Relationship between migratory behavior and environmental features revealed by genetic structure of *Sardina pilchardus* populations along the Moroccan Atlantic coast

Malika Chlaida[1*], Cécile Fauvelot[2], Omar Ettahiri[1], Najib Charouki[1], Salaheddine. Elayoubi[1] & Serge Planes[3,4]

1. Institut National de Recherche Halieutique. 2, BD Sidi Abderrahmane. Ain Diab , Casablanca 20030, Maroc.
2. Institut français de   Recherche et Développement (IRD – UR128). Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne, Université de Perpignan, 52 Av. Paul Alduy. F-66860 Perpignan cedex, France.
3. UMR 5244 EPHE/ CNRS/UPVD. Université de Perpignan. F-66860 Perpignan Cedex. France.
4. UMS 2978 EPHE / CNRS. Centre de Recherches Insulaires et Observatoire de l'Environnement, BP 1013, Papetoai, Moorea, French Polynesia.

Abstract. We used genetic markers, namely allozymes, to study the genetic structure (stock unit) and the sardine stocks movement along the Moroccan Atlantic coast and its relationship regarding the environmental features, especially upwelling. In this study, we have combined previous results obtained by analyzing eight samples collected during the spawning season (winter 2004) (chlaida et al.2008) and new data obtained by analyzing eight samples gathered during the feeding season (summer 2006). Therefore, we compiled 765 individuals from an earlier study and the 2006 summer sampling and compared seasons' results. In winter, a substantial heterogeneity (F_{st} =0.205) is described, with a significant genetic break in the Agadir Bay (latitude 30° 48' N) that cuts the coastal sardine populations in the Moroccan Atlantic into two stocks (north and south). In summer, the genetic structure showing two groups is maintained (F_{st}= 0.135). Still, the genetic break separating the two stocks arises southward, near Tarfaya (latitude 28°08'10" N), suggesting a spreading out towards the south of the northern stocks. This result seems to be related to the sardine movement along the Moroccan Atlantic coast regarding reproduction needs in winter and for trophic reasons in summer. The species' observed genetic break and seasonal activity along the Moroccan coast are expected to result from the Cape Ghir Hydrological barrier, impermeable in winter and semi-permeable in summer. This barrier comprises currents, gyres, and different mesoscale structures related to upwelling dominating in this zone.

Keywords: *Sardina pilchardus*, migratory behavior, genetic structure, upwelling, Moroccan Atlantic coast.

1. Introduction

Small pelagic population size and abundance fluctuate significantly from year to year, mainly due to strong variability of recruitment, overfishing (Parrish et al. 1989; Gaggiotti et al. 1999; Schwartzlose et al. 1999; Cendrero et al. 2002). However, the real challenge is the management of small pelagic fisheries due to climatic and hydrological variations, as well as variation in seasonal migrations of species (Lluch-Belda et al. 1989; Cury 1994; Guisande et al. 2001; FAO 2004). Therefore, the assessment of intra-specific diversity and determining the geographical extent of sustainable populations or groups of sub-populations linked by gene flow is vital for managing marine resources to ensure lasting exploitation (Iles & Sinclair 1982; Grant et al. 1999). For example, the European sardine (*Sardina pilchardus* Walbaum 1792) is a clupeoid found in the Atlantic, from the Celtic Sea and the North Sea to south Mauritania, together with populations in the Mediterranean and the Black Sea. On the other hand, populations of Madeira, the Azores, and the Canary Islands are at the western limit of the distribution (Parrish et al.1989). Occasionally, populations may be found as far south as Senegal during episodes of low water temperature (Corten et al. 1996; Binet et al. 1998).

Sardines are the most abundant and commercially important fish species on the Moroccan shelf, with annual purse seine catches exceeding 650,000

tons. These total catches represent about 70% in the 2000s (FAO 2008). However, the stocks and populations dynamics of this species remain not well-known. Former studies conducted on sardine population's identification in (CHLAIDA et al. 2005; LAURENT et al. 2007; ATARHOUCH et al. 2007; CHLAIDA et al. 2008)] and its ichthyologic aspect FURNESTIN & FURNESTIN 1970; BELVÈZE 1984; ETTAHIRI et al. 2003; BERRAHO 2007) brought important information regarding the reproduction and the genetic structure of sardine stocks. Nevertheless, the stock definition requires knowledge of the fish's life history, migrations, mortality, and strategic adaptation to deal with the environmental fluctuations to which the species is permanently exposed (AGENBAG et al. 2003). Moreover, this knowledge can help understand this pelagic fish's behavior with relatively high migratory capacities. Indeed, this species is characterized by a high gene flow that is accelerated by a strong dispersion. In addition, the adequate size of this population opposes genetic drift (WAPLES 1989; GONZLES & ZARDOYA 2007). Homogenizing forces linked to the hydrodynamic environment characterize this flow. This is notably the case of the northwestern African coasts with the Canary Current and the upwelling phenomenon (LE FLOCH 1974; BELVÈZE &ERZINI 1983) For this reason, each piece of the information constitutes a new element in the understanding of sardine stocks.

