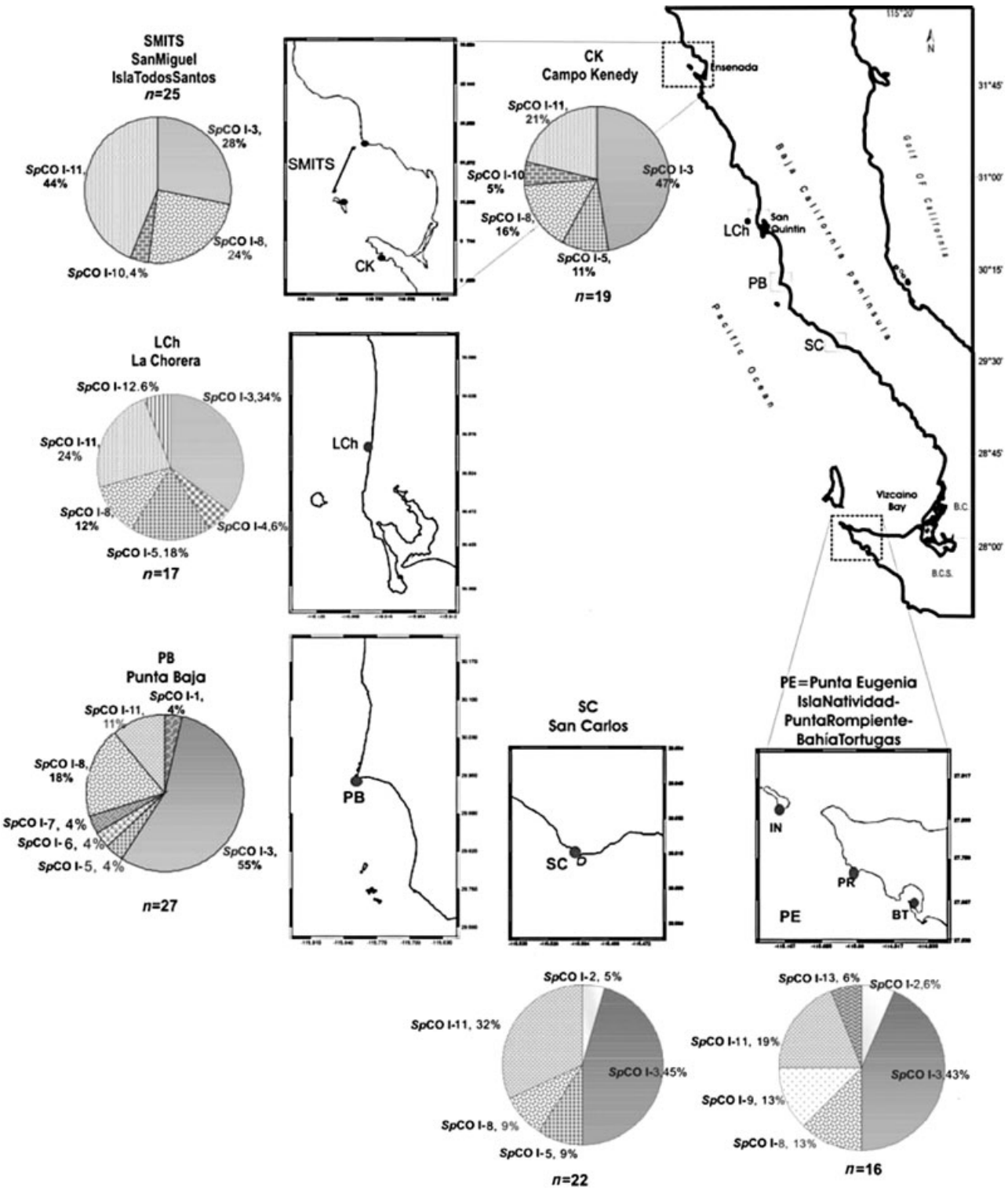

Fig. 2 mtDNA *COI* gene haplotype frequency distribution of the populations of *Strongylocentrotus purpuratus* of the west coast of Baja California. SMITS, San Miguel and Todos Santos Island; CK, Campo Kenedy; LCh, La Chorera; PB, Punta Baja; SC, San Carlos; PE, Natividad Island, Punto Rompiente and Bahía Tortugas. Pie charts show the haplotydic frequencies of each site.

