

# Testing the Habitat Safety Hypothesis with behavioural field experiments: amphipod orientation on sandy beaches with contrasting morphodynamics

Lucia Fanini<sup>1,\*</sup>, Omar Defeo<sup>2</sup>, Cecilia Do Santos<sup>2</sup>, Felicita Scapini<sup>1</sup>

<sup>1</sup>Dipartimento di Biologia Evoluzionistica 'Leo Pardi', Università di Firenze, 50125 Florence, Italy

<sup>2</sup>Unidad de Ciencias del Mar (UNDECIMAR), Facultad de Ciencias, Universidad de la República, PO Box 10773, 11400 Montevideo, Uruguay

**ABSTRACT:** Understanding behavioural adaptations in sandy beach macrofauna has been a major step in theoretical development of sandy beach ecology. In particular, behavioural studies in supralittoral amphipods have been useful in understanding macrofaunal responses and adaptations to environmental changes in these dynamic ecosystems. The predictions of the Habitat Safety Hypothesis (HSH) were tested for the first time on *Atlantorchestoidea brasiliensis* through orientation experiments carried out on 2 sandy beaches, one dissipative and the other reflective. Orientation patterns of *A. brasiliensis* followed the trend predicted by the HSH: even though sandhoppers oriented seawards on both beaches using a sun compass, the orientation on the reflective beach was more precise than on the dissipative one. Thus, stability conditions in the supralittoral zone of the reflective beach favoured a higher precision of the sun compass. The precision of seawards orientation on the dissipative beach increased when landscape references were added to the sun compass mechanism. The response to an unexpected object was also experimentally tested by use of a visual pattern, and a higher individual variability in the orientation of the reflective beach population was found. Thus, orientation strategies in sandy beach environments seem to respond to the stability of the supralittoral zone, widening the general pattern predicted by the HSH for the supralittoral fauna to the behavioural traits of the population.

**KEY WORDS:** Sandy beaches · Habitat Safety Hypothesis · Orientation · *Atlantorchestoidea brasiliensis* · Sun compass

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Dissipative microtidal and reflective microtidal sandy beaches were first described from a physical point of view by Short (1996), distinguishing beaches where the wave energy is dissipated along a gentle slope (dissipative beaches) or reflected seawards by a steep slope (reflective beaches). As the physical features are inter-connected and driven by energy flow, a set of characteristics can be related to each beach type: dissipative beaches are characterised by gentle slopes, fine sand, long swash periods and low turbulence, while reflective beaches are characterised by steep slopes,

coarse sand, short swash periods and high turbulence (McLachlan & Brown 2006).

During the last few decades, several ecological hypotheses have been postulated to explain the influence of morphodynamics on life history traits (Defeo & McLachlan 2005). The Swash Exclusion Hypothesis (SEH) states that species richness decreases from dissipative to reflective beaches until, under extreme reflective conditions, no intertidal species occur and only supralittoral forms remain (McArdle & McLachlan 1991, 1992); experimental results have provided strong support for this prediction (McLachlan & Dorvlo 2005 and references therein). The Habitat Harshness Hypo-

\*Email: sandhopper@unifi.it

thesis (HHH) incorporated predictions of the original SEH at the population level (Defeo et al. 2001, 2003), and postulated that the harsh environment of reflective beaches forces organisms to divert more energy towards maintenance, resulting in lower abundance, fecundity, growth and survival rates as compared to dissipative beaches. Results documented worldwide have provided support for the HHH, particularly for truly intertidal species affected by the swash climate (Brazeiro 2005, Celentano & Defeo 2006 and references therein).

In contrast, supralittoral forms appeared to be favoured by reflective environments, notable examples including cirrolanid isopods (Defeo et al. 1997, 2003, Defeo & Martínez 2003, Contreras et al. 2003) and amphipods (Gómez & Defeo 1999). These supralittoral species are less influenced by the swash climate and generally engage in autonomous active movement on upper beach levels (Giménez & Yannicelli 1997). These observations are also supported by geomorphologic considerations: Short (1996) defined reflective beaches as the most stable beach type with low backshore mobility. The combination of short swashes and steep slopes may in fact make microtidal reflective beaches more stable and safer environments for supralittoral species, because here their risk of immersion is substantially lower than on dissipative beaches. Thus, Defeo & Gómez (2005) postulated the habitat safety hypothesis (HSH) for supralittoral forms, which predicts that populations (total, ovigerous females and juveniles) and individual sizes will increase in abundance from dissipative to reflective beaches (i.e. a trend opposite to that predicted by the HHH). This separates intertidal and supralittoral forms, taking into account both swash and sand effects as well as differences in life histories (McLachlan & Dorvlo 2005).