Based on biological certainties, these informations allow sardine stocks delimitation that characterizes its migratory flow (direction and amplitude) and adapts management plans for Moroccan sardine fisheries. We used enzyme polymorphism (allozymes) to compare opposite seasons (winter and summer) and to understand the sardine movement along the Moroccan Atlantic coast by investigating the relationship between genetic results and migratory behavior with the upwelling conditions (CHLAIDA et al. 2008; and new data). This is due to the availability and diversity of information using genetic markers, the definition of geographical limits and stock evolution (RICO et al. 1997; EXADACTYLOS et al. 1998 ; GUARNIERO et al. 2002), as well as

life history monitoring (BORSA et al. 1997; GRANT & BOWEN 1998; GILLES et al. 2000) and the study of the migration and the estimation of the fish dispersal rate (SOTKA & PAUMBI 2006; PLANES & RAMOS 2004), we used enzyme polymorphism (allozymes) to compare opposite seasons : winter (CHLAIDA et al. 2008) and summer (new data) and understand the movement of the sardine along the Moroccan Atlantic coast by investigating the relationship between genetic results and migratory behavior in relation to the upwelling conditions.

2. Material and methods

2.1 Sampling

To compare the genetic structure observed during the 2004 spawning season (CHLAIDA et al. 2008) to that of the feeding season, another batch of 8 samples of sardines, with 50 individuals per sample, were collected along the Moroccan Atlantic coast on board the R/V "Al Amir Moulay Abdallah" in July 2006 (Fig. 1). Fishes were dissected to isolate the liver and a piece of muscle. Each piece of tissue was manually grounded in 1 ml of pure water on a bench of ice to limit any degradation of the enzymatic activity. Homogenates were sub-divided in 4 Eppendorf and then stored at -30°C.

2.2 Allozymes electrophoresis.

For 2006 Sampling, we only surveyed polymorphic loci described in earlier studies (CHLAIDA et al., 2005; Laurent et al., 2006; CHLAIDA et al., 2008), SOD* [EC.1.15.1.1] and PGM* [EC 2.7.5.1] (SHAKLEE et al. 1990) for locus nomenclature). Alleles were separated on horizontal starch gel electrophoresis following the technique of Pasteur et al. (1987) and using TG (pH=9) buffer. Alleles and genotypes were scored according to SHALKLEE et al. (1990) with the most common allele in the first sample being designated as 100. The other variants were subsequently according to SHALKLEE et al. (1990), we scored Alleles and genotypes, with the most common allele in the first sample designated 100. The other variants were subsequently numbered according to their electrophoretic mobilities relative to the most common allele.
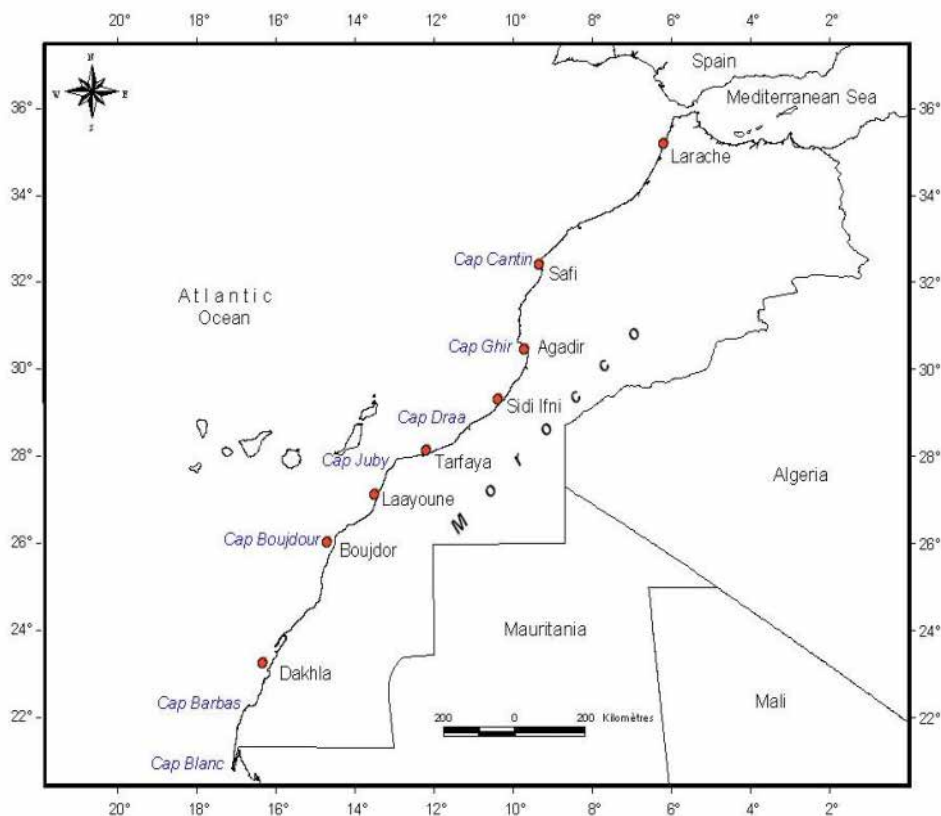
Figure 1: Map of the Moroccan Atlantic coast showing the location (red spots) of sardine sampling site.

2.3 Genetic data analysis

Allele and genotype frequencies were obtained by counting phenotypes directly from the gels and analyzed with the GENETIX 4.05 package (BELKHIR et al. 1996-2004) (http://www.univ-montp2.fr/genome-pop/genetix.htm). Departure from the Hardy-Weinberg proportions was assessed with the fixation index (FIS) and statistically tested using the Markov chain method implemented in Genepop 3.4 (RAYMOND & ROUSSET 1995). We adjust the level Significance for statistical tests according to the standard Bonferroni procedure (RICE 1989). In addition, we used Wright's standardized variance in allele frequencies (F_{ST}) to perform Genetic divergence among pairs of samples (WRIGHT 1969). Following the method of Weir and Cockerham (1984), calculate this index (F_{ST}) using the all-samples algorithm. Therefore, we adjusted the level significance according to the sequential Bonferroni procedure (RICE 1989). Finally, we tested the genetic structure using the hierarchical analysis of molecular variance (AMOVA) implemented in ARLEQUIN v. 2.000 000 (SCHNEIDER et al. 2000; EXCOFFIER et al. 1992).

