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RESEARCH ARTICLE

Abundance and orientation responses of the sandhopper *Talitrus saltator* to beach nourishment and groynes building at San Rossore natural park, Tuscany, Italy

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Abstract Beach nourishment and groynes building were implemented to counteract erosion in sandy beaches located at San Rossore natural park (Tuscany, Italy), near the mouth of Arno river. From 2000 to 2003, nine groynes were built along 3.6 km of coastline at intervals of *ca.* 400 m, and two of the eight beach segments were filled with marble gravel. Here, we analysed the effects of these beach changes on the abundance and behaviour of the amphipod *Talitrus saltator*, using field and laboratory observations. Sampling with pitfall traps in order to use the capture frequency as a proxy of abundance was performed bimonthly from September 2004 to January 2006, and orientation experiments were carried out in autumn (2004 and 2005), and spring and summer 2005. Physical variables (beach width, swash width, beach slope, sand penetrability, mean grain size and salinity) were also recorded. The abundance of *T. saltator* increased with the distance from the river mouth, towards sites with: negligible amounts of marble locally used for nourishment; higher beach width and salinity; lower slope and penetrability values; medium grain sizes, and during the spring/summer seasons. A Generalized Linear Model with a predictive power of 64.5% considered three main descriptors in the model as significant: distance from the river mouth, sand penetrability and a seasonal factor. Orientation experiments showed a highly variable behaviour among sites, depending on coastal stability: at the site stabilized by the concurrent actions of nourishment and groynes protection measures, sandhoppers were oriented to the shoreline direction by using a sun compass; alternatively, at a site situated only 2 km from the nourished sites, they showed scattered orientation. These between-site differences in orientation, described through Spherically Projected Linear Models, were consistent throughout the study period. Different responses obtained at the individual (orientation) and population (captures) levels stress the need to account for several bioindicators to characterize biotic responses to both natural and anthropogenic changes in sandy beaches.

Introduction

Sandhoppers occur all along the morphodynamic continuum from reflective to dissipative sandy beaches (McLachlan and Jaramillo 1995), spending their whole life cycle on the supralittoral zone and occasionally visiting the intertidal area and the sand dunes. Since sandhoppers have branchial respiration, they are linked to wet sand conditions, and behavioural adaptations are needed to actively maintain their position across the beach, avoiding both dry surfaces and displacement by waves. If removed from their position, they actively recover the burrowing zone (Scapini 2006 for a review). Consequently, the distribution tends to be aggregated into elliptical patches, with the major axis parallel to the shoreline (Defeo and McLachlan 2005), selecting a

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specific position on the beach as a response to environmental and individual characteristics (Scapini et al. 1992; Fallaci et al. 2003). To achieve this goal, an orientation behaviour based on a sun compass mechanism is fixed under stable conditions, and a simple phototaxis and a response to visual cues, such as landscape features, can be used as non-mutually exclusive mechanisms in cases of environmental instability (Scapini 2006).

The sandhopper *Talitrus saltator* is a widely distributed species (North and South Mediterranean, Baltic, European and African Atlantic coasts) that has been suggested as a useful bioindicator of anthropogenic impacts on sandy beaches (Wesławski et al. 2000; Scapini et al. 2002), showing a rapid recolonisation capability of the habitat (Fanini et al. 2005). The short time span between generations (months, Marques et al. 2003) makes this species suitable as a bioassay for rapid impact assessments. Another potentially useful characteristic of *T. saltator* as a bioassay is its orientation capability (Scapini et al. 1995, 2005; Borgioli et al. 1999). Behaviour in talitrid amphipods represents an integration of environmental information, which is expressed under contingent conditions and continuously updated through a feedback with the environment (Hartwick 1976; Ugolini et al. 1988). Therefore, orientation represents more than a snapshot of environmental characteristics and related dynamics. In this setting, sandhopper orientation was affected by beach erosion/accretion and a variety of human impacts on beaches, such as trampling and building on the dunes (Scapini 1997; Scapini et al. 2005; Fanini et al. 2007). The orientation of *T. saltator* rapidly changes in unstable habitats, whereas under stable conditions, the species tends to genetically fix a sun compass orientation mechanism (Scapini and Fasinella 1990; Scapini et al. 1995). Thus, sandhopper orientation could be considered as a suitable indicator of beach changes.

The characteristics for a suitable ecological indicator of the ecosystem status were reviewed by Salas et al. (2006). It was paid attention to both the ecological and the management perspective, since on sandy beaches those different environmental components are acting at the time and are therefore indissoluble: in synthesis, a suitable indicator should (a) have an agreed scientifically sound meaning, (b) be representative of an important environmental aspect for the society, (c) provide valuable information with a readily understandable meaning, (d) be meaningful for external audiences, (e) help in focusing information necessary for answering important questions and (f) assist decision-making by being efficient and cost-effective in terms of use.

