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ORIGINAL PAPER

Population morphometric variation of the endemic freshwater killifish, *Fundulus lima* (Teleostei: Fundulidae), and its coastal relative *F. parvipinnis* from the Baja California Peninsula, Mexico

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Abstract The population morphometric variation of the endangered freshwater killifish (*Fundulus lima*) was evaluated and compared with that of its euryhaline coastal relatives (*F. parvipinnis parvipinnis* and *F. p. brevis*) on the basis of 384 specimens from the Baja California peninsula, Mexico. Forty five standardized body distances were compared by means of discriminant function analysis (DFA). Sixteen body distances were significant to distinguish two groups of populations for *F. lima*: a first group represented by the Bebelamas and San Javier basins, and second group composed by the basins of San Ignacio, La Purísima, San Luis, San Pedro and Las Pocitas. When all freshwater and coastal populations were compared, the southernmost population of *F. lima* (Las Pocitas) showed a higher morphometric similarity with the southern coastal subspecies (*F. p. brevis*), while another southern population (San Pedro) had an intermediate position between the freshwater and coastal forms. This study suggests the presence of five evolutionary units (three freshwater and two coastal) for the genus *Fundulus* in the Baja California peninsula.

Keywords Morphometry · *Fundulus lima* · *Fundulus parvipinnis* · Baja California peninsula

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1 Introduction

The family Fundulidae belongs to the order Cyprinodontiformes, a group of freshwater and estuarine small fishes commonly referred to as killifishes, or "guayacones", of Gondwanan origin (Nelson 2006). The family is restricted to the North American continent and includes four genera and approximately 50 species (Berra 2001). Within Fundulidae, the genus *Fundulus* is the most diverse with 30 known species (Nelson 1994; García-Ramírez et al. 2006), most of them occur in the Atlantic drainages. However, two species are confined to the Pacific drainages (Parenti 1981, Bernardi and Powers 1995), the California killifish *Fundulus parvipinnis* Girard 1854, which is distributed along the Californian coastal province (Miller and Lea 1972) and belongs to the euryhaline marine component (Follett 1960; Castro-Aguirre 1978; Castro-Aguirre et al. 1999); and the Baja California killifish, *Fundulus lima* Vaillant 1894, endemic to the oases of Baja California Sur (Follett 1960; Ruiz-Campos 2000) and currently categorized in danger of extinction (Ruiz-Campos et al. 2003a). The possible ancestor of Baja California killifish is assumed to have stemmed from a euryhaline population of *F. parvipinnis* that invaded the freshwater environment and later became isolated with the hydrological conditions changes that prevailed after the late Pleistocene (Camarena-Rosales et al. 2001; Ruiz-Campos et al. 2003a; Bernardi et al. 2007).

At least two nominal subspecies of California killifish have been recognized, the northern form (*F. parvipinnis parvipinnis* Girard 1854) from Morro Bay, California (Miller and Lea 1972) to Laguna Ojo de Liebre, Baja California Sur (De la Cruz-Agüero et al. 1996); and the southern form (*F. p. brevis* Osburn and Nichols 1916) from Punta Eugenia (Bernardi and Talley 2000; Bernardi et al. 2007) to Bahía Magdalena, Baja California Sur (Camarena-Rosales et al. 2001).

At the same time, Bernardi et al. (2007), based on an analysis of the sequence of the mitochondrial control region (D-loop) of continental and coastal populations of the genus *Fundulus* on the Baja California peninsula, determined that the two subspecies of *F. parvipinnis* plus *F. lima* appeared to form an unresolved trichotomy that separated and were isolated between 200,000 and 400,000 years ago, where each one of them represents a distinct evolutionary unit. However, Camarena-Rosales et al. (2001) proposed that the genetic separation of the two coastal subspecies resulted from a parapatric process favored by the California Current. In the case of the freshwater form, *F. lima*, it is inferred that all its populations were first connected and later were perhaps separated by geological and hydrographical episodes (Follett 1960), although Camarena-Rosales et al. (2001) argued, based on phylogeographical aspects, that each population might have originated individually by means of a process of radiation through discontinuous founders. If this latter process did indeed occur, each discontinuous population would be a genuine species under the concept of evolutionary species (*sensu* Mayden and Wood 1995).

The morphological description of *F. lima* has been exclusively based on specimens from the typical locality of San Ignacio oasis (cf. Vaillant 1894; Evermann 1908; Camarena-Rosales 1999; Camarena-Rosales et al. 2001), therefore, the magnitude of its morphological variation throughout its distributional range is not known (Ruiz-Campos et al. 2003a). Recent genetic analyses for populations of *F. lima* indicated certain differences in the composition and frequency of mitochondrial DNA sequences (Bernardi et al. 2007), and haplotypes (Ruiz-Campos et al. 2008), yet lacked the additional morphological analyses necessary to fully appreciate the evolutionary picture of the group.

For the present study, we evaluated the variation of 45 linear body distances among populations of *Fundulus lima* through its distribution range. Additionally, we compared these same characters with those of the two euryhaline coastal subspecies (*F. parvipinnis parvipinnis* and *F. p. brevis*) in order to determine diagnostic characteristics, identification, taxonomic position and evolutionary relationships in this group.

2 Study area

The study area comprises the freshwater wetlands (oases) and coastal wetlands (estuaries and salt marshes) in the Pacific drainage from the Río Cantamar (Baja California) to Río Las Pocitas (Baja California Sur), Mexico (Fig. 1). The surface hydrology in the northwestern region consists of a series of small coastal streams originating on the western slope of the Sierra Juárez and Sierra San Pedro Mártir. Most of these streams become intermittent in their middle and lower courses during extremely dry conditions (Tamayo and West 1964). The mouths of most streams are blocked from the ocean by sandbars, except for extraordinary flooding events of high tides that produce riverine-estuarine conditions (Ruiz-Campos 2002). Salt marsh habitats with tidal influence are found in Todos Santos Bay (Punta Banda), San Quintín Bay, Guerrero Negro lagoon, San Ignacio lagoon, La Bocana and Magdalena Bay. The freshwater environments of the study area are represented

