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Comparative phylogeography of sympatric sister species, *Clevelandia ios* and *Eucyclogobius newberryi* (Teleostei, Gobiidae), across the California Transition Zone

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Abstract

It is paradigmatic in marine species that greater dispersal ability often, but not always, results in greater gene flow and less population structure. Some of the exceptions may be attributable to studies confounded by comparison of species with dissimilar evolutionary histories, i.e. co-occurring species that are not closely related or species that are closely related but allopatric. Investigation of sympatric sister species, in contrast, should allow differences in phylogeographic structure to be attributed reliably to recently derived differences in dispersal ability. Here, using mitochondrial DNA control region sequence, we first confirm that *Clevelandia ios* and *Eucyclogobius newberryi* are sympatric sister taxa, then demonstrate considerably shallower phylogeographic structure in *C. ios* than in *E. newberryi*. This shallower phylogeographic structure is consistent with the higher dispersal ability of *C. ios*, which most likely results from the interaction of habitat and life-history differences between the species. We suggest that the paradigm will be investigated most rigorously by similar studies of other sympatric sister species, appended by thorough ecological studies, and by extending this sister-taxon approach to comparative phylogeographic studies of monophyletic clades of sympatric species.

Keywords: coastal marine evolution, dispersal, estuary, mtDNA control region, phylogeography

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Introduction

Recent molecular studies have demonstrated considerable phylogeographic structure in several coastal marine taxa whose ranges span the California Transition Zone in the northeastern Pacific Ocean (Burton 1998; Marko 1998; Bernardi 2000; Dawson *et al.* 2001). The deepest phylogeographic breaks in three species, *Tigriopus californicus* (Burton 1998), *Embiotoca jacksoni* (Bernardi 2000) and *Eucyclogobius newberryi* (Dawson *et al.* 2001), co-occur geographically in the vicinity of Los Angeles indicating long-term inhibition of gene flow across this region (Dawson 2001). However, gene flow in other species has apparently not been affected by physical discontinuities in the Los Angeles region (LAR; Palumbi 1995; Burton 1998; Dawson 2001). This dichotomy may be attributable to differences in dispersal potential due to habitat or life-history preferences. For example, the species displaying phylogeographic structure across the LAR, such as *T. californicus*, *E. jacksoni* and *E. newberryi*, are generally poor dispersers that inhabit patchy supra-tidal, shallow-water or estuarine habitats, respectively (Burton & Lee 1994; Bernardi 2000; Dawson *et al.* 2001). In contrast, species lacking phylogeographic structure across the LAR, such as the solitary coral *Paracyathus stearnsii* (Beauchamp & Powers 1996; Hellberg 1996), generally have planktonic larvae and high dispersal potential, and inhabit more continuous habitat and often deeper water (see Waples 1987; see also Wares *et al.* 2001). Indeed, in marine species, greater dispersal ability is accompanied sufficiently frequently by increased gene flow and decreased population structure (e.g. Waples 1987; Avise 1992; see also Doherty *et al.* 1995) that this relationship has achieved the

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status of a paradigm (Palumbi 1995) despite a number of exceptions (e.g. Knowlton & Keller 1986; Shulman & Bermingham 1995; Barber *et al*. 2000).

Exceptions to the paradigm might be attributable to historical events. Often, correlative studies compare sympatric species that are not closely related (e.g. Waples 1987; Avise 1992; Borsa & Benzie 1996; Hellberg 1996) or species that are closely related but inhabit dissimilar ranges (e.g. McMillan *et al*. 1992; Palumbi 1995). Consequently, species may be separated by many millions of years or thousands of kilometres and by differences in their evolutionary histories that had important phylogeographic effects at the time but that are not identifiable from a modern viewpoint. Thus, although the paradigm that dispersal ability determines population structure is compelling, in some cases other factors, such as species-specific or regional patterns of extinction and recolonization, may have had important influences on population structure (Palumbi 1995; Cunningham & Collins 1998; Vogler 1998). More robust studies of the factors affecting historical gene flow and phylogeographic structure therefore must 'control' for such historical events by comparing species that differ minimally in both range and phylogenetic history, i.e. sympatric sister species. Sympatric sister species, by definition, co-occur geographically and share the most recent common phylogenetic history possible and therefore have experienced the same environmental influences throughout their evolutionary history — in essence, they were the same species prior to cladogenesis and occupied the same region after cladogenesis. Differences in the phylogeography of sympatric sister species should be attributable to recently derived, species-specific, characteristics.

Here we investigate the effects of habitat and life-history on the dispersal ability and phylogeographic structure of the arrow goby, *Clevelandia ios*, and the tidewater goby, *Eucyclogobius newberryi*. In contrast to *C. ios*, and other eastern Pacific bay gobies, *E. newberryi* has low dispersal potential due to unique habitat preferences and life-history characteristics (Table 1; MacGinitie 1935; Weisel 1947; Prasad 1959; Barlow 1961, 1963; Miller & Lea 1972; Hart 1973; Brothers 1975; Watson 1996; Kent & Marliave 1997; Swenson 1999). Prior molecular analyses demonstrated that *E. newberryi* is also highly phylogeographically structured (Dawson *et al*. 2001). Hypothetically therefore, the phylogeographic structure of *E. newberryi* may be attributable to its uniquely low dispersal potential and its putative sister species *C. ios* (Ginsburg 1945; C.C. Swift unpublished results) should have higher gene flow and less phylogeographic structure. Here, first, we investigate the sister taxa relationship of *C. ios* and *E. newberryi* within the monophyletic clade of eastern Pacific bay gobies (minus *Gillichthys*, *Lethops* and *Typhogobius*) as established by morphological studies (Ginsburg 1945; C.C. Swift unpublished results) and, second, we explore the dispersal–gene flow hypothesis by comparative phylogeographic analyses of variation in the mitochondrial control region (mtCR) of *C. ios* and *E. newberryi* across the California Transition Zone.

