Belg. J. Zool. - Volume 129 (1999) - issue 1 - pages 83-94 - Brussels 1999

A GENETIC COMPARISON OF ATLANTIC AND MEDITERRANEAN POPULATIONS OF A SALTMARSH BEETLE

KONJEV DESENDER (1) AND JOSÉ SERRANO (2)

(1) KBIN, Department of Entomology, Vautierstraat 29, B-1000 Brussels, (Belgium)
(2) Department of Animal Biology, Univ. Murcia Aptdo. 4021. 30071 Murcia (Spain)
e-mail : kdesender@kbinirsnb.be

Abstract. Enzyme and dispersal polymorphism in the saltmarsh carabid beetle *Pogonus chalceus* Marsham were compared between 30 Atlantic and nine Mediterranean European populations. Allozyme results showed that Mediterranean beetles (France, Spain) are genetically distinct from Atlantic populations. All Mediterranean beetles screened showed complete fixation at one locus (IDH1), which in Atlantic populations nearly always varied, whereas some unique Mediterranean alleles were observed for another locus (MPI). Genetic differentiation (allozymes) between Mediterranean populations, although highly significant, appeared to be much lower (F_{ST} =0.098) than between Atlantic populations (F_{ST} =0.178). Beetles from the Mediterranean showed a remarkably high dispersal power in all populations studied, whereas Atlantic populations showed wing polymorphism and reduced dispersal power to much more varying degrees. These results, along with relatively lower levels of *Pogonus chalceus* abundance in many Mediterranean saltmarshes, strongly suggest increased levels of extinction/recolonisation in relation to a lower degree of habitat persistence in Mediterranean compared with most Atlantic saltmarshes. Conclusions are relevant to issues in both evolutionary and conservation biology.

Key words : population genetics, genetic differentiation, dispersal power, gene flow, habitat fragmentation, allozymes, wing polymorphism, saltmarshes, Atlantic, Mediterranean, ground beetles (Carabidae), *Pogonus chalceus*.

INTRODUCTION

Geographic genetic structure – the distribution and abundance of genotypes between and within populations – is a fundamental part of ecology and evolution, combining both demographic and genetic processes, such as extinction/recolonisation, gene flow, drift and natural selection (RODERICK, 1996). Insects, with their extreme diversity and abundance, in many cases have evolved special features, and are increasingly used as model species in population and conservation genetics. For example, many insect species display dispersal polymorphism (*e.g.* DENNO *et al.*, 1996), which can be used to evaluate directly the effect of migration on geographic structure. Such data can then be compared with those obtained indirectly from genetic studies (RODERICK, 1996).

Natural areas in Europe have been severely reduced and highly fragmented. Many species therefore persist only in small and isolated populations. Habitat fragmentation in general results

in a reduced biodiversity (e.g. ANDRÈN, 1994), but may also lead to an increased genetic differentiation (HASTINGS & HARRISON, 1994; YOUNG *et al.*, 1996) as a result of reduced gene flow (SLATKIN, 1994). In theory, the negative influence of fragmentation on biodiversity is supposed to be caused by lowered genetic diversity and adaptability of species, eventually leading more rapidly to their extinction (FRANKHAM, 1995). Recently, we started studying population genetic consequences of fragmentation on a variety of beetle species, with emphasis on saltmarsh and woodland species. The rationale which formed the basis of this study is outlined in more detail elsewhere (DESENDER & TURIN, 1989; DESENDER *et al.*, 1998).

West-European saltmarshes are relatively recent habitats, in many cases well documented historically. They can mostly be considered true habitat islands, a prerequisite for the study of population genetic effects of isolation and fragmentation. Recent estimates all over western Europe show a dramatic decrease of the surface area of saltmarshes (DIJKEMA *et al.*, 1984). This is expected to enhance isolation and its negative effects on the genetic diversity of the highly specialised terrestrial arthropod fauna, including many halobiontic species, i.e. many ground beetles (Coleoptera, Carabidae). Mediterranean saltmarshes, although in general studied less intensively than Atlantic marshes, also are inhabited by an array of highly specialised terrestrial invertebrates, with again beetles as one of the most prominent groups (BIGOT, 1965). Also in this area, human impact on coastal habitats (especially estuaries) has been very pronounced during the twentieth century (e.g. GUILLEN & PANALQUES, 1997).

Ground beetles show large variation in morphological traits related to dispersal power, and many species even display dispersal polymorphism or dimorphism (DEN BOER *et al.*, 1980; DESENDER, 1989). Gene flow of such species can be quantified more or less directly by means of morphological or biometrical knowledge on the hind wings and flight muscles. In earlier work, we have documented the life cycle and population densities of such a wing polymorphic and halobiontic carabid beetle *Pogonus chalceus* (Marsham, 1802) from an Atlantic population (DESENDER, 1985). *P. chalceus* occurs exclusively in saltmarshes (THIELE, 1977), at densities generally between about 1-20 ind/m^2 (DESENDER & SEGERS, 1985; GAUTIER, 1979). The geographical distribution extends along the Atlantic coasts from Denmark to and including the major part of the Mediterranean (TURIN *et al.*, 1977). The species can be found on inland saline habitats (EVERSHAM *et al.*, 1996; DESENDER & MAELFAIT, in press), especially in the Iberian Peninsula (ZABALLOS & JEANNE, 1994).

