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Relationships between biological characteristics of the crustacean amphipod *Talitrus saltator*, including behavioural responses, and local environmental features. Case studies of Zouara and Korba (Tunisia)

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Abstract. A geomorphological and biological multidisciplinary approach was performed to analyse the relationships between the biological characteristics of the crustacean amphipod *Talitrus saltator*, including behavioural responses, and local environmental features. To this aim, two Tunisian sandy beaches, Zouara and Korba, located respectively on the western and eastern Mediterranean coasts, were investigated. These two localities present different physical, morphological, and landscape characteristics. Zouara beach is a well-developed beach backed by considerable coastal dunes and is one of the most extended beaches in Tunisia. It is very exposed to the north-western winds, being part of a coastal sector well known for storm frequency and violence mainly during the winter season. Korba beach is located on the eastern coast of the Cap Bon Peninsula and is protected from northern and north-western winds. It is also characterized by the presence of *sebkhas* and *chotts* in the retrodunal area, which constitute one of the most striking aspects of the morphology of this coast. Orientation behaviour, activity rhythms and genetic diversity were investigated in *Talitrus saltator* populations from the two beaches to assess the potential relations of the different beach characteristics on this species. Orientation experiments under dry conditions showed that the Korba population had a mean escape direction not substantially deviating from the theoretical escape direction seawards, whereas the Zouara population exhibited a higher dispersion with a significant deviation from the local seawards direction. Regarding the locomotor activity under constant laboratory conditions, the data indicated a significant difference in the circadian period and rhythmicity rate between the two populations. The most clearly defined circadian rhythms were found in the Korba population. The genetic diversity, analysed through allozymic analysis, showed a greater variation in the Korba population than in the Zouara one. The analysis of the polymorphism of the mtDNA COI gene indicated a similar tendency. The different approaches converged on a relation between the characteristics of the beach and the biological responses of *T. saltator*, showing the highest biological stability on the less exposed beach of Korba.

Key words: *Talitrus saltator*, orientation, activity rhythms, genetic diversity, geomorphological characterization, Tunisian sandy beaches.

Résumé. *Relations entre les caractéristiques biologiques du crustacé amphipode Talitrus saltator, y compris les réponses de comportement, et les aspects environnementaux locaux : Cas des sites de Zouara et Korba (Tunisie).* Une approche multidisciplinaire, géomorphologique et biologique, a été entreprise, et la réponse de *Talitrus saltator* aux caractéristiques environnementales a été analysée. Pour ce faire, deux plages sableuses tunisiennes, Korba et Zouara, appartenant respectivement aux côtes ouest et est méditerranéennes, ont été choisies. Ces deux sites présentent des caractéristiques physiques, morphologiques et paysagères différentes. La plage sableuse de Zouara est bien développée avec des dunes côtières considérables et est très exposée aux vents dominants du nord et du nord-ouest, et tout particulièrement durant la saison hivernale ; la plage sableuse de Korba est protégée des vents nord et nord-ouest et est caractérisée par la présence, en arrière des dunes, de *sebkhas* et de *chotts* caractéristiques de la géomorphologie de cette côte. L'orientation, le rythme d'activité, ainsi que la diversité génétique ont été étudiés chez les deux populations de *Talitrus saltator* de ces deux sites, en vue d'estimer l'impact potentiel des caractéristiques géomorphologiques et climatiques de ces deux plages sur cette espèce. Les expériences d'orientation ont montré que la population de Korba a une direction moyenne d'orientation proche de la direction théorique d'orientation (DTO), alors qu'une plus grande dispersion, avec une déviation significative de la DTO, a été observée pour la population de Zouara. L'analyse des données de l'activité locomotrice a mis en évidence une différence significative de la période circadienne et du taux d'activité entre les deux populations; le rythme circadien le plus régulier étant celui de la population de Korba. Par ailleurs, la diversité génétique, analysée à travers l'étude allozymique, a montré une plus grande variabilité chez la population de Korba. Une tendance similaire a été également mise en évidence par l'analyse du polymorphisme d'un fragment du gène de la cytochrome oxydase (COI) de l'ADN mitochondrial. Les différentes approches convergent vers l'hypothèse de l'existence d'une relation entre les caractéristiques de la plage et les réponses biologiques de l'espèce *Talitrus saltator*. En effet, une plus grande stabilité biologique a été enregistrée au niveau de la plage la moins exposée de Korba.