Materials and methods

Collection, DNA extraction, polymerase chain reaction and sequencing

Data describing *Eucyclogobius newberryi* were taken from Dawson *et al*. (2001) and supplemented with new sequences from 14 *E. newberryi* collected at the Santa Clara River (eight specimens) and Oxnard (six specimens) in 1999 to match, as well as possible, the geographical distribution and sizes of samples of *Clevelandia ios* collected between 1997 and 2000 (Fig. 1; Table 2). In addition, four other bay gobies [*Gillichthys mirabilis*, *Ilypnus gilberti*, *Lepidogobius lepidus*, *Quietula y-cauda* (*Evermannia* was not included following Birdsong *et al*. 1988; nor *G. seta*)] and one outgroup (*Lythrypnus* sp.) were collected during 1999–2000 from coastal California waters (Fig. 1). Fish were caught in seine nets (or plankton trawls in the case of larval *Q. y-cauda* from Morro Bay), marked individually, and stored at minus 80 °C (*E. newberryi*, *C. ios*, *Q. y-cauda*) or in 70–100% ethanol (other species). DNA extraction, polymerase chain reaction (PCR), cloning and sequencing of mtCR followed protocols modified from Dawson *et al*. (2001). The modifications included amplification of most mtCR using primers CR-A (Lee *et al*. 1995) and GoDi-H (5′-gcgctgcactctgaaatgc-3′) and variation of the PCR annealing temperature between 49 °C and 52 °C depending on the species of template DNA.

Sequence, phylogenetic and phylogeographic analyses

Goby mtCR sequences were aligned in CLUSTALX (Jeanmougin *et al*. 1998) using the default settings except for gap-opening (= 5, 10, or 20) and gap-extension (= 1) penalties. The alignments were checked by eye, and any obvious misalignments in the 5 : 1 gap-opening : gap-extension alignment were corrected manually in SE-AL v1.0A1 (Rambaut 1996). Additional *E. newberryi* and *C. ios* sequences were aligned by eye with conspecific sequences in PAUP 4.0b5a for PowerMac (Swofford 2001). The ratio of transitions to transversions (ti : tv) was calculated using ARLEQUIN 2.0 for Macintosh (Schneider *et al*. 2000) and used to identify an appropriate weighting scheme for phylogenetic analyses. (For robustness, other weighting schemes were also explored, see Results section.) Phylogenies were reconstructed using unweighted or weighted maximum parsimony, as appropriate (see Results section), in PAUP 4.0b5a. Gapped positions were both included in and excluded from phylogenetic analyses

Table 1 Comparison of attributes of *Clevelandia ios* and *Eucyclogobius newberryi*

Species	*Clevelandia ios*	*Eucyclogobius newberryi*
Range[*,3,4,5,6]	23–48° N, 3200 km, Magdalena Bay to Vancouver Island Puget Trough	33–42° N, 1200 km, Carlsbad submarine canyon (Agua Hedionda lagoon) to Smith River
Distribution[6]	Few large populations; widely separated, often by > 100 km	Many small populations; few large gaps, mostly 1–20 km apart
Juvenile & adult habitat[4,5,6,10,11]	Large estuaries, benthic, year-round in muddy burrows of invertebrates	Coastal lagoons, small seasonally closed estuaries, benthic†
Salinity range[6,10]	15–35‰ (preference) 0–55‰ (tolerance)	0–15‰ (preference) 0–55‰ (tolerance)
Burrowing[4,6]	Year-round, including breeding	Only during breeding
Adult size[4,6]	Up to approx. 60 mm total length	Up to 55 mm total length
Longevity[5,6,8,13]	Annual in southern California; lives 2–3 years in Puget Sound	Annual; has lived to 3 years in captivity
Reproduction[2,4,11]	Year-round, peaks late-winter to early summer	Year-round, peaks in late-spring and early summer
Fecundity[4,5,6,7,13]	~3×10^2–1.2×10^3 Multiple batches (number unknown)	10^2–10^3 (mean 4×10^2) Four to six batches annually
Larval habitat[5,10,13†]	Principally estuarine; also coastal waters at least to 0.5 km offshore but generally less than 18 fathoms	Coastal lagoons, small seasonally closed estuaries; coastal waters?
Larval duration[4,9,10,12]	2–4 weeks‡	Likely < 1 month, possibly as little as a few days.§

*Approximate distance in kilometres 'as the crow flies'.

†Presence/absence data (Lafferty *et al*. 1999a,b) indicated cycles of extirpation–recolonization that must involve movement of *E. newberryi* larvae, juveniles, or adults in coastal waters. However, during the 1900s there was only one record of adult and one record of putative larval *E. newberryi* from coastal waters (Dawson 2000).

‡Larval duration of *C. ios* estimated by extrapolating from time to achieve 7 mm (10 days; Hart 1973) to time to achieve average settlement size of 13 mm (Kent & Marliave 1997). Also, larval life was estimated at approximately 1 month by Brothers (1975).