Wing development in *P. chalceus* appears to be a polygenic trait with high heritability (DESENDER, 1985, 1989). An earlier population genetic study on the same species (based on allozymes as well as wing polymorphism) compared ten Atlantic populations (varying in size and isolation in space and time), and showed significant genetic differentiation (DESENDER *et al.*, 1998). The dispersal power in small populations was larger than in large populations, suggesting that the former are unstable and/or young. Dispersal power declined with increasing age of the saltmarsh, probably due to a continuous emigration of winged individuals. Age and size of saltmarshes, although difficult to study independently, both appeared to be important in determining the genetic structure of saltmarsh beetles. Population genetic data of *P. chalceus* are not yet available for the Mediterranean area.

In the present study, we therefore compared the geographic genetic structure in the halobiontic *P. chalceus* from 30 Atlantic and nine Mediterranean European populations. In particular, we investigated the following questions:

(1) Can Mediterranean *P. chalceus* populations be distinguished genetically from Atlantic populations?

(2) Is genetic differentiation between populations within each region comparable between the two regions?

(3) Are there general differences in dispersal power between populations in the two regions and, if so, can these be understood and related to allozyme genetic structure?

Results related to genetic diversity will be presented in a forthcoming paper.

MATERIAL AND METHODS

Study sites and sampling

Since 1992 we have collected *P. chalceus* beetles from 30 Atlantic and nine Mediterranean saltmarshes varying in size and isolation. Atlantic populations were sampled from several areas in the UK, France, The Netherlands and Belgium, including four small and relatively young populations on inland sites from Flanders and the southern part of the Netherlands (cf. DESENDER *et al.*, 1998). Nine Mediterranean populations were sampled from southern France (three coastal populations from lagoons) and Spain (including three coastal populations and three populations from inland high elevation salt ponds (elevation ca 600-800 m) near Albacete). The study areas are indicated on Fig. 1. In several areas, different populations were studied (Table 1).

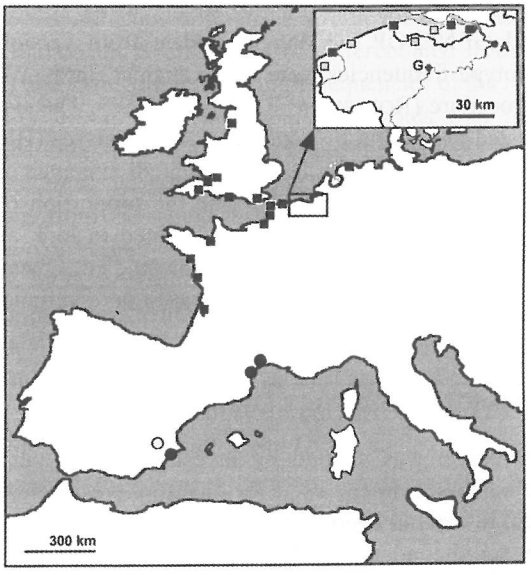

Fig. 1. – Geographic location of sampled saltmarsh areas (in some areas, more than one population was sampled; for names, see Table 1); square symbols: Atlantic areas, grey-filled: small/young inland marshes; circular symbols: Mediterranean areas, grey-filled: high elevation inland salt ponds near Albacete.

Beetles were collected by standardised handcatches (unit of effort), mostly by using an aspirator, or by flotation whenever brackish water was available in the immediate surroundings of a sampling site. Beetles were transported alive, counted and identified with a binocular dissecting microscope, and mostly kept at low temperature for some days without food to allow the gut to empty. They were then frozen in liquid nitrogen until subjected to electrophoresis.

Allozyme electrophoresis

Individuals were prepared for electrophoresis by homogenising part of the body in 50 µl of distilled water, and kept in eppendorf tubes on ice. Only the head and thorax of beetles were used for electrophoresis, while the abdomen was retained for morphological study and verification of identification. Variation at enzyme loci was analysed using cellulose acetate electrophoresis (HEBERT & BEATON, 1989), permitting the examination of each individual for variation at multiple enzyme loci. If available, about 30 to 50 individuals from each population were analysed. Overall, more than 2000 beetles were processed for this study. Results from six polymorphic enzyme loci (95%-criterion) are used in this paper: Aldehyde Oxidase (AO, E.C. 1.2.3.1), Glucose-6-phosphate Isomerase (GPI, E.C. 5.3.1.9), Isocitrate Dehydrogenase 1 and 2 (IDH1, IDH2, E.C. 1.1.1.42), Mannose Phosphate Isomerase (MPI, E.C. 5.3.1.8) and Phosphoglucomutase (PGM, E.C. 2.7.5.1). For more details on other enzymes tested, protocols of electrophoresis and buffer systems used, we refer to DESENDER *et al.* (1998).