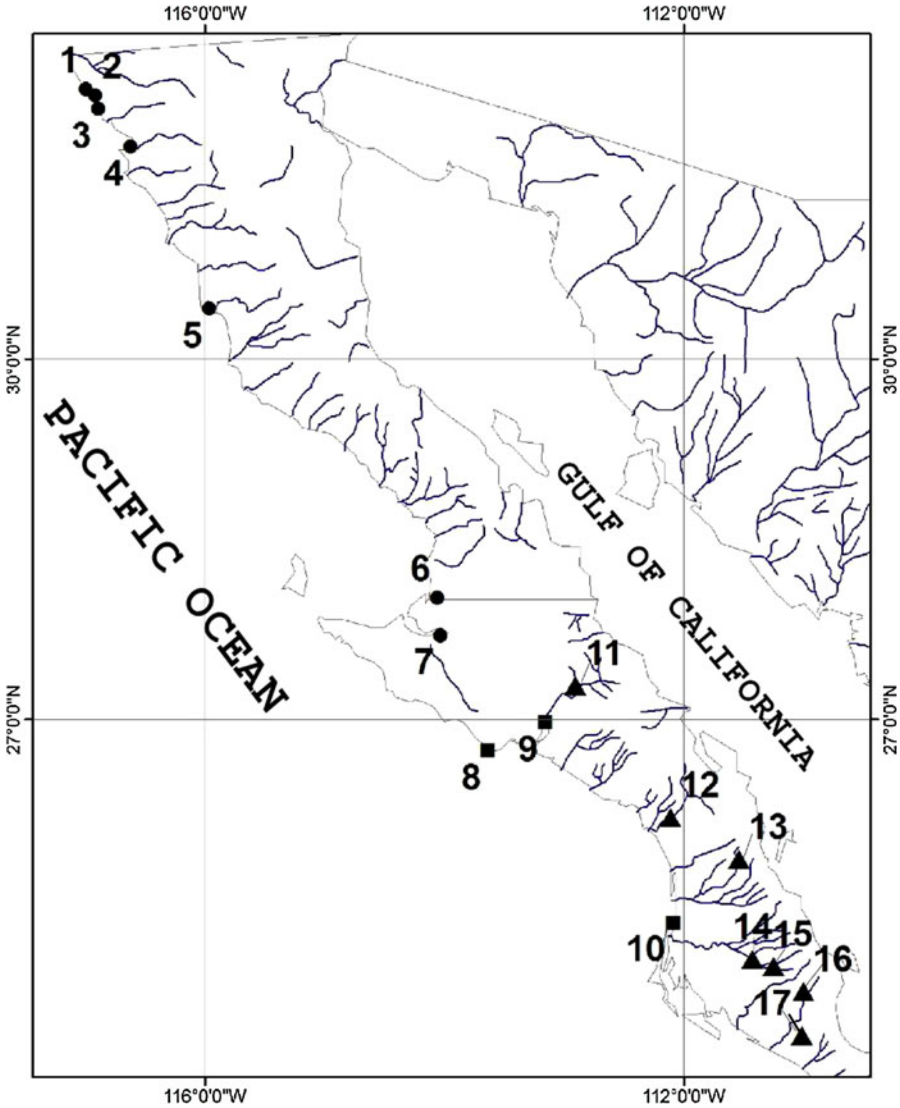

Fig. 1 Studied basins for *Fundulus* spp. (filled circle = *F. p. parvipinnis*, filled square = *F.p. brevis*, and filled triangle = *F. lima*) in the Baja California peninsula, Mexico. (1) Cantamar, (2) El Descanso, (3) La Misión, (4) Estero de Punta Banda, (5) San Simón, (6) Laguna de Guerrero Negro, (7) Laguna Ojo de Liebre, (8) La Bocana, (9) Laguna de San Ignacio, (10) Bahía Magdalena, (11) San Ignacio, (12) La Purísima, (13) San Javier, (14) Bebelamas, (15) San Luis [Gonzaga], (16) San Pedro [de la Presa], and (17) Las Pocitas

by a complex of oases through the Pacific drainage of the central and southern peninsular regions, from the Río San Ignacio to Río Las Pocitas. These oases are produced by springs that create permanent ponds within each basin and are intermittently connected during flooding events (Ruiz-Campos et al. 2003a). The vegetation of coastal saltmarshes includes *Spartina foliosa, Frankenia grandifolia, Salicornia bigelovii, Distichlis spicata, Suaeda californica* and *Limonium californicum* (Delgadillo 1992). The oases include macrophytes of the genera *Typha, Potamogeton, Scirpus, Utricularia, Zannichellia,* and *Azolla* (Wiggins 1980), as well as riparian elements such as native fan palm (*Washingtonia robusta*), exotic date palm (*Phoenix dactylifera*), common reeds (*Phragmites australis*) and mule's fat (*Baccharis salicifolia*) (Arriaga et al. 1997). The water physicochemical characteristics of the study area are described in Ruiz-Campos et al. (2003a, 2006, 2008).

3 Methods

The specimens of the genus *Fundulus* examined for this study were collected from 17 coastal and freshwater basins through the Pacific drainage of

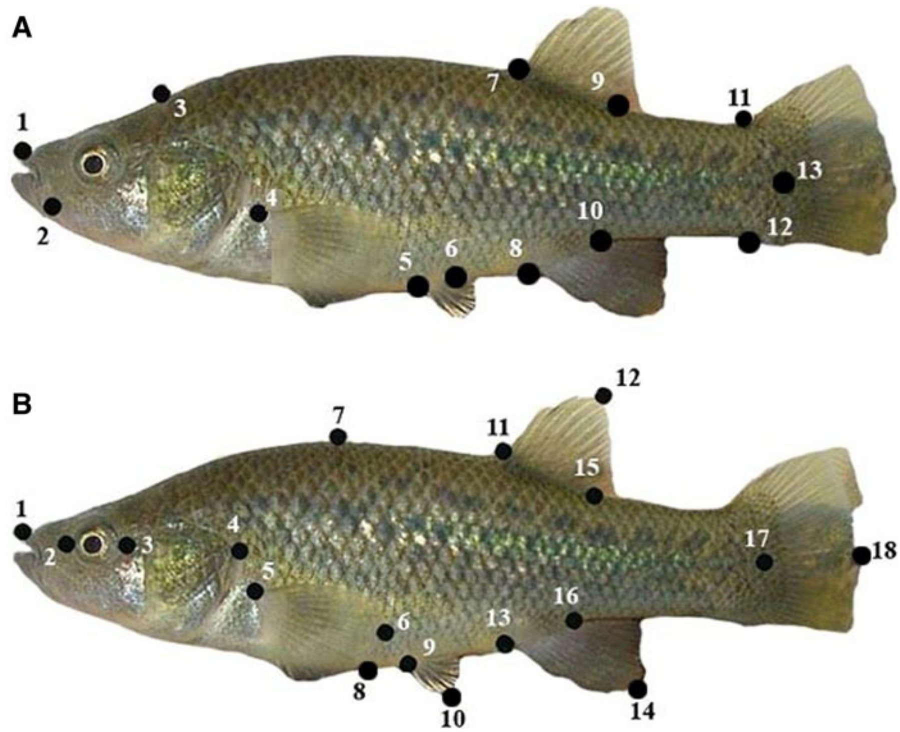

Fig. 2 Landmarks of morphometric distances used for the comparative analysis of the genus *Fundulus* from the Baja California peninsula, Mexico. **a** "Box truss" protocol of Bookstein et al. (1985). **b** Standard method of Hubbs and Lagler (1958)

the Baja California peninsula, during 1977 to 2005 (Fig. 1). The fish specimens were deposited in the following Mexican ichthyological collections: Universidad Autónoma de Baja California (UABC) at Ensenada, Baja California; Universidad Autónoma de Nuevo León (UANL) at Monterrey, Nuevo León; and Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional-IPN (CI-CICIMAR) at La Paz, Baja California Sur.

Specimens of the species and subspecies of the genus *Fundulus* were selected for the morphometric analysis (cf. material examined in Appendix 1). Forty-five linear measures (M) based on box truss protocol of Bookstein et al. (1985) and the standardized method of Hubbs and Lagler (1958) were considered for the morphometric analysis of the specimens (Fig. 2a, b). All the measurements were made on the left side of each specimen using a digital caliper (precision, 0.01 mm) connected to a PC. Linear measures (distances) based on box truss protocol (Fig. 2a) and traditional protocol (Fig. 2b) as well as other measures are described in Table 1.