§Larval duration of *E. newberryi* is poorly documented but seems unlikely to exceed the larval duration of closely related species. Indeed, Capelli (1997) and Ballard *et al*. (1999) suggest the duration may be as little as a few days or 1 week.

References are indicated by the following superscript numbers: [1]MacGinitie (1935), [2]Prasad (1959), [3]Miller & Lea (1972), [4]Hart (1973), [5]Brothers (1975), [6]Swift *et al*. (1989), [7]Matarese *et al*. (1989), [8]Brown & Swenson (1994), [9]Watson (1996), [10]Capelli (1997), [11]Kent & Marliave (1997), [12]Ballard *et al*. (1999), [13]Swenson (1999).

because their utility may vary between datasets (e.g. Swofford *et al*. 1996; van Dijk *et al*. 1999). Parsimony analyses used the heuristic search option employing accelerated transformation, tree-bisection–reconnection, and random sequence addition. Each search consisted of 10 000 replicates, saving and swapping on all shortest trees. Bootstrap analyses were completed using the same heuristic search options but only 100 heuristic replicates were completed for each of the 1000 bootstrap replicates. The Templeton test (Templeton 1983; Swofford *et al*. 1996), as employed in PAUP 4.0b5a, was used to test *a posteriori* the hypothesis that *C. ios* and *E. newberryi* are sister taxa.

Haplotype diversity, nucleotide diversity, and mismatch distributions were calculated using haplotypes inferred from distance (pairwise sequence difference) matrices constructed by ARLEQUIN 2.0. Phylogeographic structure was assessed using analysis of molecular variance (AMOVA, 10 000 permutations; Excoffier *et al*. 1992) in ARLEQUIN v.2.0 by defining phylogeographic groups in accordance with historical barriers to gene flow in the vicinity of Los Angeles and Morro Bay-Big Sur (Fig. 1; Table 2; Burton 1998; Bernardi 2000; Dawson *et al*. 2001; Dawson 2001). Two variations on this structure — placing the southern break (i) north of Ballona, or (ii) south of Anaheim, instead of between Ballona and Long Beach — were investigated in *C. ios* due to the distribution of sample locations in the Los Angeles region. These alternatives produced AMOVA results that differed from the original by < 1% at all hierarchical levels and so were not investigated further. The Mantel test (10 000 permutations) was used

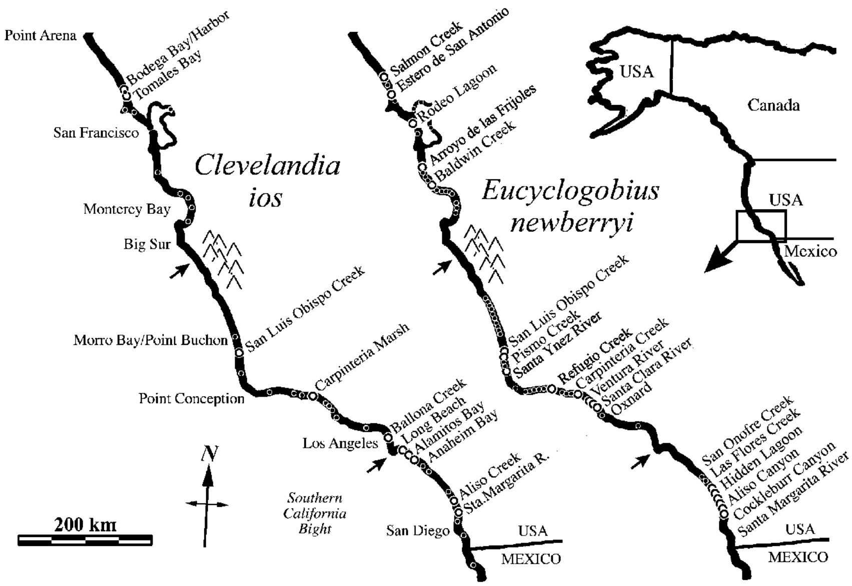

Fig. 1 Map of study area showing collection localities (named, open circles), other current or known twentieth century populations (closed circles) of *Clevelandia ios* and *Eucyclogobius newberryi*, and coastal topographic features associated with phylogeographic structure in coastal California taxa. Three major cities (San Francisco, Los Angeles, San Diego) are identified as landmarks. The California Transition Zone, between approximately Los Angeles and Monterey Bay, is a region of gradual species replacement between Oregonian and Californian biogeographic provinces (Seapy & Littler 1980). Three regions consistent with phylogeographic structure identified previously in *E. newberryi* (Dawson *et al.* 2001), and demarcated in the figure by arrows, were also defined for AMOVA. Additional locations mentioned in Fig. 2 include Stone Lagoon (*E. newberryi* Stone 3) approximately 400 km north of Bodega (see Dawson *et al.* 2001) and San Clemente Island (*Lythrypnus* sp.) in the Southern California Bight (approximately south of Ballona and east of San Diego).

to test for correlation between mean pairwise sequence and geographical distances (R PACKAGE 4.0; Casgrain & Legendre 1999).