Table 1 Mitochondrial DNA *COI* gene haplotypic diversities for *Strongylocentrotus purpuratus* populations along the Pacific coast of Baja California peninsula

Site	SMITS	CK	LCh	PB	SC	PE	*n*	Haplotypic diversity
SMITS	–	0.08199	0.08176	0.23277	0.13587	0.04819	25	0.6967 ± 0.0498
CK	0.06934 ± 0.0065	–	–0.03904	0.01362	–0.04319	–0.02312	19	0.7310 ± 0.0805
LCh	0.07422 ± 0.0074	0.80176 ± 0.0097	–	0.04053	–0.03638	–0.03165	17	0.8162 ± 0.0607
PB	0.00098 ± 0.0010	0.26367 ± 0.0181	0.12402 ± 0.0100	–	0.02069	0.03437	27	0.6638 ± 0.0876
SC	0.02637 ± 0.0042	0.86133 ± 0.0105	0.74219 ± 0.0153	0.22559 ± 0.0147	–	0.00383	22	0.7076 ± 0.0679
PE	0.11719 ± 0.0099	0.58594 ± 0.0164	0.71191 ± 0.0159	0.15039 ± 0.0101	0.29199 ± 0.0151	–	16	0.7833 ± 0.0852

F_{ST} *P*-values showed significant differences among sites with respect to the population as a whole ($F_{ST} = 0.0494$, $P < 0.0010$) below diagonal (value ± standard deviation), and F_{ST} values above diagonal; *n*, sample size of each site.

where recruits settle from larvae that have originated, been retained and completed development within a fiord, and where reduced larval exchange provides a mechanism for the observed genetic differentiation of this population.[17] The SMITS population, in a similar way, may be a self-recruiting population that is genetically isolated and haplotype-poor compared to other surrounding populations, as a result of the large bay of Todos Santos.

South of Ensenada and north of San Quintín, the California Current once again comes near shore in a feature called the Ensenada front[27] (north of this area, the California Current is much further offshore). This feature could connect populations in the southern California Bight (USA) with populations south of the Ensenada front through the connectivity of the California Current when it comes back onshore, and at the same time leaves populations in the Ensenada region isolated from populations both in the southern California Bight and further south of Ensenada.

In comparison with all other sampling areas, the PB region is characterized by the occurrence of a strong coastal southward current[35] and eddies.[26,32,48] Such distinctive oceanographic features in this area allow year-round upwelling, and high primary production (up to 8 mg/m^3 of chlorophyll-a[33,48]). Durazo and Baumgartner[32] indicate the dominance of poleward motion associated with considerable recirculation both in the onshore–offshore and alongshore directions. A distinct narrow flow tending shoreward and poleward, and associated return flows, divides the region into northern and southern areas. This shoreward–poleward flow can be traced approximately at 27°N, cutting across the survey region to its convergence with the coast just to the north of 30°N. This separated flow could explain the differences between the SMITS and PB sites; local recruitment could occur at each site, so that the unique haplotypes of PB do not reach the SMITS sites, as flow is rarely northward. The southward flowing California Current could bring common haplotypes to the PB area, while at the same time the recirculation flow associated with upwelling shadows[18,49] could create areas of retention and self-recruitment of unique haplotypes that would never be transported to the north because of the strong southward-flowing California Current. According to our results, the absence or reduction of reproductive and larval abundance peaks of purple sea urchin *S. purpuratus* [20] could not affect the haplotydic frequency, because *S. purpuratus* is well represented. This is not the case for PB, which has the greatest unique frequency but minimal represented percentage.