The AMOVA provided estimates of the portion of the observed total variance accounted for within and among groups of samples. The objective was to test for the best grouping by maximizing the variance among groups while minimizing the variance within groups. Statistical significance was determined using a permutation of genotypes among groups (> 1000 permutations).

3. Results and discussion

Statistical analyses showed that overall samples analysis was in Hardy-Weinberg equilibrium (FIS = -0.0306, p<0.732). Furthermore, the Observed heterozygosity (Ho) in Laâyoune 2006 and Safi 2004 is respectively ranged from 0.071 to 0.310; while the expected heterozygosity (He) is ranged among similar values, from 0.067 (in Laâyoune 2006) to 0.276 (in Safi 2004), (Table 1). Thus, all samples were in Hardy-Weinberg equilibrium after standard Bonferroni correction of the threshold value.

The overall genetic differentiation was highly significant with $F_{ST} = 0.135$ (p<0.000). This differentiation is the result of the variation of a single locus, enzymatic system SOD (Super Oxyde Dismutase). A comparison of SOD* allele frequencies (Table 1) shows a structured spatial variation of allele frequency with a north-south gradient as well as and a temporal variation (i.e., see allele frequencies in Tarfaya in 2004 compared as in 2006). The test of genetic differentiation test for all pairs of samples illustrates allele frequencies differences (Table 2). In both seasons, the F_{ST} estimates obtained for the southern samples (Dakhla, Laâyoune, Boujdour) are indeed not significant with F_{ST} estimates of 0 - 0.02 (all p-values non-significant after Bonferroni corrections). Consequently, these populations can be considered to be homogenous. Also, the northern samples (Agadir, Safi, and Larache) belong to a second homogeneous group irrespective of the season (F_{ST} estimates obtained among these samples of 0 – 0.106, all p-values non-significant after Bonferroni correction) (Table 2). Among the two seasons, we noticed differences in the transition zone between northern and southern groups identified earlier. Indeed, the Tarfaya sample appeared genetically homogeneous to the southern group in winter (F_{ST} of 0.00). At the same time, in summer it made a homogenous entity with the northern group, being then significantly different from the southern group (F_{ST} of 0.142-158, p<0.001, Table 2). Likewise, Sidi Ifni appeared homogeneous to the northern stock in summer while it was significantly differentiated from it in winter (though F_{ST} estimates < 0.10). The global F_{ST} estimate reaches 0.205 (p<0.000) (result of CHLAIDA et al. 2008) in winter and 0.135 (p<0.000) in summer (2006 data), suggesting summertime movement and/or a mixture of the two stocks. We evaluated the best groupings by testing the significance of two different segregations with an AMOVA (Table 3).

The results of the AMOVA showed that grouping the samples in 2 groups (North and South) with the Sidi Ifni sample of 2004 in the northern group explained 20.12 % of the total variance (p<0.000), with 1.65 % (p<0.000) of the total variance being explained within groups. However, when the Sidi Ifni sample of 2004 (winter) is included in the southern group, the results are nearly identical, explaining 19, 65 % (p<0.000) of the total variance (1.72% (p<0.000) being explained within groups). This result confirms the intermediate position of the Sidi Ifni sample from 2004 (CHLAIDA et al. 2008) suggesting that this sample may be composed of a mix of the two stocks.

The electrophoresis allozyme survey, during winter and summer, reveals the existence of two large sardine populations segregated along the Moroccan coast. The first one was located on the southern coast of Morocco and included the samples from Laâyoune, Boujdour, and Dakhla; the second northern population consisted of Agadir, Safi, and Larache samples (See sample location on Fig. 1). Although SOD* loci mainly drove the analyses, this genetic structure was stable during the two winter seasons, 2003 and 2004 (CHLAIDA et al. 2005; 2008) and 2006 data of summer season. These two large homogeneous populations are set apart by more than 200 km transition zone located between Cape Juby (latitude ~28°N) and the Agadir-bay (latitude 30°38'N) (Fig. 1). Considering the switch in allele frequencies, in summer and winter periods, the Tarfaya samples and the distinctiveness of the Sidi Ifni sample (northern and southern stocks), our results suggest that this zone is successively occupied in winter by sardine of the southern stock and in summer by those of northern stock. Thus, the limit of the two stocks is placed between Laâyoune and Tarfaya in summer (possibly at Cape Juby) and around Sidi Ifni in winter. (see Figure 2 for seasonal distribution).

Table 1: Allele frequencies and gene diversity for each sample of S. pilchardus. N = sample size (N), Ho = observed heterozygosity, He = expected heterozygosity, Fis = Wrights' fixation index.

Locus/Population

SOD	Lar.04	Saf.04	Aga.04	S.Ifni.04	Tarf.04	Lay.04	Boj.04	Dakh.04	Lar.06	Safi.06	Aga.06	S.Ifni.06	Tarf.06	Lay.06	Boj.06	Dakh.06
(N)	49	50	43	50	50	50	50	30	46	50	50	49	50	49	50	49
80	0.459	0.440	0.337	0.230	0.080	0.090	0.040	0.067	0.565	0.370	0.310	0.316	0.300	0.061	0.050	0.051
100	0.541	0.560	0.663	0.770	0.920	0.910	0.960	0.933	0.435	0.630	0.690	0.684	0.700	0.939	0.950	0.949