The values of distances (body measures) were standardized by means of regression (Elliott et al. 1995) in order to remove the size component from the shape measurements (allometry) and to homogenize their variances (Jolicoeur 1963). This standardization was performed by taxon and for each character (distance) using the following equation: $Ms = Mo\ (Ls/Lo)^b$, where Ms = standardized measurement, Mo = measured character length (mm), Ls = overall (arithmetic) mean standard length (mm) for all individuals from all populations of each species, Lo = standard length (mm) of specimen, and "b" was estimated for each character from the observed data using the non-linear equation, $M = a\ L^b$. Parameter "b" was estimated as the slope of the regression of log Mo on log Lo, using every fish in every population of each taxon.

Standardized morphometric values were compared among taxa and populations by means of discriminant function using Statistica 6.0 software (StatSoft Inc., Tulsa, OK 2002). This multifactorial analysis allowed us to determine which combination of variables (distances) discriminated best among populations or taxa, and detected which populations were the most different (Elliott et al. 1995; Ruiz-Campos et al. 2003b).

Table 1 Linear measures (distances) based on box truss protocol, traditional protocol and other measures considered in the morphometric analysis of *Fundulus* spp. from Baja California peninsula, Mexico

Code	Morphometric character
M1–2	Snout tip to upper jaw tip
M1–3	Snout tip to occiput
M2–3	Upper jaw tip to occiput
M2–4	Upper jaw tip to pectoral fin origin
M2–7	Upper jaw tip to dorsal fin origin
M2–9	Upper jaw tip to posterior insertion of dorsal fin
M3–4	Occiput to pectoral fin origin
M3–5	Occiput to pelvic fin origin
M3–7	Occiput to dorsal fin origin
M4–5	Pectoral fin origin to pelvic fin origin
M4–7	Pectoral fin origin to dorsal fin origin
M4–9	Pectoral fin origin to posterior insertion of dorsal fin
M5–6	Basal length of pelvic fin
M5–7	Pelvic fin origin to dorsal fin origin
M5–9	Pelvic fin origin to posterior insertion of dorsal fin
M6–8	Posterior insertion of pelvic fin to anal fin origin
M7–8	Dorsal fin origin to anal fin origin
M7–9	Basal length of dorsal fin
M7–10	Dorsal fin origin to posterior insertion of anal fin
M8–9	Anal fin origin to posterior insertion of dorsal fin
M8–10	Basal length of anal fin
M9–10	Posterior insertion of dorsal fin to posterior insertion of anal fin
M9–11	Posterior insertion of dorsal fin to superior origin of caudal fin
M9–12	Posterior insertion of dorsal fin to inferior origin of caudal fin
M10–11	Posterior insertion of anal fin to superior origin of caudal fin
M10–12	Posterior insertion of anal fin to inferior origin of caudal fin
M11–12	Superior origin of caudal fin to inferior origin of caudal fin
M11–13	Superior origin of caudal fin to mid caudal base
M12–13	Inferior origin of caudal fin to mid caudal base
M1–2 (2)	Preorbital length
M1–4 (2)	Head length
M1–11 (2)	Predorsal length
M2–3 (2)	Eye diameter
M3–4 (2)	Postorbital length
M5–6 (2)	Pectoral fin length
M7–8 (2)	Maximum depth
M9–10 (2)	Pelvic fin length
M11–12 (2)	Dorsal fin length
M13–14 (2)	Anal fin length
M15–17 (2)	Postdorsal length
M16–17 (2)	Postanal length
M17–18 (2)	Caudal fin length
M1–2 (3)	Mouth width (between commisures)
M3–4 (3)	Interorbital space
M5–6 (3)	And head width

4 Results and discussion

The descriptive statistics (median, standard deviation and coefficient of variation) of the 45 morphometric characteristics for each one of the three taxa of *Fundulus* are shown in Table 2.

4.1 Morphometric comparison among populations of *Fundulus lima*

The specimens of *Fundulus lima* used for the morphometric analysis were grouped by hydrological basin (Fig. 3a–g). The analysis of discriminating function (ADF) indicated that 16 of the 45 characteristics examined were statistically significant ($P < 0.01$) (Table 3). The highest tolerance values (> 0.5) were registered for the basal length of pelvic fin (M5-6), superior origin of caudal fin to mid caudal base (M11-13) eye diameter (M2-3[2]), pelvic fin length (M9-10[2]), and caudal fin length (M17-18[(2]). The canonical variable 1 (cv 1) accounted for 93.1% of the total variation (Table 4). In cv 1, one linear characteristics exerted the greatest effect: M1-11 (2) (predorsal length, $Y_1 = 0.7958$).

Based on squared Mahalanobis' distances (D^2), 100% of the individuals were correctly classified in their respective populations (Fig. 4). The resulting categorization of the individuals on the basis of the canonical roots 1 and 2 showed again a notable separation of the Bebelamas and San Javier basins from the remaining basins (Fig. 4).

4.2 Morphometric comparison of *Fundulus p. parvipinnis* versus *F.p. brevis*

In the ADF applied to compare the two subspecies of *F. parvipinnus,* seven of the 45 characteristics examined were significant ($P < 0.01$) in discriminating the two taxa: M2-9 (upper jaw tip to posterior insertion of dorsal fin); M4-7 (pectoral fin origin to dorsal fin origin), M1-4[2] (head length), M1-11[2] (predorsal length). M15-17[2] (postdorsal length), M16-17[2] (postanal length) and M17-18[2] (caudal fin length) (Table 3). The tolerance values of the characteristics ranged from 0.10 (M1-11[2], predorsal length) to 0.63 (M5-6, basal length of pelvic fin). The cv 1 accounted the 100% of the total variation (Table 4) and was associated to two lineal characters: M2-9 (upper jaw tip to posterior insertion of dorsal fin, $Y_1 = -0.8107$) and M1-11[2] (predorsal length, $Y_1 = -0.8121$). The percentage of correct classification of individuals in the two compared subspecies was 100%.

4.3 Morphometric comparison of populations of *Fundulus lima* versus *F. parvipinnis* spp.

In the ADF applied to all the populations of the genus *Fundulus lima* and *Fundulus parvipinnis* by taxa, 24 of the 45 characteristics examined turned out to be statistically significant ($P < 0.01$): M2-4 (upper jaw tip to pectoral fin origin), M2-9 (upper jaw tip to posterior insertion of dorsal fin), M3-4 (occiput to pectoral fin origin), M4-5 (pectoral fin origin to pelvic fin origin), M5-6 (basal length of pelvic fin), M5-7 (pelvic fin origin to dorsal fin origin), M5-9 (pelvic fin origin to posterior insertion of dorsal fin), M6-8 (posterior insertion of pelvic fin to anal fin origin), M7-9 (basal length of dorsal fin), M9-10 (posterior insertion of dorsal fin to posterior insertion of anal fin), M9-12 (posterior insertion of dorsal fin to inferior origin of caudal fin), M1-2[2] (preorbital length), M1-4[2] (head length), M1-11[2] (predorsal length), M2-3[2] (eye diameter), M7-8[2] (maximum depth), M9-10[2] (pelvic fin length), M11-12[2] (dorsal fin length), M13-14[2] (anal fin length), M15-17[2] (postdorsal length), M16-17[2] (postanal length), M17-18[2] (caudal fin length), M3-4[3] (interorbital space) and head width (M5-6[3]) (Table 3).

The cv1 contributed 86.17% of the total variation (Table 4), principally correlated with two linear characteristics: M2-9 (upper jaw tip to posterior insertion of dorsal fin, $Y_1 = 0.6317$), and M1-11[2] (predorsal length, $Y_1 = 0.6439$).