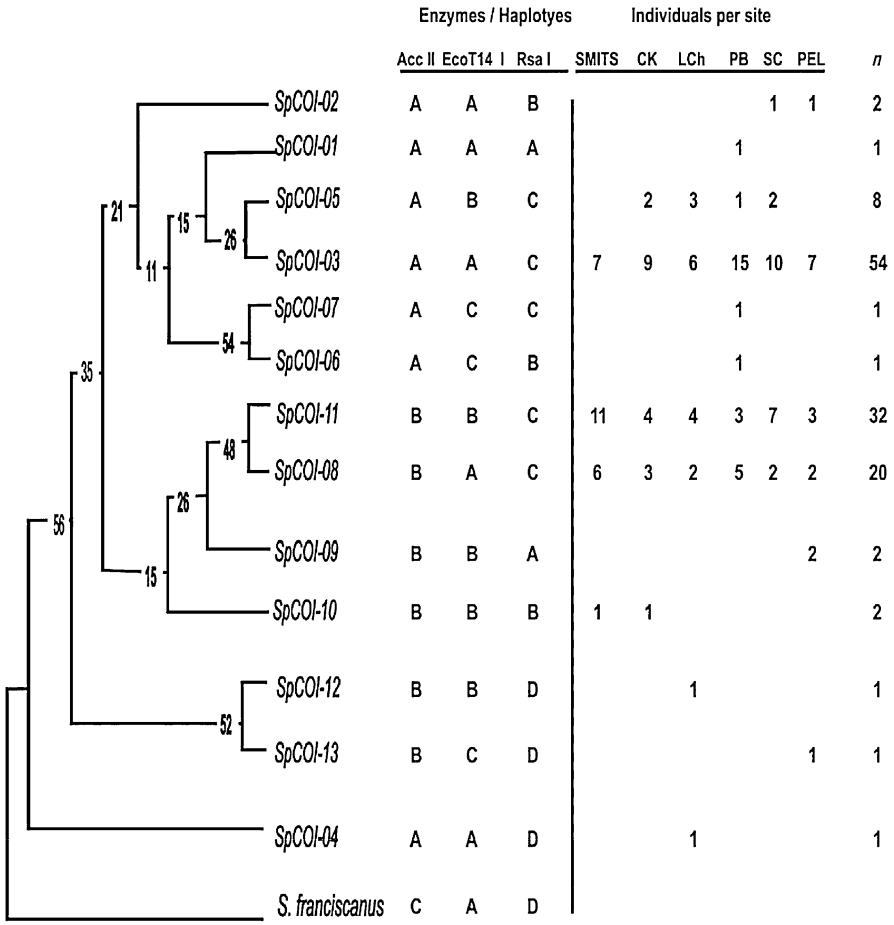

Fig. 3 Neighbor-joining tree of mtDNA *COI* gene haplotypes of *Strongylocentrotus purpuratus* along the western coast of Baja California. Numbers on branches are bootstrap scores. Right-hand columns show mtDNA *COI* gene haplotype code; *n*, number individuals of each haplotype per site.

Supporting the above hypothesis, PB exhibits the highest densities of purple sea urchin along Baja California. Similarly, red sea urchin *S. franciscanus* densities at PB of 5.9 inds/m^2 (Palleiro-Nayar J, pers. comm., 2003) support the most intense and productive fishery of the species along the Baja California west coast, contrasting with the lowest densities at SMITS (2.6 inds/m^2). PB may be an area of accumulation of common northern haplotypes due to the unidirectional current along the coast, while at the same time is a refuge for unique haplotypes due to recirculation in the Vizcaino Bay, causing self-recruitment of rare haplotypes. Again, because this area has one of the highest sampling numbers, we do no believe this is an artifact. In addition, Ganz and Burton[50] reported PB as a genetically distinct location along the Baja California peninsula in a study on the copepod *Trigriopus californicus*.