Mots clés : *Talitrus saltator*, orientation, rythmes d'activité, diversité génétique, caractérisation géomorphologique, plages sableuses tunisiennes.

INTRODUCTION

Sandy beaches are highly dynamic ecosystems. They harbour a fauna that exhibits behavioural and morphological adaptations shown to depend largely on physical processes (McLachlan & Brown 2006). Among crustacean amphipods, *Talitrus saltator* is a common inhabitant of sandy beaches and has been considered as a

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bioindicator of the quality of sandy beaches (Weslawski *et al.* 2000, Scapini *et al.* 2002). The behavioural adaptation of this species has been studied across its geographical range, considering orientation and rhythmicity of locomotor activity (Borgioli *et al.* 1999, El Gtari *et al.* 2000, Fanini & Scapini 2008, Nardi *et al.* 2003, Nasri-Ammar & Morgan 2005, 2006, Rossano *et al.* 2008, 2009, Scapini *et al.* 1995, 1999, 2002, 2005b, Morgan et al. 2002). These behaviours have been proven to be of high survival value for the species and critical for its fitness; a good orientation seawards is needed, for example, to avoid death by dehydration. The rhythmic behaviour constitutes also, a fundamental factor for the species survival, as it determines its spatio-temporal distribution (Scapini *et al.* 1992, Borgioli *et al.* 1999). These traits were correlated with the local environmental factors, species intrinsic characters and beach morphology (Borgioli *et al.* 1999, Scapini *et al.* 2002, Nardi *et al.* 2003, Scapini *et al.* 2005b, Nasri-Ammar & Morgan 2006).

Genetic variation of the species has been also studied to a great extent to assess intra- and inter-populations' variation (Bulnheim & Scholl 1986, De Matthaeis *et al.* 1995, Bulnheim & Schwenzer 1999, Bouslama *et al.* 2001, Ketmaier *et al.* 2003, 2005), and some authors hypothesised a correlation between genetic variation and the beach stability, and therefore their potential use as bioindicators of the stability of sandy beaches (Ketmaier *et al.* 2003). Furthermore, Scapini *et al.* (1995) provided an elegant approach on the assessment of the relationship of both species orientation and heterozygosity with beach stability.

In this paper, we combined two approaches: the first one is related to the geomorphologic characteristics of two sandy beaches, Zouara and Korba belonging to the northern and eastern coasts of Tunisia, respectively; in the second approach, some biological features of the species *Talitrus saltator* were assessed. The aim of this study was to investigate the trends of variations among the different biological responses, and also to highlight their relationship with the local factors, mainly the geomorphological ones and human impacts on the beach.

MATERIAL AND METHODS

The study was carried out at two sandy beaches on the Mediterranean coasts of Tunisia (Fig. 1).

Zouara site

Zouara Beach (37°0'41''N 08°53'26''E) is located on the north-western coast of Tunisia. Exposed to northern and north-western winds and bathed by a relatively deep sea known for its frequent storms and strong waves, the Zouara beach is bordered by an extended dune field. The dunes penetrate several kilometres inland and are largely wooded, but their seaward margin can show many excavations due to the sand reactivation consecutively to the destruction of the vegetation. The sections exposed reveal that the recent sand is covering different generations of dunes, the oldest thereof are consolidated and date back to the Tyrrhenian Age or the late Pleistocene (Fig. 2). Theses are generally separated from the recent dunes by continental runoff deposits. As for the beach, it is relatively extensive (Fig. 2), thick and constituted by relatively coarse material, in which the average grain size of the sandy fraction (the most often between 0.400 to 0.580 mm) is significantly coarser than for dunes (0.280-0.350 mm). The vertical growth of this dune that may locally constitute a real ridge isolating the beach from the hinterland is accelerated by mechanical obstacles made of different types of twigs and branches. The transition between this ridge and the beach is characterized by the multiplication of small *nebkas* fixed by various psammophile plant species. Such a dynamics suggests that the beach is not directly subject to marine erosion that constitutes a serious threat to beaches in other Tunisian areas (Oueslati 2004). However, it seems that this situation will not be perpetuated because of the reduction of the terrigenous inputs of Oued Zouara since the building of the Sidi El Barrak dam ended in year 1999. The fore dune has there lost a significant part of its sandy body and the retreat of the shoreline has led to the destruction of the rare constructions built in the inner part of the beach (Oueslati 2004).

