Genetic Study of the Atlantic/Mediterranean Transition in Sea Bass (*Dicentrarchus labrax*)

M. Naciri, C. Lemaire, P. Borsa, and F. Bonhomme

We report on the genetic differentiation among populations of the common (or European) sea bass (*Dicentrarchus labrax*) from the North Sea, Britanny, Portugal, Morocco, the Alboran Sea, and the western Mediterranean. Based on allele-frequency variation at six microsatellite loci, a distance tree inferred from Reynold's coancestry coefficient showed that sea bass populations clustered into two distinct groups of populations, an Atlantic group which includes the Alboran Sea east of Gibraltar Strait, and a western Mediterranean group. While no clear geographical pattern emerged within each of these two entities, the sharp transition led us to postulate that the divide may correspond to the Almeria–Oran oceanographic front. This divide was evidenced by a small but highly significant F_{ST} value (0.018, $P < .001$), corresponding at equilibrium to an average effective number of migrants *Nm* on the order of 14 individuals per generation. We emphasize the idea that the passive retention of larvae on either side of the oceanographic front is not a sufficient explanation for the persistence of this divide.

The delimitation of discrete populations is a long-standing challenge in the marine environment because of the absence of obvious geographical barriers and the frequent existence of passive and active dispersal mechanisms at larval and adult stages. High expectations have been associated with indirect genetic methods to objectively determine geographical limits to populations. The literature on marine populations shows that the actual levels of structuring can be higher than what could be suspected solely on the basis of passive larval dispersal (reviewed in Avise 1994; Burton 1983; Hilbish 1996; Palumbi 1992, 1994). The question of the mechanisms involved in the limitations to effective genetic dispersal however remains unresolved. Places where genetic transitions occur on a limited geographical scale may provide opportunities to study these mechanisms, and therefore ought to receive particular attention. The existence of such zones has been hypothesized in the northeastern Pacific around Cape Mendocino on the Californian coast, Cape Hatteras, and the Florida peninsula in the western Atlantic (Avise 1994; Palumbi 1994) and Gibraltar Strait between the northeastern Atlantic and the Mediterranean (Borsa et al. 1997). Not all taxa however show a sharp transition across these zones (Avise 1992, 1994, 1996; Borsa et al. 1997; Foltz DW, unpublished manuscript). The present study was intended to test the existence of a transition zone in the European sea bass (*Dicentrarchus labrax* L., 1758) (Teleostei, Perciformes, *Moronidae*). To do this, we investigated the geographical structure of Atlantic and Mediterranean populations of this species.

The sea bass is a euryhaline and eurythermic species living in marine, lagoonal, and estuarine habitats. It ranges from Norway to Morocco in the northeastern Atlantic and from the western Mediterranean to the Black Sea (Whitehead et al. 1986). Eggs hatch in the sea 4–9 days after fertilization depending on water temperature (Jennings and Pawson 1992). The duration of the planktonic larval stage varies from 2 to 3 months, at the end of which larvae are able to colonize coastal waters, estuaries and lagoons where they grow for 2 years (Barnabé 1980). Adults gather and migrate to offshore spawning grounds each year (Barnabé 1980; Kelley 1979). Since the sea bass is a highly valued commercial species, several authors have attempted to investigate its genetic structure at the regional scale using allozyme (Castilho and McAndrew 1998; Child 1992) or mitochondrial DNA markers (Patarnello et al. 1993). Only two other studies included samples from both the Atlantic and the Mediterranean (Allegrucci et al. 1997; Benharrat et al. 1983). These two studies, which used allozymes, reported substan-

From Laboratoire Génome, Populations, Interactions, Université Montpellier II, Sète, France (F. Bonhomme, P. Borsa, and C. Lemaire), Institut de Recherche pour le Développement, France (P. Borsa), and Laboratoire de Biologie et Zoologie Générale, Université Mohamed V, Rabat, Morocco (M. Naciri). We wish to thank D. W. Foltz for his unpublished review, F. J. García de León for providing unpublished data, and R. Castilho, H. Kara, V. Sbordoni, and F. Volckaert for providing some of the samples. We also extend our thanks to L. Bahri, N. Bierne, G. Kotoulas, and F. Volckaert for helpful discussions and to anonymous referees for helpful suggestions. This work was financed partly by contract IFREMER URM n°16 to LGPI. Address correspondence to F. Bonhomme, Laboratoire Génome, Populations, Interactions, Station Méditerranéenne de l'Environnement Littoral, 1 Quai de la Daurade, 34200 Sète, France, or email: bonhomme@univ-montp2.fr.