PGM																
(N)	50	50	50	50	50	50	50	30	50	50	50	49	50	50	50	50
100	0.990	0.970	0.990	0.950	0.960	0.970	0.950	0.967	0.990	0.990	0.960	0.980	0.970	0.990	0.970	0.910
150	0.010	0.030	0.010	0.050	0.040	0.030	0.050	0.033	0.010	0.010	0.040	0.020	0.030	0.010	0.030	0.090
Ho	0.245	0.310	0.254	0.240	0.120	0.120	0.090	0.100	0.249	0.300	0.270	0.194	0.270	0.071	0.080	0.101
He	0.258	0.276	0.233	0.225	0.112	0.111	0.086	0.094	0.256	0.243	0.252	0.236	0.239	0.067	0.077	0.130
Fis	0.063	-0.115	-0.077	-0.059	-0.061	-0.071	-0.038	-0.042	0.036	-0.225	-0.060	0.189	-0.119	-0.047	-0.034	0.238

Table 2: F_{ST} pairwise estimates among all sites with emboldened values representing statistically significant differences after Bonferroni correction

	Safi.04	Aga.04	S.Ifni.04	Tarf.04	Lay.04	Boj.04	Dakh.04	Lar.06	Safi.06	Aga.06	S.Ifni.06	Tarf.06	Lay.06	Boj.06	Dakh.06
Lar.04	-0.008	0.019	**0.092**	**0.274**	**0.263**	**0.334**	**0.273**	0.010	0.006	0.034	0.029	0.040	**0.320**	**0.328**	**0.300**
safi.04		0.011	**0.073**	**0.244**	**0.234**	**0.301**	**0.242**	0.020	0.002	0.022	0.019	0.028	**0.288**	**0.295**	**0.268**
Aga.04			**0.018**	**0.159**	**0.147**	**0.220**	**0.163**	0.086	-0.007	-0.007	-0.011	-0.006	**0.200**	**0.210**	**0.191**
S.Ifni.04				**0.054**	**0.047**	**0.096**	**0.059**	0.184	0.035	0.004	0.007	0.002	**0.084**	**0.090**	**0.077**
Tarf.04					-0.009	-0.001	-0.012	**0.390**	**0.186**	**0.119**	**0.130**	**0.113**	-0.003	-0.004	0.003
Lay.04						0.005	-0.010	**0.380**	**0.175**	**0.109**	**0.119**	**0.104**	-0.003	-0.001	0.010
Boj.04							-0.007	**0.449**	**0.245**	**0.170**	**0.185**	**0.166**	0.004	-0.007	-0.003
Dakh.04								**0.386**	**0.189**	**0.122**	**0.133**	**0.118**	-0.009	-0.011	-0.001
Lar.06									0.062	0.106	0.102	0.117	**0.439**	**0.445**	**0.409**
Safi.06										0.000	-0.004	0.003	**0.228**	**0.237**	**0.216**
Aga.06											-0.010	-0.009	**0.155**	**0.163**	**0.144**
S.Ifni.06												-0.010	**0.167**	**0.176**	**0.160**
f.06													**0.149**	**0.158**	**0.142**
Lay.06														-0.006	0.021
Boj.06															0.006

Table 3: AMOVA results comparing two groups of *Sardina pilchardus*. (A) Group 1 = samples from Larache 2004, Larache 2006, Safi 2004, Safi 2006, Sidi Ifni 2004, Agadir 2004, Agadir 2006, Sidi Ifni 2006, Tarfaya 2006; Group 2 = samples from Tarfaya 2004, Laayoune 2004, Laayoune 2006, Boujdour 2004, Boujdour 2006, Dakhla 2004, Dakhla 2006. (B) same grouping except that Sidi Ifni 2004 is moved to Group 2.

	Source of variation	d. f.	Variance components	%
A	Among groups	1	33.93	20.12***
	Among samples within groups	14	7.3	1.65***
	Within samples	1544	263.37	78.23***
B	Among groups	1	33.76	19.65***
	Among samples within groups	14	7.46	1.72***
	Within samples	1544	263.37	78.23***
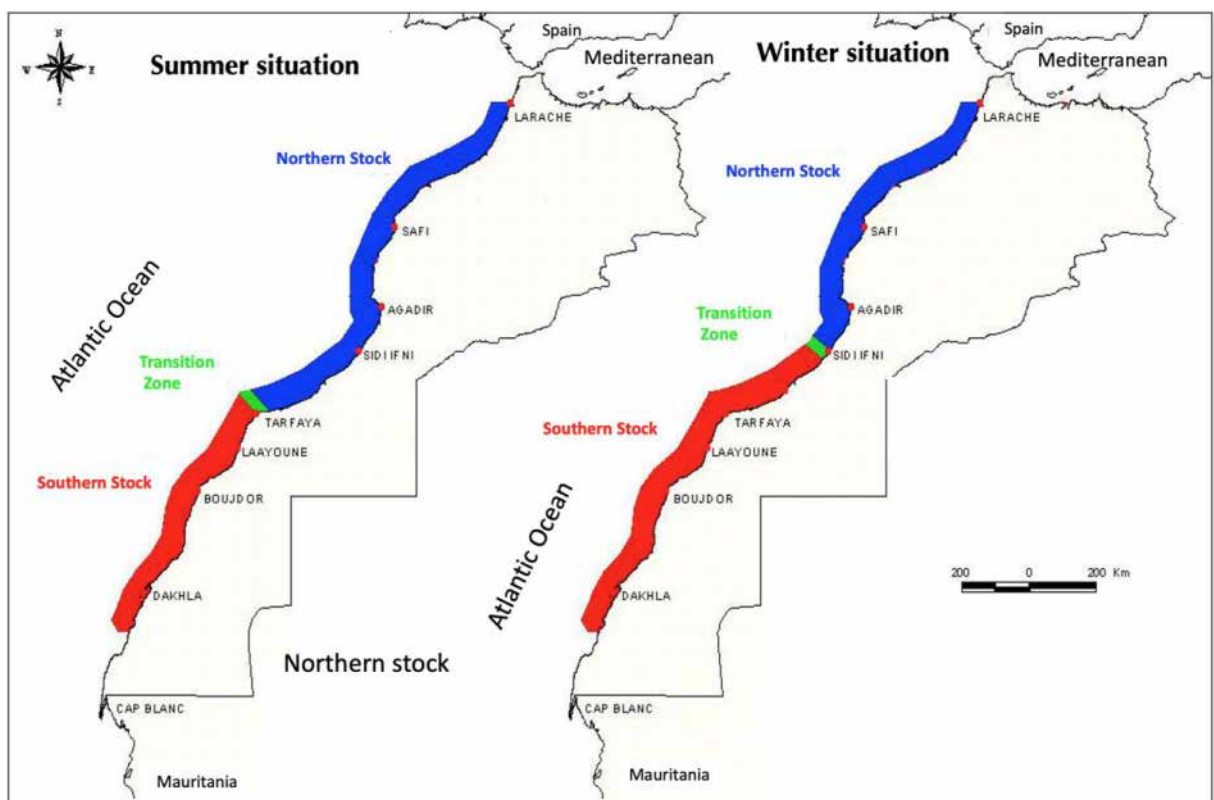
Figure 2: Summary Map showing seasonal distribution of sardine stocks along the Moroccan Atlantic coast