Relevant behavioural characteristics common to sandy beach macrofauna comprise mobility, burrowing capability, rhythmicity, orientation capability and plasticity (Schlacher et al. 2008). The orientation capability of supralittoral species is one of the most studied among these, although field experiments on orientation mechanisms under natural conditions are often avoided due to the difficulty of isolation and control of environmental variables. Behaviour is the result of the integration of environmental information, generated by the continuous feed-back of environmental conditions, by resident fauna. Recent findings have shown significant correlations between the orientation capability of the crustacean amphipod *Talitrus saltator* and beach dynamics, the landscape stability, and human actions aimed at counteracting erosion and stabilising the shoreline (Scapini et al. 2005, Fanini et al. 2007, Fanini & Scapini 2008). When removed from their burrows during daytime, these amphipods re-

cover seawards to the burrowing zone (represented by the wet sand stripe above high tide marks) by using a sun compass as the main orientation mechanism; increasing precision is shown on beaches characterised by higher stability. In cases of low environmental stability and a more unpredictable environment, the smaller degree of sun compass precision requires that it is integrated with other cues (Ugolini et al. 1986); additionally, individual variability is increasingly limited by the harsher conditions (Lerner 1954). Orientation is expressed by individuals within a population, but can be analysed as a population characteristic by considering features such as precision around the mean direction, orientation mechanisms displayed (e.g. sun compass, scototaxis, phototaxis) and variability of orientation performances within populations. All these features depict behavioural characteristics beyond the individual level (Batschelet 1981) and can be related to the environmental stability affecting sandhopper populations (see theoretical background in Fig. 1). Despite the demonstrated importance of morphodynamics in explaining population patterns in sandy beach macrofauna, field studies aimed at testing the main predictions of HSH on behavioural features of supralittoral species are lacking.

The sandhopper *Atlantorchestoidea brasiliensis* occurs from the supralittoral to the upper midlittoral zone across the whole morphodynamic spectrum of exposed sandy shores of Uruguay and Brazil (Cardoso & Veloso 1996, Defeo & Gómez 2005). Thus, this amphipod is expected to display sun compass orientation consistent with the behavioural strategies known in its taxonomic group. This study aims to integrate behavioural strategies into the HSH by testing the orientation of this supralittoral species on 2 Uruguayan sandy beaches with contrasting morphodynamics. To this end, the main visual components in the orientation mechanism of *A. brasiliensis* were tested: sun compass, the response to 'natural' visual cues such as landscape vision,

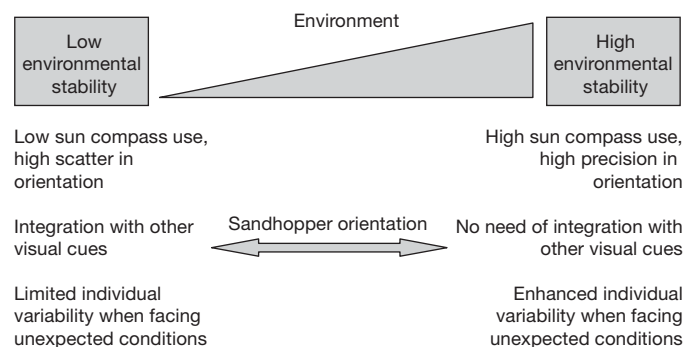


Fig. 1. *Atlantorchestoidea brasiliensis*. Theoretical background model of orientation performances (considered as a population characteristic) related to environmental stability

and the response to an 'unnatural' visual pattern (scototaxis). According to the HSH, on a reflective beach (where the supralittoral zone is more protected from the wave energy, and the environment is more stable than on a dissipative beach), the sun compass orientation of *A. brasiliensis* ought to be more precise. On reflective beaches, the higher risk of dehydration encountered by supralittoral species (due to coarser sand and lower water content) is also expected to define a higher sandhopper orientation precision than on dissipative beaches. Differences in the response to visual cues would be expected: on the less stable supralittoral fringe of a dissipative beach, a less precise sun compass mechanism would require the integration of additional cues (e.g. landscape vision, phototaxis) to increase orientation precision. Conversely, a more precise sun compass orientation is expected on the more stable supralittoral fringe of a reflective beach, together with a higher variability in response to other visual references; in the face of multiple cues, this would lead to increasingly scattered sandhopper orientation.

## MATERIALS AND METHODS

**Study sites.** Barra del Chuy (33° 45' S, 53° 23' W) and Punta del Diablo (34° 01' S, 53° 32' W) beaches were chosen on the basis of several years of data collection, including a previous study testing the main predictions of the HHH and HSH on abundance, reproductive features and population structure of *Atlantorchestoidea brasiliensis* (Defeo & Gómez 2005). These beaches are located along the continuous Uruguayan coastline (Fig. 2), and can be classified as dissipative (Barra del

Chuy) and reflective (Punta del Diablo): mean values and Confidence Intervals (CI) of the main physical variables from the 2 beaches do not overlap, and define Barra del Chuy as a beach with shallower slope, smaller grain size, higher sand compaction and higher water content than Punta del Diablo (Defeo & Gómez 2005). Both beaches have developed dune belts, and are not affected by any relevant human disturbance.

