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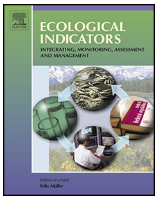

Talitrid orientation as bioindicator of shoreline stability: Protected headland-bays versus exposed extended beaches

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ABSTRACT

The behaviour of talitrids, being a local adaptation to beaches, is known to be related to environmental stability. The use of behavioural responses of resident populations as bioindicator of shoreline stability has been tested under various conditions, including after soft and hard engineering actions to stabilise eroded beaches. Port structures likely have impact on sediment longshore transportation and shoreline stability. The question was whether talitrid orientation behaviour could be proposed as bioindicator of impacts also for sandy bays of limited extension and highly used for recreation, such as those in the vicinity of touristic port structures. Orientation experiments were carried out on a set of sandy beaches of different extension and morphology, each of them in the vicinity of a touristic port, across the Mediterranean coasts. The protocol included field orientation tests of populations of talitrids, then analysed in terms of orientation precision seawards (considering sun compass orientation as the most locally adapted behavioural mechanism) in different seasons (before and after the touristic season) and times of day. The populations from more protected (either naturally or artificially) headland-bays showed a higher precision of orientation with respect to the shoreline direction than those from extended beaches, more subject to changes in longshore sedimentary transport as consequence of natural and human activities. The distance from the port and touristic pressure had no influence on talitrid orientation. An important stabilising factor for the sandy beach ecosystems, including talitrid populations and their behavioural adaptation, appeared to be the presence of seagrass banquette. The behavioural data point out that biotic information proceeding from local animal populations linked to beach sediments may complement sedimentology data and allow scaling the impacts occurring on a developed coastline. This becomes particularly relevant when considering interdisciplinary approaches to monitoring strategies.

1. Introduction

1.1. Talitrids: fine tuning to a changing environment

Sandy beaches host abundant and diverse arthropod communities in the intertidal and supra-littoral zones exploiting the wrack deposited by tides and waves (Schlacher et al., 2014). Within the mobile arthropod fauna communities, talitrids (Crustacea, Amphipoda, Talitridae) are keystone species that show peculiar behavioural adaptations tuned to the environmental features of sandy beaches (Scapini, 2006, 2014; Walsh et al., 2010). Talitrids inhabiting sandy beaches are night-active, but may express solar orientation seawards during the day in case of displacement by mechanical factors (e.g., waves, predators) or to face a dehydration risk while buried in the sand in the supra-littoral zone. This is particularly evident in Mediterranean microtidal beaches, where talitrids occupy a zone very close to the waterline (Scapini et al., 1997; Colombini et al., 2002; Fallaci et al., 2003). Differences in orientation capability, with the use of alternative mechanisms and cues, were found related to the stability of beaches (Scapini, 2006). On Italian shores, sun orientation was shown to be adapted to the

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shoreline direction and inherited on more stable beaches, while on changing shorelines a scatter toward various directions was observed in the samples (Scapini et al., 1995). The interpretation of these results, supported by population genetics data, was that stable beaches offered a longer time for behavioural adaptation to be fixed by natural selection and/or learning. The study of Scapini et al. (1995) was integrated by relating behavioural and genetic adaptation with the changes of shoreline through time (decades) as reported in the topographic maps of Italy (C.N.R.-M.U.R.S.T, 1997). These hypotheses remained indeed to be tested in a wider context, to avoid bias due to differences in coastline morphology, such as uneven presence of headlands, river mouths and rocky shores (see e.g. Barsanti et al., 2011, regarding Italian coasts). Later studies led however to similar conclusions: differences in orientation precision toward the shoreline were shown by populations from different points along the same continuous beach on the Tyrrhenian coasts of Italy, subject to different erosion/accretion dynamics (Scapini et al., 2005; Ketmaier et al., 2010). Also Bouslama et al. (2011) found a link between talitrid behaviour and environmental stability on two beaches of the Tunisian coasts comparing behavioural traits (orientation and locomotor activity rhythms). On the Atlantic coast of Uruguay, Fanini et al. (2009) compared the orientation of talitrids from beaches differing in morphodynamics and observed a more precise orientation on a reflective beach than on a dissipative one, due to the protected position of talitrid populations across the beach, where the wave energy is reflected by the beach slope (Habitat Safety Hypothesis, Defeo and Gómez, 2005). On the Pacific coasts, in Chile, on oceanic macrotidal intermediate beaches, a better adapted seaward orientation was observed on a protected beach than on an exposed one (Scapini and Dugan, 2008). Although the relation of talitrid behavioural adaptation/plasticity with respect to stable/changing shoreline was not clearly stated among the hypotheses to be tested, the relationship between population features and sandy beach ecology and morphology appeared clear from literature (Soares et al., 1999; McLachlan and Brown, 2006; Defeo et al., 2009). In summary, there is a consistent indication across geographical macro-areas, of talitrid adaptation (allowed by a high behavioural plasticity) to the stability of the shoreline inhabited by the populations. While the debate about the meaning of “shoreline stability” is still open (depending on the perspective of each discipline), the information provided by local talitrid populations can provide an integration of those features, which are relevant to the species-environment perspective.