Analyses of electrophoretic data were carried out using BIOSYS-1 (SWOFFORD & SELANDER, 1981) and GENEPOP (version 3; update from version 1.2: RAYMOND & ROUSSET, 1995). Genotype frequencies were tested against Hardy-Weinberg expectations using an exact test procedure (ROUSSET & RAYMOND, 1995). The significance of genetic differentiation was tested per region by contingency X^2-analyses (BIOSYS-1) and evaluated quantitatively by F_{ST}-statistics (NEI, 1977) (weighted) averaged over the six polymorphic (95%-criterion) enzymes. F_{ST}-values describe the proportion of diversity found in populations. Hierarchical F_{ST}-values were also calculated to look at partitioning of the genetic variance within and between the two regions studied. Overall genetic similarity between the populations was visualised in a PCA based on a variance-covariance matrix of allelic frequencies.

Dispersal polymorphism

Dispersal polymorphism was studied by investigation of wing and flight muscle development, on the same specimens used for electrophoresis as well as on additional alcohol-fixed samples. In carabid beetles in general, wing size follows an allometric relationship to body size, and the index «% MAX ALL» (DESENDER *et al.*, 1986) corrects for this allometry. Wing length and width, as well as elytral length and width are needed to calculate these values. Wing length x width is then expressed as a percentage of the maximal wing size for a beetle of a given (elytral) size. Population frequency distributions of «% MAX ALL» values were plotted for ten Atlantic populations (showing the range of variation in all studied Atlantic populations, see also DESENDER *et al.*, 1998) and the nine

Mediterranean populations. The plots were ordered according to decreasing mean population values, and the frequencies of individuals with functional flight muscles were separately indicated.

RESULTS AND DISCUSSION

Genotype frequencies were first tested against Hardy-Weinberg expectations and showed only very few significant deviations, which could be expected by chance alone. These results suggest that the studied populations were all in Hardy-Weinberg equilibrium.

Allelic frequencies of the polymorphic loci are given in Table 1. The PCA-plot (based on allelic frequencies) along the first and second axis is given in Fig. 2. Dispersal power, expressed as % MAX ALL, is shown in frequency distributions for ten Atlantic populations (Fig. 3) and for the nine Mediterranean populations (Fig. 4.).

The allozyme results showed that the beetles from the Mediterranean (France, Spain) were genetically distinct from those in the Atlantic populations. All Mediterranean beetles screened showed complete fixation in one enzyme (IDH1) – which in Atlantic populations nearly always varied (except for one population on an inland site, see further) – whereas some unique Mediterranean alleles were observed for another locus (MPI). Moreover, allelic frequencies regularly differed between the two regions for AO (AO A allele most frequent in coastal Mediterranean populations only), and for GPI (GPI A allele most frequent for coastal Mediterranean sites, and GPI B allele most frequent in Mediterranean populations). There were thus also a number of differences within the Mediterranean area, where all coastal populations (France and Spain) could be differentiated from the inland salt ponds near Albacete (Spain) due to the presence of high frequencies of the AO A and GPI A allele. Whether the similarity between coastal populations holds true for other parts of the Mediterranean remains to be investigated, but is not immediately expected because of the more or less discontinuous distribution of the species in other parts of the area (TURIN *et al.*, 1977). The populations from the inland marshes of Belgium and the southern part of the Netherlands (small and/or young populations of *P. chalceus*) showed near-fixation in the IDH1 B allele (in the MOK population even complete fixation, but relatively low sample size) and in this way mimic the Mediterranean populations. This explains why these Atlantic populations are situated closer to the Mediterranean ones along the first and second axis of the PCA-plot based on allelic frequencies (Fig. 2). The table with allelic frequencies, however, shows that they still can be discriminated from Mediterranean populations by the complete absence of the MPI A, MPI D, GPI A and GPI B alleles.

Genetic differentiation (allozymes) between Mediterranean populations, although highly significant for at least two enzymes (Table 2), appeared to be much lower (F_{ST}=0.098) than between Atlantic populations (F_{ST}=0.178). This difference cannot be explained by the difference in the number of populations screened so far for both regions. Indeed, recalculating F_{ST}-values for several sets of randomly chosen groups of only ten populations of the Atlantic region yielded only slightly lower mean values than those obtained from 30 populations. Hierarchical F-statistics showed an overall F_{ST}=0.244 (all 39 populations), F_{ST}= 0.150 within regions and F_{ST}= 0.094 between regions.