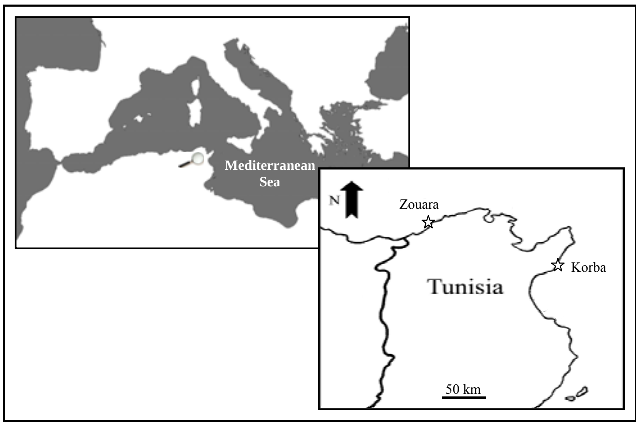

Figure 1: Sampling localities of the studied populations.

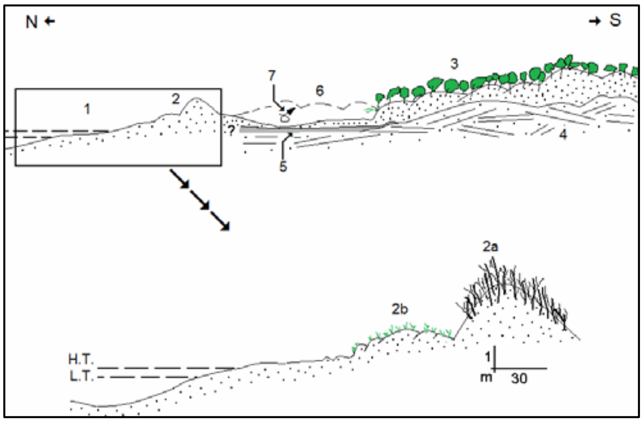

Figure 2: Main components of the geomorphological landscape in the Zouara locality.
1-beach ; 2-foredune (2a-dune developed by artificial fixation of the sand ; 2b-nebkas fixed by natural vegetation) ; 3-recent dunes ; 4-consolidated dunes ; 5-continental runoff deposits ; 6-former profile of the dunes ; 7-wind erosion ; H.T., L.T.: high and low tide levels.

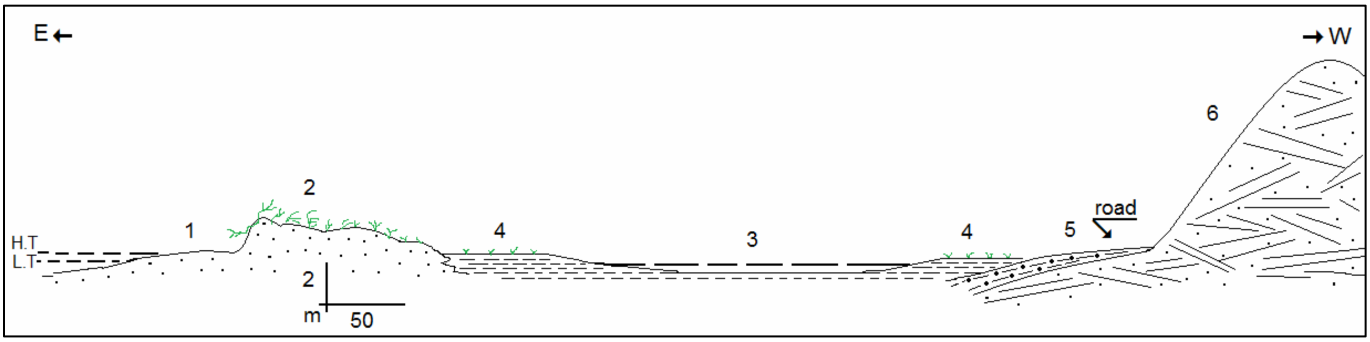

Figure 3: Main components of the geomorphological landscape in the Korba locality.
1-beach; 2-foredune ; 3-lagoon ; 4-chott ; 5-alluvial plain ; 6-Tyrrhenian consolidated beach barrier. H.T., L.T.: high and low tidal levels

Korba site

Korba beach (36°37’58’’N 10°54’26’’E) is on the east coast of the Cap Bon peninsula. Unlike the Zouara area, the Korba one pertains to an open landscape. It also differs by its relatively shallow sea and eastern exposure. This shelters it from the northern and north-western winds and high energy waves. Differences appear also across the hinterland, which doesn’t contain considerable dunes. The beach is backed by a lagoon communicating episodically with the open sea and fringed by a typical *chott* or a very narrow alluvial plain. This coastal system is limited from the inner side by a series of small hills lying parallel to the coast and interpreted as a Pleistocene barrier beach (Fig. 3).