Results

Bay goby phylogeny

The homologous fragment of mtCR amplified from all seven species of gobies ranged in length from 506 (*Gillichthys mirabilis*) to 554 (*Lepidogobius lepidus*) nucleotides. The mean per cent base composition was 16.6G : 34.6A : 29.5T : 19.3C. The aligned length was 651 nucleotides, of which 443 positions were polymorphic; there were 198 transitions, 179 transversions and 252 indels. Mean pairwise sequence differences and unweighted and weighted (ti : tv, 1 : 9 and 1 : 20) maximum parsimony analyses of all three alignments supported a sister-taxon relationship between *Clevelandia ios* and *Eucyclogobius newberryi* (Table 3; Fig. 2). Templeton (1983) tests of relationships within the *E. newberryi–C. ios–L. lepidus* clade indicated the most parsimonious arrangement shown in Fig. 2 differed significantly from both a three-way polytomy ($n = 10$, $T = 0$, $P = 0.002$) and sister taxa relationship between *E. newberryi* and *L. lepidus* ($n = 12$, $T = 13$, $P = 0.021$) but did not differ significantly from a clade in which *E. newberryi*

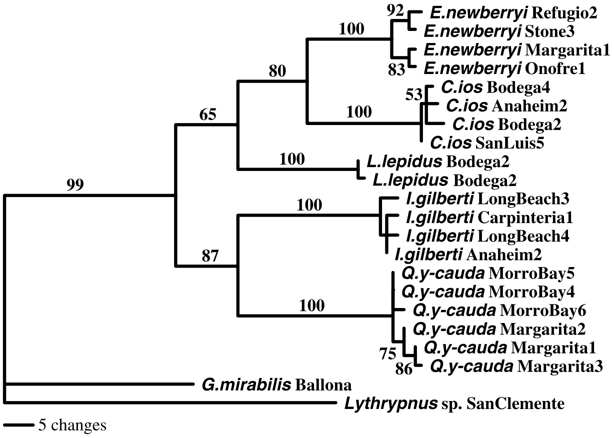

Fig. 2 Mitochondrial control region gene tree of California bay gobies showing the sister taxa relationship of *Clevelandia ios* and *Eucyclogobius newberryi*. One of 35 most parsimonious gene trees (10 000 heuristic searches; tree length = 297; CI = 0.7980) retrieved by unweighted maximum parsimony analysis of the 'gap-opening : gap-extension = 5 : 1' CLUSTALX alignment, corrected by eye, excluding gapped and ambiguous positions. Numbers by branches are bootstrap support values (1000 replicates). Weighted (ti : tv = 1 : 9, 1 : 20) and unweighted maximum parsimony analysis of two additional, uncorrected, CLUSTALX alignments (opening : extension = 9 : 1 and 20 : 1) also supported a sister taxa relationship of *C. ios* and *E. newberryi* if *Lythrypnus* sp. was excluded from analyses to avoid long-branch attraction.

Table 2 Geographic structure of sampling, regions and populations defined in AMOVA, and sample sizes of *Clevelandia ios* and *Eucyclogobius newberryi*

Region	*Clevelandia ios* Population (n)	*Eucyclogobius newberryi* Population ('aggregate') location (n)
North	Bodega Bay/Harbor (9)	'Bodega'
		Salmon Creek (2)
		Estero de San Antonio (4)
	Tomales Bay (7)	'San Francisco'
		Rodeo Lagoon (3)
		Arroyo de las Frijoles (5)
		Baldwin Creek (2)
Central	San Luis Obispo Creek (6)	'San Luis'
		San Luis Obispo Creek (2)
		Pismo Creek (3)
		Santa Ynez River (1)
	Carpinteria Marsh (5)	'Carpinteria'
		Refugio Creek (2)
		Carpinteria Creek (3)
		Ventura River (4)
		Santa Clara River (8)
	Ballona Creek (6)	Oxnard (9)
South	Long Beach (3)	
	Alamitos Bay (5)	
	Anaheim Bay (4)	
	Aliso Creek (1)	Aliso Canyon (2)
	Santa Margarita River (20)	'Santa Margarita'
		San Onofre Creek (3)
		Las Flores Creek (5)
		Hidden Lagoon (2)
		Cockleburr Canyon (1)
		Santa Margarita River (4)

Populations of *E. newberryi* were aggregated for use in AMOVA so that they compared better with the distribution and sizes of samples of *C. ios*. Locations are listed from north to south (Fig. 1).

occurred basal to *C. ios* and *L. lepidus* ($n = 15$, $T = 40$, $P = 0.197$).

Clevelandia ios

Five hundred and twenty-three nucleotides of mtCR from 66 *C. ios* were aligned unambiguously. The mean per cent base composition of this fragment was 18.0G : 33.0A : 29.5T : 19.6C. It contained 69 polymorphic sites including 59 transitions (ti), 13 transversions (tv), and three indels. Pairwise sequence differences were distributed normally with mode 6 and range 0–14 nucleotides (mean 6.36; standard deviation 3.05), the mismatch distribution was not significantly different from the expected distribution for a rapidly expanding population (Fig. 3a; $P_{[\text{Simulated sum of squared deviations (Sim. SSD)} \geq \text{Observed SSD}]} = 0.45$; 200 bootstrap replicates; Schneider *et al*. 2000). Sixty-five unique haplotypes were recognized; haplotype diversity was 0.9995 (SD 0.0028) and nucleotide diversity was 0.0123 (SD 0.0065). Weighted (ti : tv = 1 : 5) and unweighted maximum parsimony analyses of *C. ios* mtCR revealed a shallow, poorly resolved gene tree (Fig. 4a). Genetic variation was not significant among regions (AMOVA: −0.6%, Φ_{CT} −0.0056, $P = 0.397$, d.f. 2) as variation occurred principally at the intrapopulation level (AMOVA: 97.2%, Φ_{ST} 0.0281, $P = 0.054$, d.f. 56) and to a considerably lesser extent among populations within regions (AMOVA: 3.4%, Φ_{SC} 0.0335, $P = 0.087$, d.f. 7). At the scale of these analyses there was no correlation between mean nucleotide differences and geographical distances between populations in *C. ios* (Mantel's $r = -0.0453$; $P = 0.59$) and therefore no evidence of isolation by distance.