Sandhoppers are recognized to fulfil some of the characteristics listed above, since they are strictly linked to the supralittoral environment, and their response to environmental variation, as previously described, represent updated and integrated environmental information. Their wide distribution supplies the possibility of comparisons between geographical areas and ecological environments. Also the economic feasibility is a strength point of such an environmental indicator. This work represented a test for the use of sandhoppers as ecological indicators to follow up and quantify beach stability conditions. Osenberg and Schmitt (1996) also stressed the need of the choice of indicators fitted to the aim of the monitoring process, and the consideration of multiple indicators in order to depict an unbiased indication. Consequently, in this study, we defined our setting as the variation in beach stability conditions after nourishment and groynes building, to be observed in the scale of kilometres and the time span of years. The indicators under test were the two different levels (abundance and behaviour) of sandhopper population and individuals, respectively. They were considered as mutually integrative indicators and analysed at the same time.

This latter proposal was motivated by the fact that abundance and orientation changes in sandhoppers can be observed over the same life span (*ca.* 3 months, F. Scapini, personal observation), but these two kinds of population bioindicators are sensitive to different phenomena. Sandhopper orientation is an individual feature that depends on both a genetic background and individual experience, and thus it is likely to be affected in the short term. Orientation can also change on a small spatial scale ranging from metres to few kilometres, because it is fitted to the local environment (Scapini et al. 2005; Fanini et al. 2007). On the other hand, variations in abundance depend on dynamic processes like recruitment, mortality and growth, which are sensitive to changes in habitat and food quality and availability. Seasonal variations in environmental conditions could also affect both abundance and behaviour of *T. saltator* (Marques et al. 2003; Nardi et al. 2003; Scapini et al. 2005), and thus the time scale needed to assess variations in these two features should consider this seasonality to avoid biases in data and misinterpretation of results.

Beach nourishment is a human-induced change affecting sandy beach ecosystems (Peterson and Bishop 2005). Nourishment has often been carried out worldwide on beaches extending only a few kilometres, and it is considered a soft measure against erosion. However, studies on the effects of nourishment on sandy beach macrofauna are rare (Peterson and Bishop 2005; Peterson et al. 2006). In San Rossore, a regional natural park in Tuscany (Italy), a project of stabilization of shoreline against erosion (i.e. beach nourishment and groynes building) was carried out in the last few years. In this study, we investigated the effects of these human-induced perturbations on *T. saltator* abundance and orientation by means of field observations and laboratory experiments. The time span covered by the study (17 months, equivalent to several sandhopper cohorts) and the sampling periodicity (bimonthly) used to monitor

T. saltator allowed us to discriminate continuous trends from seasonal dynamics. In addition, as the marsh system backing the beaches under study constitutes a natural reserve, according to the Park's management plan, visitors do not have access to the littoral, thus allowing us to isolate the impact of shoreline protection actions (nourishment and groynes building) from other human impacts that commonly affect sandy beaches, such as trampling and beach grooming.

Material and methods

Study area

San Rossore-Migliarino-Massaciuccoli Regional Park, in northern Tuscany (N 43°41′ E 10°16′), is situated on the right side of the Arno river mouth. One century ago, the silting up of Gombo cliffs interrupted sand transport alongshore (Cipriani et al. 2001), causing a severe erosion of the beach that is still going on nowadays on the sandy beaches situated to the right of the Arno river mouth. From 2000 to 2003, measures were taken to nourish the eroding sandy beach stretch close to the river. To this end, nine groynes built at irregular distances from the river mouth artificially created eight beach segments of differing length, ranging from 0.3 to 0.8 km, along 3 km of coast (Fig. 1). In addition, marble gravel extracted from a nearby mine was used as filling material, and nourishment was carried out on the two beach segments nearest to the river mouth. The beach segments have the general shape of a natural pocket beach that results from engineered structures interacting with waves and currents.

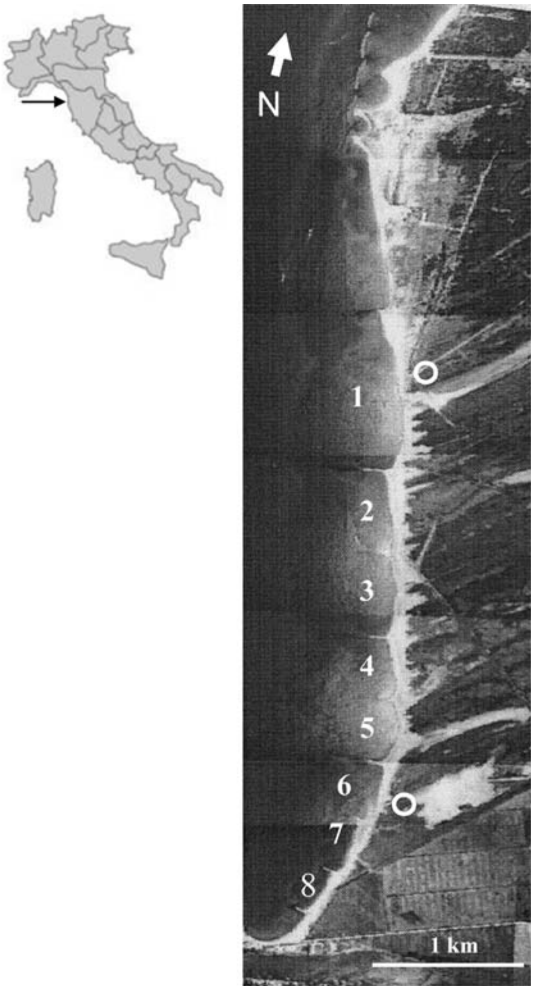


Fig. 1 Study area, on the right side of the Arno river mouth. The *numbers* indicate the beach segments sampled, and *circles* indicate the sites (1 and 6) where orientation of *Talitrus saltator* was tested (from Archivio Regione Toscana)