Predictive classification of individuals in each basin and taxon showed that 100% of the individuals were correctly classified in their respective populations and taxa. Based on canonical roots 1 and 2, and according to squared Mahalanobis' distances (Fig. 5a), two population groups could be identified: the first included the freshwater populations of San Javier and Bebelamas, the second comprised both fresh water and coastal populations. In that second group, we could distinguish (1) association between the southernmost population of *F. lima* (Rio Las Pocitas basin) with the southern coastal subspecies

Table 2 Mean and coefficient of variation (CV) of standardized morphometric characters for populations of *Fundulus* spp. from the Baja California peninsula, Mexico

Code	1	2	3	4	5	6	7	CV	8	9	CV	TOTAL	CV
Ml–2	3.58	3.01	2.21	1.89	4.16	2.98	2.64	**26.60**	2.92	2.64	**7.25**	**2.89**	**23.52**
Ml–3	13.65	12.15	9.12	6.11	15.27	13.25	11.83	**26.53**	13.37	11.53	**10.45**	**11.81**	**23.15**
M2–3	11.87	10.53	8.14	5.18	13.34	11.74	10.53	**26.80**	11.92	10.21	**10.92**	**10.39**	**23.44**
M2–4	17.90	16.27	11.76	9.60	20.23	16.79	14.32	**23.95**	16.82	14.23	**11.82**	**15.32**	**21.11**
M2–7	38.45	34.01	24.02	19.24	40.24	33.58	30.25	**24.08**	34.30	29.10	**11.60**	**31.46**	**21.22**
M2–9	45.56	40.57	28.80	23.44	48.27	42.00	37.88	**23.53**	44.25	36.80	**13.01**	**38.62**	**20.85**
M3–4	12.15	10.91	7.71	5.83	13.59	11.56	10.14	**26.03**	11.46	9.92	**10.18**	**10.36**	**22.72**
M3–5	26.13	23.42	16.31	14.59	28.32	22.62	20.27	**22.99**	23.10	19.69	**11.28**	**21.61**	**20.36**
M3–7	27.47	24.51	16.58	14.70	27.97	22.92	20.68	**23.11**	23.15	19.89	**10.70**	**21.98**	**20.51**
M4–5	15.57	13.67	9.66	7.53	16.31	13.01	12.60	**24.69**	13.50	11.18	**13.34**	**12.56**	**22.01**
M4–7	22.91	19.59	13.75	10.13	23.58	20.02	18.01	**26.54**	20.30	17.06	**12.28**	**18.37**	**23.31**
M4–9	29.07	25.43	17.95	13.95	30.16	27.01	24.76	**24.77**	28.80	23.68	**13.80**	**24.53**	**22.02**
M5–6	2.42	2.26	1.61	1.45	2.97	2.45	2.40	**23.70**	3.27	2.93	**7.67**	**2.42**	**25.01**
M5–7	16.76	14.66	10.07	7.70	18.71	14.80	13.18	**27.65**	15.58	13.01	**12.73**	**13.83**	**24.24**
M5–9	19.26	16.91	11.76	9.48	20.54	17.83	16.56	**24.95**	19.82	16.14	**14.47**	**16.48**	**22.38**
M6–8	6.52	5.17	3.77	2.85	5.60	5.22	5.88	**25.38**	5.92	4.91	**13.22**	**5.09**	**22.44**
M7–8	14.73	13.16	9.14	7.21	17.07	14.05	12.03	**27.00**	14.76	11.90	**15.14**	**12.67**	**23.90**
M7–9	7.71	6.95	5.03	4.71	8.86	8.59	8.02	**23.34**	10.49	8.13	**17.96**	**7.61**	**24.06**
M7–10	15.45	14.05	9.71	8.18	18.09	15.75	14.13	**25.63**	17.22	13.58	**16.70**	**14.02**	**23.21**
M8–9	13.59	12.21	8.28	6.92	15.41	13.03	11.76	**25.83**	14.31	11.35	**16.30**	**11.87**	**23.18**
M8–10	6.25	5.78	4.30	3.85	7.74	6.79	6.44	**23.44**	7.64	6.23	**14.36**	**6.11**	**21.73**
M9–10	10.04	9.23	6.09	4.95	11.06	9.50	8.96	**25.75**	10.01	7.99	**15.88**	**8.65**	**22.92**
M9–11	11.66	10.94	7.83	6.56	12.51	11.84	11.63	**21.90**	13.38	10.17	**19.27**	**10.72**	**20.66**
M9–12	15.36	14.24	10.02	8.64	17.21	15.66	14.59	**22.97**	16.82	13.24	**16.83**	**13.98**	**20.93**
M10–11	14.86	13.61	9.70	7.89	15.94	13.81	13.68	**22.67**	16.65	13.17	**16.48**	**13.26**	**21.24**
M10–12	11.06	10.01	7.24	5.64	11.27	9.95	10.06	**22.40**	12.88	10.22	**16.28**	**9.82**	**22.05**
M11–12	8.91	8.11	5.75	4.74	10.29	8.45	7.34	**24.76**	9.25	7.60	**13.85**	**7.83**	**22.06**
M11–13	5.20	4.75	3.38	3.07	6.07	5.40	4.55	**23.34**	5.78	4.71	**14.44**	**4.77**	**21.20**
M12–13	5.17	4.73	3.38	2.81	6.17	5.38	4.18	**25.82**	5.76	4.62	**15.56**	**4.69**	**23.32**
M1–2 (2)	6.36	5.54	3.69	2.89	6.94	5.66	4.75	**28.15**	5.59	4.78	**11.05**	**5.13**	**24.64**
M1–4 (2)	19.68	17.44	12.44	10.54	21.70	18.23	15.62	**23.93**	18.40	15.75	**10.98**	**16.64**	**21.00**
M1–11 (2)	40.39	35.57	25.08	20.10	42.37	35.51	31.86	**24.31**	35.76	30.52	**11.17**	**33.02**	**21.40**