The beach is less wide than that of Zouara and characterized by a very weak slope. It also differs for its finer material as the grain size averages range between 0.200 to 0.315 mm in the outer part and between 0.200-0.250 mm in the fore dune. The latter remains hardly evident in the landscape mainly because of its very low altitudes not higher than three meters. For its width, this beach may give the impression of lacking problems related to marine erosion. But, it is quite vulnerable. On the one hand, the fore dune is often characterized by a dissymmetric profile. Its outer side is episodically truncated by waves and often shows barefoot vegetation. This means that the sediment loss caused by storms is not always compensated by calm seas. On the other hand, the beaches of the adjacent areas, which pertain to the same natural context and show similar geomorphological patterns, show evidences of a regressive trend during recent times. In some cases the proof of the regressive trend comes from archaeological data. It was demonstrated, for example, that waves have eroded important roman ruins which were originally located on the fore dune (Slim *et al.* 2004). In other cases, the cliff shaped in the outer side of the fore dune cuts both sandy and clayey materials. Only a shoreline retreat can explain such a situation because the latter is in fact material of clay dunes that were originally formed behind the sandy beach system in relation to wind erosion acting in summer on the dry sectors of the lagoon.

Orientation experiments

The orientation tests of adult individuals of the species of *Talitrus saltator* were carried out on the beach near the capture points. At the two localities, the TED (theoretical escape direction seawards) was measured using a magnetic compass, and was 324° and 112° at Zouara and Korba respectively. Groups of 10-15 individuals were released at the centre of a circular arena with a diameter of 40°, made of Plexiglas, surrounded by 72 pitfall traps, protected from wind with a Plexiglas transparent screen and positioned horizontally on the beach. The releases were repeated 3-6 times successively at different times of the day (morning, noon and afternoon), and were carried out during two sunny days, in spring and summer. The angular distributions were analysed with the statistics of circular distributions. Sample angles were transformed by subtracting the TEDs to allow the comparison between the two populations from the two beaches that had distinct orientation. More details are provided in previous papers, in which part of these data were published (El Gtari *et al.* 2000, Scapini *et al.* 2002, Morgan *et al*. 2002).

Activity rhythms

Sixteen individuals of each population were transferred to a controlled environment cabinet in the laboratory. Monitoring of the locomotor activity of the individuals was performed in annual chambers equipped with an infrared activity recording system. The animals were kept in a light-dark cycle (LD) for the first 7 days of recording. They were then transferred to constant darkness (DD) for at least another week of recording. The period of the activity rhythm was detected by time series analysis, using the periodogram techniques. The material used and the statistical analyses performed are detailed in previous papers, in which part of these data, namely those of Korba, were published (Morgan *et al*. 2002, Nasri-Ammar & Morgan 2005, 2006).

Genetic diversity

For allozyme study, 9 enzymatic proteins coded by 13 gene loci were tested in the two populations. These enzymes are Me (*Me*); Ao (*Ao*); Ca (*Ca-1*; *Ca-2*); Got (*Got-1*; *Got-2*); Hk (*Hk*); Mpi (*Mpi*); Pep (*Pep-1*; *Pep-2*; *Pep-3*); Pgm (*Pgm*); Phi (*Phi*). Details for the electrophoresis procedures are given in other papers, in which data of the same populations were analysed (Bouslama *et al.* 2001, Ketmaier & De Matthaeis 2002). The genetic variability was estimated by the observed and expected heterozygosity under Hardy-Weinberg equilibrium. The mean number of alleles per locus and the proportion of polymorphic loci were also compared between the two populations.