TABLE 1

Allele frequencies (zero-values not printed) and number of individuals scored (n) for polymorphic enzymes (95%-criterion) in Pogonus chalceus; populations (from left to right) arranged in four groups: (1) Atlantic, coastal, n=26; (2) Atlantic, inland, n=4; (3) Mediterranean, inland, n=3; (4) Mediterranean, coastal, n=6; population codes: France, Atlantic: AFM: Authie estuary, Fort Mahon; APM: Authie, Port Madelon; CAN= Canche estuary; FOR: le Fort Vert; GAC: la Gachère; GFP: Grand Fort Philippe; GIR: Gironde estuary; GUA-GUD: la Guérande: MSM: Mont St Michel; SOC: Somme estuary, le Crotoy; SOH: Somme, Cap Hornu; UK: EXE: Exe estuary; MOR: Morecambe Bay; RYE: Rye estuary; SEA-SEB: Severn estuary; THO: Thorney Island; The Netherlands: FRI: Friesland, Ferwerd-Holwerd; OSS: Ossenisse; SAE: Saeftinghe; BRA: the Braakman; Belgium: NIE: Nieuwpoort, IJzer estuary; ZWR- ZWC: the 'Zwin'; MOE: De Moeren; MOK: Molenkreek; OOS: Oostende; Spain: COR: Cordovilla; ELS: El Saladar; PET: Petrola; MAT: La Mata; PED: La Pedrera; POL: Sta Pola; France, Mediterranean: MAR: la Marende; LAP: Lapalme; SAL: Salses

	ATLANTIC COASTAL																									ATLANTIC INLAND				MEDITERRANEAN INLAND				
POPUL.	AFM	APM	CAN	EXE	FRI	FOR	GAC	GFP	GIR	GUA	GUB	GUC	GUD	MOR	MSM	NIE	OSS	RYE	SAE	SEA	SEB	SOC	SOH	THO	ZWR	ZWC	BRA	MOE	MOK	OOS	COR	ELS	PET	MAT	PED
allele:																																			
AOA	.038	.087	.039	.083	.119	.089	.007	.125	.051	.022					.125	.088	.143	.020	.219	.077	.178	.094	.130	.085	.107	.185	.054	.009	.019	.130	.048	.015	.061	.478	.750
AOB	.363	.338	.304	.250	.357	.389	.089	.328	.205	.090	.122	.076	.250		.444	.262	.452	.122	.300	.231	.305	.271	.349	.162	.375	.303	.446	.284	.259	.185	.323	.294	.333	.250	.063
AOC	.300	.300	.373	.472	.292	.256	.521	.344	.282	.455	.541	.758	.750	.100	.297	.371	.262	.592	.210	.269	.229	.396	.336	.338	.250	.265	.161	.440	.333	.442	.274	.265	.288	.188	.188
AOD	.250	.262	.235	.194	.202	.267	.384	.203	.462	.388	.338	.167		.900	.122	.228	.095	.153	.214	.413	.288	.229	.171	.415	.250	.210	.298	.155	.370	.116	.177	.250	.121	.063	
AOE	.050	.013	.049		.030					.045					.013	.051	.048	.112	.057	.010		.010	.014		.018	.038	.042	.112	.019	.127	.177	.176	.197	.063	
MPIA																															.031	.100	.029		
MPIB		.071			.012	.056		.045							.019	.008			.042			.025	.017	.045	.022	.037	.125			.094	.125	.143	.100	.125	.063
MPIC	1.000	.929	1.000	1.000	.988	.944	1.000	.955	1.000	1.000	1.000	1.000	1.000	1.000	.981	.992	1.000	1.000	.958	1.000	1.000	.975	.983	.955	.978	.963	.875	1.000	1.000	.906	.828	.743	.829	.875	.938
MPID																															.016	.014	.043		
IDH1A									.012			.172																							
IDH1B	.587	.250	.280	.066	.546	.807	.153	.710	.049	.615	.029	.359	.625	.000	.623	.611	.214	.076	.337	.323	.170	.202	.143	.367	.268	.438	.853	.856	1.000	.921	1.000	1.000	1.000	1.000	1.000
IDH1C	.412	.650	.720	.934	.446	.193	.847	.290	.841	.385	.971	.469	.375	1.000	.377	.389	.786	.924	.663	.677	.830	.798	.857	.633	.732	.562	.147	.144		.079					
IDH1D					.008				.098																										
IDH2A		.013				.011				.007			.063			.009			.010			.010			.008					.016	.043	.014		
IDH2B	1.000	.988	.980	1.000	.994	.989	1.000	1.000	1.000	.993	1.000	1.000	.938	1.000	.997	.991	1.000	1.000	.976	1.000	.992	.990	.987	1.000	1.000	.988	1.000	1.000	1.000	1.000	.969	.957	.971	1.000	1.000
IDH2C			.020		.006										.003				.014		.008		.013								.016		.014		
IDH2D																									.004										
GPIA	.028	.013			.012		.013		.012	.043			.063		.009			.010	.005	.038	.025	.010	.023			.018								.063	.063
GPIB																															.016	.014			.188
GPIC		.013					.006								.009							.031							.148			.043	.029	.063	.063
GPID	.972	.975	1.000	1.000	.988	1.000	.981	.970	.988	.957	1.000	1.000	.938	1.000	.978	1.000	1.000	.970	.995	.962	.975	.959	.977	1.000	1.000	.982	1.000	1.000	.852	1.000	.953	.914	.943	.875	.688
GPIE								.030							.003			.020													.031	.029	.029		
PGMA			.028																			.013									.016		.014		
PGMB	1.000	1.000	.972	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.938	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.988	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.984	1.000	.971	1.000	1.000
PGMC													.063																				.014		
n =	40	40	51	38	88	45	77	33	43	69	37	33	8	5	163	160	23	52	105	53	61	49	75	65	30	128	51	58	27	146	32	35	35	8	8