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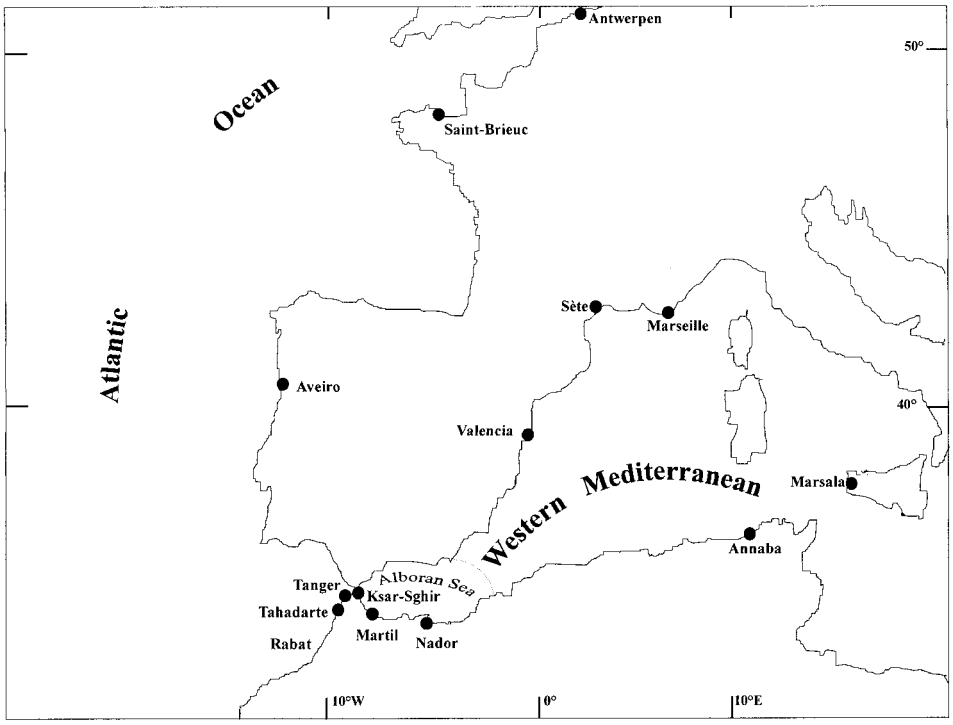

Figure 1. Collection sites of *Dicentrarchus labrax.* Sampling locations (closed circles); dotted line represents the Almeria–Oran oceanographic front.

tial genetic differentiation of the Mediterranean versus Atlantic samples, in contrast with broad-scale homogeneity within the Mediterranean, although the genetic distance estimates they provided were different. Both studies included a single Atlantic sample, which was insufficient to geographically delineate populations. Moreover, these were based on completely different sets of loci, some of which may be subject to natural selection (Allegrucci et al. 1997).

Presumably neutral microsatellite markers may overcome the above mentioned difficulties. In a preliminary study of genetic variation at six microsatellite loci, García de León (1995) found an F_{ST} value of about 0.035 between sea bass sampled in Brittany and other samples from the western Mediterranean, whereas García de León et al. (1997), using the same set of microsatellites to approach the question of stock assessment at a microgeographic scale, found an average F_{ST} estimate of 0.001 among samples collected in the Golfe-du-Lion (western Mediterranean). Since the allele-frequency differences between Portuguese and Mediterranean samples also exceeded by far the differences that were observed within the Mediterranean (Allegrucci et al. 1997), we postulated that some genetic transition occurred over a relatively small geographical area. Indeed, when considering the supraspecific level, some authorities have considered the region around Gibraltar as a biogeographical boundary (e.g., Briggs 1974; Quignard 1978), although this does not conform with the ideas of others (see, for instance, Ekman 1968). Geographic population structure is generally (though not necessarily) associated with the boundaries between biogeographic provinces (reviews in Avise 1994, 1996; Borsa et al. 1997; Cunningham and Collins 1994; Palumbi 1994). We report here on the geographic structure of sea bass in the northeastern Atlantic and the western Mediterranean, with emphasis on a possible transition zone in the Gibraltar region. We shall address the following questions: How homogeneous are the populations on each side? Does the genetic transition proceed gradually or abruptly? In either case, can we locate the maximum gradient and to which biological or environmental factors can we relate it?