Several authors have already described massive sardine movements along the Moroccan Atlantic coast (FURNESTIN & FURNESTIN 1970; JOHANNESON et al. 1975; FAO 1978; LAMBOUF 1977; BELVÈZE & ERZINI, 1983; BELVÈZE, 1972, 1984). The small pelagic fish can undertake large migrations seasonally. Therefore, our results confirm that sardines undergo seasonal drifts along the Atlantic coast. These movements depend on the developmental stage, nutrient availability, reproduction, and thermal conditions of the study area (OLIVAR et al. 2001; RIVEIRO et al. 2000).

The global hypothesis suggests that the sardine coming from the south migrate northwards during the summer season. This idea is supported by significant sardine catches conducted by fishing vessels operating between Safi and Sidi Ifni. Encouraged by wide sardine availability, fishing

activity indeed increases during the summer season (BELVÈZE, 1984; FAO 1985; KIFANI. 1991). Authors of the abovementioned studies stated that the sardines migrate back to the south for reproduction purposes during winter. Other works reported that sardines from the south concentrate in Dakhla during this spawning season (DOMANOVSKI & BARKOVA 1976). However, neither the direction nor the amplitude of this migratory flow has been verified using molecular techniques or tagging experiments. Near the Moroccan Atlantic Coast, in the North-Eastern Atlantic, and within the framework of SARDYN Project (2002-2005), only one trial of sardine tagging has been undertaken. The results of this campaign were promising regarding the survival in captivity of the marked individuals. Still, the experiment was not concluding about fish movement, primarily because of the meager percentage of recaptured (SARDYN report).

Regarding the direction of this migration, our results confirm that Moroccan sardines undergo seasonal migrations, except that these are not consistent with what has been admitted. The genetic analyses have revealed that in winter, the southern population scatters from the Cape Blanc (19°03'N) to the south of Sidi Ifni (29°12' N) (CHLAIDA et al. 2005; ATTARHOUCH et al. 2007; CHLAIDA et al. 2008; and summer samples included in this study), While in the summer, its northern limit arose south to the winter season limit, between Laâyoune and Tarfaya (28°08'10"N). Consequently, our results suggest a sardine migration towards the south in summer, contrary to previously stated.

The winter season corresponds to the main spawning period since 90% of the analyzed sardines were spawning (unpublished personal data). Furthermore, the eggs and larvae study carried out between 1996-2006 (ETTAHIR et al. 2003; BERRAHO et al. 2007). confirms our results. The latter indicates that during winter, the south stock undergoes an extension northward to spread out towards the Sidi Ifni zone during spawning reasons. In contrast, the northern stock concentrates north of Sidi Ifni, yielding the niche available for the southern stock. This winter migration pattern would correspond to a need

from genitors to spawn in propitious zones for early survival stages (BAKUN, 1989; 1996). Indeed, several spawning grounds have been identified along the Moroccan coast, between Cape Ghir (30°37'N) - Cape Cantin (~32°30'N), between Cape Juby - Cape Draa (~28°N -29° N), and between Cape Boujdour and Cape Barbas in the south (~26°-22°N) (see Fig. 1 for caps location). These areas have favorable hydrological and/or geomorphological characteristics (wide and shallow continental shelf) in favor of better water retention, as well as nutrients for adult species (BKAUN, 1996; ETTAHIRI, 1996).

In summer, the reverse phenomenon would occur. The southern stock will be concentrated between Dakhla and Cape Juby (its northern limit), leaving the Sidi Ifni - Tarfaya zone to the sardines of the north stock, which spreads out southwards to the south of Tarfaya. This result contradicts some previous acoustic observations in this area, indicating that, in summer, sardines coming from the south form the fisheries located between Safi and Agadir, particularly from the zone between Sid Ifni and Laâyoune (LAMBOUF, 1977; FAO, 1985). The southward drift of the northern stock is likely driven by trophic purpose since spawning is weak during this period (ETTAHIRI et al. 2003; BERRAHO et al. 2007). This expansion would then occur after the spawning period and recruitment of new individuals (June-July). Indeed, during summer, the upwelling activity increases along the Atlantic Moroccan coast, ensuring a significant abundance of nutrients and subsequent primary production (BELVÈZE 1984; MAKAOUI et al. 2005). Concerning the area of Dakhla, the upwelling activity is permanent with intensification in summer, guaranteeing enough nutrients for each member of the population. Therefore, individuals of the southern stock would not have to move northward in search of food.