Eucyclogobius newberryi

Five hundred and twenty-nine nucleotides of mtCR (homologous to the 523 nucleotides from *C. ios*) from 65

Table 3 Mean pairwise sequence differences within and between bay gobies

	Eucyclogobius newberryi	*Lepidogobius lepidus*	*Ilypnus gilberti*	*Quietula y-cauda*	*Clevelandia ios*	*Gillichthys mirabilis*	*Lythrypnus* sp.
E. newberryi	28.0						
L. lepidus	170.5	1.0					
I. gilberti	221.6	209.8	12.7				
Q. y cauda	237.2	243.3	209.2	8.9			
C. ios	147.8	146.5	219.3	238.3	13.7		
G.mirabilis	256.0	257.5	266.5	305.5	246.8	—	
Lythrypnus sp.	359.3	349.5	366.8	374.0	355.8	290.0	—

Diagonal: average number of pairwise differences within species.
Below diagonal: uncorrected average pairwise difference between species.
Aligned length is 651 therefore percentage difference = difference/651 × 100 (e.g. 28.00 = > 4.3%).

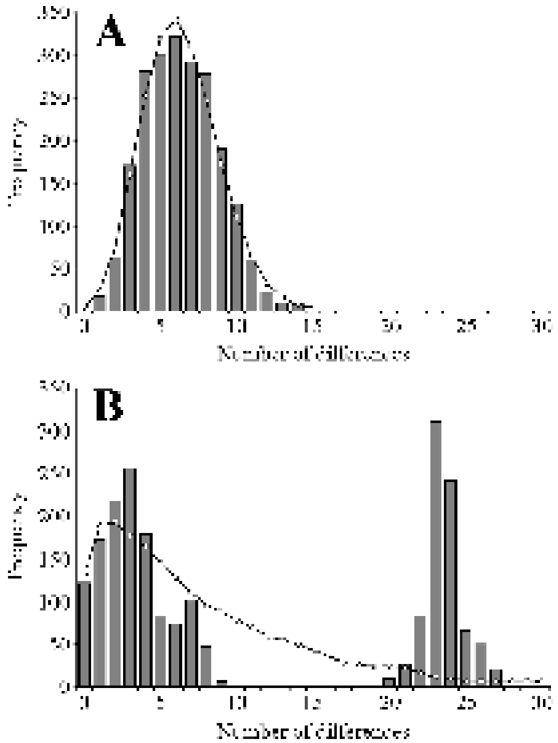

Fig. 3 Mismatch distributions (histograms) constructed using uncorrected pairwise differences among mtCR sequences from (A) 66 *Clevelandia ios* ($\vartheta_0 = 0.35$, $\tau = 6.08$, HRI = 0.010) and (B) 65 *Eucyclogobius newberryi* ($\vartheta_0 = 8.01$, $\tau = 0.56$, HRI = 0.028). Mismatch distributions expected for rapidly expanding populations (white circles, solid line) match closely the distribution observed in *C. ios* ($P_{[\text{Sim. SSD}\geq\text{Observed SSD}]} = 0.45$) but differ considerably from that observed in *E. newberryi* ($P_{[\text{Sim. SSD}\geq\text{Observed SSD}]} = 0.06$).

E. newberryi were aligned. The mean per cent base composition of this fragment was 16.0G : 35.0A : 30.9T : 18.1C. It contained 51 polymorphic sites including 34 transitions, 16 transversions, and one indel. Pairwise sequence differences were distributed bimodally with modes of 3 (range 0–8) and 23 mutations (range 20–29), the mismatch distribution differed considerably from the expected distribution for a rapidly expanding population (Fig. 3b; $P_{[\text{Sim. SSD} \geq \text{Observed SSD}]} = 0.06$; 200 bootstrap replicates; Schneider *et al.* 2000). Thirty-one unique haplotypes were recognized; haplotype diversity was 0.9413 (SD 0.0158) and nucleotide diversity 0.0215 (SD 0.011). Weighted (ti : tv = 1 : 2) and unweighted maximum parsimony analyses revealed a deeply bifurcated gene tree separating populations south of LAR from those north of LAR (Fig. 4b). Genetic variation in *E. newberryi* was distributed principally among regions (AMOVA: 83.9%, Φ_{CT} 0.8392, $P = 0.014$, d.f. 2) and, to a considerably smaller extent, among populations within regions (AMOVA: 6.3%, Φ_{SC} 0.3924, $P < 0.001$, d.f. 6) and within populations (AMOVA: 9.8%, Φ_{ST} 0.9023, $P < 0.001$, d.f. 56). At the scale of these analyses, there is indication that geographical distance contributes to genetic isolation in *E. newberryi* (Mantel's $r = 0.2808$; $P = 0.07$; see also Dawson *et al.* 2001).