**Orientation experiments.** Experiments were carried out simultaneously on both beaches, with tests in spring (October 2006) and autumn (April 2007) so as to avoid the extreme meteorological conditions of winter and summer. An orientation chamber was placed horizontally on each beach and screened with transparent Plexiglas so that sandhopper movements would be unaffected by the wind. The chamber was made of Plexiglas and was of circular shape (40 cm diameter), with 72 pitfall traps (7 cm depth) along its rim (each one subtending 5°; the intrinsic error of the device was therefore estimated as  $\pm 5^\circ$ ). By placing trap number 72 towards magnetic North, the orientation angles chosen by individual sandhoppers could be calculated (Scapini 2002). Following a standard procedure, replicate groups of ~10 individuals freshly collected from the beach were placed in the centre of the orientation chamber by means of a Plexiglas tube and then released. Individual directions were recorded; tested sandhoppers were preserved in 75% alcohol and transferred to the laboratory. Individual sandhopper orientation was assumed to be independent, following the experimental approach of Scapini et al. (1981) and the theoretical model developed by Codling et al. (2007). The influence of landscape vision was tested by screening the landscape off with white cardboard along the rim of the arena, alternating releases with and without landscape vision. Orientation tests started at 09:00 and 15:00 h (solar time), with releases every 15 min for a total number of 8 releases per session. In correspondence to each release, we recorded air temperature (°C), relative air humidity (%), cloud cover (ranging from 0/8 to 8/8), sun visibility (3 levels: bright, visible, overcast) and sun azimuth (° to the North).

To analyse the influence of scototaxis, a dark pattern of 35 × 10 cm was placed at 230–260° and maintained in this position during alternate releases, with and without landscape vision. In this case, experiments were only conducted in the morning, because this was the time of day when the direction to the sea, the sun azimuth and the direction towards or away from the pattern could be clearly discriminated.

**Morphometric characteristics.** It was assumed that all individuals collected had experienced the beach conditions, and were able to integrate this experience into their behaviour and cope with the immediate environmental conditions. However, behavioural dif-

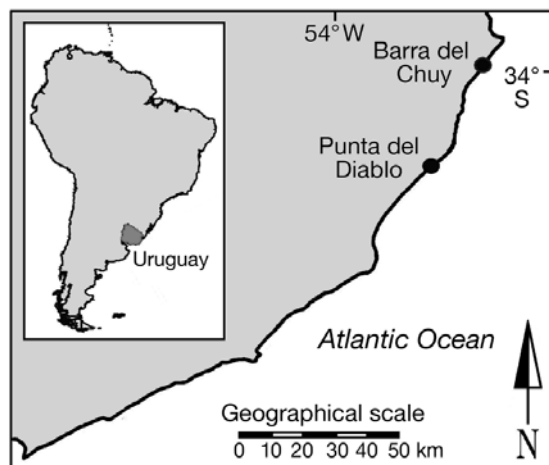


Fig. 2. Map of the Uruguayan Atlantic coast, showing locations of the 2 beaches analyzed in this study: the dissipative Barra del Chuy (33° 45' S, 53° 23' W), and the reflective Punta del Diablo (34° 01' S, 53° 32' W)

ferences could also be related to individual characteristics such as size, age and sex (Borgioli et al. 1999). For this purpose, the cephalic length (mm) of each individual was measured to obtain a proxy of the size (Marques & Anastácio 2002), whilst the age was estimated by the number of tagma on the second antenna (Williams 1983). Sex was identified by the presence of sexual appendages (oostegites or penis); individuals that presented neither a well-developed second gnathopod (males) nor oostegites (females) were classified as 'juveniles'.

**Statistical analysis.** Circular distributions were obtained and tested for randomness with the Rayleigh test (Batschelet 1981). Mean vector length ( $r$ ) and Sample Circular Dispersion were used to estimate the precision around the mean angle of orientation (Fisher 1993). While  $r$  indicates the precision around the mean angle of a circular distribution and ranges from 0 (homogeneous distribution) to 1 (maximum orientation precision), the Sample Circular Dispersion is a non-standardised parameter of concentration (from 0 to  $N$ ), allowing for an immediate comparison of distribution scatter. The concentrations of the distributions obtained from the 2 beaches were compared by means of the concentration parameter ( $k$ ) (Batschelet 1981), which estimates the relative precision around the mean. The Theoretical Escape Direction (TED) was defined as the direction perpendicular to the shoreline: the shortest seaward direction, measured locally with a compass in the field. At Punta del Diablo the TED was  $145^\circ$ , and at Barra del Chuy the TED was  $140^\circ$  (after local measurement with a compass). To verify the use of a sun compass mechanism, the inclusion of local TED within the 95% CI of the distributions, with and without landscape vision, was checked (Batschelet 1981).