Captures

Biological samples and environmental data were collected bimonthly from September 2004 to January 2006. In each of the eight beach segments artificially created by the nine groynes built, two transects were set up perpendicularly to the shoreline and spaced 5 m apart. The transects were located at the middle of each beach segment in order to maximize the catching effort (Defeo and McLachlan 2005) and to avoid disturbance due to water currents associated to groyne presence (K. Nordstrom, personal communication). In each transect, pitfall traps were placed every 2 m, starting from the upper level of the swash zone up to the first plants observed in sand dunes. In the absence of dunes, the road built during the construction of the groynes was used as a reference point for ending the transect. The traps were left on each site for 24 h in order to intercept animals spontaneously moving during night and day. In the laboratory, the sandhoppers were counted and their cephalic length measured as an estimate of the total length, thus avoiding biases due to telson measurements (Marques and Anastácio 2002). "Adults" and "juveniles" were classified using the threshold values of 1 mm cephalic length and the 14th tagma of the second antenna, after the measurements of the orientation sample (see below). The number of sandhopper captures for each sampling date and beach segment was estimated by summing up the total number of amphipods retained in all the traps set in the two transects. This indirect method of assessing abundance has been shown by Fallaci et al. (2003) to provide an accurate proxy for counts. As we conducted a systematic sampling design within exactly the same zone (i.e. from the upper level of the swash to the first dune plants or road) in each transect, our total counts of sandhoppers capture can be considered as an unbiased proxy of abundance.

During each sampling session and for each site, we measured the following physical variables: beach width (m, from the upper level of the swash to the first dune plants or road-zone defined above), swash width (m, defined as the difference between final run-up and run-down of broken waves after collapsing on the sand), beach slope (degrees, average of measurements taken every 2 m), beach orientation (degrees from N), mean particle size (mm) and sea-water salinity (gNa/l, recorded with Salintest, Hanna Instruments, Woonsocket, RI, USA). At the level of each pitfall, we measured sand penetrability (cm), using a 5 mm diameter iron rod of 21.41 g weight that was dropped through a plastic tube of 1 m height (Colombini et al. 2003). Because of the presence of marble gravel, granulometric analysis was performed by dividing the sediment samples into two fractions: grain size <4 mm and grain size >4 mm, the latter being estimated as percentage in weight of the total substrate sample weight. Granulometric parameters for the first fraction were estimated according to Folk and Ward (1957).

Orientation experiments

Laboratory experiments on *T. saltator* orientation were carried out in October 2004 and in April, June, August and October 2005, at least two weeks after field sampling. During a pilot sampling conducted on September 2004, not enough sandhoppers were found at nourished sites 7 and 8, and thus the experimental sites chosen were site 1 (2.7 km from river mouth) and site 6 (0.7 km from river mouth), i.e. the farthest and the nearest to the nourished beaches (Fig. 1). Animals were collected in each site by means of pitfall traps, which were set over 24 h. Some 80 individuals were collected at each site for the performance of the experiments. As field experiments in the protected area were not allowed, orientation tests were carried out on the terrace on the top of the tower of the Department of Animal Biology and Genetics in Florence, within the 48 h immediately after collection. Groups of ten individuals were released in a circular orientation chamber, horizontally placed and without landscape vision. The chamber was divided into 72 small pitfall traps (5° each) around its circumference to record the orientation of individuals released in its centre (Scapini et al. 2002). Tests were carried out in two sessions, one starting at 9.00 a.m. solar time, and one starting at 3.00 p.m. solar time, with alternated releases from the two sites every 15 min. Environmental variables recorded in each release were: air temperature (°C), air relative humidity (%), sky cover (0–8/8) and sun visibility (three levels: bright, visible, overcast). Four groups from each site were observed in each session. Landscape vision was avoided by positioning a white cardboard of 10 cm height all around the rim of the arena device. After orientation tests, the animals were stored in alcohol 75°. For each individual, the sex was identified, and cephalic length and tagma of the second antenna (as a proxy of age) were estimated (Scapini et al. 1999; Marques and Anastácio 2002).

Data analysis

Captures

As only two of the eight sites were nourished, the variable “marble” was categorized using a threshold value of 1% of marble presence to classify the sites as “with” and “without” marble. We discriminated two annual periods, hereafter called “autumn–winter: AW” (September, November, January) and “spring–summer: SS” (March, May, July).

The relationships between the distance from the river mouth and environmental variables (mean estimates for each site) were modelled by linear or non-linear fitting. Generalised Linear Models (GLMs) were used to model the relationship between sandhopper number of captures and environmental variables, using a logarithmic link function. The time factor was included separately as month (temporal trend) and as season (AW and SS). The use of GLMs is more appropriate than multiple comparison procedures that use discrete categorization of continuous variables to depict patterns (Guisan et al. 2002). Given the over-dispersion in captures data generated during field samplings, a negative binomial distribution (i.e. with the variance not equal to the mean) was assumed for GLM. Interactions between variables and non-linear effects were checked. A stepwise selection procedure was used to discriminate the effects of independent variables on sandhopper captures. In the model selection process, we used the Akaike Information Criterion (AIC), i.e. the maximum likelihood with the minimum number of parameters. To evaluate the significance of each variable included within the best model, we used Likelihood Ratio Tests (LRT), comparing the best model and the nested model without the variable considered. The predictive power of the resultant model was measured by the linear correlation between the observed and the fitted values (Agresti 2002). All models were estimated using the GLM functions contained in the MASS libraries and plotted using the package effects of R language (2006 version).

