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PHYLOGEOGRAPHY AND DEMOGRAPHY OF SYMPATRIC SISTER SURFPERCH SPECIES, *EMBIOTOCA JACKSONI* AND *E. LATERALIS* ALONG THE CALIFORNIA COAST: HISTORICAL VERSUS ECOLOGICAL FACTORS

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Abstract.—With 18 closely related endemic species that radiated in a diversity of ecological niches, the California surfperches (Embiotocidae) species flock is a good candidate for the study of sympatric speciation. Resource partitioning has been suggested as an important driving force in the radiation of the surfperch family. Within the family, two congeneric sister species, *Embiotoca jacksoni* and *E. lateralis*, are known to compete strongly for a preferred single food resource and may be used as a model of ecological interactions for the family. Along the California coast, the distribution of the two species differs. *Embiotoca jacksoni* has a continuous range, whereas *E. lateralis* shows a disjunction with a distribution gap in the Southern California Bight. Two hypotheses may explain this disjunct distribution. Ecological competition may have displaced *E. lateralis* in favor of *E. jacksoni*. Alternatively, a common vicariant event may have separated the species into northern and southern populations, followed by secondary contact in *E. jacksoni* but not in *E. lateralis*. The two hypotheses predict different phylogeographic and demographic signatures. Using a combined phylogeographic and coalescent approach based on mitochondrial control region data, we show that vicariance can only account for a portion of the observed divergences. Our results are compatible with a significant role played by ecological competition in the southern range of the species.

Key words.—Demography, *Embiotoca*, phylogeography, surfperches, sympatric speciation.

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Sympatric speciation is currently experiencing a renewed interest in theoretical and empirical evolutionary biologists (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999; Via 2001; Bolnick 2004). Several modes of sympatric speciation have been proposed (Turelli et al. 2001), including ecological speciation (Via 2001). Ecological speciation results from divergent selection on traits, which in turn leads to reproductive isolation (Schluter 2001). In fish systems, only a few studies have investigated in detail the factors that are likely to be responsible for ecological speciation. Microallopatry, including depth segregation (Fryer and Iles 1972) and environmental segregation (Schluter 2000; McKinnon et al. 2004), have been documented. Resource competition may also play an important role in ecological speciation in fish, yet little direct evidence has been gathered (Schluter 1994; Seehausen 1996, 2000). For example, the explosive radiation of Lake Malawi endemic cichlid fishes, which occurred in three stages, involved the partition of food resources coupled with the evolutionary adaptation of the morphology of the jaw (Liem 1991; Danley and Kocher 2001; Albertson et al. 2003). Alternatively, speciation may result from allopatric situations that either occurred in the past (historical allopatry) or are still effective in the present time, where vicariant events separated populations that accumulated mutations through drift (Bermingham et al. 1997; Bernardi et al. 2003). Populations may later rejoin through secondary contact, making it difficult to distinguish from true sympatric speciation (Coyne and Orr 2004).

Study System, Hypotheses, and Predictions

In this study, we have focused on two congeneric sister species of marine fishes, the black surfperch, *Embiotoca jacksoni*, and the striped surfperch, *E. lateralis*. These two northeastern Pacific reef species compete for resources, a potential situation for ecological speciation (Hixon 1980; Schmitt and Coyer 1983; Holbrook et al. 1985; Holbrook and Schmitt 1986, 1989, 1992, 1995; Schmitt and Holbrook 1986, 1990). *Embiotoca jacksoni* are present continuously from northern California to central Baja California. A previous genetic study has shown that *E. jacksoni* experienced a vicariant event that separated populations in the Los Angeles region (Bernardi 2000). *Embiotoca lateralis* ranges from Alaska to northern Baja California (Punta Cabras), with a distribution gap from Santa Barbara to Punta Banda (Fig. 1), resulting in a disjunct population restricted to the region comprised between Punta Banda and Punta Cabras (Fig. 1).

The goal of this study was to determine if competitive exclusion by the congeneric *E. jacksoni* or if a similar historical (vicariant) event was responsible for the southern California distribution gap observed in *E. lateralis*. Importantly, if the distribution gap resulted from a vicariant event, subsequent secondary contact between northern and southern populations of *E. lateralis* may have been prevented by ecological competition with *E. jacksoni*, but in this case competition would not be its primary cause.