Spherically projected linear models (SPLM: Presnell et al. 1998) were used to estimate the effect of environmental and intrinsic variables on orientation (Marchetti & Scapini 2003). These models represent a multiple regression analysis adapted for angular data (i.e. assuming a projected normal distribution of the data after Presnell et al. 1998), and were used to avoid spurious results deriving from single correlation analyses between the angles of orientation (dependent variable) and independent variables: if such correlations were taken singly, they would not allow for an overall integrated vision of orientation under natural conditions (Scapini 2002). The multiple regression analysis began

with an additive model that included all the independent variables recorded (beach of origin, season, time of the day, pattern vision, landscape vision, air temperature, air relative humidity, cloud cover, sun visibility, sun azimuth, size, sex, age), and the best additive model was selected through backward selection. The library, created ad hoc (Marchetti & Scapini 2003), highlights the eventual multi-collinearity among variables before starting the analysis to avoid bias in correlation values. The Akaike Information Criterion, i.e. the maximum likelihood with the least number of variables (expressed as score), was used to select the model that best explained the distribution of orientation angles of *Atlantorchestoidea brasiliensis*. When interactions between variables were found, different models were developed separately for each level of the interacting variables. The significance of the variables included in the best model was checked with the Likelihood Ratio Test by comparing the best model and the nested model without the variable being tested (Marchetti & Scapini 2003).

## RESULTS

Environmental variables recorded during the experiments showed minimal seasonal differences in air temperature and sun visibility, while air humidity (in particular) and cloud cover markedly differed between seasons (Table 1).

The number of juveniles found in the samples was low (3.5%); juveniles were therefore excluded from further analysis. Circular distributions related to both beaches included the Theoretical Escape Direction (TED) seawards; on the reflective sandy beach (Punta del Diablo) the mean angle of orientation was closer to the TED, and the orientation was more precise than on the dissipative beach (Barra del Chuy) ( $k$  test for concentration between the 2 distributions under natural conditions without visual pattern,  $p < 0.05$ ; Fig. 3, Table 2). The effect of landscape vision on orientation highlighted further differences between the behavior

Table 1. Environmental variables recorded during the experiments on the beach. Seasonal data with median and range are reported

	Air temperature (°C)	Air relative humidity (%)	Sun visibility (Bright–Visible–Overcast)	Cloud cover (0–8/8)
<b>Spring (October)</b>				
Median	26.0	47.0	Bright	0
Range	20.0–31.5	38.0–63.0	Bright–Bright	0–0
<b>Autumn (April)</b>				
Median	26.8	77.0	Bright	3
Range	23.8–34.7	43.0–85.0	Bright–Overcast	1–8

of the 2 populations: an increase in precision, and a mean angle of orientation closer to the TED was obtained on the dissipative beach as compared to the conditions without landscape vision, while the opposite effect was observed on the reflective beach (i.e. an increase in scatter with landscape vision). No photo-

taxis effect was found, reflected in the lack of differences in distributions attributable to the time of day (result confirmed by the SPLM below). In all cases, the TED was included within the CI (Fig. 3, Table 2). On both beaches the response to the visual pattern included a component representing a negative scoto-