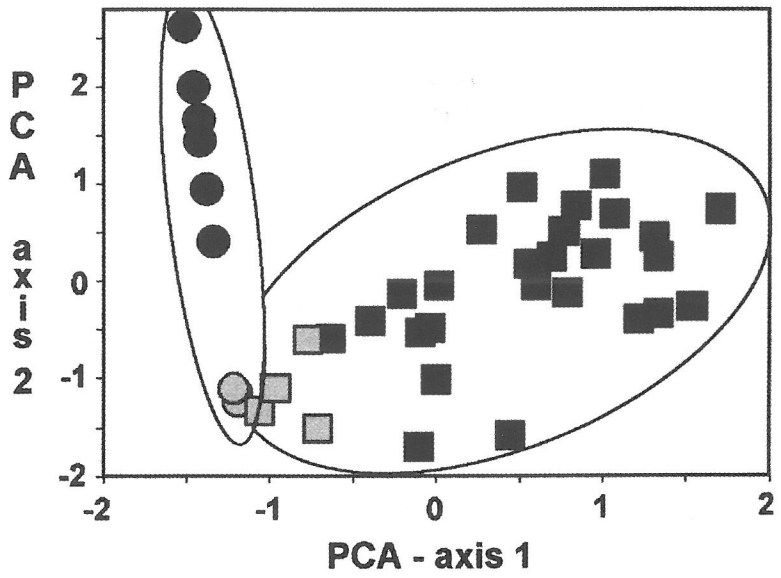

Fig. 2 . – PCA-plot along first and second axis based on allelic frequencies of 39 populations of *Pogonus chalceus*; square symbols: Atlantic populations, grey-filled: small/young inland marshes; circular symbols: Mediterranean populations, grey-filled: high elevation inland salt ponds; ellipses regroup Mediterranean and Atlantic populations, respectively.

TABLE 2

Contingency X^2-analyses at all polymorphic enzyme loci for (A) 30 Atlantic and (B) nine Mediterranean populations of Pogonus chalceus*; highly significant values ($p<0.01$) in bold italic*

Locus	No. of alleles	X^2-value	d.f.	p
(A) AO	5	742.28	116	***0.0000***
(A) MPI	2	46.17	29	0.0225
(A) IDH1	4	1758.88	87	***0.0000***
(A) IDH2	4	91.76	87	0.3429
(A) GPI	4	385.27	87	***0.0000***
(A) PGM	3	149.15	58	***0.0000***
(A) totals		3173.51	464	***0.0000***
(B) AO	5	147.55	32	***0.0000***
(B) MPI	4	34.09	24	0.0831
(B) IDH2	3	11.0	16	0.8046
(B) GPI	5	97.52	32	***0.0000***
(B) PGM	3	20.72	16	0.1893
(B) totals		310.97	120	***0.0000***

Beetles from the Mediterranean, moreover, showed a remarkably high dispersal power in all populations (Fig. 4), whereas Atlantic populations showed wing polymorphism and reduced dispersal power to much more varying degrees (Fig. 3). The population mean values for Atlantic populations ranged from 84 down to 32 % of maximal relative wing size, whereas for the Mediterranean populations these values were as high as 91 to 93 %. X^2-tests between adjacent distributions showed many statistically significant differences between Atlantic populations (Fig. 3). The reverse was true for Mediterranean populations, all showing near-maximum dispersal power as well as high frequencies of individuals with functional flight muscles, but no significant differences between populations, not even between coastal or inland populations (Fig. 4). Additional data for the Mediterranean area, especially from parts other than the Western Mediterranean, are needed to test the generality of these results.