Discussion

Bay goby phylogeny and the evolution of Clevelandia ios *and* Eucyclogobius newberryi

Traditionally, morphological systematics places *Gillichthys* and *Lepidogobius* basal to a derived monophyletic clade containing the remaining four or five genera of northeastern Pacific bay gobies [*Clevelandia, Eucyclogobius, Ilypnus, Quietula and* variously, *Evermannia* (e.g. Ginsburg 1945; Barlow 1961; cf. Birdsong *et al.* 1988; C.C. Swift unpublished results)]. *Eucyclogobius* is considered a generally primitive member of the derived clade and relatively closely related to *C. ios* or *Quietula y-cauda*, with a sister taxa relationship between *C. ios* and *E. newberryi* being preferred (Ginsburg 1945; C.C. Swift unpublished results). The molecular phylogenetic analyses and pairwise sequence differences presented here are consistent with the basal position of *G. mirabilis* and affirm the close, indeed sister taxa, relationship of *C. ios* and *E. newberryi* (Fig. 2, Table 3). However, these analyses also suggest that a derived clade that excludes *L. lepidus* would be paraphyletic and that *E. newberryi* is not basal within that derived clade. Rather, molecular data demonstrate that *E. newberryi* is a relatively recently derived lineage.

Based on a cytochrome apoenzyme b molecular clock, extant molecular variation in *E. newberryi* mtDNA probably arose within the last 1–2 million years (Dawson *et al.* 2001). Using this figure to calibrate mtCR divergences in *E. newberryi* (4.3%; Table 3) and among other bay gobies suggests that the *C. ios* and *E. newberryi* lineages diverged approximately 5–10 million years before the present (Myr BP) (22.7%), and the *C. ios*/*E. newberryi* lineage separated from the *L. lepidus* lineage approximately 6–12 Myr BP (24.3%). The origin of the northeastern Pacific bay gobies is estimated at 10–20 Myr BP (40.9%). However, these older dates will be underestimates if mtCR sequences > 15–20% different (uncorrected) are mutationally saturated (Yang 1998), as indicated by ti : tv ratios greater than one within species (*C. ios*, *E. newberryi*) but approximately equal to one among all gobies.

Considering this time-scale, the derived status of *E. newberryi*, and life-history characteristics common to all of the other bay gobies, it is highly likely that during the Late Miocene and into the Pliocene the ancestors of modern bay gobies possessed life-history characteristics — such as pelagic larval stages of several weeks to months duration — that fostered relatively distant dispersal despite the semi-enclosed bay or estuarine environments of adults, low-to-moderate fecundity (10^3–10^4 eggs), and spawning and development of eggs in burrows (MacGinitie 1935;

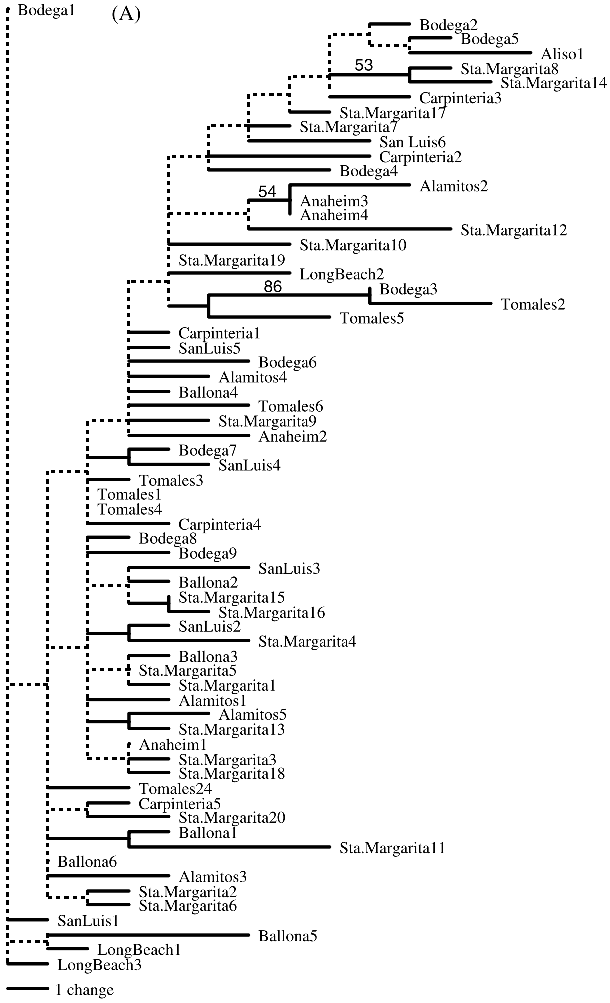

Fig. 4 Intra-specific phylogenetic hypotheses for *Clevelandia ios* and *Eucyclogobius newberryi*. (A) One of 2863 most parsimonious mtCR gene trees for *C. ios* (10 000 heuristic searches; tree length = 142; CI = 0.5211). (B) One of 1008 most parsimonious mtCR gene trees for *E. newberryi* (10 000 heuristic searches; tree length = 58; CI = 0.9138). Solid branches are present in, and broken lines absent from, the strict consensus trees for *C. ios* and *E. newberryi*. Numbers above branches are bootstrap values and are shown only if > 50% (1000 replicates).