The alternative hypotheses of ecological and historical factors predict different testable phylogeographic and demographic signatures. As mentioned above, a genetic study based on mitochondrial DNA sequences (control regions) has shown that *E. jacksoni* exhibits a strong genetic break across the Los Angeles region where, coincidentally, *E. lateralis* is absent (Bernardi 2000). This is a known region of genetic discontinuities for several coastal marine species (Dawson 2001). Historical events were suggested as the major factor in shaping these genetic patterns (Bernardi 2000; Dawson 2001; Dawson et al. 2002). Thus, one possible explanation

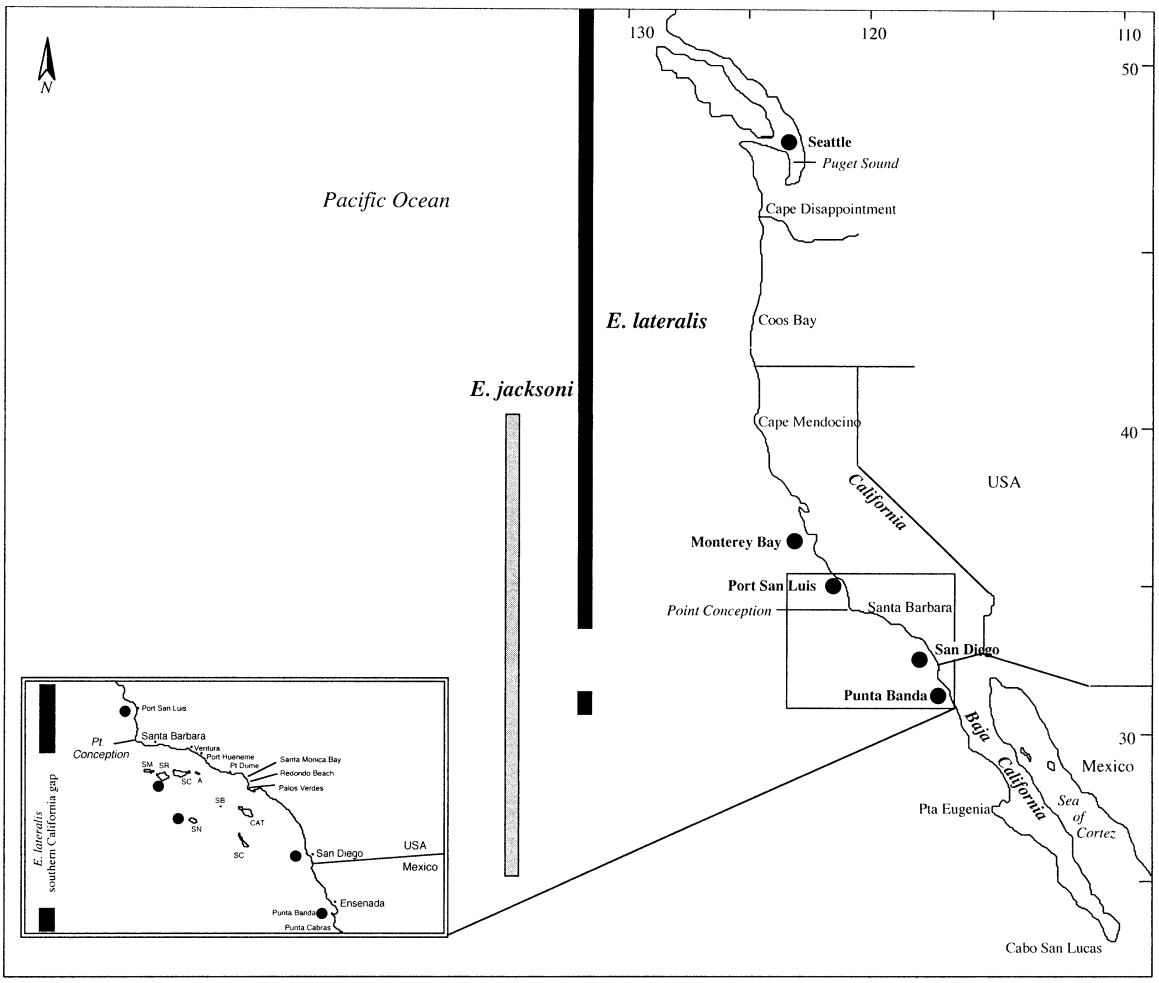

FIG. 1. Distribution map and sampling locations of *Embiotoca jacksoni* and *E. lateralis*. Left bars represent the mainland ranges of the two species.

for the present-day distributions is that populations of both *E. jacksoni* and *E. lateralis* were subjected to similar historical vicariant events. In this case, concordant phylogeographic patterns (concordant genetic breaks) would be expected (Avise 2000). The vicariant event would have been followed by secondary contact in *E. jacksoni* but not in *E. lateralis*. Thus, in addition to a phylogeographic break, the vicariance hypothesis would predict that central California populations of *E. jacksoni* that moved in from their historical separation would show signatures of immigration, followed by population expansion. Northern populations of both species may show increases due to range expansions after the last glacial maximum (LGM, Wares 2002; see also Wares and Cunningham 2001; Marko 2004), with *E. lateralis* showing a stronger increase than *E. jacksoni* as its range expanded well within the glaciated region (Fig. 1). Southern populations should show stable populations (growth equals zero) for both species.