For the mtDNA, total genomic DNA was extracted using the Tissue Kit (Promega) following the instructions of the supplier. A fragment of the mtDNA COI gene was amplified using the primers described in Ketmaier *et al.* (2006). The PCR program consisted of an initial denaturing step at 94°Cfor 10 mn, 40 amplification cycles (93°C for 1 min., 52°C for 1 min. and 15 sec. and 65°C for 1 min. and 15 sec.) and a final incubation step at 68°C for 7 min. performed in a GeneAmp PCR System 2700 (Applied Biosystems). PCR products were checked on 1.5% agarose gel. The PCR amplified fragments were purified with a PCR DNA Purification Kit from Promega. Sequences were determined using an automated ABI PRISM 377 sequencer (Applied Biosystems) following the manufacturer's protocols. Sequences were edited and aligned with BIOEDIT Sequence Alignment Editor (Hall 1999). The intra-population variation was assessed by using diversity indices, mainly haplotypes diversity, mean number of pair-wise differences and nucleotide diversity.

RESULTS

Orientation behaviour

Talitrids' pooled distributions of the orientation choices of both populations, corresponding to experiments conducted in late spring-summer and in warm sunny days with landscape view permitted (Fig. 4), showed a general orientation towards the sea in both populations. The individual angular choices were concentrated in directions near the expected direction perpendicular to the shoreline (TED) in each population.

The concentration, estimated by the mean vector length r, was higher for Korba population (r=0.781) than for Zouara one (r = 0.566), which had a more scattered orientation. The confidence interval (ci) of the mean direction, used to compare the mean directions of the angular distributions with the expected direction (TED), showed a deviation from the seaward direction in both populations. However, the deviation was higher for Zouara population.

Activity rhythms

The analysis of the actograms, corresponding to the activity of each individual under constant conditions, revealed an endogenous rhythm of locomotor activity, with a circadian period in both populations. However, the individuals of the Korba population showed a higher rate of rhythmicity than those of Zouara; this rate was estimated to 87.5% and 50% for Korba and Zouara respectively. The figure 5 shows examples of periodograms under light-dark (LD) and free-running conditions (DD). The lowest inter-individual variation was recorded in the Korba population in both LD and DD periods. The average periods were 24h04±0.13 under LD and 24h06±0.11 under DD conditions for the Korba population; 24h05±0.35 and 24h06±0.56 under LD and DD conditions respectively for the Zouara population.

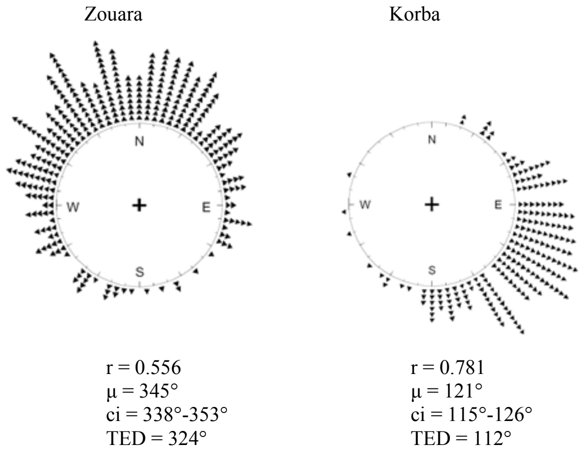

Figure 4: Orientation of *Talitrus saltator* collected from the two study sites: r, mean vector length; μ, mean direction; ci, confidence interval of the mean direction; TED, theoretical escape direction seawards.

Genetic diversity

The allozyme study revealed that the Zouara population exhibited the lowest variation; P and Ho values were 15.4 and 0.036 respectively, whereas they reached 30.8 and 0.097 for Korba (Table I).

From the mtDNA study, we obtained 384 bp sequences of COI from 11 individuals from the two studied populations. A total of 7 haplotypes were found, indicating a high degree of polymorphism. For both populations, the analysis of molecular diversity showed high values of haplotypes diversity combined with low nucleotide diversity. However, the Korba population exhibited the highest diversity indices values, compared with the Zouara population (Table II).

DISCUSSION

Despite a general orientation towards the sea, the two populations showed significant differences in orientation behaviour. In fact, *Talitrus saltator* appeared to be better oriented at Korba, whereas orientation was more scattered at Zouara, where both higher sample dispersion and higher deviation from the TED were recorded. It has been argued that differences in orientation are likely to be related to beach stability and more stable beaches allow a more precise orientation (Scapini *et al.* 1995, Fanini *et al.* 2007). Scapini & Fasinella (1990) pointed out that behavioural flexibility is frequently observed on changing beaches. In general, differences in environmental factors such as sun azimuth, temperature, wind direction, humidity or air pressure levels may explain the different behaviours observed in different populations. This behavioural variation depends also on the intrinsic characteristics of the animals (Borgioli *et al.* 1999, Scapini *et al.* 2002). In the case of Zouara and Korba populations, El Gtari *et al.* (2000) hypothesized a dependence of the observed variation on the different morphodynamics and use of the beaches, where the samples had been collected.