Weisel 1947; Prasad 1959; Barlow 1961, 1963; Miller & Lea 1972; Hart 1973; Brothers 1975; Watson 1996; Kent & Marliave 1997; Swenson 1999). Furthermore, it seems likely, by modern analogy with *C. ios*, that ancestral bay gobies experienced relatively high gene flow among populations (and had shallow phylogeographic structure), perhaps facilitated by a climate that was generally warmer and wetter than at present (Axelrod & Raven 1985) and that promoted advection of propagules out of estuaries into the connecting coastal waters. However, the advent of a generally drier, more 'Mediterranean' climate, probably around 14–11 Myr ago (see Keller & Barron 1983; Axelrod & Raven 1985; also Johnson 1977) physically altered coastal habitats, particularly in more southerly regions, reducing freshwater discharge and decreasing the size of many estuaries, often leading to the development of attenuated or seasonally closed estuaries. Evidently, these changes did not eradicate habitat suitable for most of the more widely dispersing bay gobies, but they did lead to a novel habitat that permitted the evolution of *E. newberryi* (their timing being consistent with the older molecular clock estimates of divergence times). Given this change, it seems likely that selection for modified ecological preferences (or for greater tolerances of more extreme estuarine conditions) and life-history attributes led to ecological separation and, considering the sister taxa status and modern ranges of *C. ios* and *E. newberryi*, sympatric speciation (*sensu* Bush 1969; Diehl & Bush 1989; see Lynch 1989; also Chesser & Zink 1994). However, the geological history of California is complex and included the formation and elimination of large marine, sometimes brackish, inland seas and channels (e.g. Yanev 1980) which may also have provided opportunities for local isolation and divergence.

Habitat, life history and phylogeography in C. ios *and* E. newberryi

Irrespective of the precise geographical pattern of evolution, cladogenesis of *C. ios* and *E. newberryi* resulted in sympatric sister taxa with contrasting attributes (Table 1) and different intraspecific phylogeographic patterns (Fig. 4). For example, no significant regional- or population-level genetic structure was detected in *C. ios* reflecting historically, and probably currently, relatively high gene flow ($Nm \cong 9$). Also, the mean pairwise sequence difference between *C. ios* specimens is moderate (1.19%), reflecting high haplotype diversity but low nucleotide diversity (Grant & Bowen 1998; Avise 2000) consistent with a mismatch distribution that suggests historically rapid expansion of the abundance and range of *C. ios* (Fig. 3). In contrast, considerable regional- and population-level genetic variation was detected in *E. newberryi* reflecting historically very low gene flow ($Nm \cong 0.03$; despite grouping of populations for comparative purposes which slightly underestimates phylogeographic structure and over-estimates gene flow). Also, the mean pairwise sequence difference between *E. newberryi* specimens was higher (2.10%), reflecting a slightly lower haplotype diversity (0.9413 ± 0.0158) but relatively high nucleotide diversity (0.0215 ± 0.011) which, like the bimodal mismatch distribution, indicates historically differentiated, allopatric populations and somewhat restricted expansion of the species (Fig. 3; Grant & Bowen 1998; Avise 2000; see Dawson *et al*. 2001 for a more thorough discussion of *E. newberryi* evolution and phylogeography).