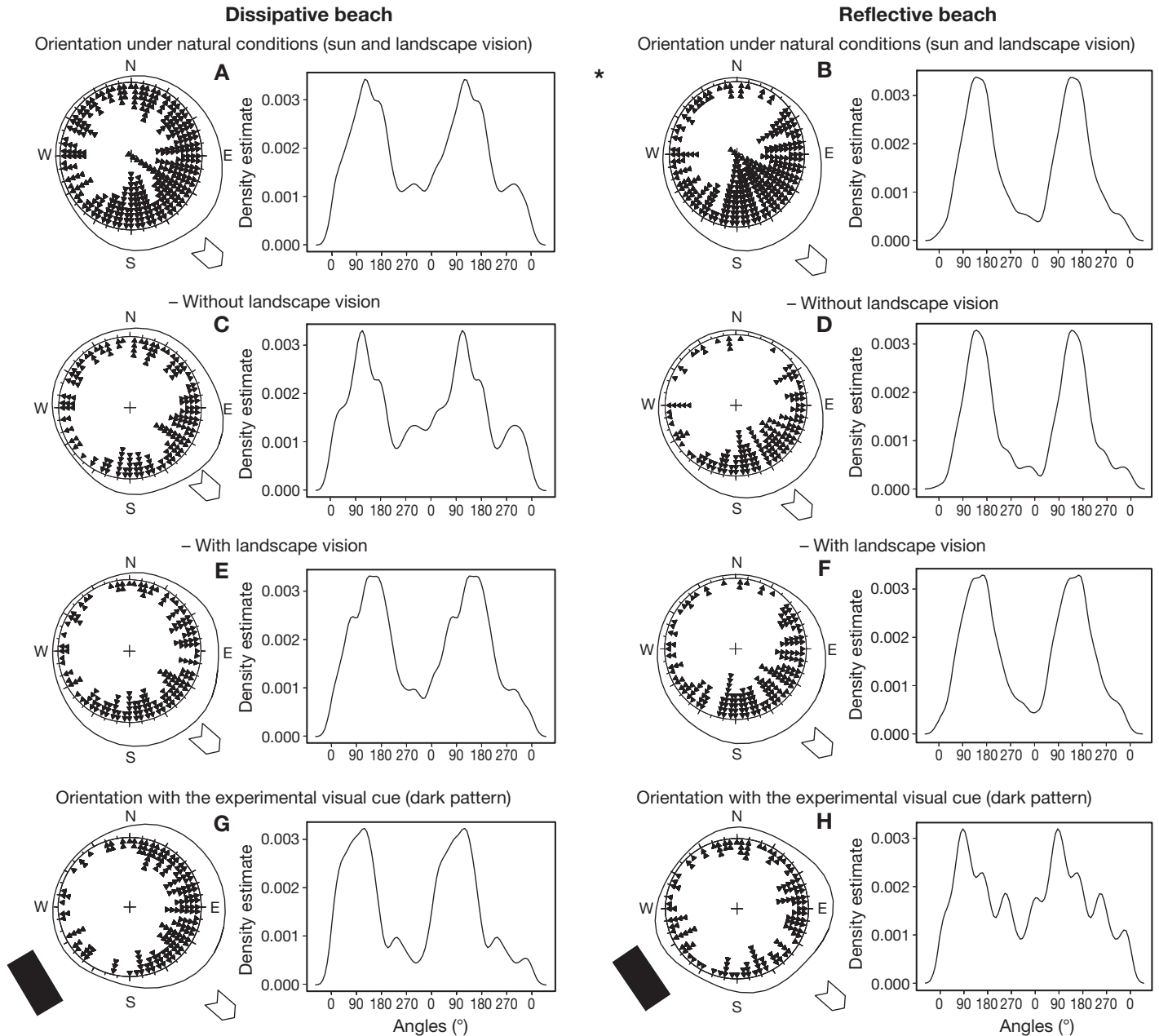


Fig. 3. *Atlantorchestoidea brasiliensis*. Orientation patterns on sandy beaches with contrasting morphodynamics: (A, C, E, G) dissipative (Barra del Chuy, Theoretical Escape Direction TED = 140°), and (B, D, F, H) reflective (Punta del Diablo, TED = 145°). White arrows: TED, i.e. the seaward direction perpendicular to the shoreline; (▲) individual angles of orientation; line: angle distribution smoothed with Kernel method (density estimate). The same distribution is represented in the graph on the right, where data are doubled to avoid the effect of interruption due to transposition of circular distribution into a Cartesian graph. The TED lay within the CI of the distribution in all cases except (C). \*Significant difference ( $p < 0.05$ ) in  $k$  test in the orientation tested under natural conditions (sun and landscape vision) (A vs. B). Black rectangles: dark pattern position in the orientation tested with experimental visual cue. Rayleigh test was significant for all distributions ( $p < 0.05$ ). Summaries of the circular orientation patterns are given in Table 2

Table 2. Summaries of the circular orientation patterns illustrated in Fig. 2

Treatment	Mean direction (°)	95% confidence intervals (°)	Mean vector length (r)	Circular dispersion	N
<b>Dissipative beach</b>					
A. Orientation under natural conditions (sun and landscape as visual cues)	125.80	111.39 – 140.29	0.29	5.54	342
C. Without landscape vision	112.30	89.80 – 134.89	0.25	6.69	175
E. With landscape vision	136.50	118.53 – 154.57	0.33	4.16	167
G. Orientation with the experimental visual cue (dark pattern)	92.61	78.69 – 106.53	0.42	2.55	169
<b>Reflective beach</b>					
B. Orientation under natural conditions (sun and landscape as visual cues)	148.50	140.25 – 156.78	0.48	1.82	338
D. Without landscape vision	147.50	136.86 – 158.13	0.52	1.41	159
F. With landscape vision	149.60	136.78 – 162.39	0.44	2.29	179
H. Orientation with the experimental visual cue (dark pattern)	105.40	72.23 – 138.52	0.21	10.58	136

taxis (orientation away from the pattern), a positive scototaxis (orientation towards the pattern) and a seaward orientation (towards the TED: Fig. 3, Table 2). These orientation components were more uniform on the reflective than on the dissipative beach, with prevailing orientation directed seaward and away from the pattern.