In contrast, if ecological competition were the primary cause for the absence of *E. lateralis* from southern California, competition could have predated the historical events that separated *E. jacksoni* populations. *Embiotoca lateralis* would then show a genetic break between its disjunct populations that would be stronger than what has been observed in *E. jacksoni*. Furthermore, the present boundaries of the range disjunction of *E. lateralis* (Santa Barbara to the north, Punta Banda to the south) would not correspond to the location of historical separation but to the boundaries of the region where *E. jacksoni* outcompetes *E. lateralis*. In this case, *E. jacksoni* populations that are found between Santa Barbara and Punta Banda (the distribution gap of *E. lateralis*) would not show a particular trend in immigration or emigration and would not show a particular trend in population fluctuations.

Life History

The genus *Embiotoca* comprises only two species *E. jacksoni* and *E. lateralis*, and is part of the small surfperch species flock, a family (Embiotocidae) restricted to the northern Pacific Ocean (Tarp 1952; Bernardi and Bucciarelli 1999). Embiotocids comprise 22 livebearing species that give birth to fully developed young that remain close to the parents, thus limiting their dispersal potential (Waples 1987; Bernardi 2000). The family is divided in two tribes, Amphisticines and Embiotocines (Tarp 1952). The Embiotocine tribe includes the two focal species of this study.

Two distinct foraging strategies have been recognized in this tribe. Most species (including *E. lateralis*) browse invertebrate species from the benthic substrate, which are then processed through mastication by the pharyngeal jaws (jaws inside the mouth; Drucker and Jensen 1991). In contrast, three species (including *E. jacksoni*) process food through oral winnowing (Laur and Ebeling 1983; Drucker and Jensen 1991). These species take mouthfuls from the benthos and efficiently separate food from debris within their mouth. Following deglutition of food, debris is ejected from the mouth (Drucker and Jensen 1991). It has been suggested that winnowing enables these three species to exploit resources that are effectively unavailable to the other sympatric surfperch species (Schmitt and Holbrook 1984a,b, 1986; Holbrook and Schmitt 1989). Thus, winnowing may allow for sympatric coexistence through resource partitioning (Drucker and Jensen 1991), which may ultimately be responsible for the radiation in the group (Laur and Ebeling 1983), not unlike the case of Lake Malawi cichlids mentioned above.

Embiotoca jacksoni and *E. lateralis* have similar adult sizes, clutch sizes, densities, and food preferences (Hixon 1980; Schmitt and Coyer 1983). When in sympatry, these two species compete strongly for a single preferred resource: dense patches of crustacean food located on the alga *Gelidium robustum* (Hixon 1980; Schmitt and Coyer 1983; Holbrook et al. 1985; Holbrook and Schmitt 1986, 1989, 1992, 1995; Schmitt and Holbrook 1986, 1990). The presence or absence of winnowing mentioned above may be the key feature that separates the two species when they are in competition. Specifically, resource competition in these two species results in space partitioning, with *E. lateralis* being more abundant in shallower water, where resources are more desirable (Schmitt and Holbrook 1990). Reciprocal removal experiments evidenced asymmetrical competition, with the removal of *E. lateralis* increasing the abundance of *E. jacksoni*, whereas the removal of *E. jacksoni* had smaller effects on the abundance of *E. lateralis* (Schmitt and Holbrook 1990). In addition to microhabitat segregation, the distribution ranges of *E. lateralis* and *E. jacksoni* differ. *Embiotoca lateralis* is found from Alaska to northern Baja California (where cold upwelled water is present) but is absent from the warmer waters of the southern California Bight, from Santa Barbara to San Diego, thus creating a disjunct distribution (Miller and Lea 1972; Fig. 1). In contrast, *E. jacksoni* seems to be more tolerant of warmer water and is found continuously from Mendocino County, California, to central Baja California, Mexico (Miller and Lea 1972). The ranges of the two congeneric species therefore overlap along an extensive stretch of coast along central California and off northern Baja California (Fig. 1). In addition, *E. jacksoni* is found in all the California Channel islands, but *E. lateralis* is only present in the cooler waters of the northern islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) and the westernmost San Nicolas Island.

The goal of this study was to combine a comparative phylogeographic approach (Grismer 2000; Arbogast and Kenagy 2001; Dawson et al. 2002; Bernardi et al. 2003) and a demographic approach (e.g., Wares and Cunningham 2001; Wares 2002; Marko 2004) to test the two alternative hypotheses that describe the present-day distribution of *E. jacksoni* and *E. lateralis*. Previous genetic studies have been done on the two *Embiotoca* species. Partial mitochondrial control regions in *E. jacksoni* showed a genetic break between northern and southern populations (Bernardi 2000). In contrast, early genetic work based on allozymes showed no genetic divergence across the southern California distribution gap for *E. lateralis* (Haldorson 1980). This result may be due to the lack of genetic divergence between these populations or to the lack of resolution of the selected molecular markers. To address the latter point, we used a fast-evolving molecular marker, the mitochondrial control region, in this comparative study. Furthermore, similar sample sizes and locations were used for both species to ensure consistency in data collection.