1.2. *Behaviour of talitrids and man-made structures: open questions*

The MAPMED project (ENPI CBC-MED programme) aimed at characterizing port areas in the Mediterranean, to develop suitable monitoring tools that can sustain Port Authorities in managing these areas. Within the project framework, a suite of possible stabilizing/destabilizing factors were taken into account that may act on a shoreline. Port structures may impact on sediment longshore transport and sandy beach stability (Poulos and Chronis, 2001). These dynamics, generated by man-made hard structures, may act with faster time than the natural ones and severely impact beach ecosystem (Dugan et al., 2008; 2013). Behavioural experiments (etho-assays) were planned on beaches at different distances updrift or down-drift from the port structures to assess the effects of the port impacts on mobile macrofauna adaptation. Three port areas were selected across the Mediterranean, in the western Mediterranean Basin (Italy, Sardinia, Port of Cagliari), in the eastern one (Greece, Crete, Port of Heraklion) and on the southern coasts (Tunisia, eastern coast, Port of El Kantaoui) (Fig. 1a). The three localities were characterised by the presence of touristic infrastructures and similar seasonality of tourism (peaks in summer months); the direct impact of human trampling and other managements were consequently supposed to be similar. To each of the selected beaches an index of beach use (Recreation and Conservation, integrating in a final score both natural and human features of the beach-dune system) was assigned (McLachlan et al., 2013). The approach of this study was based on current models developed in coastal engineering regarding the concept of “static bay beach” (Hsu et al., 2010; Barsanti et al., 2011). According to this concept, a pocket beach would be stable, while an extended beach would be subject to longshore sediment transport depending on the dominant winds, currents and waves, and thus to changes as a consequence of human actions and man-made interruptions (Barsanti et al., 2011).

1.3. *Hypotheses for behavioural tests on changing coastlines*

Arthropod community features and orientation of talitrids to the shoreline had been used in similar contexts to monitor the stability of the beach ecosystem with respect to changed sedimentary dynamics caused by soft and hard engineering measures to stabilise beaches against erosion (Fanini et al., 2007; Bessa et al., 2013; Nourisson et al., 2014). Measurable changes in talitrid orientation parameters, such as the precision with respect to the shoreline direction, would provide a tool for a monitoring programme of the impact of man-made structures on the beach ecosystem (Scapini, 2014). In a complex system such as the touristic areas under analysis, it is relevant, first of all, to know to which of the above mentioned factors (direct tourism impact or effects of human made structures on the sedimentary transport) will respond the local talitrid population.

In this study current paradigms were considered, which summarize the stability condition of a sandy beach under the perspective of different disciplines, and were tested via the behaviour of local talitrid populations. It was assumed that on more stable beaches (in the present case on pocket beaches, eventually stabilised by the presence of wrack, Dugan et al., 2003, 2013) talitrids would show an orientation precisely adapted to the (stable) shoreline, while on beaches more exposed to winds, currents and waves, and stressed by changes in sedimentary longshore transport, talitrid orientation would be more scattered. The interference of port structures with longshore sedimentary drifts was expected to have a consequence on resident populations, likely detectable in behavioural adaptation.

Alternative not mutually exclusive hypotheses that have been considered by this study were:

(1). The intensity of recreation activities (expressed by the Recreation index, McLachlan et al., 2013) would have a negative impact on the mobile macrofauna.
(2). The vicinity of the port structure (distance from the port) would have a negative impact on the talitrid populations and their behavioural adaptation.
(3). The extension of the beach (pocket beach vs. extended beach) would affect the talitrid behavioural adaptation to the shoreline direction.
(4). The presence of dunes and wrack (Conservation index, McLachlan et al., 2013, or local ecological stabilisation) would positively impact on the behavioural adaptation.