Orientation

The angles of orientation resulting from the experiments were plotted into circular distributions and probability density functions were estimated, smoothed with the Kernel method. From the distributions, we calculated the resultant vectors (r) and the null hypothesis of uniform distribution was tested with Rayleigh’s test at a P level <0.05. The Theoretical Escape Direction (TED) was estimated in the field as the perpendicular to the shoreline (shortest direction seawards). Significant deviations of the mean vector from the

TED were checked using the 95% Confidence Intervals (95% CI) of the mean direction. In case of axial orientation (i.e. orientation towards two opposite directions), its significance was checked by maximising the vector *r* by doubling the angles (Fisher 1993). Spherically Projected Linear Models (SPLMs), i.e. a multivariate analysis adapted to angular data (Marchetti and Scapini 2003), were used to analyse the effect of environmental and intrinsic variables, as follows: site, month, season, time of the day ("a.m." and "p.m."), air temperature, air relative humidity, cloudiness, sun visibility, sun azimuth (calculated in relation to solar time of each release), beach slope and beach orientation (sites 1 and 6), sex, cephalic length and number of tagma of antenna. At both sites, shoreline orientation varied through time <5°, corresponding to the intrinsic error of the orientation chamber (each trap subtending 5°). Therefore, this variable was considered constant over time and excluded from the analysis. In case of significant interactions between factors, two or more additive models, discriminated by the interacting factor, were developed. When factors were correlated, the most informative ones were used for testing, and the final model was selected according to the AIC. The significance of each variable in the best model was assessed by LRT, comparing the best model and the nested model without the variable being tested (Marchetti and Scapini 2003).

Results

The habitat

Marble represented 47% of the total sediment weight at site 8 (0.3 km from Arno river mouth) and 7% at site 7 (0.5 km from Arno river mouth), whereas at sites 1–6 the coarse sediment fraction (including marble) was negligible and did not exceed 0.14% of the total weight (mean for the six sites = 0.06%). The mean size of marble pebbles found in both nourished sites was 3.2 cm, while the mean particle size of the sand fraction at all eight sites ranged from 0.30 to 0.44 mm (Fig. 2). Beach width, beach slope, particle size and salinity were significantly related to the distance from the river mouth, whereas sand penetrability and swash width were not so (Fig. 2). Beach width increased with increasing distances from the river mouth, whereas beach slope decreased along with an exponential monotonic model (Fig. 2). Salinity and mean particle size were best related to distance from the river mouth through quadratic models, increasing with distance and then decreasing to the furthest site 1 (Fig. 2).

Captures

GLMs obtained using adults and juveniles independently as response variables included the same significant variables as in the global model, and thus we used total captures (i.e. population components pooled) as response variable.

Bivariate plots showed relationships between captures of *T. saltator* and several environmental variables (Fig. 3). The capture frequency increased with the distance of the river mouth and beach width. *T. saltator* capture frequency showed a decrease with presence of marble (coarse sediment fraction >0.14%). The highest capture frequency was found at intermediate values of penetrability and salinity. However, note that the bivariate associations in some cases are spurious, including combined effects of the other variables.

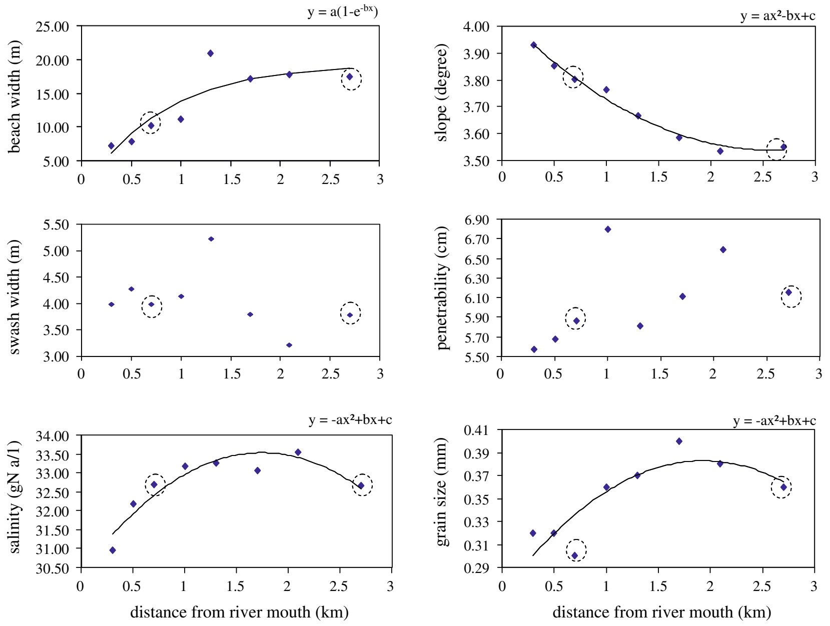


Fig. 2 Spatial patterns of physical parameters (averages of the whole sampling period) as a function of distance from the river mouth. *Dashed circles* indicate the orientation study sites. *Lines* indicate significant ($P \leq 0.05$) patterns. Equations are reported on the *graphs*

Despite the above trends (Fig. 3), a single additive GLM retained three main descriptors in the model as significant explanatory variables of spatio-temporal variations in *T. saltator* captures, with a predictive power of 64.5%: season, distance from the river mouth and sand penetrability (Table 1). The model showed an increase in *T. saltator* capture frequency with the distance from river mouth, during the SS season and a decrease in captures with increasing sand penetrability values (Fig. 4).