The few estimates of *P. chalceus* abundance known to us from Mediterranean saltmarshes (Camargue area, GAUTIER, 1979) indicate a maximum of less than 1.5 ind/m^2, even in preferred habitats. Ecological studies from the same and other areas in the Western Mediterranean invariably mention strong fluctuations of numbers during the course of a year in these salty habitats, possibly mediated through changes in temperature and humidity (GAUTIER, 1979; VERDIER & QUÉZEL, 1951). Severe circumstances indeed regularly occur due to temporal desiccation of many lagoons from July onwards. Populations of *P. chalceus* in parts of the Mediterranean therefore are probably to be viewed as metapopulations made up of ephemeral local populations (cf. OLIVIERI & GOUYON, 1997). Along with the observed relatively low abundance levels of *P. chalceus* in many Mediterranean saltmarshes, our dispersal power data thus strongly suggest increased levels of extinction/recolonisation in Mediterranean compared with most Atlantic saltmarshes. Mediterranean populations suffer much more from temporarily dry and hot conditions during a large part of the year. The retention of a high dispersal power can then be interpreted as an adaptation for survival in temporarily more unstable marshes compared with many Atlantic saltmarshes, which would be closer to the species' optimal habitat, with less need for regular recolonisation. As a consequence of increased gene flow, one would then expect the genetic differentiation between Mediterranean populations to be lower. Our allozyme data confirm this hypothesis. Future field work, especially in other areas of the Mediterranean area, will gather more data to further test this hypothesis.

Models and (few) empirical work have shown that patterns of extinction and recolonisation indeed can influence the genetic differentiation between local populations (MCCAULEY, 1991), but that effects can be complex. The hypothesis that levels of gene flow among populations are correlated with dispersal power (« the dispersal-gene flow hypothesis ») has only recently been rigorously tested. This was done by comparing intraspecific geographic variation in dispersal strategies with levels of gene flow, as derived from genetic structure data (PETERSEN & DENNO, 1997): increased genetic structuring between populations of wing-dimorphic planthopper species was found in the region where they showed a lower dispersal power. Our results on *P. chalceus*, although still somewhat limited for the Mediterranean, present comparable evidence for the dispersal-gene flow hypothesis. PETERSEN & DENNO (1997) also investigated coastal saltmarsh-inhabiting species, in their case from the Atlantic and Gulf coasts of North America.

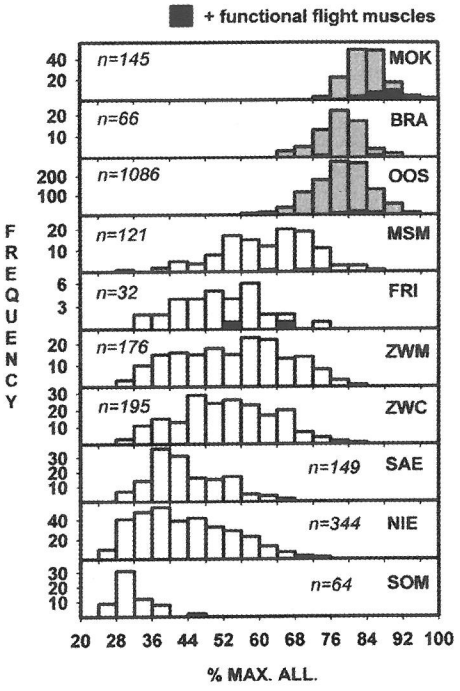

Fig. 3. – Wing polymorphism in Atlantic populations of *Pogonus chalceus*: percentage frequency distributions of % MAX ALL, arranged according to decreasing mean value of dispersal power; grey-filled histograms correspond to highly significantly differing samples from inland marshes; X^2-test results between adjacent distributions: MOK ≅ BRA ≅ OOS ≠ MSM ≠ FRI ≅ ZWM ≅ ZWC ≠ SAE ≅ NIE ≠ SOM, $p<0.01$; black columns: individuals with functional flight musculature; for population codes, see Table 1.

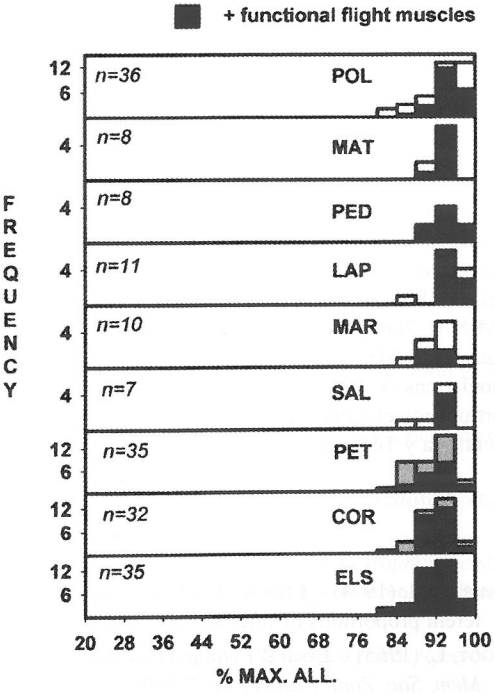

Fig. 4. – Wing polymorphism in Mediterranean populations of *Pogonus chalceus*: percentage frequency distributions of % MAX ALL; grey-filled histograms correspond to inland salt ponds near Albacete (Spain); no significant differences (X^2-test) between distributions; black columns: individuals with functional flight musculature; for population codes, see Table 1.