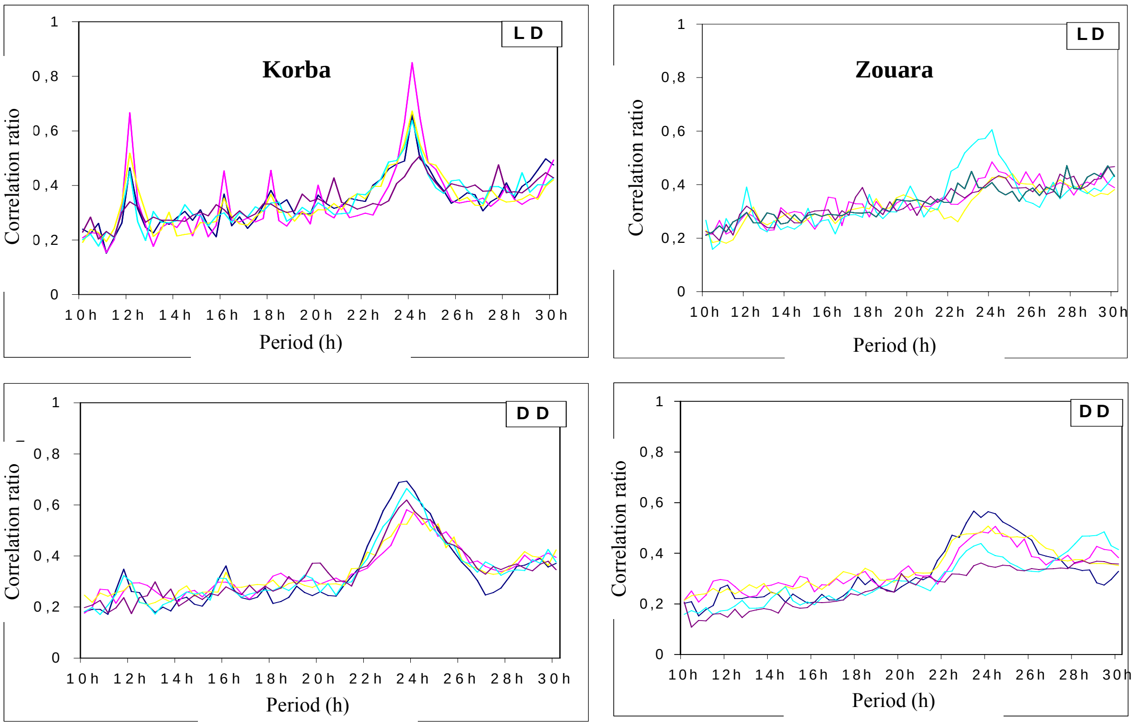

Figure 5: Examples of superimposed periodograms calculated from the endogenous activity of some individuals collected in the two populations; LD: Light-Dark; DD: Dark-Dark conditions.

Table I: Variation of parameters based on the allozyme study.

Population	Mean number of alleles per locus	Percentage of polymorphic loci	Mean heterozygosity observed (Ho)	expected (He)
Zouara	1.2 (0.2)	15.4	0.036 (0.025)	0.034 (0.023)
Korba	1.5 (0.2)	30.8	0.097 (0.042)	0.120 (0.054)

Table II: Diversity indices of the two populations studied based on the COI analysis. Nind: individual number; Nh: number of haplotypes; Np : number of polymorphic sites; h: haplotype diversity; n : mean number of pair-wise differences; π_n: nucleotide diversity; standard deviations between parentheses.

Population	Nind	Nh	Np	h	n	π_n
Korba	4	3	5	0.833 (0.222)	2.50 (1.68)	0.0065 (0.0052)
Zouara	7	4	7	0.809 (0.130)	2.38 (1.47)	0.0062 (0.0044)

Although the mean period of the activity rhythm was estimated to be close to 24 hours, variation in the period of the biological clock was observed between individuals and populations (Nardi & Morgan 2002, Nardi *et al.* 2003). This variation was hypothesised to be derived from non optimal adaptations, as in the case of changing environmental conditions, and was considered to be useful to assess ecological stability of the sand beach system. On this basis, as for orientation behaviour, the comparison of the two populations of this study showed a better defined free-running period in the population of Korba than of Zouara, where the beach exhibits a considerably higher dynamics.