Orientation

Sites 1 and 6 showed differing sandhopper orientation patterns (Fig. 5). At site 1, the orientation of *T. saltator* was scattered (i.e. randomly distributed, Rayleigh's test: $P > 0.05$, Fig. 5a). In contrast, at site 6, *T. saltator* showed significant seaward orientation, with the TED included within the 95% CI (Fig. 5b). Moreover, a significant axial orientation resulting from doubling the angles (see Methods) strongly indicated the sandhopper's orientation tendency as perpendicular to the shoreline, in both seaward and duneward directions (Fig. 5c).

Table 1 Summary of the best additive Generalized Linear Model (GLM) (negative binomial distribution) fitted to sandhopper captures data

Variables	Estimate	SE	e^{estimate}	LRT
Season	1.44	0.42	4.21	<0.001
Penetrability (cm)	−0.77	0.19	0.46	<0.001
Distance from river mouth (km)	0.54	0.25	1.71	0.03

Variables appear in decreasing order of significance. Estimated coefficients and the corresponding Standard Error (SE) are reported for the model obtained with a logarithm link function. Back-transformed coefficients (linear) are indicated (e^{estimate}). Likelihood Ratio Test (LRT) results are reported for each variable

The SPLM showed a significant interaction that minimized the AIC between the factor "site" and the other variables considered (month, season, time of the day, air temperature, air relative humidity, cloudiness, sun visibility, sun azimuth, beach slope, sex, cephalic length, tagma of the antenna). Thus, two different SPLMs, one for each site, were fitted. At site 1, a continuous decrease in beach slope

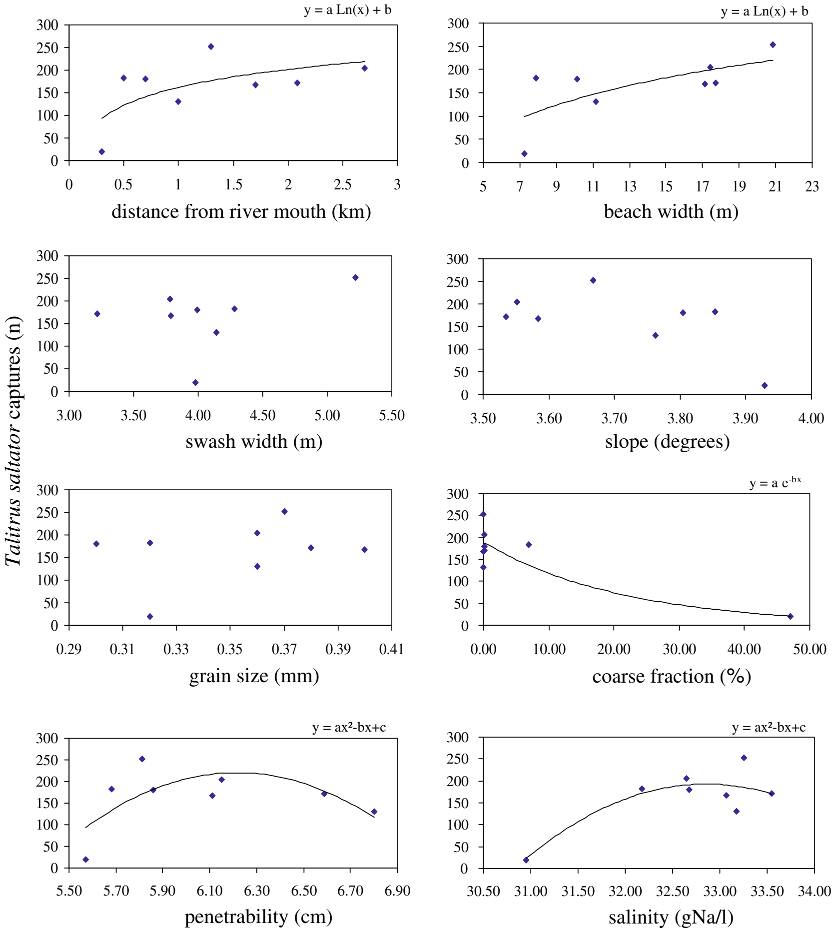


Fig. 3 Patterns of *Talitrus saltator* captures (averages on the whole sampling period) with respect to physical variables. *Lines* indicate significant ($P = 0.05$) patterns. Equations are reported on the *graphs*