Materials and Methods

Six hundred thirty sea bass (adults and juveniles) from 17 samples were included in this study (their geographic locations are given in Figure 1; other details are in Table 1). All samples collected near the Moroccan coast were obtained directly from fishermen operating by day trip with small fishing vessels within a fishing range presumably not wider than a few dozen kilometers. Samples from Saint-Brieuc, Mar-

Table 1. Description of the 17 *Dicentrarchus labrax* samples by geographic origin, size, date of collection, habitat, and collector's name

Geographic origin	Locality	Abbreviation	*N*	Sampling date	Habitat	Collector
North Sea	Antwerpen, Belgium	BANV	50	27 Sep. 1997	Estuary	F. Volckaert
Atlantic Ocean	Saint-Brieuc, France	FBRE	39	18 Aug. 1994	Sea	F. J. García de León
	Aveiro, Portugal	PAVR	50	—	Coastal lagoon	R. Castilho
	Rabat, Morocco	MRBT	60	15 Jun. 1996	Sea	M. Naciri
	Tahadarte 1, Morocco	MTH1	30	14 Dec. 1997	Coastal lagoon	M. Naciri
	Tahadarte 2, Morocco	MTH2	35	22 Jan. 1997	Coastal lagoon	M. Naciri
	Tanger 1, Morocco	MTN1	65	03 Jan. 1997	Sea	M. Naciri
	Tanger 2, Morocco	MTN2	65	15 Feb 1997	Sea	M. Naciri
Alboran Sea	Ksar-Sghir 1, Morocco	MKS1	46	08 Feb. 1997	Sea	M. Naciri
	Ksar-Sghir 2, Morocco	MKS2	14	08 Mar. 1997	Sea	M. Naciri
	Martil, Morocco	MMAR	20	02 Mar. 1997	Sea	M. Naciri
	Nador, Morocco	MNAD	9	18 Dec. 1996	Coastal lagoon	M. Naciri
Western Mediterranean Sea	Sète, France	FSET	26	26 Oct. 1994	Sea	F. J. García de León
	Marseille, France	FMRS	50	10 Feb. 1994	Sea	F. J. García de León
	Valencia, Spain	EGLV	37	14 Jul. 1994	Sea	F. J. García de León
	Annaba, Algeria	AGLA	34	01 Jan. 1994	Sea	H. Kara
	Marsala, Italy	ISCL	26	Mar. 1991	Sea	V. Sbordoni

N = sample size.

Table 2. Pairwise estimates of F_{ST} (Weir and Cockerham's θ) among 17 *Dicentrarchus labrax* samples

	FBRE	PAVR	MRBT	MTH2	MKS1	MTN2	MTH1	MTN1	MKS2	MMAR	MNAD	EGLV	FSET	FMRS	AGLA	ISCL
BANV	0.008	0.010*	0.008	0.002	0.014*	0.021*	0.023*	0.013*	0.011	0.012	0.021	0.049*	0.036*	0.046*	0.044*	0.051*
FBRE		0.002	0.003	0.009	0.009	0.010*	0.019*	0.002	0.007	0.008	0.018	0.043*	0.022*	0.037*	0.042*	0.041*
PAVR			0.008	0.008	0.004	0.012*	0.004	0.007	0.000	0.008	0.005	0.027*	0.012	0.029*	0.027*	0.026*
MRBT				0.008	0.009*	0.011*	0.017*	0.003	0.005	0.005	0.022	0.032*	0.019*	0.028*	0.032*	0.031*
MTH2					0.005	0.013*	0.012	0.004	0.005	0.005	0.011	0.024*	0.012	0.024*	0.024*	0.027*
MKS1						0.016*	0.007	0.009	0.007	0.012	0.002	0.029*	0.017*	0.035*	0.031*	0.029*
MTN2							0.024*	0.009	0.006	0.008	0.018	0.032*	0.020*	0.022*	0.031*	0.027*
MTH1								0.015	0.008	0.010	−0.001	0.021*	0.013	0.035*	0.028*	0.028*
MTN1									−0.001	−0.001	0.024	0.029*	0.017*	0.029*	0.033*	0.028*
MKS2										0.002	0.004	0.025*	0.018	0.021	0.026	0.024
MMAR											0.015	0.022*	0.014	0.020*	0.027*	0.027
MNAD												0.029	0.021	0.037	0.028	0.031
EGLV													0.000	0.008	−0.002	0.006
FSET														0.005	0.002	0.000
FMRS															0.008	0.012
AGLA																0.008