Among-populational genetic differentiation in *P. chalceus* was highly significant (Table 2), and many of the populations studied were genetically distinct, especially in the Atlantic part of the distribution area (DESENDER *et al.*, 1998). This was shown by allozyme as well as wing polymorphism data. Conserving a maximal overall genetic diversity for such a saltmarsh beetle therefore requires the protection of as much of the few remaining sites as possible.

Significant genetic substructuring (allozymes) has been reported for many insects including beetles (HSIAO, 1989; KING, 1987). Apart from the study of PETERSON & DENNO (1997), to our knowledge such substructuring has never been mentioned to be accompanied by such a difference in dispersal strategy. Geographic genetic structure in wing polymorphism nevertheless has been mentioned for many insect species (RODERICK, 1996). DENNO *et al.* (1996) gave strong evidence for an intraspecific inverse relationship between the dispersal capability of saltmarsh-inhabiting planthoppers and the persistence of their habitats.

Few genetic comparisons have been made for terrestrial coastal organisms between the Mediterranean and the Atlantic. MADEC *et al.* (1996) reported significant geographic genetic structure in the mollusc *Helix aspersa*, but some Mediterranean populations showed a stronger genetic relationship to all Atlantic ones, probably as a result of human transport in the past. The geographic genetic structure of a tephritid fly from 16 European regions (EBER & BRANDL, 1997) showed only low levels of differentiation, mainly resulting from a south-north decrease in allelic diversity. A genetic study on *Zannichellia* water plants (TRIEST & VANHECKE, 1991) showed a near-uniform intraspecific genetic structure between Mediterranean and Atlantic populations, linked to predominant inbreeding. Many more empirical population genetic studies are needed to evaluate more generally the patterns and processes linked to the geographic genetic structure of organisms, distributed both in the Atlantic and Mediterranean region.

ACKNOWLEDGEMENTS

Regional and national nature conservation authorities allowed us to sample invertebrates in their saltmarshes. Numerous students and colleagues assisted in the field work necessary for this study. Patrick Grootaert, Ann Huysseune and Peter Verdyck commented on an earlier version of the manuscript. This study is supported partly by FKFO grant 2.0128.94 and by project AMINAL/Natuur/VLINA 96/1, and is carried out within the framework of the Flemish research network FWO.010.97N (« Ecological genetics : patterns and processes of genetic variation in natural populations »). J. L. Lencina helped with collection of Spanish samples and J. Serrano had the support of project « PB95-0235 Fauna Ibérica IV », granted by the Dirección General de Investigación Científica y Técnica.

REFERENCES

ANDRÈN, H. (1994) – Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : a review. *Oikos*, **71** : 355-366.

BIGOT, L. (1965) – Essai d'Ecologie quantitative sur les Invertébrés de la « sansouire » camarguaise. *Mem. Soc. Zool. France*, **34** : 7-100.

DEN BOER, P.J., T.H.P. VAN HUIZEN, W. DEN BOER-DAANJE, B. AUKEMA & F.M. DEN BIEMAN (1980) – Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera : Carabidae). *Entomol. Gener.*, **6** : 107-134.

DENNO, R.E., G.K. RODERICK, M.A. PETERSON, A.F. HUBERTY, H.G. DOBEL, M.D. EUBANKS, J.E. LOSEY & G.A. LANGELLOTTO (1996) – Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol. Monogr.*, **66** : 389-408.

DESENDER, K. (1985) – Wing polymorphism and reproductive biology in the halobiont carabid beetle *Pogonus chalceus* (Marsham) (Coleoptera, Carabidae). *Biol. Jb. Dodonaea*, **53** : 89-100.

DESENDER, K. (1989) – Heritability of wing development and body size in a carabid beetle, *Pogonus chalceus* Marsham, and its evolutionary significance. *Oecologia*, **78** : 513-520.

DESENDER, K., TH. BACKELJAU, K. DELAHAYE. & L. DE MEESTER (1998) – Age and size of European saltmarshes and the population genetic consequences for ground beetles. *Oecologia*, **114** : 503-513.

DESENDER, K. & J.-P. MAELFAIT (in press) – Diversity and conservation of terrestrial arthropods in tidal marshes along the river Schelde : a gradient analysis. *Biol. Conserv.*

DESENDER, K., J.-P. MAELFAIT & M. VANEECHOUTTE (1986) – Allometry and evolution of hind wing development in macropterous carabid beetles. In : *Carabid beetles. Their adaptations and dynamics.* DEN BOER, P.J., M. LUFF, D. MOSSAKOWSKI & F. WEBER (Eds.) Gustav Fisher, Stuttgart : 101-112.

DESENDER, K. & H. SEGERS (1985) – A simple device and technique for quantitative sampling of riparian beetle populations with some carabid and staphylinid abundance estimates on different riparian habitats (Coleoptera). *Rev. Ecol. Biol. Sol.*, **22** : 497-506.

DESENDER, K. & H. TURIN (1989) – Loss of habitats and changes in the composition of the ground- and tiger beetle fauna in four West-European countries since 1950 (Coleoptera : Carabidae, Cicindelidae). *Biol. Conserv.*, **48** : 277-294.