Materials and Methods

Collections and DNA Samples

Fishes were collected by free or scuba diving with pole spears. After collection, tissue samples (gills, liver, fin clips, or muscle) were immediately placed in 95% ethanol and stored at ambient temperature in the field, and then at 4°C in the laboratory. Total genomic DNA was prepared from 75–150 mg of tissue by proteinase K digestion in lysis buffer (10 mM Tris, 400 mM NaCl, 2 mM EDTA, 1% SDS) overnight at 55°C. This was followed by purification using chloroform extractions and alcohol precipitation (Sambrook et al. 1989).

Polymerase Chain Reaction Amplification and Sequencing

Two datasets were used in this study, one for the phylogenetic analysis and one for the demographic analysis (Table 1). For the phylogenetic analysis, amplification of a region that comprised the complete mitochondrial control region (also called D-loop), two t-RNAs (Pro and Phe), and a portion of the 12S rRNA was accomplished with universal primers CR-A (Lee et al. 1995) and 12SBH (Kocher et al. 1989). Amplifications consisted of a 26-μl reaction containing 22.5 μl of PCR-mix (ABgene, Rochester, NY), 10–100 ng of DNA, and 0.3 mM of each primer. Cycling profiles of 45 sec at 94°C, 1 min at 50°C, 45 sec at 72°C for 35 cycles, followed by 3 min at 72°C. After purification of the PCR fragments, sequencing was performed according to standard protocols recommended by the manufacturer (Applied Biosystems, Foster City, CA) and resolved with an ABI 3100 automated sequencer. Sequencing was performed in both directions with the primers used in the PCR amplification as well as an internal primer, EJEL (5′GAG TTA AAA TCA TGA TTT ATG CTC 3′). Sampling sites and sample numbers are described in Table 1. For the demographic analysis, we used a larger dataset based on partial control region sequences. *Embiotoca jacksoni* samples were from Bernardi (2000). In the case of *E. lateralis*, we trimmed the complete control region (from this study) down to the same length as what was used in Bernardi (2000). We also sequenced 18 additional *E. lateralis* samples from Punta Banda, Baja California, Mexico, using the PCR-primers CR-A and CR-E (Lee et al. 1995). Sample numbers and locations are presented in Table 1.

Phylogenetic and Population Analyses

We used the computer program Clustal V implemented by Sequence Navigator (Applied Biosystems) to align the DNA

TABLE 1. Collection localities of *Embiotoca lateralis* and *E. jacksoni*. Columns represent the number of individuals included in the study and locality abbreviations as in Figure 2. Asterisks indicate populations that were not sampled in this study, and n/a indicates places where a species is absent. The left panel (phylogeography) is based on complete mitochondrial control regions (data for Fig. 1), and the right panel (demography) is based on partial control regions (data for Table 2).

		Phylogeography		Demography	
		E. lateralis	*E. jacksoni*	*E. lateralis*	*E. jacksoni*
Northern region				26	53
Seattle	SEA	05	n/a	05	n/a
Tomales Bay		*	*	*	10
Monterey Bay	MB	10	10	18	26
Port San Luis	PSL	03	03	03	17
North-central region				n/a	24
Ventura		n/a	*	n/a	11
Port Hueneme		n/a	*	n/a	02
Point Dume		n/a	*	n/a	11
South-central region				n/a	43
Redondo Beach		n/a	*	n/a	11
Palos Verdes		n/a	*	n/a	09
Cabrillo Beach		n/a	*	n/a	01
San Diego	PL	n/a	05	n/a	22
Southern region				28	25
Punta Banda	PB	10	10	28	12
Isla San Martin		n/a	*	n/a	02
Bahia Asuncion		n/a	*	n/a	01
Bahia Tortuga		n/a	*	n/a	01
Isla San Roque		n/a	*	n/a	09
California Channel Islands					
Santa Rosa Island	SRI	05	05	*	*
San Nicolas Island	SNI	03	03	*	*

sequences. When present, gaps were counted as single steps, regardless of size. Nucleotide sequence evolution models were evaluated using likelihood-ratio tests implemented by Modeltest v.3.06 (Posada and Crandall 1998). Phylogenetic relationships were assessed using maximum likelihood, maximum parsimony, and neighbor-joining methods implemented by the Software package PAUP ver. 4.0 (Swofford 1998). Topological confidence was evaluated with 1000 bootstrap replicates (Felsenstein 1985) for neighbor-joining and also using the fast-step method for maximum parsimony (only one tree kept at each replicate). In both neighbor-joining and maximum parsimony, bootstrapping analysis was performed with equal weighting of transitions and transversions. Maximum likelihood analyses were performed using the optimal substitution model resulting by likelihood-ratio tests with or without enforcing a molecular clock. Alternative topologies were compared using Shimodaira-Hasegawa (Shimodaira and Hasegawa 1999; Goldman et al. 2000) statistical tests implemented in PAUP.