4. Conclusion

Through this study, we have clearly shown that *Sardina pilchardus* is a small pelagic resource that is known to be a highly fluctuating marine species. This high variability is mainly attributed to their strong dependence on the marine environment and their adaptive strategies to ensure their survival in a changing environment. We have also shown

that, in addition to the spatial delimitation of stocks, genetic markers can also provide important information concerning fish migrations. For *Sardina pilchardus*, in the Moroccan Atlantic coast, the results of this genetic analysis disagree with previous assumptions related to seasonal migrations, namely those proposed by FURNESTIN & FURNESTIN (1970) and BELVÈZE & ERZINI (1983). The patterns of sardine movements drawn from the present investigation suggest that during winter, sardines carry out a migration following a south-north direction, likely linked with a reproduction purpose. During summer, they undertake a trophic north-south migration. These movements are conditioned by the hydro-climatic factors which vary according to the season (JOHNSON & STEVENS, 2000; BARTON et al., 2004; PELEGRI et al. 2005), and to the zone

(BAKUN et al. 2015; XIU et al. 2018; FAO 2018). Future research should focus on a more acceptable spatio-temporal scale analysis to provide further details concerning seasonal sardine migrations that depend on the environmental conditions that change over time and space along the Moroccan Atlantic coast.

Acknowledgements

References

AGENBAG J.J., RICHARDSON A.J., DEMARCQ H., FRÉON P., WEEKS S. & SHILLINGTON F.A. (2003): Estimating environmental preferences of south african pelagic fish species using catch size and remote sensing data. Progress in Oceanography, **59** (2-3), 275-300.

ATARHOUCH T., RAMI M., NACIRI M. & DAKKAK A. (2007): Genetic population structure of sardine (*Sardina pilchardus*) off Morocco detected with intron polymorphism (EPIC-PCR). Marine Biol,**150**, 521-528.

BAKUN A. (1989) : L'océan et la variabilité des populations marines. In : Troadec J.P. (Eds.), L'homme et les ressources halieutiques : Essai sur l'usage d'une ressource renouvelable. IFREMER, Brest, 155-188.

BAKUN A. (1996): Patterns in the ocean: ocean progresses and marine population dynamics. Upwelling of California Sea Grant, San Diego, CA, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 p.

BAKUN A., BLACK B.A., BOGRAD S.J., GARCÍA-REYES M., MILLER A.J., RYKACZEWSKI R.R & SYDEMAN W.J. (2015): Anticipated effects of climate change on coastal upwelling ecosystems. Current Climate Change Reports, **1** (2), 85–93, https://doi.org/10.1007/s40641-015-0008-4.

BARTON E.D., ARÍSTEGUI J., TETT P. & PEREZ E.N. (2004) : Variability in the Canary Islands area of filament-eddy exchanges. Progress in Oceanography, **62** (2-4), 71-94.

BELKHIR K., BORSA P., CHIKI, L. GOUDET J. & BONHOMME F. (1996–2004): Genetix version 4, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome et Populations, CNRS UPR 9060, Université de Montpellier II, Montpellier, France.

BELVÈZE H. (197 : Observation complémentaires sur le stock sardinier de l'Atlantique marocain de 1968 à 1971 et essai d'estimation de quelques paramètres. Rev. Trav. Inst. Pêches Marit,**20**, 5-55.

BELVÈZE H. & ERZINI K. (1983): The influence of hydroclimatic factors on the availability of the sardine (*Sardina pilchardus*) in the Moroccan Atlantic fishery. In Proceedings of the expert consultation to examinen changes in abundance and species composition of neritic fish resources. San Jose. Costa Rica. FAO Fishery.Report, **291(2),** 285-328.

BELVÈZE H. (1984) : Biologie et dynamique des populations de Sardine (*Sardina pilchardus*) peuplant les côtes atlantiques marocaines et propositions pour un aménagement des pêches. Doc. D'Etat. Université de Bretagne Occidental, 532 pp.

BERRAHO A. (2007) : Relations spatialisées entre milieu et ichtyoplancton des petits pélagiques de la côte Atlantique marocaine (Zones centrale et sud). Université Mohamed V, Rabat, 261 pp.

BINET D., SAMB B., TALEB SIDI M., LEVENEZ J.J. & SERVAIN J. (1998): Sardines and other pelagic fisheries changes associated with trade wind increases in the Canary current upwelling (26°N-

14°N), late 1960s-early 1990. In. Durand M.H., Mendelssohn R., Cury P., Roy C., Pauly D. (Eds). Global versus local changes in upwelling systems. Collection et Séminaires, ORSTOM, Paris, 211-233.

BORSA P., NACIRI M., BAHRI L., CHIKHI L., GARCIA DE LEON F.J., KOTOULAS G. & BONHOMME F. (1997) : Zoogéographie infra-spécifique de la mer Méditerranée : Analyse des données génétiques populationnelles sur seize espèces atlanto-méditerranéennes (Poissons et Invertébrés). Vie et Milieu, **47**, 295-305.

CENDRERO O. (2002) : Sardine and anchovy crises in northern Spain : natural variations or an effect of human activities ? ICES Marine Science Symposium, **215,** 279-285.