Table 2 continued

Code	1	2	3	4	5	6	7	CV	8	9	CV	TOTAL	CV
M2–3 (2)	4.69	4.62	3.68	3.30	5.02	4.29	4.15	**14.14**	4.80	4.31	**7.61**	**4.32**	**12.77**
M3–4 (2)	9.67	8.72	6.23	5.21	10.83	8.99	7.70	**23.91**	9.21	7.75	**12.21**	**8.26**	**21.08**
M5–6 (2)	10.60	9.13	6.55	5.58	11.04	9.65	7.76	**23.85**	10.82	8.74	**15.06**	**8.88**	**21.68**
M7–8 (2)	17.82	15.90	11.03	8.30	20.11	16.00	12.81	**28.04**	16.60	13.89	**12.53**	**14.72**	**24.55**
M9–10 (2)	5.26	4.42	3.12	2.73	5.79	5.72	5.09	**26.76**	6.98	5.67	**14.59**	**4.98**	**27.13**
M11–12 (2)	12.58	10.89	7.27	6.47	14.51	12.97	11.51	**27.38**	15.80	11.95	**19.61**	**11.55**	**26.44**
M13–14 (2)	11.87	10.41	7.07	5.86	14.14	15.08	12.32	**31.43**	16.62	13.40	**15.17**	**11.87**	**30.09**
M15–17 (2)	15.41	14.37	10.12	8.36	17.06	15.32	14.42	**23.10**	17.43	13.40	**18.47**	**13.99**	**21.51**
M16–17 (2)	14.59	13.45	9.86	8.02	15.98	14.09	13.14	**21.99**	17.09	13.25	**17.90**	**13.27**	**21.25**
M17–18 (2)	11.11	9.27	7.02	6.18	11.09	10.81	8.82	**21.69**	11.60	9.91	**11.10**	**9.53**	**19.99**
M1–2 (3)	6.06	5.23	3.69	3.24	7.17	5.07	4.28	**27.59**	4.86	4.27	**9.09**	**4.88**	**24.77**
M3–4 (3)	7.80	6.93	5.16	4.32	8.89	7.25	5.75	**24.19**	6.79	5.54	**14.30**	**6.49**	**21.96**
M5–6 (3)	11.83	10.16	7.51	6.10	13.47	10.50	8.62	**26.01**	10.06	8.38	**12.87**	**9.62**	**23.33**
CV	**65.58**	**65.22**	**64.56**	**64.18**	**62.68**	**61.88**	**62.42**	**63.79**	**59.61**	**60.69**	**60.15**	–	–
N	60	60	15	5	29	12	16	**197**	127	60	**187**	**384**	–
SL (ave.)	62.59	56.65	40.30	33.03	67.67	59.29	54.02	**58.28**	63.27	51.59	**59.52**	**58.88**	–
SL (min)	45.73	36.21	30.55	29.04	34.45	30.88	42.96	**29.04**	38.46	40.38	**38.46**	**29.04**	–
SL (max)	82.00	80.55	64.21	46.21	109.47	94.35	61.97	**109.47**	95.11	65.59	**95.11**	**109.47**	–

Codes for characters are described in text. Basins or taxa are depicted with numbers: 1 (San Ignacio), 2 (La Purísima), 3 (San Javier), 4 (Bebelamas), 5 (San Luis), 6 (San Pedro), 7 (Las Pocitas), 8 (*F. p. parvipinnis*), and 9 (*F. p. brevis*)

N Number of specimens, *SL* No transformed standard length

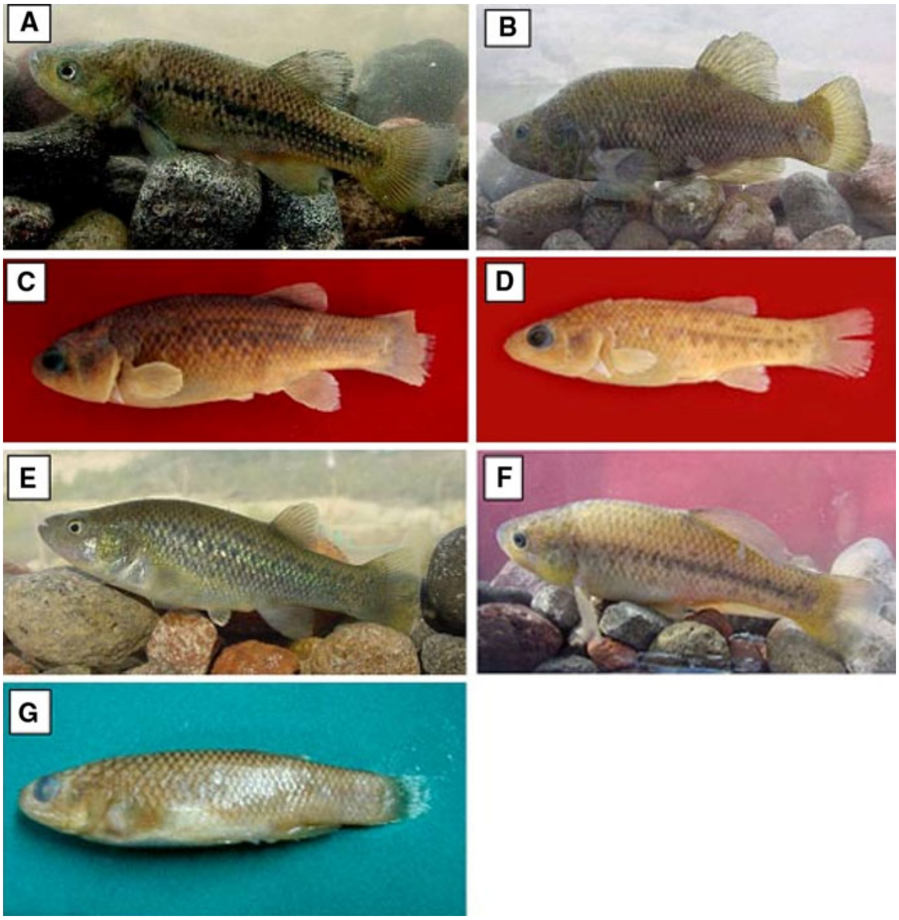

Fig. 3 Specimens of *Fundulus lima* from different hydrological basins through its distribution range. **a** San Ignacio, **b** San Luis, **c** San Javier, **d** Bebelamas, **e** La Purísima, **f** San Pedro, and **g** Las Pocitas. Photographs by Gorgonio Ruiz-Campos

F. parvipinnis brevis, (2) association between the northernmost of *F. lima* (Rio San Ignacio basin) with the northern coastal subspecies *F. parvipinnis parvipinnis*, and (3) the intermediate position of the population of *F. lima* from the San Pedro basin in regard to those freshwater (La Purísima basin) and coastal (*F. p. brevis*) (Fig. 5b).

5 Final considerations

The specimens of *Fundulus lima* examined are representative of the different hydrological basins along its distributional range. Several populations have recently been eliminated due to the introduction of redbelly tilapia (*Tilapia* cf. *zilli*) such as those in the oases of San Javier (San Javier Mission), San Luis Gonzaga (mission and Las Cuedas) and San Pedro de la Presa (Ruiz-Campos et al. 2008).

It is important to mention that our results derived from the comparative morphometric analysis among the three nominal taxa of *Fundulus* in the Baja California peninsula made it possible to have a broader perspective regarding the inter- and intra-population variation of *F. lima*, as well as the identification of diagnostic characteristics to distinguish it from the two coastal subspecies of *F. parvipinnis* (Table 3). In a previous morphometric analysis of the genus *Fundulus* of the Baja California peninsula, Camarena-Rosales et al. (2001) only included one population per taxon, so the interpopulational variation of *F. lima* and its geographic relationship with the coastal subspecies could not be adequately evaluated. Although these authors

Table 3 Values of lambda of Wilks, significance (*P*) and tolerance for morphometric variables calculated from the forward stepwise discriminant function analysis for freshwater and coastal of populations of the genus *Fundulus* in the Baja California peninsula, Mexico