Near the southern limit of the species, the PE sites showed a homogeneous haplotype frequency. This protruding point, the largest on the entire peninsula of Baja California, has connectivity with the California Current through the anticyclone eddy of San Sebastian in Vizcaino Bay.[35] This eddy brings large amounts of water from the north through the California Current. However, in contrast to the PB area, PE would not have any recirculation current to trap and self-recruit unique haplotypes as they occur on the open coast near a deep shelf where the California Current comes very close to shore. They would, therefore, have little connection with the PB area and at the same time a large connection with more northern sites. Our genetic data support this hypothesis.

In agreement with the observations of Edmands *et al.*[24] and Flowers *et al.*,[25] we found that overall haplotype diversity increased southwards, with most of the rare and unique haplotypes occurring south of LCh. A possible explanation of this pattern is that dispersal of local rare haplotypes is limited to local coastal currents and eddies where local oceanography supports self-recruitment. Therefore, larvae may only be transported between adjacent areas, as was the case with haplotypes *SpCOI*-5 (CK, LCh, PB and SC), *SpCOI*-10 (SMITS and CK) and *SpCOI*-2 (PE and SC). However, given the stronger and longer influence of the California Current system on the study area, dispersal is favored southwards, preventing the rare haplo-

types from reaching northern areas while causing northern haplotypes to be homogenous across the study site.

PB seems to be a key location to maintain genetic diversity of the entire population because it maintains the highest haplotypic diversity, but LCh is the site that has haplotypes that are present in the three branches of the neighbor-joining tree and must be particularly considered in any fishery management scheme for the purple urchin fishery. Just as the North American sea urchin population has been divided into northern and southern fishery stocks in the area of Point Conception, California, USA,[3,24] we suggest a new purple sea urchin fishery stock definition in the Baja California peninsula, considering the areas south of LCh and all areas near PB as separate stocks.

ACKNOWLEDGMENTS

This work was made possible by a scholarship to NO-B from CONACyT (164625-OIBN780628). This research was financially supported by the Centro de Investigación Científica de Educación Superior de Ensenada (CICESE and the Biological Oceanography Department), FCM-UABC, the Molecular Biology Laboratory of the Facultad de Ciencias-UABC, AMELIS CONACyT Young Researcher Project J37689 grant to LBL, and UC MEXUS Key Intertidal Species project grant also to LBL. Special thanks to A Grant for comments and review. Thanks to the ICE team and to those who helped with sea urchin sampling.