Gene Flow and Genetic Divergence

Genetic divergence was estimated using Kimura two-parameter distance. To account for polymorphism in each population (or species), divergence was estimated as the average pairwise distance between populations minus the average pairwise distance within a population. Genetic divergence (as a proxy for population divergence) estimates based on a single mitochondrial locus, however, may differ from the actual time of separation between populations (see Edwards and Beerli 2000). Gene flow (N_em, where N_e is the effective population size and m the migration rate; F_{ST}), Haplotype numbers (Hn) and haplotype diversity (Hd) were calculated using the software package DNAsp (Rozas and Rozas 1997).

Historical Demography

Historical demography was evaluated using a larger dataset (145 individuals) from Bernardi (2000) based on partial mitochondrial control regions of *E. jacksoni*. The same region was used for 54 *E. lateralis* individuals. Coastal populations were divided into four groups: two groups adjacent to the Central California gap (north and south), and two groups within the gap (north-central and south-central). Population specifications and sample numbers are given in Tables 1 and 2. Population parameters Θ ($= 2N\mu$, where μ is the mutation rate for mitochondrial DNA) and g (the exponential growth parameter in units of μ^{-1}) were estimated using a coalescent approach with FLUCTUATE 1.4 (Kuhner et al. 1998). The parameter Θ was estimated with population growth (parameters are estimated jointly) or with growth kept constant ($g = 0$). Both estimates were obtained by running five replicates, which generated a mean value and its associated standard deviation. Analysis of each dataset was done with 10 short Monte Carlo chains of 4000 steps each and five long chains of length 20,000, with a sampling increment of 20. Fluctuate generated a random topology for initial searching.

Migration between the four groups was analyzed with the software MIGRATE 1.7.3 (Beerli 2003), which is a maximum likelihood estimator based on the coalescent theory. It uses a Markov chain Monte Carlo approach to investigate possible genealogies with migration events. Analysis of each dataset was also done with 10 short Monte Carlo chains of 4000 steps each and five long chains of length 20,000, with a

TABLE 2. Historical demography of *Embiotoca jacksoni* and *E. lateralis*. Columns represent the regions investigated, sample numbers, haplotype numbers (Hn), haplotype diversity (Hd), immigration, theta with no growth, theta with growth, and growth (*g*). The latter four columns are averages of 5 replicates, between parentheses are their standard deviations. Immigration is given for *E. jacksoni*, where Nm represents the number of migrants into the populations from the adjacent population (e.g. there were 5.72 migrants from the north-central region into the northern region).

Species	Population	*N*	Hn	Hd	Immigration (N_em)	θ (no growth)	θ (growth)	*g*
E. jacksoni	northern	53	10	0.52	5.72 (±1.19)	0.0145 (±0.0028)	0.0755 (±0.0240)	1276.5 (±379.1)
	north-central	24	6	0.73	643.32 (±395.11)	0.0103 (±0.0006)	0.0151 (±0.0055)	168.5 (±111.2)
	south-central	43	12	0.55	0.17 (±0.45)	0.0115 (±0.0007)	0.0292 (±0.0063)	341.2 (±106.9)
	southern	25	5	0.72	2.59 (±2.14)	0.0047 (±0.0010)	0.0152 (±0.0091)	750.8 (±273.4)
E. lateralis	northern	26	9	0.53		0.0116 (±0.0008)	0.0956 (±0.0946)	9523.2 (±908.0)
	southern	28	5	0.71		0.0045 (±0.0005)	0.0038 (±0.0005)	−37.55 (±39.4)

sampling increment of 20. For each estimate, five replicates were used to generate a mean value of migration (N_em) and its associated standard deviation.

RESULTS

Sequences

PCR amplifications and sequencing resulted in a fragment that was 1330 bp long. Of these, 12 bp were in the tRNA Pro region (partial sequence); 816 bp were in the control region (complete sequence), which corresponded to 61.3% of the region studied here; 67 bp were in the tRNA Phe region (complete sequence); and 435 bp were in the 12S rRNA region (partial sequence). Of the aligned 1330 bp, 141 bp were variable, and 112 were phylogenetically informative. The control region was the most variable section, with 103 variable sites (73% of all variable sites). Eight indels (insertions and deletions) of one nucleotide each were observed between *E. jacksoni* individuals, one indel of one nucleotide was observed in a single *E. lateralis* individual. Due to their close phylogenetic relationship, only 16 short indels corresponding to a total of 17 nucleotides were observed between the two species. When testing evolution models using Modeltest (Posada and Crandall 1998), we found that the HKY + G model (Hasegawa et al. 1985), with a transition/transversion ratio of 2.038 and a gamma distribution shape parameter of 0.0714 best fitted our data. A molecular phylogeny based on the neighbor-joining method is presented in Figure 2. The topology of this tree was statistically indistinguishable to the topologies found with the maximum likelihood method (with or without enforcing a molecular clock) and with the maximum parsimony methods.