CHLAIDA M., KIFANI S., LENFANT P. & OURAGH L. (2005) :First approach for the identification of sardine populations Sardina pilchardus (Walbaum 1792) in the Moroccan Atlantic by allozymes. Marine Biol, **149,** 169–175.

CHLAIDA M., LAUREN, V., KIFANI S., BENAZZOU T., JAZIRI H., & PLANES S. (2008): Evidence of a genetic cline for Sardina pilchardus along the Northwest Africa coast. ICES Journal of Marine Science,**66,** 264-271.

CORTEN A. & VAN KAMP G. (1996): Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind. ICES Journal of Marine Science,**53,** 1113-1119.

CURY P. (1994): Obstinante nature: ecology of individuals. Thoughts on reproductive behaviour and biodiversity.Can.J Fish. Aquat. Sci, **51,** 1664-1673.

DOMANEVSK, L.N.& BARKOVA N.A. (1976): Some peculiarities of sardine (*Sardina pilchardus*.) distribution and spawning along the Northwest Africa. Int. Coun. Explor. Sea, **6,** 15.

ETTAHIRI O. (1996) : Etude de la phase planctonique de la sardine, *Sardina pilchardus*, et de l'anchois, Engraulis encrasicolus des côtes atlantiques marocaines. Doc. d'université. Université de Bretagne Occidentale, 262 pp.

ETTAHIRI O., BERRAHO A., VIDY G., RAMDANI M. & DO CHI T. (2003): Observation on the spawning of *Sardina* and *Sardinella* off the south Moroccan Atlantic coast (21-26°N). Fisheries Research,**60,** 207-222.

EXADACTYLOS A., GEFFEN A.J., THORPE J.P. (1998): Population structure of the Dover sole, Solea solea L., in a background of high gene flow. Journal of Sea Research,**40**, 117-129.

EXCOFFIER L., SMOUSE P. & QUATTRO J. (1992): Analysis of molecular variance inferred from metric distance among DNA haplotypes: Application to human mitochondrial DNA restriction data. Genetics, **131,** 479-491.

FAO (1978) : Les pêches dans l'Atlantique Centre – Est. rapport du Groupe de Travail sur l'unification de la détermination de l'âge de la sardine (Sardina pilchardus walb.). COPACE Rapport tech,**78/8/Dakar**, 8 pp

FAO (1985) : Rapport de la troisième réunion du Groupe de travail ad hoc sur Sardina pilchardus (Walb.). COPACE/PACE SERIES 85/39/Rome, 157 pp.

FAO (2004): Report of the working Group on the assessment of small-pelagic fish off northwest Africa. FAO Fish. Rep. 762, 135 pp.

FAO (2008): Report of the working Group on the assessment of small-pelagic fish off northwest Africa. FAO Fisheries and Aquaculture Report, **882,**117-118.

FAO (2018) : Impacts du changement climatique sur les pêches et l'aquaculture : synthèse des connaissances actuelles, options d'adaptation et d'atténuation. Résumé du Document technique sur les pêches et l'aquaculture 627 de la FAO. Rome, 48 pp. Licence: CC BY-NC-SA 3.0 IGO.

FURNESTIN J. & FURNESTIN M.L. (1970) : La sardine marocaine et sa pêche : migrations trophiques et génétiques en relation avec l'hydrologie et le plancton. Rapp. P.V CIEM, **159,** 165-175.

GAGGIOTTI O.E. & VETTER R.D. (1999): Effect of life history strategy. Environmental variability. and overexploitation on the genetic diversity of pelagic fish populations. Canadian Journal of Fisheries and Aquatic Sciences, **56**, 1376-1388.

GILLES A., MIQUELIS A., QUIGNARD, J-P. & FAURE E. (2 000) : Molecular phylogeography of western mediterranean dusky grouper Epinephelus marginatus. Comptes Rendus de l'Académie des Sciences de Paris, **323,** 195-205.

GONZALEZ E.G. & ZARDOYA R. (2007): Relative role of life-history traits and historical factors in shaping genetic population structure of sardines (*Sardina pilchardus*). BMC Evolutionary Biology, **7,**197.

GRANT W.S., GARCIA-MARIN J.L. & UTTER F.M. (1999) : Defining Population Boundaries for Fishery Management , 27-72. In: Mustafa,. S. (Eds), Genetics in Sustainable fisheries Management. Fishing News Books. Blackwell Science. Oxford. UK, 223p.

GRANT W.S. & BOWEN B.W. (1998): Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. Journal of Heredity, **89,** 415-426.

GUARNIERO I., FRANZELLITTI S., UNGARO N., TOMMASINI S., PICCINETTI C. & TINTI F.(2002):

Control region haplotype variation in the central Mediterranean common sole indicates geographical isolation and population structuring in Italian stocks. Journal of Fish Biology, **60,** 1459-1474.

GUISANDE C., CABANAS J.M., VERGARA A.R. & RIVEIRO I. (2001) : Effect of climate on recruitment success of Atlantic Iberian sardine *Sardina pilchardus*. Marine Ecology Progress. Series, 223, 243-250.

ILES T.D. & SINCLAIR M.(1982): Atlantic Herring: Stock discreteness and abundance. Science. **,215,** 627-633.

JOHANNESSON K., VILLEGAS L. & LAMBOUF M. (1975) : Estimation acoustique quantitative de l'importance et de la distribution des ressources sardinières de la côte atlantique du Maroc. Trav. Doc. Dev. Pêche Maroc,**11,** 23pp.

JOHNSON J. & STEVENS I. (2000) : A fine resolution model of the eastern North Atlantic between the Azores, the Canary Islands and the Gibraltar Strait. Deep Sea Research,**47,** 875–899.