* Value significant after sequential Bonferroni adjustment of type I error level (Rice 1989).
Abbreviations for samples as in Table 1.

seille, and Annaba were from a previous study (García de León 1995).

For each individual, a piece of muscle and a fin clip were stored in 80% ethanol. DNA was extracted from a fragment of about 1 mm^3 of either muscle or fin tissue after alcohol was evaporated at room temperature, using Chelex 100® resin (Bio-Rad, Richmond, CA) as detailed in García de León et al. (1995).

Genotyping of microsatellites was as in García de León et al. (1997) for the six microsatellite loci *Labrax-3, Labrax-6, Labrax-8, Labrax-13, Labrax-17,* and *Labrax-29.* Briefly, primers were end-labeled with γ-^{33}P-ATP (Amersham Life Science, Cleveland, OH) using T_4 polynucleotide kinase (Eurogentec, Liège, Belgium). Polymerase chain reaction (PCR) amplifications were carried out in a Crocodile III thermocycler (Appligène, Strasbourg, France) in microtiter-plate wells with 10 μl final volume containing 4 μl DNA solution, 2.8 ng radioactively labeled primer, 2.8 ng reverse primer, 2.5 mM $MgCl_2$, 0.12 mM each dNTP, 1× polymerase buffer, and 0.3 U *Taq* polymerase. Each well was overlaid with 20 μl of paraffin oil. Program parameters were 3 min at 94°C, followed by 7 cycles of 1 min at 94°C, 1 min at hybridization temperature (*Labrax-3,* 58°C; *Labrax-6* and *Labrax-8,* 55°C; *Labrax-13, Labrax-17,* and *Labrax-29,* 59°C), 23 cycles of 45 s at 94°C, 45 s at hybridization temperature, and a final 5 min elongation step at 72°C.

Six microliters of each PCR product was mixed with 15 μl loading buffer and subjected to electrophoresis in a vertical denaturing polyacrylamide gel [6% Acrylogel 5 (BDH, Poole, England), 7 M urea, and 1× TBE buffer] at 50 W for 2 h. Gels were transferred to Whatman paper, vacuum dried at 80°C, and autoradiographed against X-Omat film (Eastman Kodak, Rochester, NY). The resolution was sufficient to distinguish 1 bp size differences. Microsatellite alleles were sized relative to the controls used by García de León et al. (1997), so that allelic nomenclatures matched exactly.

All calculations were performed using the GENETIX software (Belkhir et al. 1996). F_{IS} and global- and pairwise F_{ST} were estimated, respectively, by Weir and Cockerham's (1984) f and θ estimators. Nei's unbiased gene diversity (H_{exp}) was also computed. In order to test for the significance level of a given parameter, the GENETIX software performs permutations of the dataset to estimate its distribution under the null hypothesis (for instance, permutations of alleles within samples to simulate panmixia and to test the significance of heterozygote deficiencies F_{IS}). The sequential Bonferroni method (Rice 1989) was used to compute tablewide significance levels.

A tree was inferred from the matrix of Reynolds et al.'s (1983) coancestry genetic distance [$D_{Reynolds} = -\ln(1 - F_{ST})$] using the neighbor-joining algorithm (Saitou and Nei 1987) implemented as the NEIGHBOR procedure of the PHYLIP 3.57 program package (Felsenstein 1995). The robustness of each node was evaluated by bootstrapping over loci (100 replicates, SEQBOOT procedure of PHYLIP).