Phylogenetic Relationships

Embiotoca jacksoni and *E. lateralis* clustered in two reciprocally monophyletic assemblages defined by 82 fixed differences (6.6%, Kimura two-sequence divergence; Fig. 2). In addition, *E. jacksoni* and *E. lateralis* showed similar intraspecific phylogenetic relationships, where northern and southern populations grouped into two well-separated monophyletic clades, and California Channel Island individuals grouped with the northern clade (Shimodaira-Hasegawa test, $P > 0.1$; Fig. 2). Northern populations included Monterey Bay, Port San Luis, and northern Channel Islands individuals for both species, as well as Seattle individuals for *E. lateralis* (where *E. jacksoni* is absent). The southern clade included all the individuals collected at Punta Banda for both species, as well as Point Loma individuals for *E. jacksoni* (where *E. lateralis* is absent). Most California Channel Island individuals formed a paraphyletic cluster that was closely related to the northern clade for both species (Fig. 2).

Gene Flow and Genetic Divergence

Fixed differences between northern and southern clades resulted from an absence or limited gene flow between these regions (no gene flow was detectable). Southern individuals were characterized by 11 and seven unique substitutions compared to the northern individuals in *E. jacksoni* and *E. lateralis*, respectively. This result expanded previous observations

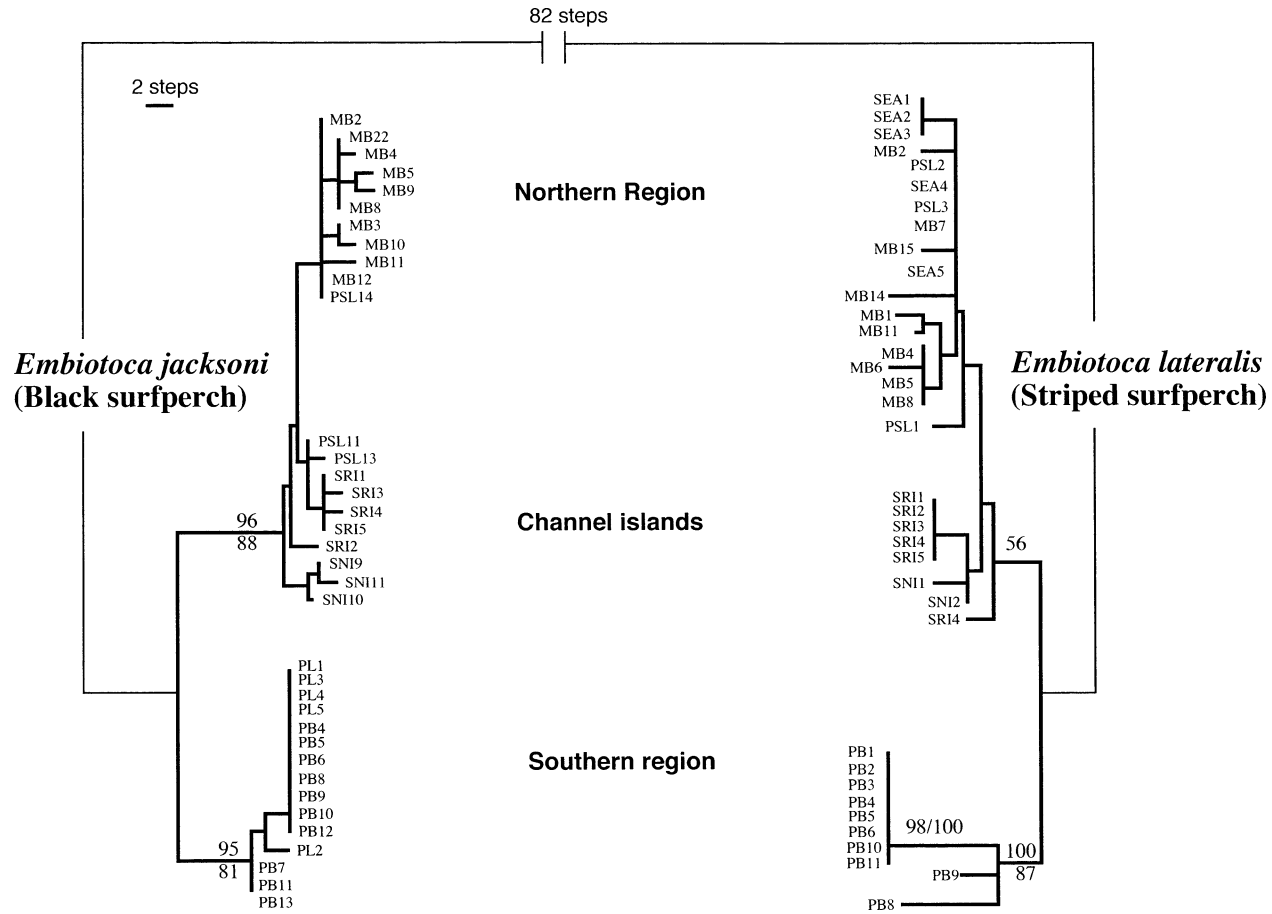

FIG. 2. Molecular phylogeny of *Embiotoca jacksoni* and *E. lateralis* based on the mitochondrial control region marker using the neighbor-joining method (using Kimura two-parameter distances). Bootstrap support is shown when above 50%, neighbor-joining bootstrap support is shown above the nodes, maximum parsimony bootstrap support is shown below the nodes. Scale bar represents two steps.

on *E. jacksoni* where evidence of limited gene flow could only be observed in populations directly north and south of the Santa Monica Bay/Los Angeles region (Bernardi 2000). Based on the evolution model obtained using Modeltest, northern and southern clades exhibited a control region sequence divergence of 1.37% and 0.62% in *E. jacksoni* and *E. lateralis*, respectively. These values were also very similar to divergence values based on Kimura two-parameter distances (1.18% and 0.54%, respectively). When using a control region molecular clock calibrated for transisthmian fish species (3.6 ± 0.45% per million years Kimura distance; Donaldson and Wilson 1999), these divergences corresponded to an approximate separation that occurred 328,000 (±36,000) years ago and 150,000 (±17,000) years ago respectively. These values were smaller than between populations of the tidewater goby, *Eucyclogobius newberryi*, another California coastal fish that shows a similar phylogeographic break (1–2 million years ago, Dawson et al. 2001, 2002). Levels of genetic divergence within clades were in the same order of magnitude for the *E. jacksoni* and *E. lateralis* with average pairwise divergences in the northern clade of 0.39% and 0.16% and 0.10% and 0.20% in the southern clade for *E. jacksoni* and *E. lateralis*, respectively. In addition, gene flow levels between northern mainland populations and the northern Channel Islands were low and almost identical in *E. jacksoni* and *E. lateralis*. Number of migrants per generation between these regions were 0.77 for *E. jacksoni* (F_{ST} = 0.39) and 0.75 for *E. lateralis* (F_{ST} = 0.40).