KIFANI S. (1991) : Approche spatio-temporelle des relations hydroclimatiques des espèces pélagiques en région d'upwelling : cas de la sardine du stock central marocain. Thèse Doc.d'université en Oceanographie halieutique. Université de Bretagne Occidentale, 216pp.

LAMBOUF M. (1977) : Estimation acoustique quantitative de l'abondance et de la distribution de sardine marocaine en janvier 1977.Trav.Doc.Dév.Pêche Maroc,**22,** 11p.

LAURENT V., VOISIN M. & PLANES S. (2006) : Genetic clines in the Bay of Biscay provide estimates of migration for Sardina pilchardu. Journal of Heredity, **97,** 81–88.

LAURENT V., MAGOULAS A., CANECO B. & PLANES S. (2007):Isolation by distance and selection effects on genetic structure of sardine Sardina pilchardus Walbaum. Journal of Fish Biology, **71,** 1–7.

LE FLOCH J.(1974) Quelques aspects de la dynamique et de l'hydrologie des couches superficielles dans l'Ouest marocain Campagne CINECA-CHARCOT I et III. Tethys, **6 (1-2),** 53-68.

LLUCH-BELDA D., CRAWFORD R.J.M., KAWASAKI T., MCCALL A.D., PARRISH R.H., SCHARTZLOSE R.A. & SMITH P.E.(1989):World-wide fluctuations of sardine and anchovy stocks: the regime problem. South African Journal of Marine Sciences, **33,** 195-205.

MAKAOUI A., ORBI A., HILMI K., ZIZAH S., LARISSI J. & TALBI M. (2005) : L'upwelling de la côte Atlantique du Maroc entre 1994 et 1998. C.R.Geoscience,**337,** 1518-1524.

OLIVAR M.P., SALAT J. & PALOMERA I.(2001) :Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Marine Ecology Progress, **217,** 111-120.

PARRISH R.H., SERRA R. GRANT W.S. (1989) The monotypic sardines. sardina and sardinops : their taxonomy.distribution. stock structure and zoogeography. Canadian Journal of Fisheries and Aquatic Sciences,**46**, 2019-2036.

PASTEUR N., PASTEUR G., BONHOMME F., CATALAN J. & BRITTON-DAVIDIAN J. (1987) : Manuel de génétique par électrophorèses des protéines. Paris : Collection techniques et documentation, Lavoisier. 232 pp.

PELEGRI J. L., ARI stegui L., CANA M., GONZALEZ-DA VILA A., HERNA ndez-GUERRA S., HERNANDEZ-LEO 'N A. & MARRERO-DIAZ M. F. (2005) : Coupling between the open ocean and the coastal upwelling region off Northwest Africa: water recirculation and off- shore pumping of organic matter. Journal of Marine Systems,**5,**3–37.

PLANES S. & ROMANS P. (2004): Evidence of genetic selection for growth in new recruits of a marine fish. Molecular Ecology,**13,** 2049–2060.

RAYMOND M. & ROUSSET F. (1995): GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. Journal of Heredity, **86,** 248-249.

RICE W. R. (1989): Analyzing tables of statistical tests. Evolution, 43, 223–225.

RICO C., IBRAHIM K.M., RICO I. & HEWITT G.M. (1997) Stock composition in North Atlantic populations of whiting using microsatellite markers. Journal of Fish Biology,**51,** 462-475.

RIVEIRO I., GUISANDE C., LLOVES M., MANEIRO I. & CABANAS J.M.(2000) Importance of parental effects on larval Survival in Sardina pilchardus. Marine Ecology Progress. Series, **205**, 249-258.

SARDYN Project: Sardine dynamique and stock structure in the north-eastern Atlantic, Q5 RS-2002-000818,2002-2006.

SCHNEIDER S., ROESSLI D. & EXCOFFIER L.(2000) Arlequin Ver 2.000: A software for population genetics data analysis. Genetics and Biometry Laboratory, Dept. of Anthropology, University of Geneva, Switzerland.

SCHWARTZLOSE R. A., ALHEIT J., BAKUN A., BAUMGARTNER T. R., CLOETE R., CRAWFORD R. J. M., FLETCHER W. J., GREEN-RUIZ Y., HAGEN E., KAWASAKI T., LLUCH-BELDA D., LLUCH-COTA S. E., MACCALL, A. D., MATSUURA Y., NEVA 'REZ-MARTINEZ M. O., PARRISH R. H., ROY C., SERRA R., SHUST K. V., WARD M. N. & ZUZUNAGA J. Z. (1999): Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science, **21,** 289-347

SHAKLEE J.B., ALLENDORF F.W., MORIZOT D.C. & WHITT G.S. (1990): Gene nomenclature for protein-coding loci in fish. Transactions of the American Fisheries Society,**119,** 2-15.

SOTKA E.E. & PALUMBI S.R. (2006): Genetic clines and dispersal distance of marine larvae. Ecology, **87(5),** 1094–1103.

WAPLES R.S. (1989): A generalized approach for estimating effective population size from temporal changes in allele frequency. Genetics, **121,** 379-391.

WEIR B.S. & COCKERHAM C.C.(1984): Estimating F-statistics for the analysis of population structure. Evolution,**41,** 1358-1370.

WRIGHT S. (1969): Evolution and the genetics of populations.2: The theory of gene frequencies. University of Chicago Press, Chicago

XIU P ; CHAI F., CURCHITSER E.N. & CASTRUCCIO F.S.(2018) : Future changes in coastal upwelling ecosystems with global warming: the case of the California Current System. Scientific Reports, **8 ,** art :2866 [en ligne]:(http://doi.org/10.1038/s41598-018-21247-7)