Results

Seventeen sea bass samples from the continental shelf of the western European Atlantic and the western Mediterranean Sea were genetically compared (Figure 1). Table 2 gives pairwise estimates of F_{ST} over six microsatellite loci. The divergence data contained in this matrix are summarized in Figure 2 by a distance tree produced with the neighbor-joining clustering method. It is clear from this figure that the samples separated into two main branches, one grouping the 12 samples from the northeastern Atlantic ocean together with those of the Alboran Sea, the other clustering the 5 samples from the western Mediterranean Sea. Bootstrapping over loci showed that the separation between the two clades is robust (with a bootstrap score of 100%), whereas most values within each cluster were well below the 50% threshold. This is equivalent to saying that all loci contributed to the Atlantic/Mediterranean genetic divergence, but individually provided conflicting resolution of nodes within each cluster. In particular, the two branches within the northeastern Atlantic/Alboran Sea clade (that we shall hereafter term Atlantic) were not well supported and apparently did not match the geography, since Alboran Sea samples appeared to be intermingled with Portuguese and Moroccan samples. Nevertheless the genetic signal between the two basins was strong, as was already mentioned; that it was obtained with rather small divergence values is noteworthy: pairwise F_{ST} estimates between populations from either group ranged between 0.012 and 0.051. This estimate was 0.023 ($P < .001$) when considering each group as an entity.

Table 3 summarizes the estimates of the main genetic parameters for each sample and each locus. All populations showed a high number of alleles per locus, with some variation among loci, in keeping with García de León et al. (1997) on a restricted set of western Mediterranean samples. Since the number of alleles is