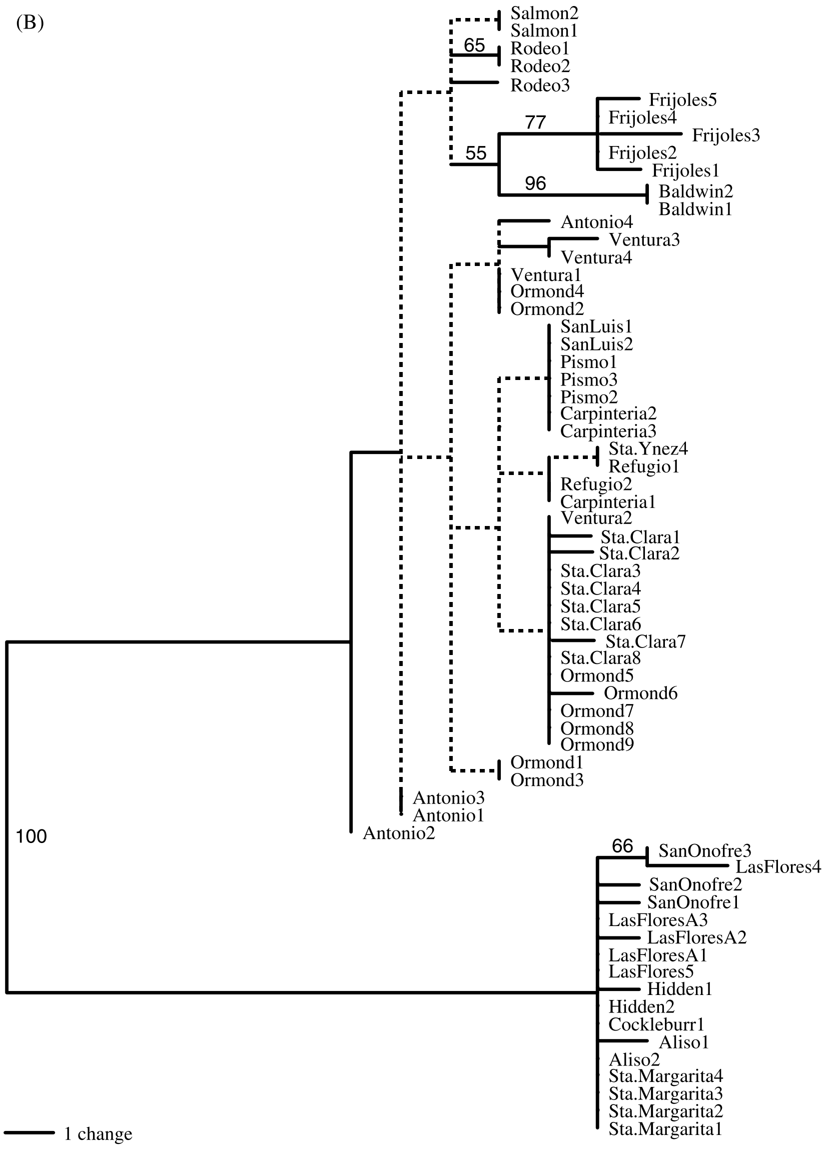

Fig. 4 *Continued*

Intuitively, given that the evolution of *C. ios* and *E. newberryi* occurred sympatrically, differences in intraspecific phylogeographic structure were probably determined by attributes specific to the species. It is likely that some abiotic environmental factors strongly influenced the phylogeographic differences between *C. ios* and *E. newberryi*. For example, the habitat of *C. ios* is tidal and open to the ocean all year round, but that of *E. newberryi* is often nontidal and seasonally closed during peaks in reproductive activity, differences that should facilitate greater dispersal of *C. ios* larvae and lead to shallower phylogeographic structure in *C. ios*, as observed. Additionally, geological-scale events, such as Miocene-Pliocene uplift of large Northern Channel Islands (Sorlien 1994; Ingersoll & Rumelhart 1999), Plio-Pleistocene transition of LAR from a marine to terrestrial environment (Davis *et al.* 1989), and a dozen or so major, and many more minor, Pleistocene cycles of climate and sea-level change (Shackleton 1987; Harland *et al.* 1989) might have locally influenced *C. ios* and *E. newberryi* differently via destruction and creation of habitat (e.g. see above; Lafferty *et al.* 1999a,b; Schimmelman *et al.* 1992, 1998; Dawson *et al.* 2001). More recently, human activities have modified coastal Californian habitats (Swift *et al.* 1989; Lafferty *et al.* 1996), again with potentially species-specific effects, including an increase in open tidal habitat for *C. ios* and a decrease in seasonally closed nontidal habitat for *E. newberryi* across LAR.

However, abiotic environmental factors alone may have been insufficient to cause the different phylogeographic structures of *C. ios* and *E. newberryi*, life-history may also have been important. First, seasonal closure of estuaries alone is insufficient to explain the greater phylogeographic structure in *E. newberryi* because *C. ios* and *E. newberryi* co-occur in several estuaries (e.g. Humboldt Bay, Santa Margarita River, and historically in San Francisco Bay, Morro Bay, Gaviota Creek) and because *E. newberryi* habitat is closed for only part of each year. Second, ecological data suggest that while summer closure of estuaries prevents dispersal of most larvae, winter rains occur when estuaries are open and facilitate the dispersal of *E. newberryi* (Lafferty *et al*. 1999a,b) possibly as larvae, juveniles, or adults. Greater dispersal of *C. ios* may also result from its occurrence in greater numbers than *E. newberryi* (C.C. Swift, personal observation) which leads, probabilistically, to greater dispersal of a greater number of propagules. Third, although historical events undoubtedly did alter the distribution of habitat patches of *C. ios* and *E. newberryi*, regional patterns of extirpation were probably geographically similar in both taxa (e.g. during uplift of LAR). In these regions, differences in phylogeographic patterns are therefore more likely to reflect the capacity of life-history strategies to overcome such disturbances than the disturbances themselves. This point is illustrated directly by the occurrence of a deep phylogeographic break in *E. newberryi* across LAR but no congruent break in *C. ios*. Finally, due to its depth, this LAR phylogeographic break in *E. newberryi* is unlikely to have resulted from anthropogenic effects (Dawson *et al*. 2001).

Thus, the shallower phylogeographic structure of *C. ios* (cf. *E. newberryi*) is most likely attributable to interactions between habitat and life-history differences, including its generally more open habitat, greater abundance, and, potentially, longer larval duration. The impact of probably small differences in fecundity between *C. ios* and *E. newberryi* may be negligible. In general, however, the relative importance of different factors has proved difficult to determine at this time due to often insufficient data describing precisely the ecologies of these sister taxa. Irrespective of this difficulty, the correlation between dispersal ability and phylogeographic structure in *C. ios* and *E. newberryi* is consistent with comparisons of other, albeit more divergent, California coastal taxa of varying dispersal abilities (e.g. Hellberg 1996; summary in Dawson 2001) and habitats (Waples 1987). It is also consistent with studies that positively correlate dispersal ability with gene flow (e.g. Waples & Rosenblatt 1987; Waples 1987; Palumbi 1995) and with geographical range (e.g. Scheltema 1968; Victor & Wellington 2000).

Conclusions

Based on habitat structure and life-history differences *C. ios* has greater dispersal ability than its sister taxon *E. newberryi*, and this is reflected in its much shallower phylogeographic structure. This result is consistent with the paradigm that greater dispersal ability will lead to greater gene flow. However, there remain many apparent exceptions to the paradigm (e.g. Waples 1987; Palumbi 1995; Cunningham & Collins 1998). These exceptions may, in part, be due to comparisons of species generally more geographically or phylogenetically distant than the sympatric sister taxa compared here (e.g. Waples 1987; see also Victor & Wellington 2000) and, consequently, attributable to confounding factors contingent on historical events. They may also be due, in part, to insufficiently detailed natural history data. While a diversity of approaches has merit, we suggest that such issues can be investigated most rigorously by extending the sister-taxon approach used here to comparative phylogeographic studies of groups of closely related sympatric species, such as the clade of eastern Pacific bay gobies, and gathering additional life-history data (e.g. see *Q. y-cauda* in Fig. 2; also Huang & Bernardi 2001).

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