SPLM analysis of orientation showed an interaction between the 'pattern' factor and all the other variables considered. Two models were consequently developed: one for the orientation under natural conditions (sun and landscape vision), and one for the orientation with the visual pattern. The latter included an interaction between the 'site' variable and all the other variables. This implies that only one model explained the orientation of *Atlantorcheostoidea brasiliensis* (integrating sun compass and landscape vision: Table 3), while scototaxis was best explained by 2 different models, depending on the beach type (Table 4). Within the best model explaining orientation under natural conditions (Table 3), the 'site' and 'landscape' variables defined

orientation precision in the seaward direction. The highest precision was observed on the reflective beach (Punta del Diablo) in absence of landscape vision ( $r = 0.52$  and Sample Circular Dispersion = 1.41), while the highest scatter was observed on the dissipative beach (Barra del Chuy) in absence of landscape vision ( $r = 0.25$  and Sample Circular Dispersion = 6.69). The 'season' variable defined a seasonal variation in precision, with an increase in scatter during April (autumn), when the most humid conditions were also found. The 'landscape' and 'season' variables were included in the best models developed for the scototactic response (Table 4): on both beaches the landscape vision enhanced the negative scototaxis (escape away from the pattern) and in autumn the seawards direction was enhanced. 'Air humidity' was the only continuous variable retained in the models. This variable was present in the orientation model under natural conditions, but reached statistical significance only in the 2 models obtained for scototaxis (Table 4). A higher scatter of individuals was observed in general under higher air

Table 3. Spherically projected linear models for orientation under natural conditions (sun compass and landscape vision). Orientation is the dependent variable, expressed in degrees (circular data). Significance to the Likelihood Ratio Test (LRT): (\*)  $p \leq 0.05$ ; (\*\*)  $p \leq 0.01$ . Variables not significant to the LRT but which contribute to the lowest Akaike Information Criterion (AIC) score were included in the model

Model	Factors and variables included in the model	AIC score	df
Additive model with all factors and variables	Orientation $\approx$ beach of origin + season + pattern vision + time of day + landscape vision + size + age + sex + air temperature + air humidity + azimuth + sun visibility + cloud cover	3356.95	955
Best model for orientation by means of sun compass and landscape vision	Orientation $\approx$ beach of origin** + season** + air humidity	2276.88	672

Table 4. Spherically projected linear models for orientation as a response to a visual pattern (scototaxis). Orientation is the dependent variable, expressed in degrees (circular data). Significance to the Likelihood Ratio Test (LRT): (\*)  $p \leq 0.05$ ; (\*\*)  $p \leq 0.01$ . Variables not significant to the LRT but which contribute to the lowest Akaike Information Criterion (AIC) score were included in the model

Model	Factors and variables included in the model	AIC score	df
Additive model with all factors and variables	Orientation $\approx$ beach of origin + season + pattern vision + time of day + landscape vision + size + age + sex + air temperature + air humidity + azimuth + sun visibility + cloud cover	3356.95	955
Best model for response to pattern vision on the dissipative beach	Orientation $\approx$ season** + landscape vision** + air humidity** + cloud cover**	518.94	159
Best model for response to pattern vision on the reflective beach	Orientation $\approx$ season* + landscape vision** + sex* + air humidity* + air temperature	449.48	124

relative humidity. Only on the reflective beach was an effect of the 'sex' variable on orientation observed in response to the visual pattern (Table 4), males being more scattered than females.

## DISCUSSION

Sun compass was confirmed as the main cue for orientation under natural conditions in *Atlantorchestoidea brasiliensis*, the direction seawards being maintained either with or without landscape vision (Williamson 1951). No differences between morning and afternoon (related to the sun azimuth) were found, confirming a compensation mechanism for sun movement and highlighting scarce phototactic behaviour under natural conditions (Pardi & Papi 1953).

In agreement with the main predictions of the HSH, significant differences were observed between beaches: when the landscape vision was screened off and the sun was the only visual reference, the precision of the orientation seawards was higher on the reflective beach than on the dissipative one. By adding a visual pattern, a major scatter in the orientation of sandhoppers inhabiting the reflective beach was observed. On the dissipative beach, such an additional visual cue caused the opposite effect on orientation precision. Thus, a reflective beach type favours sun compass over local visual cues, while the individual variability is enhanced by the higher stability of the supralittoral zone.

Scototactic behaviour, analysed as the response to a pattern placed in a position usually free of references (i.e. different from the sea-dune axis and from the sun azimuth during testing), also differed between beaches; this is highlighted by the different SPLMs obtained to explain the angle distributions. Environmental factors and variables had different weights in the best models obtained for the 2 beaches, and the intrinsic 'sex' vari-

able affected the behaviour of sandhoppers on the reflective beach only. Scototactic responses were in agreement with those observed for sandhoppers from microtidal beaches of the Mediterranean (Scapini 1997) and the Baltic Sea (Nardi et al. 2000). However, the higher scatter observed in scototaxis on the reflective beach with respect to the dissipative one could be attributed to different strategies (e.g. escape from the pattern, escape seawards, or attraction to the pattern), as highlighted by the different distributional patterns of the orientation responses (Fig. 3). Between-sex differences also influenced the response to the visual pattern on the reflective beach, as pointed out by the significance of the 'sex' variable in the model. The higher scatter displayed by males with respect to females could be explained by their exploratory behaviour, as was also observed by Scapini et al. (2005) on a Mediterranean sandy shore; males (less linked to the wet sand stripe than juveniles and females carrying eggs) oriented not only seawards but also long-shore. On the Uruguayan dissipative sandy beach, no intrinsic characteristics, such as sex, age or dimension, had significant effects on orientation.