Linear character	*Fundulus lima*				*Fundulus parvipinnis* spp.				*Fundulus lima* versus *F. parvipinnis* spp.			
	Wilks' Lambda	F-remove	*P*-level	Toler.	Wilks' Lambda	F-remove	*P*-level	Toler.	Wilks' Lambda	F-remove	*P*-level	Toler.
M1–2	–	–	–	–	0.01345	3.064	0.082	0.566	0.00004	1.865	0.065	0.646
M1–3	0.00004	1.618	0.146	0.170	–	–	–	–	0.00004	1.223	0.284	0.230
M2–3	0.00004	2.462	0.027	0.165			–		0.00004	1.952	0.052	0.252
M2–4	0.00004	1.809	0.101	0.378	0.01348	33.381	0.068	0.369	0.00004	3.039	0.003	0.398
M2–7	0.00004	1.795	0.104	0.187	0.01350	3.662	0.058	0.109	0.00004	1.745	0.087	0.142
M2–9	0.00004	2.159	0.050	0.318	0.01595	32.348	0.000	0.266	0.00004	5.656	0.000	0.317
M3–4	0.00005	8.526	0.000	0.389	0.01346	3.099	0.080	0.437	0.00004	10.563	0.000	0.424
M3–5	0.00004	2.740	0.015	0.376	–	–	–	–	0.00004	1.503	0.155	0.400
M3–7	0.00004	3.569	0.002	0.215	0.01332	1.538	0.217	0.160	0.00004	2.046	0.041	0.180
M4–5	0.00004	3.686	0.002	0.347	0.01357	4.478	0.036	0.367	0.00004	3.963	0.000	0.252
M4–7	0.00004	1.644	0.139	0.213	0.01392	8.533	0.004	0.108	0.00004	2.144	0.031	0.167
M4–9	0.00004	1.796	0.103	0.232	0.01323	0.396	0.530	0.179	0.00004	1.741	0.088	0.221
M5–6	0.00004	3.033	0.008	0.694	0.01363	5.121	0.025	0.631	0.00004	6.594	0.000	0.701
M5–7	0.00004	1.673	0.131	0.189	0.01350	3.608	0.059	0.175	0.00004	3.549	0.001	0.204
M5–9	0.00004	3.630	0.002	0.220	0.01353	3.980	0.048	0.221	0.00004	3.080	0.002	0.559
M6–8	0.00004	6.308	0.000	0.436	0.01330	1.240	0.267	0.490	0.00004	6.153	0.000	0.474
M7–8	0.00004	1.406	0.216	0.201	0.01343	2.811	0.096	0.334	0.00004	2.086	0.037	0.302
M7–9	0.00004	0.973	0.445	0.381	0.01332	1.468	0.228	0.331	0.00004	3.437	0.001	0.350
M7–10	0.00004	2.631	0.019	0.365	–	–	–	–	0.00004	1.688	0.100	0.450
M8–9	–	–	–	–	0.01341	2.506	0.115	0.258	0.00004	1.637	0.113	0.238
M8–10	0.00004	2.056	0.062	0.388	0.01341	2.525	0.114	0.406	0.00004	2.067	0.039	0.435
M9–10	0.00004	3.189	0.006	0.382	–	–	–	–	0.00004	4.610	0.000	0.479
M9–11	–	–	–	–	–	–	–	–	0.00004	1.439	0.179	0.429
M9–12	0.00004	2.459	0.027	0.428	–	–	–	–	0.00004	3.872	0.000	0.451
M10–11	0.00004	2.237	0.043	0.446	0.01355	4.212	0.042	0.261	0.00004	1.303	0.241	0.245
M10–12	–	–	–	–	–	–	–	–	0.00004	1.477	0.164	0.374
M11–12					0.01365	5.379	0.022	0.405	0.00004	2.029	0.043	0.380
M11–13	0.00004	1.101	0.364	0.609	0.01332	1.499	0.223	0.531	0.00004	2.150	0.031	0.616
M12–13	0.00004	1.983	0.071	0.582	–	–	–	–	–	–	–	–

Table 3 continued

Linear character	*Fundulus lima*				*Fundulus parvipinnis* spp.				*Fundulus lima* versus *F. parvipinnis* spp.			
	Wilks' Lambda	F-remove	*P*-level	Toler.	Wilks' Lambda	F-remove	*P*-level	Toler.	Wilks' Lambda	F-remove	*P*-level	Toler.
M1–2 (2)	0.00004	2.512	0.024	0.434	–	–	–	–	0.00004	3.250	0.001	0.450
M1–4 (2)	0.00004	2.588	0.020	0.217	0.01380	7.082	0.009	0.237	0.00004	2.960	0.003	0.442
M1–11 (2)	0.00004	4.449	0.000	0.158	0.01411	10.792	0.001	0.100	0.00004	2.832	0.005	0.146
M2–3 (2)	0.00004	6.191	0.000	0.652					0.00004	7.081	0.000	0.754
M3–4 (2)	0.00004	2.563	0.022	0.486	0.01344	2.852	0.093	0.448	0.00004	1.290	0.248	0.527
M5–6 (2)	0.00004	2.922	0.010	0.568	0.01333	1.652	0.201	0.620	0.00004	2.063	0.039	0.583
M7–8 (2)	0.00004	4.683	0.000	0.350	0.01337	2.052	0.154	0.280	0.00004	8.807	0.000	0.371
M9–10 (2)	0.00004	2.641	0.018	0.603	–	–	–	–	0.00004	3.240	0.001	0.439
M11–12 (2)	0.00004	5.138	0.000	0.172	–	–	–	–	0.00004	7.579	0.000	0.096
M13–14 (2)	0.00005	8.342	0.000	0.266					0.00004	4.251	0.000	0.140
M15–17 (2)	0.00004	3.087	0.007	0.400	0.01663	40.405	0.000	0.546	0.00004	7.563	0.000	0.375
M16–17 (2)	–	–	–	–	0.01380	7.152	0.008	0.222	0.00004	2.980	0.003	0.300
M17–18 (2)	0.00004	5.466	0.000	0.737	0.01389	8.181	0.005	0.567	0.00004	10.682	0.000	0.595
M1–2 (3)	0.00004	2.037	0.064	0.470	0.01372	6.143	0.014	0.518	0.00004	2.077	0.037	0.521
M3–4 (3)	0.00004	3.092	0.007	0.484	0.01332	1.455	0.230	0.605	0.00004	6.115	0.000	0.584
M5–6 (3)	0.00004	3.959	0.001	0.380	0.01337	2.040	0.155	0.364	0.00004	3.883	0.000	0.340
Total by grouping	0.00003	F (234,911) = 18.123	<0.0000	–	0.01319	F (31,155) = 374	<0.0000	–	0.00004	F (352,2634) = 19.978	<0.0000	–

Number of steps for *F. lima* = 39, for *F. parvipinnis* spp. = 31, and both taxa combined = 35

Table 4 Standardized coefficients of the first canonical variables (roots) resulting from the discriminant function analysis for specimens of the genus *Fundulus* from the Baja California peninsula, Mexico