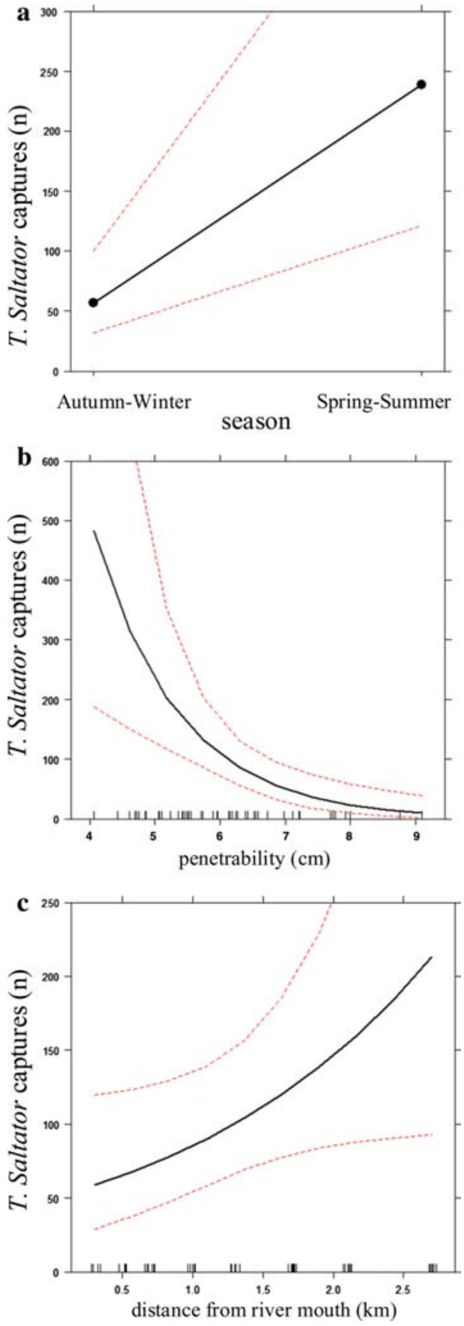
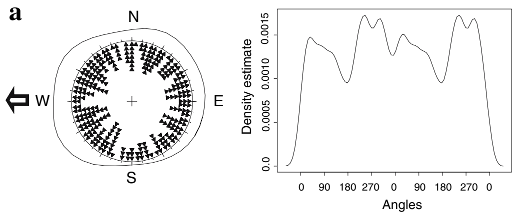
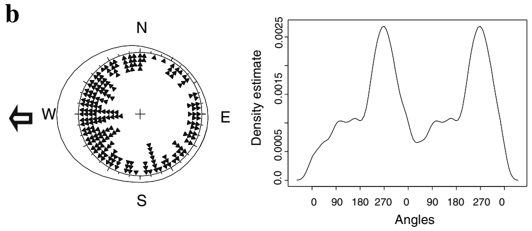


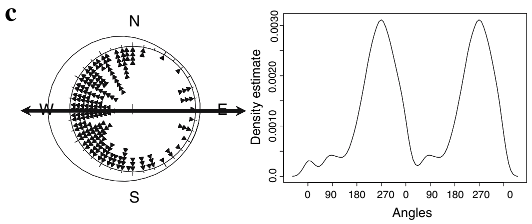
Fig. 4 Results of the Generalized Linear Model (*GLM*) showing the relationship (*solid line*) between *Talitrus saltator* captures and each meaningful variable: **a** season; **b** sand penetrability and **c** distance from the river mouth. *Dashed lines* indicate 95% CI, and the "rug plots" on the *X*-axis indicate the data points



mean angle of orientation 310.10°
r length 0.08 n.s.
Sample Circular Dispersion 75.770
N. of observations 288
TED 254°



mean angle of orientation 263.50°
r length 0.30**
Sample Circular Dispersion 4.447
N. of observations 214
CI 95% 247.10°-279.93°
TED 265°



mean angle of orientation 268.9°=> axis 268.9°-88.9°
r length 0.53**
Sample Circular Dispersion 1.508
N. of observations 214
TED 265°

Fig. 5 Orientation experiments for **a** site 1; **b** site 6 and **c** site 6 axial distribution after doubling angles: summary statistics, plots of circular distributions (on the *left*) and double plotted density functions (on the *right*). *Points* indicate individual orientation choices. *Asterisks* indicate significance for Rayleigh test *<0.05; **<0.01. *White arrows* indicate the TED. Resultant vectors (*r*) have the direction of the mean resultant angle of orientation and a length between 0 and 1. *Black arrows* indicate the resultant axis of orientation

over time, coupled with an increase in mean grain size, was observed, whereas no significant temporal trends in these variables were found at site 6 (Fig. 6). As for intrinsic (animal-related) information, the sex ratio (male:female) was biased towards males at both sites (3.35 at site 1 vs. 1.87 at site 6).