The influence of meteorological variables on orientation was expected, as this behaviour represents a response to immediate environmental conditions (Borgioli et al. 1999). This was confirmed in this case as well, with the presence in all best models of those variables related to a dehydration risk for sandhoppers: air humidity and season (the latter grouping higher air humidity values under increasing cloud cover in autumn, consistent with the seasonality expected at this latitude). The behavioural response of sandhoppers to a lesser dehydration risk was to increase in scatter; this was observed at the seasonal and immediate (relative variation of air humidity within the season) levels.

In summary, the results obtained in this experimental field study can be integrated into the current hypotheses that link physical and biotic components in

sandy beach ecology. The more benign physical conditions of the littoral zone on dissipative beaches did not explain variations in sandhopper behaviour (as expected by the SEH and the HHH), but instead responded to the higher stability found on a smaller scale (i.e. the supralittoral zone of the reflective beach), as predicted by the HSH. A precise mechanism such as sun compass, paired with a higher variability in individual behaviour, was favoured by the more stable supralittoral conditions on the reflective beach. Individual variability appeared when sandhoppers were subjected to unexpected visual cues, such as a dark pattern on the horizon (here added experimentally, but it could be a predator or a stranded object for animals under natural conditions). By contrast, on a dissipative beach the sun compass was less precise and adjustment to the natural landscape was needed. In this case, individual variability was higher when the only visible cue allowed was the sun. The analysis of sandhopper behaviour as a population trait provides strong support for the HSH, and represents an argument in favour of the consideration of animal behaviour characteristics when describing sandy beach environments.

*Acknowledgements.* This study was partly funded by the International Cooperation between the University of Florence, the University of the Republic of Uruguay, and by PEDECIBA Uruguay. We are also grateful to J. Gómez, J. P. Lozoya, E. Celentano, G. Martínez, S. Horta and S. Saucó, who shared with us the fieldwork, and to the Lercari and de Alava families. We are grateful to Professor G. M. Marchetti for his support in checking the sections regarding statistical analysis, and ensuring intelligibility without losing correctness.

#### LITERATURE CITED

- Batschelet E (1981) Circular statistic in biology. Academic Press, London
- Borgioli C, Martelli L, Porri F, D'Elia A, Marchetti GM, Scapini F (1999) Orientation in *Talitrus saltator* (Montagu): trends in intra-population variability related to environmental and intrinsic factors. *J Exp Mar Biol Ecol* 238:29–47
- Brazeiro A (2005) Geomorphology induces life history changes in invertebrates in sandy beaches: the case of mole crab *Emerita brasiliensis* in Chile. *J Mar Biol Assoc UK* 85:113–120
- Cardoso RS, Veloso VG (1996) Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha beach, Brazil. *Mar Ecol Prog Ser* 142:111–119
- Celentano E, Defeo O (2006) Habitat harshness and morphodynamics: life history traits of the mole crab *Emerita brasiliensis* in Uruguayan sandy beaches. *Mar Biol* 149: 1453–1461
- Codling EA, Pitchford JW, Simpson SD (2007) Group navigation and the 'many-wrongs principle' in models of animal movement. *Ecology* 88:1864–1870
- Contreras H, Jaramillo E, Duarte C, McLachlan A (2003) Population abundances, growth and natural mortality of the crustacean macroinfauna at two sandy beach morphodynamic types in southern Chile. *Rev Chil Hist Nat* 76: 543–561
- Defeo O, Gómez J (2005) Morphodynamics and habitat safety in sandy beaches: life history adaptations in a supralittoral amphipod. *Mar Ecol Prog Ser* 293:143–153
- Defeo O, Martínez G (2003) The Habitat Harshness Hypothesis revisited: life history of the isopod *Excirrolana brasiliensis* in sandy beaches with contrasting morphodynamics. *J Mar Biol Assoc UK* 83:331–340
- Defeo O, McLachlan A (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Mar Ecol Prog Ser* 295:1–20
- Defeo O, Brazeiro A, de Alava A, Riestra G (1997) Is sandy beach macrofauna only physically controlled? Role of substrate and competition in isopods. *Estuar Coast Shelf Sci* 45:453–462
- Defeo O, Gómez J, Lercari D (2001) Testing the swash exclusion hypothesis in sandy beaches populations: The mole crab *Emerita brasiliensis* in Uruguay. *Mar Ecol Prog Ser* 212:159–170
- Defeo O, Lercari D, Gómez J (2003) The role of morphodynamics in structuring sandy beach populations and communities: What should be expected? *J Coast Res* 35S: 352–362
- Fanini L, Scapini F (2008) Variable orientation within a natural population of the sandhopper *Talitrus saltator* (Crustacea:Amphipoda) as a response to a variable environment: The case-study of Berkoukesh beach, Tunisia. *Estuar Coast Shelf Sci* 77:163–168
- Fanini L, Marchetti GM, Scapini F, Defeo O (2007) Abundance and orientation responses of the sandhopper *Talitrus saltator* to beach nourishment and groynes building at San Rossore Regional Park, Tuscany, Italy. *Mar Biol* 152: 1169–1179
- Fisher NI (1993) Statistical analysis of circular data. Cambridge University Press, Cambridge
- Giménez L, Yannicelli B (1997) Variability of zonation patterns in temperate microtidal Uruguayan beaches with different morphodynamic types. *Mar Ecol Prog Ser* 160: 197–207
- Gómez J, Defeo O (1999) Life history of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda) in sandy beaches with contrasting morphodynamics. *Mar Ecol Prog Ser* 182:209–220
- Lerner IM (1954) Genetic homeostasis. Oliver and Boyd, London
- Marchetti GM, Scapini F (2003) Use of multiple regression models in the study of sandhopper orientation under natural conditions. *Estuar Coast Shelf Sci* 58(S): 207–215
- Marques JC, Anastácio P (2002) Integration and interpretation of ecological data at population level. In: Scapini F (ed) Baseline research for the integrated sustainable management of Mediterranean sensitive coastal ecosystems. A manual for coastal managers, scientists and all those studying coastal processes and management in the Mediterranean. Istituto Agronomico per l'Oltremare, Società Editrice Fiorentina, Florence, p 155–164
- McArdle S, McLachlan A (1991) Dynamics of the swash zone and effluent line on sandy beaches. *Mar Ecol Prog Ser* 76:91–99
- McArdle S, McLachlan A (1992) Sand beach ecology: Swash features relevant to the macrofauna. *J Coast Res* 8: 398–407
- McLachlan A, Brown A (2006) The ecology of sandy shores, 2nd edn. Academic Press, London