Codes	*Fundulus lima*			*Fundulus parvipinnis* spp.	*Fundulus lima* versus *F. parvipinnis* spp.	
	Root 1	Root 2	Root 3	Root 1	Root 1	Root 2
M1–2	–	–	–	−0.19	−0.03	−0.14
M1–3	−0.01	0.23	−0.41	–	0.10	−0.12
M2–3	−0.12	−0.55	0.03		0.07	0.11
M2–4	−0.24	0.28	−0.17	−0.24	0.21	−0.37
M2–7	−0.13	0.53	0.27	−0.46	–	–
M2−9	−0.29	0.02	0.15	−0.81	0.63	0.19
M3–4	0.17	−0.71	−0.07	0.21	−0.15	0.34
M3–5	−0.13	0.08	−0.52		0.12	−0.12
M3−7	0.26	0.42	0.24	0.25	−0.09	−0.37
M4–5	−0.36	−0.03	0.28	−0.28	0.23	−0.08
M4–7	0.20	−0.17	−0.12	0.70	−0.18	0.10
M4–9	−0.22	−0.34	−0.15	−0.12	–	–
M5–6	0.02	−0.08	−0.19	0.23	−0.10	0.25
M5–7	0.48	0.23	−0.07	0.36	−0.45	−0.48
M5–9	−0.37	0.00	0.54	−0.34	0.34	0.22
M6–8	−0.19	−0.21	0.50	−0.13	0.23	0.29
M7–8	0.27	0.37	0.01	0.23	−0.11	0.34
M7–9	0.04	−0.22	−0.12	−0.17	0.10	0.51
M7–10	0.06	−0.10	−0.51		−0.03	0.15
M8–9	–	–	–	0.25	−0.07	−0.24
M8–10	−0.22	0.23	0.13	−0.20	0.23	−0.15
M9–10	−0.08	−0.21	0.14	–	0.04	−0.20
M9–11	–	–	–	–	0.03	0.09
M9–12	−0.29	−0.12	−0.23	–	0.13	−0.08
M10–11	−0.10	−0.22	0.38	−0.32	0.14	0.04
M10–12	–	–	–	–	−0.03	0.02
M11–12	–	–	–	−0.29	0.09	0.05
M11–13	−0.09	−0.01	0.11	−0.14	0.18	0.−08
M12–13	−0.13	−0.16	−0.28			
M1–2 (2)	0.08	0.27	0.16	–	0.01	−0.16
M1–4 (2)	−0.19	−0.26	0.42	0.43	−0.03	0.27
M1–11 (2)	−0.80	−0.39	−0.13	−0.81	0.64	−0.23
M2–3 (2)	−0.04	0.14	0.18		0.03	0.06
M3–4 (2)	0.10	0.20	−0.43	−0.20	−0.03	−0.10
M5–6 (2)	0.17	0.16	0.33	0.13	−0.13	0.03
M7–8 (2)	−0.07	0.38	−0.54	−0.22	0.11	−0.23
M9–10 (2)	−0.21	−0.29	−0.03	–	0.07	0.32
M11–12 (2)	−0.42	0.53	0.58	–	0.30	−0.80
M13–14 (2)	−0.04	−0.73	−0.48	–	−0.24	0.18
M15–17 (2)	−0.41	−0.23	0.22	−0.62	0.44	0.43
M16–17 (2)	–	–	–	−0.45	0.33	−0.04
M17–18 (2)	−0.19	−0.03	0.07	−0.30	0.26	0.18
M1–2 (3)	0.17	−0.15	0.26	0.27	−0.12	0.01

Table 4 continued

Codes	*Fundulus lima*			*Fundulus parvipinnis* spp.	*Fundulus lima* versus *F. parvipinnis* spp.	
	Root 1	Root 2	Root 3	Root 1	Root 1	Root 2
M3–4 (3)	−0.05	0.30	−0.43	−0.12	0.07	−0.32
M5–6 (3)	−0.12	0.28	−0.04	−0.19	0.09	−0.12
Eigenval	160.20	5.99	2.62	74.80	103.37	12.66
Cum. Prop	0.93	0.97	0.98	1.00	0.86	0.97

See abbreviations of morphometric characters in text

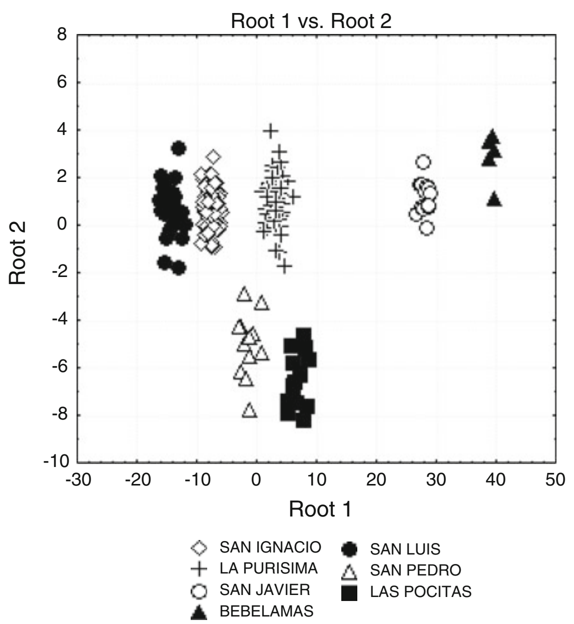

Fig. 4 Classification of individuals based on squared Mahalanobis' distances for populations of *Fundulus lima*

suggested that *F. lima* (from San Ignacio oasis) was more closely related to the coastal subspecies *F. parvipinnis brevis*, our morphometric analyses identified that the southernmost population of *F. lima* (Rio Las Pocitas basin) was in fact more similar to *F.p. brevis* (Fig. 5). Bernardi et al. (2007) determined, based on an analysis of mitochondrial DNA (D-loop) that the freshwater and coastal populations of *Fundulus* of the Baja California peninsula seem to form an unresolved trichotomy, which possibly diverged from 200,000 to 400,000 years ago, for this reason each branch could represent a distinct evolutionary unit. Bernardi et al. (*op. cit.*) also determined that the two coastal subspecies of *F. parvipinnis* are separate from the genetic point of view, between the northern and southern ends of Punta Eugenia (B.C.S.). These same authors suggest a greater affinity between *F. p. brevis* from Puerto San Carlos and La Bocana with the population of *F. lima* from Río San Pedro basin. This last relationship could be explained by two possible scenarios: 1) a recent episode of invasion by *F. p. brevis* into the San Pedro and Las Pocitas rivers, and 2) the possible existence of hybridization between *F. lima* and *F. parvipinnis brevis* (Bernardi et al. 2007), an observation that may be consistent with the mis-assignments based on morphological characteristics mentioned above.

At the level of populations of *F. lima*, the segregation of individuals of the Bebelamas and San Javier oases from the rest of the populations is noteworthy, in the measurements of at least 16 somatic characteristics (cf. Table 3). These differences suggest the distinction of a new freshwater form of the genus *Fundulus* in the Baja California peninsula, which was first referred to by Ruiz-Campos and Contreras-Balderas (1987) as *Fundulus* sp. for the San Javier oasis [mission of San Francisco Javier]. Each of the freshwater populations could represent an independent historical colonization via fluvial dispersal by a euryhaline coastal ancestor (Camarena-Rosales et al. 2001).

Comparative meristic and osteological studies of the three taxa of *Fundulus* from the Baja California peninsula are necessary to support and strengthen the genetic study that suggests the recognition of *F. parvipinnis brevis* as full species (Bernardi et al. 2007), as well as the presence of three freshwater forms of *Fundulus* for the Baja California peninsula, the first comprised by the populations of the San Ignacio, La Purísima and San Luis basins; the second by the populations of San Javier and Bebelamas; and the third by the southern population of the San Pedro basin. Finally, the southernmost freshwater population (Rio Las Pocitas) reported as *F. lima*