The SPLM fitted for site 1 included the following variables or factors (Table 2): month, number of tagma and cephalic length (intrinsic variables), air relative temperature, and beach slope. Orientation resulted scattered (n.s. for the Rayleigh test) in each replicate. The significance of the factor "month" in the model resulted from a systematic shift through time in the mean direction from SE (landward: October 2004) to SW–NW (seaward: April, June and August 2005) and then to N (longshore: October 2005). Differences in orientation linked to individual size/age could be explained by a trend of juveniles to orient landwards whenever scattered, whereas adults, also scattered, tend to orient seawards. Mean sandhopper orientation was

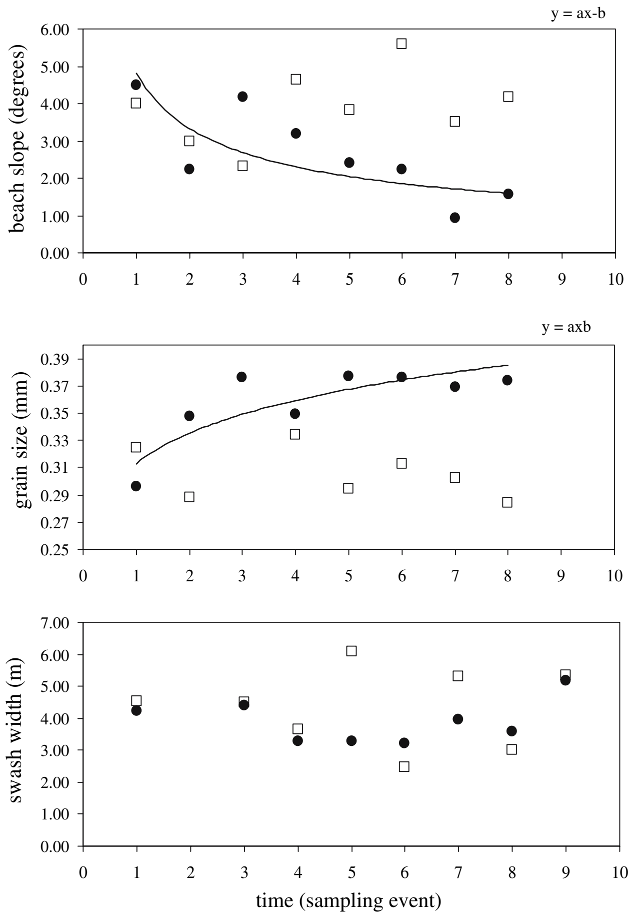


Fig. 6 Temporal patterns of physical parameters (on the *Y*-axis) at the orientation study sites (*dots*, site 1 and *squares*, site 6). *Lines* indicate significant ($P \leq 0.05$) patterns. Equations are reported on the *graphs*. During sampling session number 9 (January 2006), the whole beach surface was swashed by waves, therefore only swash width values were recorded

landward with the highest beach slopes (>4°), seaward or longshore at intermediate slopes (4° < slope < 1°), and seaward when the lowest slope occurred (<1°).

The SPLM fitted for site 6 included (Table 2): season (AW or SS), sun azimuth, air temperature, air relative humidity and beach slope. No intrinsic variables were significantly related to orientation at this site. The significance of the factor "season" in the model (Table 2) is explained by the increase in seaward concentration during the "SS season", whereas beach slope significantly explained variations in orientation as follows: at slopes >4°, axial orientation (both seawards and landwards) was observed, whereas a seaward orientation was observed at intermediate beach slopes.

Discussion

We showed abundance and behavioural responses of the sandhopper *T. saltator* to changes in the sandy beach environment on a spatial scale from a hundred metres to a few km. The number of individuals collected increased towards sites without marble, at higher beach widths and salinities, and lower slope and penetrability values. In contrast, sandhoppers were better oriented with respect to the shoreline direction at site 6, closer to the sites nourished with marble, whereas at site 1, situated 2 km from site 6, they showed scattered orientation patterns. Thus, the orientation differences observed on a small spatial scale could be explained in terms of stability/instability of environment, and support the perception of orientation as a local feature, since orientation is linked to environment in which the sandhoppers find themselves during their excursions (i.e. meters: Scapini et al. 1992).

The GLM showed that a relevant explanatory variable of the spatio-temporal patterns in sandhopper captures was the distance from the river mouth. This can be defined as an aggregated variable (see Lercari and Defeo 2006) that is accompanied by different simultaneous effects in the nearshore beach environment and in the resident fauna. In this setting, beach width, an indicator of habitat availability for the resident macrofauna, significantly increased with the distance from the river mouth and sandhopper abundance followed the same pattern, suggesting the importance of habitat availability for population development. This reinforces previous evidence that showed significant decreases in beach width and sandy beach macrofauna abundance close to river mouths (Lercari and Defeo 2006; Colombini et al. 2007) or to man-made canal discharges (Lercari and Defeo 2003; Lozoya and Defeo 2006). The low presence of sandhoppers at sites 7 and 8, in concurrence with the highest marble content (4 and 45%, respectively) and a very narrow beach width, could be an additional negative factor affecting habitat availability and suitability. The ongoing desegregation process of calcium carbonate may also have long-term effects on sand composition and beach morphology (S. Tommasini; C. Martín Cantarino, personal communication) and could affect the environmental characteristics of the beach, with consequent deleterious effects on the species and biota.