Orientation and activity rhythms are apparently correlated. In fact, the better oriented population, in this case Korba, had better defined activity rhythms and a lower inter-individual variability in orientation (Ugolini & Frittelli 1998, Ugolini *et al.* 2007). Moreover, Scapini *et al.* (2005a) clearly demonstrated that the same chronometric mechanism regulates both the locomotor rhythm and sun compensation. Differences in other biological features of the species in the two localities were also observed in previous studies. In addition to the totally different patterns of zonation with respect to Korba population, the population at Zouara showed a sex ratio significantly female biased and a recruitment frequency relatively slow, whereas a sex ratio slightly female biased and a high recruitment frequency were observed at Korba (Charfi *et al.* 2000, Marques *et al.* 2003, Bouslama *et al.* 2007, 2009) Orientation behaviour is likely genetically controlled (Scapini *et al.* 1995). Nevertheless, the species exhibits a high flexibility related to the local environmental factors (sun azimuth and meteorological variables) and also to the intrinsic species characteristics (sex, size, age and eye left/right asymmetry) (Borgioli *et al.* 1999).

Both allozyme and mtDNA studies showed a higher genetic variation in the Korba population than in the Zouara one. Generally, this variation is considered as an adaptive trait of natural populations and was used, therefore, as a suitable tool to assess the stability of sandy beaches (Theisen *et al.* 1995). Previous studies clearly showed a correlation between *Talitrus saltator* heterozygosity and beach stability; populations from stable beaches being more polymorphic than populations from changing beaches (Scapini *et al.* 1995, Bouslama *et al.* 2001, Ketmaier *et al.* 2003). Therefore, the Korba shoreline, from an ecological point of view, might be much more stable than the Zouara one.

Intrinsic species' features and environmental factors are important in shaping the behaviour and genetic structure of the populations; similar trends were shown in orientation, activity rhythms and genetic variation, which are likely correlated with coastal stability. In fact, despite the geographical closeness of the two localities, Zouara and Korba beaches show differences in physical, morphological and landscape features.

Two possible explanations can be proposed for the results on the Zouara population. (1) At Zouara, environmental conditions are harsh, and winds' and waves' actions are both unpredictable and violent involving a high beach dynamics, even though it has been showed that this beach was in equilibrium between accretion and erosion until a recent date (Oueslati 2004). This is also attested by the beach morphology and landscape variation even throughout short times; seasonal variations of the beach level are remarkable, mainly because of the high waves' energy in winter and storm frequency. Moreover, energy shift between waves of autumn-winter and spring-summer is considerable. On the other hand, the Korba shoreline, despite its apparent regressive tendency, might be considered more stable, and the regression of the beach occurs slowly enough to allow the population to adapt both on behavioural and genetic levels. In fact, this beach has not shown drastic variations on short periods, at least from a landscape point a view. (2) The Sidi El Barrak dam, recently built at Zouara and functional since 1999, is a source of the reduction of the terrigenous inputs of Oued Zouara (Oueslati 2004) and may be considered a source of perturbation for the beach populations, namely *Talitrus saltator*, and may therefore affect behavioural and genetic variation of this species (Scapini *et al.,* 2005b). We are inclined to be in favour of the first explanation, since a part of this study, notably orientation, was performed before the dam be functional. However, the two hypotheses are not mutually exclusive. Further researches would be interesting and useful to more accurately assess, the effect of the dam on both beach dynamics and biological responses of *Talitrus saltator* population.

Even though parallel trends between biological characteristics of the species and beach stability have been highlighted by this study, no correlations could be analysed because the present data were limited to only two populations. This suggests the necessity to extend such investigations on other localities and populations, in order to get a more accurate overall view of the interdependence between the parameters considered. Further studies will be interesting on physical, morphological and landscape characteristics and trends of change of these beaches, which are the most important factors influencing the biology of *Talitrus saltator*.

As a whole, we have confirmed that *Talitrus saltator* populations exhibit adaptations at different levels according to the local features of their beaches of origin, highlighting a relatively high behavioural flexibility and genetic variation, thus providing a basis for bioassays of sandy beach quality. This study also enforces the usefulness of management plans that take into account both a geomorphological and a biological approach.

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