- McLachlan A, Dorvlo A (2005) Global patterns in sandy beach macrobenthic communities. *J Coast Res* 21:674–687
- Nardi M, Persson LE, Scapini F (2000) Diel variation of visual response in *Talitrus saltator* and *Talorchestia deshayesii* (Crustacea: Amphipoda) from high latitude beaches of low tidal amplitude. *Estuar Coast Shelf Sci* 50:333–340
- Pardi L, Papi F (1953) Ricerche sull'orientamento di *Talitrus saltator* (Montagu) (Crustacea – Amphipoda). *Z Vgl Physiol* 35:459–489
- Presnell B, Morrison SP, Littel RC (1998) Projected multivariate linear models for directional data. *J Am Stat Assoc* 93:1068–1077
- Scapini F (1997) Variation in scototaxis and orientation adaptation of *Talitrus saltator* populations subjected to different ecological constraints. *Estuar Coast Shelf Sci* 44:139–146
- Scapini F (2002) Baseline research for the integrated sustainable management of Mediterranean sensitive coastal ecosystems: A manual for coastal managers, scientists and all those studying coastal processes and management in the Mediterranean. Istituto Agronomico per l'Oltremare, Florence, [www.meco.unifi.it/MECO\\_manual.pdf](http://www.meco.unifi.it/MECO_manual.pdf)
- Scapini F, Ugolini A, Pardi L (1981) Analysis of astronomical orientation in littoral amphipods (Crustacea, Amphipoda) using individual and group tests. *Monit Zool Ital* 15:77–86
- Scapini F, Chelazzi L, Colombini I, Fallaci M, Fanini L (2005) Orientation of sandhoppers at different points along a dynamic shoreline in southern Tuscany. *Mar Biol* 147:919–926
- Schlacher TA, Schoeman DS, Dugan J, Lastra M, Jones A, Scapini F, McLachlan A (2008) Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. *PSZN I: Mar Ecol* 29(S1):70–90
- Short AD (1996) The role of wave height, period, slope, tide range and embaymentisation in beach classification: a review. *Rev Chil Hist Nat* 69:589–604
- Ugolini A, Scapini F, Pardi L (1986) Interaction between solar orientation and landscape visibility in *Talitrus saltator* (Crustacea: Amphipoda). *Mar Biol* 90:449–460
- Williams JA (1983) Environmental regulation of the burrow depth distribution of the sand-beach of the amphipod *Talitrus saltator*. *Estuar Coast Shelf Sci* 16:291–298
- Williamson D (1951) Studies in the biology of Talitridae (Crustacea: Amphipoda): visual orientation in *Talitrus saltator*. *J Mar Biol Assoc UK* 30:91–99

*Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany*

*Submitted: November 14, 2008; Accepted: July 15, 2009  
Proofs received from author(s): October 8, 2009*