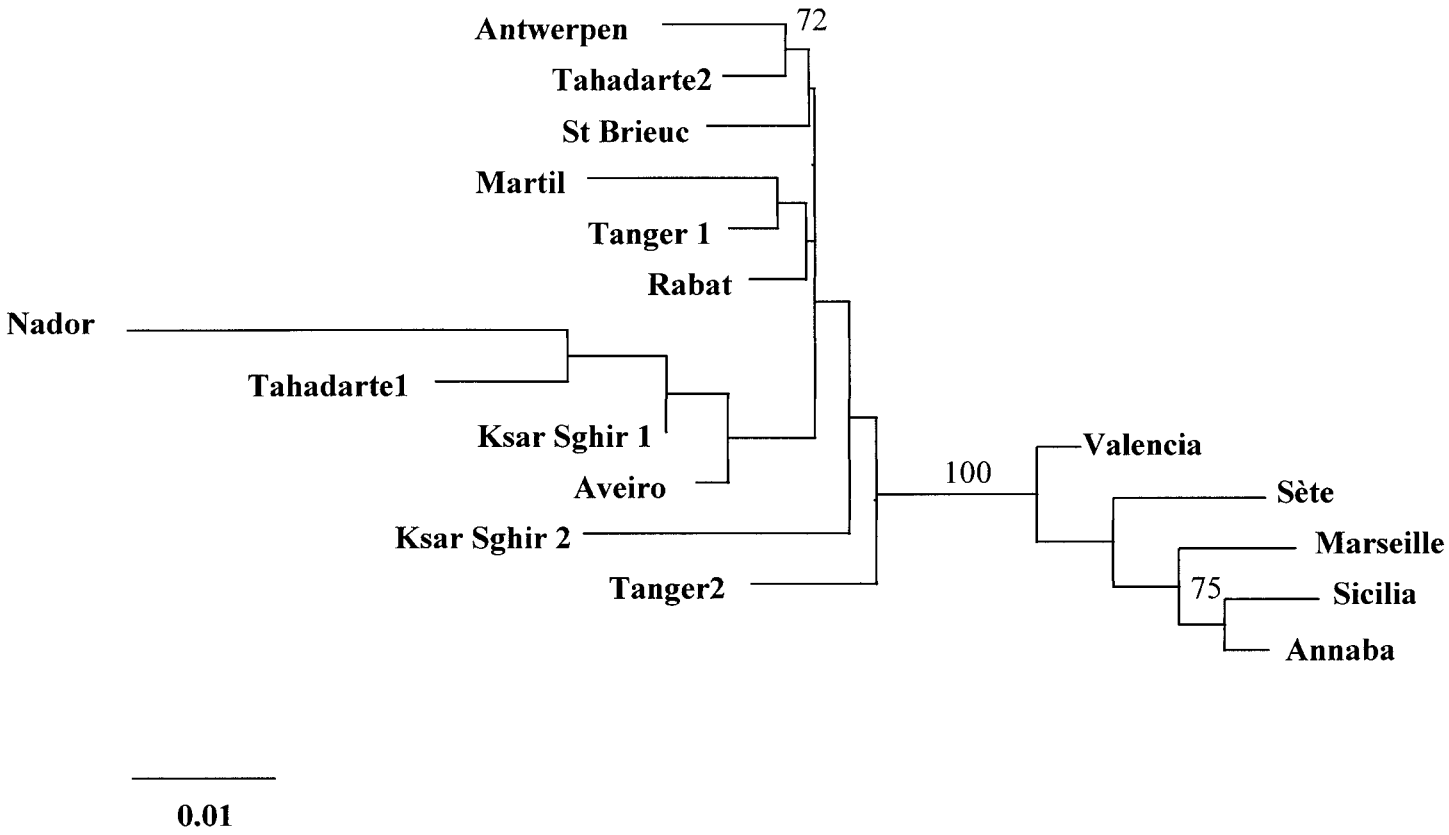

Figure 2. Unrooted neighbor-joining tree inferred from Reynolds' genetic distance based on variation at six microsatellite loci in 17 *Dicentrarchus labrax* samples. Only bootstrap scores greater than 50% are indicated.

sensitive to sample size, gene diversities (H_{exp}) should be preferred for comparisons. The average (with 95% confidence interval) within-clade gene diversity was significantly higher in the Atlantic (H_{exp} = 0.896 ± 0.019) than in the western Mediterranean (H_{exp} = 0.847 ± 0.025).

In Table 3 are indicated the estimates of Wright's F_{IS}, which is sensitive to heterozygote deficits. Locus *Labrax-6* appeared as an outlier, as it was the only locus showing pronounced heterozygote deficiencies (F_{IS} = 0.122 in the Atlantic and 0.302 in the western Mediterranean). This was already the case in the study of García de León et al. (1997), where possible causes, including the existence of null alleles, have been postulated. Omitting this outlier, the average multilocus F_{IS} value in a clade was null in the western Mediterranean (F_{IS} = −0.004, not significant), and

Table 3. Genetic variability and F_{IS} estimates at 6 microsatellite loci in 17 *Dicentrarchus labrax* samples

Sample	*A*	H_{exp}	H_{obs}	F_{IS}						Multilocus F_{IS}	
				Labrax-3	*Labrax-6*	*Labrax-8*	*Labrax-13*	*Labrax-17*	*Labrax-29*	All loci	Without *Labrax-6*
BANV	21.6	0.89 (0.08)	0.86 (0.09)	0.063	0.028	0.048	−0.024	0.064	0.005	0.030	0.030
FBRE	19.8	0.89 (0.06)	0.83 (0.09)	0.061	0.111	0.078	0.003	0.107	0.020	0.061	0.053
PAVR	22.0	0.91 (0.04)	0.80 (0.08)	0.127	0.205	0.126	0.111	0.118	0.048	0.121*	0.106
MRBT	23.2	0.89 (0.07)	0.89 (0.13)	−0.027	0.148	−0.073	−0.049	0.016	0.015	0.000	−0.024
MTH2	19.8	0.88 (0.06)	0.82 (0.13)	0.151	0.254	0.070	−0.019	−0.077	0.039	0.068	0.035
MTN2	24.5	0.90 (0.06)	0.87 (0.06)	0.029	0.055	0.033	0.056	−0.034	0.089	0.038	0.035
MKS1	20.2	0.89 (0.05)	0.89 (0.09)	0.025	0.064	−0.079	−0.054	−0.018	0.058	−0.002	−0.014
MTH1	19.7	0.88 (0.06)	0.80 (0.08)	0.024	0.184	0.028	0.070	0.152	0.144	0.100*	0.084*
MTN1	20.0	0.89 (0.06)	0.82 (0.11)	0.094	0.223	0.018	0.018	0.050	0.091	0.079*	0.054
MKS2	13.6	0.91 (0.03)	0.85 (0.16)	−0.049	0.350	0.055	−0.043	0.008	0.144	0.074	0.021
MMAR	16.3	0.88 (0.06)	0.83 (0.12)	−0.001	0.056	0.019	−0.051	0.206	0.136	0.055	0.058
MNAD	9.7	0.89 (0.05)	0.90 (0.08)	0.111	−0.085	−0.051	−0.108	0.000	0.052	−0.013	0.000
EGLV	15.2	0.83 (0.07)	0.79 (0.08)	0.030	0.079	0.110	0.036	−0.072	0.095	0.046	0.041
FMRS	19.6	0.85 (0.07)	0.81 (0.19)	0.051	0.361	0.081	−0.100	0.000	−0.071	0.044*	−0.010
FSET	14.3	0.86 (0.05)	0.83 (0.18)	−0.080	0.416	−0.098	−0.048	0.010	−0.008	0.038	−0.029
AGLA	16.2	0.85 (0.08)	0.82 (0.23)	−0.067	0.464	0.055	−0.025	−0.138	−0.038	0.028	−0.043
ISCL	13.2	0.84 (0.08)	0.78 (0.19)	0.053	0.285	−0.039	−0.106	0.015	0.259	0.066	0.031
W. Mediterranean	22.8	0.84 (0.06)	0.81 (0.12)	0.020	0.321	0.034	−0.051	−0.037	0.035	0.046*	−0.004
Atlantic Ocean	32.7	0.85 (0.06)	0.85 (0.10)	0.056	0.150	0.029	0.007	0.052	0.069	0.059*	0.042*