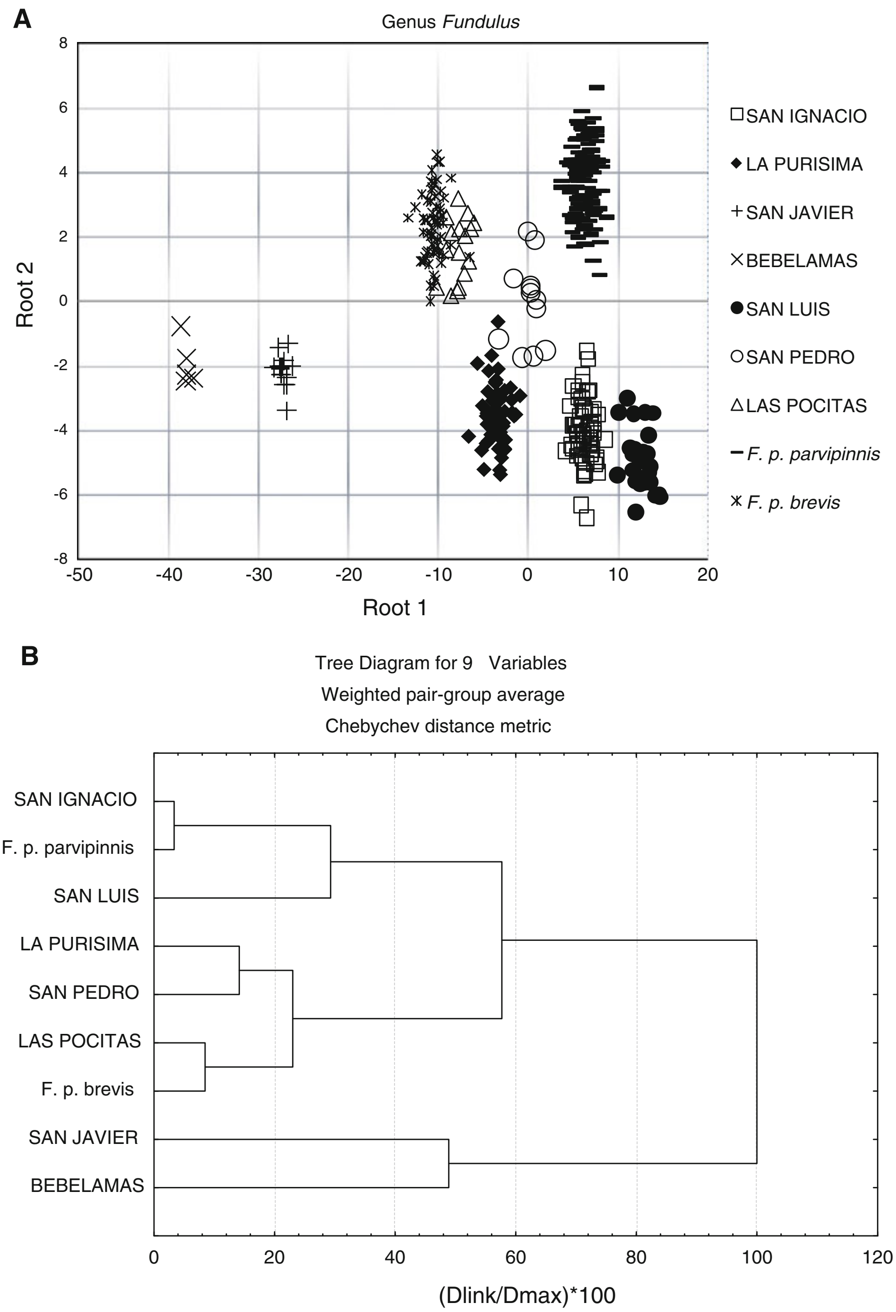

Fig. 5 **a** Classification of individuals based on squared Mahalanobis' distances for freshwater populations (*Fundulus lima*) and the two coastal taxa (*F. parvipinnis parvipinnis* and *F.p. brevis*) from the Baja California peninsula, Mexico. **b** Tree diagram resulting from the clustering analysis

(cf. Ruiz-Campos et al. 2003a, b) should be considered a recent stock derived from the southern coastal killifish, *F. parvipinnis brevis*.

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Appendix 1: Material examined of the genus *Fundulus* from the Baja California peninsula, Mexico. Numbers of examined specimens are depicted in square brackets

Fundulus lima. **Río San Ignacio Basin:** oasis San Ignacio between spring and Rancho El Tizón (UABC-1617 [15]), 26-I-2006), Poza Larga (UABC-1312 [8], 15-IV-2002; UABC-1327 [6], 14-IV-2002; UABC-1313 [1], 14-IV-2002), Los Corralitos (UABC-1385 [3], 5-II-2003; UABC-1512 [12], 4-VII-2004), and San Sabas (UABC-1486 [1], 5-II-2003; UABC-1380 [14], 5-II-2003). **Río La Purísima Basin:** Ojo de Agua (UABC-1463 [1], 12-II-2004; UABC-1516 [14], 1-VII-2004; UABC-1383 [6], 8-II-2003; UABC-1384 [4], 8-II-2003), Carambuche [= Cuba] (UABC-758 [8], 15-III-1998), and La Purísima in front of Cerro El Pilón (UABC-1515 [12], 2-VII-2004; UABC-1381 [8], 8-II-2003). **Río San Javier Basin:** Presa San Javier at San Javier (UANL-2571 [15], 27-IV-1977). **Río Bebelamas Basin:** Arroyo Bebelamas at San Lucas [= Poza Honda] (UABC-745 [5], 16-IV-1998). **Río San Luis Basin:** Arroyo San Luis at Misión de San Luis Gonzaga (UABC-740 [5], 16-IV-1998), Rancho Las Cuedas (UABC-1325 [2], 18-IV-2002; UABC-743 [21], 16-IV-1998), San Basilio (UABC-779 [1], 15-V-1998), and Merecuaco (UABC-789 [1], 16-V-1998). **Río San Pedro Basin:** Arroyo San Pedro at San Pedro de La Presa (UABC-1324 [1], 18-IV-2002; UABC-796 [3], 27-VI-1991; CICIMAR-CI 1956 [1], 27-VI-1991; CICIMAR-CI 2023 [1], 24-V-1991), San Basilio (15), and Pozo del Iritú (UABC-797 [4], 25-VI-1991; CICIMAR-CI 2005 [10], *idem*). **Río Las Pocitas Basin:** Arroyo Las Pocitas at El Caracol (UABC-798 [6], 24-V-1991; CICIMAR-CI 2025 [10], *idem*).

***Fundulus parvipinnis parvipinnis*. Mouth of Río Cantamar** (UABC-479 [6], 23-XI-1996; UABC-437 [3], 21-VIII-1996; UABC-350 [10], 24-II-1995); **mouth of Río El Descanso** (UABC-478 [10], 22-XI-1996; UABC-141 [10], 24-II-1995); **mouth of Río La Misión** (UABC-978 [10], 1-IX-1995; UABC-432 [10], 21-VIII-1996); **Bahía Todos Santos [Estero de Punta Banda] at Campo Perinsky** (UABC-984 [4], 18-III-2000) and **Rancho El Refugio** (UABC-985 [3], 19-III-2000); **mouth of Río San Simón at El Papalote** (UABC-316 [10], 27-VI-1996; UABC-587 [10], 8-III-1997); **Laguna Guerrero Negro at Estero El Chaparrito** (UABC-1600 [10], 7-VIII-2005; UABC-2122 [10], 6-VII-2007); and Laguna **Ojo de Liebre at Canal El Rincón del Dátil** (UABC-878 [20], 19-I-1997).

Fundulus parvipinnis brevis. **Laguna San Ignacio at Campo Kuyima** (UABC-1478 [20], 29-III-2004; **La Bocana**: ([10], 14-I-1998); and **Bahía Magdalena at Estero San Carlos** (UABC-961 [7], 15-I-1997; UABC-1612 [23], 6-VIII-2005).

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