Historical Demography

Migration from the adjacent regions (northern region, southern region) into the central region (north-central region, south-central region) was estimated for *E. jacksoni* (Table 2). Migration from the northern region into the north-central region was very high, 643 migrants per generation, compared to only 5.7 northbound migrants from that region (Table 2). In contrast, migration between south-central and south regions was low, with 0.17 ± 0.45 northbound migrants per generation and 2.59 ± 2.14 southbound migrants per generation (Table 2).

Population growth was found to be positive in the north-central and south-central regions (g = 168 and g = 341). Northern populations of *E. jacksoni* and *E. lateralis* showed very fast growth (g = 1276 and 9523, respectively). In contrast, while southern populations of *E. jacksoni* showed positive growth (g = 750), *E. lateralis* showed no or slightly declining population growth (g = −37; Table 2).

Discussion

Black surfperch, *E. jacksoni*, and striped surfperch, *E. lateralis*, exhibit a phylogeographic break that separates northern and southern populations (Fig. 2). In *E. lateralis*, this genetic break also coincides with a distribution gap from Santa Barbara, California, to Punta Banda, Mexico (Fig. 1). The concordant phylogenetic pattern in the two species gives us an opportunity to test alternative hypotheses that would explain the cause of the distribution gap in *E. lateralis*: historical via a similar vicariant event or ecological through resource competition.

Vicariance Hypothesis

Historical separation of populations predicts that phylogeographic patterns in the two species be concordant. This was evidenced by a strong genetic break between northern and southern populations in both species. If the same vicariant event caused these patterns, however, one would expect for the genetic break to be of similar magnitude. The genetic divergence between northern and southern clades is approximately twice as large in *E. jacksoni* than in *E. lateralis*. This difference in genetic divergence could be due to different vicariant events or to intrinsic genetic differences between the species. For example, this result would be consistent with a historically maintained higher level of mitochondrial DNA diversity in *E. jacksoni* due to a larger effective population size. However, this does not seem to be the case, as values of Θ for the two species are not significantly different (Table 2). Thus, different vicariant events are a more likely explanation for the differences in the observed population divergences. The southern California region has been geologically and climatically very active, producing genetic breaks in the Los Angeles region in several species of fish and invertebrates (Dawson 2001). It is therefore possible that a combination of glaciating and tectonic events produced the patterns observed in *Embiotoca* species. For example, the timing of the Illinoian glaciation, which resulted in a lowered sea level and its associated changes in coastal contours, approximately 400,000 years ago, does match the timing of the separation of northern and southern *E. jacksoni* populations. More recent events could have caused the separation of *E. lateralis* populations, which resulted in a similar phylogeographic pattern but with a smaller genetic divergence.