Sandhopper captures also increased with the gentle slopes and coarser grain sizes that characterized the furthest sites. The unexpected increase in grain size as the beach slope decreased (Fig. 3) could be related to the effect of groynes on longshore sediment transport (E. Pranzini, personal communication). These results are also in agreement with previous work that showed higher sandhopper abundances on sandy beaches with accreting shores (as opposed to eroded ones: Colombini et al. 2007) and coarser grain sizes (Defeo and Gómez 2005). The GLM showed that sand penetrability was more informative than the presence of marble gravel. In the San Rossore case, a higher penetrability means dry sand and consequently a less

Table 2 Summary of the best Spherically Projected Linear Models (SPLMs) obtained for orientation at sites 1 and 6

Site 1		Site 6	
Orientation ~ month + tagma of the second antenna + cephalic + air relative humidity + slope		Orientation ~ season + azimuth + air relative humidity + air temperature + slope	
AIC of the model containing all variables = 1,842.65		AIC of the model containing all variables = 1,838.42	
AIC = 1,036.60		AIC = 694.60	
Number of parameters = 10		Number of parameters = 12	
df = 278		*df* = 202	
Variable	LRT	Variable	LRT
Month	<0.001	Season	<0.001
Tagma of the second antenna	<0.001	Azimuth	<0.001
Cephalic length	~0.05	Air relative humidity	<0.05
Air relative humidity	<0.001	Air temperature	<0.001
Slope	<0.05	Slope	<0.001

Akaike Information Criterion (AIC) scores comparing the best model with the model containing all variables are reported. Likelihood Ratio Test (LRT) results are reported for each variable

favourable environment, thus explaining the decreasing *T. saltator* abundance with increasing sediment penetrability. However, the lowest penetrability value of the sediment was concurrent with the highest percentage of marble found at site 8, suggesting that, despite its statistical lack of significance in the GLM, marble may play an ecological role as a causative factor of the lowest number of sandhopper caught at site 8.

Capture frequency notably increased in summer, indicating a clear seasonal trend. This finding is in agreement with the seasonal variations in abundance commonly found for *T. saltator* in the Mediterranean (Scapini et al. 1992; Fanini et al. 2005). The fact that an identical model was useful to describe variations in captures for both juveniles and adults suggests a concurrent response of all population components to changes in habitat quality.

The two sites investigated showed significant differences in sandhopper orientation. They were better oriented at the site closer to the nourished ones, where the shoreline was artificially stabilized. In contrast, they showed scattered orientation patterns at the site furthest from the nourishment action. Thus, the observed orientation trends could be explained in terms of stability/instability of the environment, confirming previous findings that showed that more stable beaches allow the development of more precise orientation mechanisms than unstable ones (Scapini et al. 1995, 2005; Fanini et al. 2007).

Talitrus saltator orientation was affected by a time factor at both sites. At site 1, the decreasing beach slope (and increasing changes in sand particle size) over time (see Fig. 5) had a marked effect on orientation patterns, suggesting a short-term adaptation to environmental instability. This behavioural flexibility could be an adaptive response to a changing environment (Scapini et al. 2005; Fanini et al. 2007). These results confirm the general hypothesis of an increase in the precision and adaptation of orientation to local environmental features under dynamic equilibrium conditions of sea shores (Scapini 2006). Other factors acting on the scattered orientation patterns observed at this site may be the presence of a wide beach with a large amount stranded detritus (since the management of the Park does not allow mechanical beach cleaning), thus making *T. saltator* populations less dependent on the wet sand stripe at water's edge (Borgioli et al. 1999; Nardi et al. 2003). At site 6, a sun compass has been likely fixed, leading to maintenance of the direction irrespective of the time of the day (i.e. morning and afternoon experiments). At this site, ecological variables presented small fluctuations around a mean value throughout the study period, indicating a relative stability of the environment through time.

Behaviour has a contingent character, being expressed by individuals under certain circumstances (Scapini 2006). This is confirmed by the significant effects of immediate meteorological variables found in SPLM analysis. At site 6, orientation of sandhoppers significantly depended on air relative humidity (which was also significant at site 1) and temperature (see Table 2), avoiding both dryness and high temperatures. The axial orientation found at site 6 could be explained by the presence of halophyle vegetation landwards, which could provide shelter in the direction opposite to the sea. During the hot and dry season and in absence of storms, the seawards component of the axis was found enhanced.

At site 1, intrinsic variables such as individual size (cephalic length) and age (number of tagma) were significantly included in the SPLM. The effect of these intrinsic characteristics on orientation could indicate differences in the behavioural strategy depending on the developmental stage. In this context, juveniles are more dependent on the wet sand environment, near the shoreline, and are expected to be better oriented seawards (Kennedy et al. 2000; Fallaci et al. 2003). At site 6, the lack of effect of size/age on orientation patterns could be explained by an orientation response common to the whole population.

In summary, abundance and orientation of *T. saltator* responded to beach nourishment and groynes building in a dissimilar manner. Captures increased with distance from the nourished sites, whereas orientation was scattered at the farthest site, defined as an unstable environment. Therefore, it cannot be assumed that an abundant population is also well oriented (see Scapini et al. 2005). Close to the sites stabilized by the concurrent actions of nourishment and groynes protection measures (e.g. site 6), orientation appears to be adapted to the shoreline direction, suggesting a short-term sandhopper response to overcome risky environments.

The results highlighted the sensitiveness of sandhoppers to those changes acting on sandy beaches, in terms of stability and instability linked to the maintenance or the ongoing changes affecting suitable habitats. Changes were detected at the scale of kilometres and during few years from the impact that modified beach dynamics. The different responses obtained on the individual (orientation) and population (abundance) levels stress the need to account for different kinds of bioindicators to characterize biotic responses to both natural and anthropogenic changes. The results also highlighted the suitability of sandhoppers for monitoring the conditions of dynamic environments like sandy beaches, characterized by intrinsic ecological and economical value at the time.

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