DIJKEMA, K.S., W.G. BEEFTINK, J.P. DOODY, J.M. GEHU, B. HEYDEMANN & S. RIVAS MARTINEZ (1984) – *La végétation halophile en Europe (prés salés)*. Council of Europe, Strasbourg, 179 pp.

EBER, S. & R. BRANDL (1994) – Ecological and genetic spatial patterns of *Urophora cardui* (Diptera : Tephritidae) as evidence for population structure and biogeographical processes. *J. Anim. Ecol.*, **63** : 187-199.

EVERSHAM, B.C., D.B. ROY & M.G. TELFER (1996) – Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. *Ann. Zool. Fennici*, **33** : 149-156.

FRANKHAM, R. (1995) – Conservation genetics. *Annu. Rev. Genet.*, **29** : 305-327.

GAUTIER, G. (1979) – Etude écologique des communautés de Tréchidés des bords d'étangs en Camargue laguno-marine. I. Le milieu et la faune (composition, structure et dynamique). *Bull. Ecol.*, **10** : 181-202.

GUILLÉN, J. & A. PALANQUES (1997) – A historical perspective of the morphological evolution in the lower Ebro river. *Environm. Geol.*, **30** : 174-180.

Hastings, A. & S. Harrison (1994) – Metapopulation dynamics and genetics. Annu. Rev. Ecol. Syst., 25 :167-188.

Hebert, P.D.N. & M.J. Beaton (1989) – *Methodologies for allozyme analysis using cellulose acetate electrophoresis.* Helena Laboratories, Beaumont.

HSIAO, T.H. (1989) – Estimation of genetic variability amongst Coleoptera. In : *Electrophoretic studies on agricultural pests*. LOXDALE, H.D. & J. DEN HOLLANDER (Eds.). Clarendon Press, Oxford :143-180.

KING, P.S. (1987) – Macro- and microgeographic structure of a spatially subdivided beetle species in nature. *Evolution*, **41** : 401-416.

McCauley, D.E. (1991) – Genetic consequences of local population extinction and recolonization. *Trends Ecol. Evolut.*, **6**: 5-8.

Madec, L., A. Bellido & A. Guiller (1996) – Signification statistique des modèles géographiques de variation morphologique et biochimique chez l'escargot terrestre *Helix aspersa*. *C. R. Acad. Sci. Paris*, **319**: 225-229.

Nei, M. (1977) – F-statistics and analysis of gene diversity in subdivided populations. *Ann. Hum Genet., Lond.*, **41**: 225-233.

Olivieri, I. & P.H. Gouyon (1997) – Evolution of migration rate and other traits – the metapopulation effect. In: *Metapopulation Biology*. Hanski, I., & M.E. Gilpin (Eds.). Academic Press, San Diego: 293-323.

Petersen, M.A. & R.F. Denno (1997) – The influence of intraspecific variation in dispersal strategies on the genetic structure of planthopper populations. *Evolution*, **51**: 1189-1206.

Raymond, M. & F. Rousset (1995) – GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.*, **86**: 248-249.

Roderick, G.K. (1996) – Geographic structure of insect populations: gene flow, phylogeography, and their uses. *Annu. Rev. Entomol.*, **41**:3 25-352.

Rousset, F. & M. Raymond (1995) – Testing heterozygote excess and deficiency. *Genetics*, **140**: 1413-1419.

Slatkin, M. (1994) – Gene flow and population structure. In: *Ecological genetics*. Real, L.A. (Ed.). Princeton University Press, Princeton: 3-17.

Swofford, D.L. & R.B. Selander (1981) – BIOSYS-1. A Fortran program for the analysis of electrophoretic data in population genetics and systematics. *J. Hered.*, **72**: 281-283.

Thiele, H.U. (1977) – *Carabid beetles in their environments*. Springer Verlag, Berlin, Heidelberg, New York (369 pp.).

Triest, L. & L. Vanhecke (1991) – Isozymes in European and Mediterranean *Zannichellia* (Zannichelliaceae) populations: a situation of predominant inbreeders. In: *Isozymes in Water Plants*. Triest, L. (Ed.). *Op. Bot. Belg.*, **4**: 133-166.

Turin, H., J. Haeck & R. Hengeveld (1977) – Atlas of the carabid beetles of the Netherlands. *Verh. Ned. Kon. Akad. Wet.*, **68**: 1-228.

Verdier, P. & P. Quezel (1951) – Les populations de carabiques dans la région littorale languedocienne. Leurs rapports avec le sol et sa couverture végétale. *Vie Milieu*: 69-94.

Young, A., T. Boyle & T. Brown (1996) – The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evolut.*, **11**: 413-418.

Zaballos, J.P. & C. Jeanne (1994). *Nuevo catálogo de los carábidos (Coleoptera) de la Península Ibérica*. Monografías de la Sociedad Entomológica Aragonesa, 1. Zaragoza. 159 pp.