A = average number of alleles per locus; H_{exp} = Nei's (1987) gene diversity (across-locus standard deviation in brackets); H_{obs} = observed heterozygosity; *significant after sequential Bonferroni adjustment of type I error level (Rice 1989).

Abbreviations for samples as in Table 1.

small although significant in the Atlantic (F_{IS} = 0.036, $P < .001$), indicating that the populations were either at or nearly at panmixia.

Discussion

Phylogeographic inference from hypervariable loci such as microsatellites has sometimes been questioned because of a possible large amount of homoplasy from high levels of mutation (reviewed in Jarne and Lagoda 1996). Nevertheless, our results showed that significant genetic differentiation can be evidenced, even in a species with large effective population sizes, large numbers of alleles per locus, and high potential for dispersal: the distance algorithm clustered the western and eastern sea bass samples without ambiguity into two distinct groups. This is an indirect proof that homoplasy, if any, did not obliterate the genetic signal.

Our results shed light on two separate issues. First, there was no evidence of genetic continuity between the northeastern Atlantic and the Mediterranean sea bass populations, but rather significant change in allelic frequencies over a comparatively short distance. The place of the genetic transition is located within the Mediterranean basin, northeast of Gibraltar Strait (Ksar-Sghir) and east of Nador, and southwest of Valencia and west of Annaba (see Figure 1). Genetic discontinuities between the northeastern Atlantic and the western Mediterranean have been reported or suspected in a number of marine species including pelagic and demersal fishes, the mussel *Mytilus galloprovincialis* and one echinoderm (reviewed in Borsa et al. 1997; Foltz DW, unpublished manuscript). Detailed sampling in *M. galloprovincialis* showed that the genetic discontinuity for this species is located east of Almeria in southern Spain (Quesada et al. 1995), whereas in the hake (*Merluccius merluccius*), the transition zone appeared to be located west of Gibraltar Strait (Roldán 1995; Roldán et al. 1998).

Although the sampling grid for sea bass was not as detailed as that of Quesada et al. (1995), it was sufficiently accurate to rule out Gibraltar Strait as the zone of genetic discontinuity, leaving the Almeria–Oran oceanographic front (AOOF) as a possible zone of transition in sea bass. The AOOF, which is the effective boundary between Atlantic and Mediterranean surface waters, is the major oceanographic discontinuity in the western Mediterranean (Beckers et al. 1997; Millot 1987; Tintore et al. 1988). This corresponds to a major ecological break with drastically different planktonic communities on either side (Estrada et al. 1985). The encounter of Atlantic surface water with higher density Mediterranean water off Almeria on the southern coast of Spain induces a jet toward North Africa. A part of the Atlantic water returns westward to form the Alboran gyre and another part flows eastward along the coast of North Africa. The presence of this gyre could provide an explanation for the Atlantic/Mediterranean ecological and genetic discontinuity: current-transported sea bass larvae spawned in the Alboran Sea would be retained in the Alboran gyre until recruitment.