REFERENCES

1. Sagarin RD, Gaines SD. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *J. Biogeogr.* 2002; **29**: 985–998.
2. Ricketts EF, Calvin J. *Between Pacific Tides*. 3rd Rev. edn. 1962 by J.W. Hedgpeth. XII 516. Stanford University Press, Stanford, CA. 1939.
3. Workman G. *A Review of the Biology and Fisheries for Purple Sea Urchin (Strongylocentrotus purpuratus, Stimpson, 1957) and Discussion of the Assessment Needs of a Proposed Fishery*. Canadian stock assessment secretariat research document 99/163. Fisheries and Oceans Canada, Ottawa 1999.
4. Pérez SM, Calderón-Aguilera LE. Analysis of the biological fishing purple hedgehog *Strongylocentrotus purpuratus,* a new fishery in Baja California. *Oceanología* 1996; **2**: 7–16.
5. Botsford LW, Morgan LE, Lockwood DR, Wilen JE. Marine reserves and management of the northern California red sea urchin fishery. *Reports of California Cooperative Oceanic Fisheries Investigations (CalCOFI Report)* 1999; **40**: 87–93.
6. Strathmann RR. Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. *J. Exp. Mar. Biol. Ecol.* 1978; **34**: 23–27.
7. Shanks AL. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar. Ecol. Prog. Ser.* 1983; **13**: 311–315.
8. Shanks AL. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward L (ed.). *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL. 1995; 323–367.
9. Pineda J. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 1991; **253**: 548–551.
10. Pineda J. Circulation and larval distribution in internal tidal bore warm fronts. *Limnol. Oceanogr.* 1999; **44**: 1400–1414.
11. Shanks AL, Largier JL, Brink L, Brubaker J, Hoof R. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol. Oceanogr.* 2000; **45**: 230–236.
12. Farrel TM, Bracher D, Roughgarden J. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr.* 1991; **36**: 279–288.
13. Hawkins SJ, Hartnoll RG. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J. Exp Mar. Biol. Ecol.* 1982; **62**: 271–283.
14. Shanks AL. The onshore transport of an oil spill by internal waves. *Science* 1987; **235**: 1198–1200.
15. Pineda J. Internal tidal bores in the nearshore: warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. *J. Mar. Res.* 1994a; **52**: 427–458.
16. Mace AJ, Morgan SG. Larval accumulation in the lee of a small headland: implications for the design of marine reserves. *Mar. Ecol. Prog. Ser.* 2006; **18**: 19–29.
17. Lamare MD. Origin and transport of larvae of the sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea) in a New Zealand fiord. *Mar. Ecol. Prog. Ser.* 1998; **174**: 107–121.
18. Shanks AL, Eckert GL. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. *Ecol. Monogr.* 2005; **75**: 505–524.
19. Palumbi SR. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* 2003; **13** (Suppl.): S146–S158.
20. Miller BA, Emlet RB. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. *Mar. Ecol. Prog. Ser.* 1997; **148**: 83–94.
21. Wing SR, Largier JL, Botsford LW, Quinn JF. Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnol. Oceanogr.* 1995; **40**: 316–329.
22. Burton RS. Protein polymorphisms and genetic differentiation of marine invertebrate populations. *Mar. Biol.* 1983; **4**: 193–206.
23. Palumbi SR, Wilson AC. Mitochondrial DNA diversity in the sea urchins *Strongylocentrotus purpuratus* and *S. droebachiensis*. *Evolution* 1990; **44**: 403–415.
24. Edmands S, Moberg PE, Burton RS. Allozyme and mitochondrial DNA evidence of population subdivision in the purple sea urchin *Strongylocentrotus purpuratus*. *Mar. Biol.* 1996; **126**: 443–450.
25. Flowers JM, Schroeter SC, Burton RS. The recruitment sweepstakes has many winners: genetic evidence from the