In addition to phylogeographic signatures, a vicariant event should also leave demographic signatures. While *E. lateralis* northern and southern populations are separated by a large geographic gap, *E. jacksoni* populations are continuous, probably resulting from secondary contact at Santa Monica Bay (Bernardi 2000). *Embiotoca jacksoni* populations that moved in from their historical separation (called here north-central and south-central populations) should exhibit signatures of migration and population expansion. The north-central population, which ranges from Santa Barbara to Santa Monica Bay, does show both signatures (immigration, $N_em = 643$, and population growth, $g = 168$). In contrast, the south-central population, which ranges from Santa Monica bay to Punta Banda, exhibited population growth ($g = 341$), but did not show evidence of immigration ($N_em = 0.17$). These data suggest that the evolutionary history of the north-central and south-central regions may be different. The north-central region may correspond to the area where both *E. jacksoni* and *E. lateralis* were historically displaced, with *E. jacksoni* showing demographic signatures of recolonization, while preventing *E. lateralis* from recolonizing the area. In contrast, the south-central region may simply be a region where *E. jacksoni* was always present. In this case, competitive exclusion of *E. lateralis* from that region cannot be ruled out.

Resource Competition Hypothesis

The resource competition hypothesis can be distinguished from the historical hypothesis by the different phylogeographic and demographic patterns it predicts. If the Santa Barbara/Punta Banda distribution gap observed in *E. lateralis* were due to competitive exclusion by *E. jacksoni*, one would expect the competition to have been in effect since the sympatric coexistence of the species, probably predating the genetic break observed in *E. jacksoni*. This would result in a genetic divergence between northern and southern populations of *E. lateralis* to be larger than in *E. jacksoni*. The observed phylogeographic patterns do not support this hypothesis, because the opposite pattern is observed (genetic divergence is larger in *E. jacksoni* than in *E. lateralis*). At the demographic level, the north-central region supports the vicariant hypothesis also; however, the south-central region is a site where resource competition may have driven the displacement of *E. lateralis*. Indeed, between Santa Monica Bay and Punta Banda, there is no evidence of immigration for *E. jacksoni*, indicating that populations may very well have been in that region for a very long time. The absence of *E. lateralis* from that region may again be due to several causes including historical factors and ecological competition. A historical vicariant hypothesis seems unlikely because it should have affected both *E. lateralis* and *E. jacksoni*, yet *E. jacksoni* does not show any evidence of recolonization in that region. In the absence of vicariance, ecological competition remains a possible explanation. When in competition, *E. lateralis* are found in shallower water, where habitat and food is more desirable (Schmitt and Coyer 1983; Holbrook and Schmitt 1986). Since *E. lateralis* is better adapted to colder waters compared to *E. jacksoni*, a contributing factor for the absence of *E. lateralis* from that region is that shallow water there is too warm for that species. The region from Santa Monica Bay to San Diego has indeed the warmest surface water of the distribution range of *E. lateralis*. Warm water alone, however, cannot be the sole factor for the absence of this species, as colder habitat is available below 10–15 m (Hayward and Venrick 1998), a depth where *E. lateralis* is commonly found in other regions.

Conclusion

The study of sympatry is experiencing a renaissance with a renewed interest in character displacement (Schluter and McPhail 1992; Adams and Rohlf 2000; Losos 2000), resource competition (Schluter 2000), and speciation (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999; Doebeli and Dieckmann 2000; Drossel and McKane 2000). The difficulty of working with sympatric speciation derives from the numerous factors that may prevent a positive determination

that speciation did occur sympatrically (Seehausen 2000; Turelli et al. 2001; Coyne and Orr 2004). This problem is worsened in marine systems where direct observation is difficult. In the case of the *Embiotoca* surfperches, thorough ecological work has clearly demonstrated that when in sympatry, *E. jacksoni* and *E. lateralis* compete for food resources (Hixon 1980; Schmitt and Coyer 1983; Holbrook et al. 1985; Holbrook and Schmitt 1986, 1989, 1992, 1995; Schmitt and Holbrook 1986, 1990). Unfortunately, little ecological work has been done north and south of the sympatric region where *E. lateralis* and *E. jacksoni* (respectively) live without a congeneric competitor, thus precluding us from determining how much character displacement is integral to the system. In sympatry, it seems likely that behavioral differences between the two species (presence or absence of winnowing) are a key component in determining the outcome of the competition.

Our data suggest that the absence of *E. lateralis* from southern California waters, from Santa Barbara to Punta Banda, Mexico, is due in part to historical factors, but is also likely to be, at least in part, ecologically driven.

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