Although this interpretation may seem straightforward, we would like to question the hypothesis that the AOOF alone would cause the genetic divide. Planktonic sea bass larvae are long-lived (2–3 months), and even if a small part of the water masses were exchanged, this should be sufficient for some individuals to be transported on either side of the gyre. Moreover, juveniles are tolerant to temperature and salinity changes and adult sea bass are active swimmers able to migrate over hundreds of miles (Pickett and Pawson 1994). Therefore a large potential for gene flow across the AOOF must exist. Small numbers of migrants per generation suffice to homogenize the gene pools of a species. If the differentiation we observed corresponds to an equilibrium between migration and drift for neutral genes, Wright's island model predicts that equilibrium F_{ST} should be equal to $1/(1 + 4Nm)$, where Nm is the absolute number of effective (i.e., reproductively successful) migrants per generation. This result holds true for other models of population genetic structure (Slatkin 1993, but see Whitlock and McCauley 1999). Under the assumption of equilibrium, Nm between Atlantic and western Mediterranean sea bass populations would be on the order of 10–15 effective migrants per generation. This may seem quite small even when taking into account the particular hydrologic features of the Alboran Sea.

At this point we are left with two alternative possibilities, since the assumptions underlying the above relationship between Nm and F_{ST} may not be considered realistic enough, as emphasized by Whitlock and McCauley (1999). Either what we observe is a permanent or equilibrium feature, and some mechanism other than strictly passive retention by currents is involved to maintain it (e.g., selection against larvae that cross the front, or homing behavior of spawners), or the genetic demarcation is transient, and gene flow is occurring at such a rate that genetic differences that would have built up previously (perhaps during the late Pleistocene sea level drop?) are in the process of vanishing. Note that for the latter hypothesis to be realistic over thousands of generations, gene flow has still to be very limited, which does not preclude the implication of some nonpassive mechanism to impede it.

The second issue deals with the genetic differentiation within the Atlantic and the western Mediterranean groups of populations. Even though the western Mediterranean is represented in our study by only five samples, the populations appeared to be homogeneous, with a small overall F_{ST} (0.002, not significant). This is consistent with previous estimates of genetic differentiation between Mediterranean samples from Spain and France (García de León et al. 1997), and altogether depicts the western Mediterranean group of populations as being nearly panmictic. As to the Atlantic ocean/Alboran Sea group of populations, the data do not indicate such homogeneity. This can be seen in Figure 2, where the internal branches are long, and correspond to an overall F_{ST} of 0.010 ($P < .001$). However, there does not seem to be any geographical rationale in this internal differentiation, with the possible exception of the Antwerpen sample, which may be genetically slightly different from the others (Table 2). For instance, the Alboran Sea samples do not cluster together, nor do the replicate samples from Tanger, Tahadarte, and Ksar-Sghir. Castilho and McAndrew (1998), using a set of allozymes they considered as selectively neutral, also found small but significant differences between populations from northern and southern Portugal. More evidence is needed to understand the basis of small-scale geographic differentiation. The fact that samples collected at different dates at a location did not cluster together may point toward the existence of temporal or intercohort variation.

Using presumably neutral genetic markers, we documented a clear-cut shift in allele frequencies between Atlantic and western Mediterranean populations of the common sea bass, while populations in each of the two groups appeared to be homogeneous. Does this reflect historical events and will the differences between groups eventually disappear, or are these

differences at a steady-state equilibrium between drift within, and migration between populations? In either case, the absolute number of migrants exchanged each generation between the Atlantic ocean/Alboran Sea and the western Mediterranean is likely to be small. Behavior may be important in reinforcing the physical barrier to dispersal and gene flow that is represented by the AOOF, and we suggest that behavior of sea bass spawners and larvae might be fruitful to study.

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Corresponding Editor: Bernie May