sea urchin *Strongylocentrotus purpuratus*. *Evolution* 2002; **56**: 1445–1453.
26. Hickey BM. The California Current System: hypotheses and facts. *Prog. Oceanogr.* 1979; **8**: 191–279.
27. Haury L, Venrick E, Fey C, McGowan J, Niiler P. The Ensenada front: July 1985. *Calif. Coop. Ocean. Fish. Investig. Rep.* 1983; **34**: 69–88.
28. Ladah LB. The shoaling of nutrient-enriched subsurface waters as a mechanism to sustain primary productivity off Central Baja California during El Niño winters. *J. Mar. Sys.* 2003; **42**: 145–152.
29. Wooster WS, Jones JH. The California undercurrent off northern Baja California. *J. Mar. Res.* 1970; **28**: 235–250.
30. Ladah LB, Tapia F, Pineda J, Lopez M. Spatially heterogeneous, synchronous settlement of *Chthamalus* spp. larvae in northern Baja California. *Mar. Ecol. Prog. Ser.* 2005; **302**; 177–185.
31. Chelton D, Bernal P, McGowan J. Large-scale interannual physical and biological interaction in the California current. *J. Mar. Res.* 1982; **4**: 1095–1125.
32. Durazo R, Baumgartner TR. Evolution of oceanographic conditions off Baja California. *Prog. Oceanogr.* 2002; **54**: 7–31.
33. Lavaniegos BE, Jiménez-Pérez LC, Gaxiola-Castro G. Plankton response to El Niño 1997–1998 and La Niña 1999 in the Southern region of the California Current. *Prog. Oceanogr.* 2002; **54**: 33–58.
34. Ladah LB, Zertcuhe-Gonzalez JA. Giant kelp (*Macrocystis pyrifer*a) survival in deep water (25–40 m) during El Niño of 1997–1998 in Baja California, Mexico. *Bot. Mar.* 2004; **47**: 367–372.
35. Amador-Buenrostro A, Argote-Espinoza ML, Mancilla-Peraza M, Figueroa-Rodríguez M. Short term variations of the anticyclonic circulation in Bahía Sebastián Vizcaíno, B.C. *Cien. Mar.* 1995; **21**: 201–223.
36. Botsford LW. Physical influences on recruitment to California Current invertebrate populations on multiple scales. *ICES J. Ma Sci. 58* 2001; **58**: 1081–1091.
37. Andrew NL, Agatsuma Y, Ballesteros E, Bazhin AG, Creaser EP, Barnes DKA, Botsford LW, Bradbury A, Campbell A, Dixon JD, Einarsson S, Gerring PK, Hebert K, Hunter M, Hur SB, Johnson-Craig R, Juinio-Menez MA, Kalvass P, Miller RJ, Moreno CA, Palleiro JS, Rivas D, Robinson SML, Schroeter SC, Steneck RS, Vadas RL, Woodby DA, Xiaoqi Z. Status and management of world sea urchin fisheries. *Oceanogr. Mar. Biol. Annu. Rev.* 2002; **40**: 343–425.
38. Park LK, Moran P. Development in molecular genetics techniques in fisheries. *Rev. Fish. Biol. Fisher.* 1994; **4**: 272–299.
39. Thorrold SR, Jones GF, Hellberg ME, Burton RS, Swearer SE, Niegel JE, Morgan SG, Warner RR. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bull. Mar. Sci.* 2002; **70**: 291–308.
40. Underwood AJ. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, New York, NY. 1997.
41. Sambrook J, Fritsch EF, Maniatis T. *Molecular Cloning: A Laboratory Manual*, 2nd edn. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY. 1989.
42. Miller SA, Dykes DD, Polesky HF. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Res.* 1988; **16**: 1215.
43. Jacobs HT, Elliott DJ, Math VB, Farquharson A. Nucleotide sequence and gene organization of sea urchin mitochondrial DNA. *J. Mol. Biol.* 1988; **202**: 185–217.
44. Excoffier L, Smouse PE, Quattro JM. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 1992; **131**: 479–491.
45. Felsenstein J. PHYLIP – phylogeny inference package (version 3.2). *Cladistics* 1989; **5**: 164–166.
46. Kyle CJ, Boulding EG. Comparative population genetic structure of marine gastropods (*Littorina* spp.) with and without pelagic larval dispersal. *Mar. Biol.* 2000; **137**: 835–845.
47. Avise JC. *Phylogeography, the History and Formation of Species*. Harvard University Press, Cambridge, MA. 2000.
48. Venrick E, Brograd SJ, Checkley D, Durazo R, Gaxiola-Castro G, Hunter J, Huyer A, Hyrenbach KD, Lavaniegos BE, Mantyla A, Schwing FB, Smith RL, Sydeman WJ, Wheeler PA. The state of the California Current, 2002–2003: tropical and subarctic influences vie for dominance. *Calif. Coop. Ocean. Fish. Invest. Rep.* 2003; **44**: 28–60.
49. Graham WM, Largier JL. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Cont Shelf Res.* 1997; **17**: 509–532.
50. Ganz HH, Burton RS. Genetic differentiation and reproductive incompatibility among Baja California populations of the copepod *Tigriopus californicus*. *Mar. Biol.* 1995; **123**: 821–827.