2. Material and methods

2.1. *Study sites choice and characterisation*

Orientation tests on talitrids were carried out in 2012 in two replicates: one at the beginning of the touristic season (May–June)

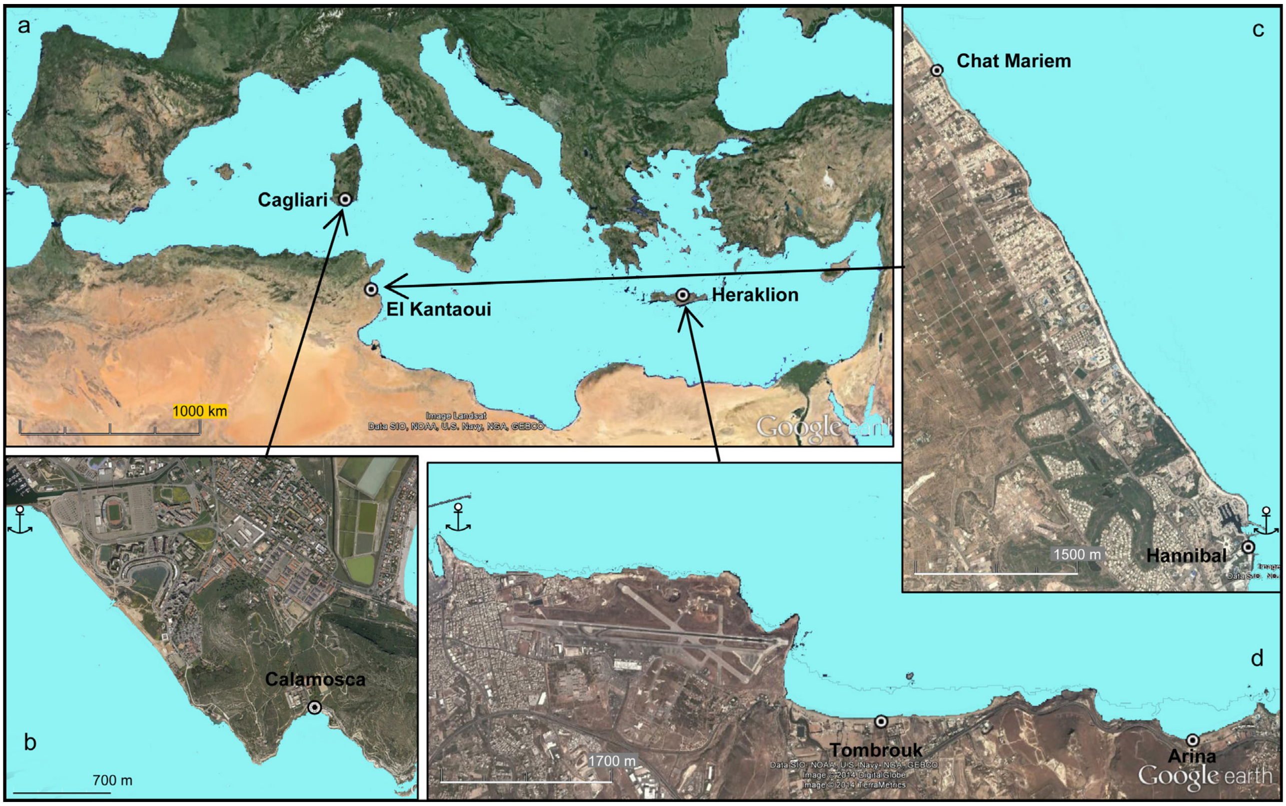

Fig. 1. (a) Location of the selected beaches across the Mediterranean coasts, near touristic ports: Cagliari (39°12′N, 9°07′E; Sardinia, Italy); El Kantaoui (35°54′N, 10°36′E; Tunisia); Heraklion (35°25′N, 25°08′E; Crete, Greece). (b) Calamosca beach (39°11′12″N, 9°09′07″E) at 3500 m from the Cagliari port; (c) Chat Mariem beach (35°55′58″N, 10°33′56″E) at 5200 m from El Kantaoui port, and Hannibal beach (35°53′29″N, 10°36′01″E) at 100 m from the El Kantaoui port; (d) Tombrouk beach (35°19′55″N, 25°12′07″E) at 5000 m from the Heraklion port, and Arina beach (35°19′49″N, 25°14′10″E) at 8000 m from the Heraklion port. North is up. Anchor symbols indicate the port position.

and one at the end of it (September) on beaches near the port of Cagliari (Italy, Sardinia; 31 May, 22 September), the port of El Kantaoui (Tunisia; 7–8 June, 26–27 September) and the port of Heraklion (Greece, Crete; 16–18 May, 12–13 September) (Fig. 1a). Consistently to the overall goals of the MAPMED Project, it was planned to study beaches on both sides of the ports to highlight eventual effects of port structures. However the natural variability of the coastlines and their features did not allow for a geometric placement of the study sites. The data analysis chosen (see below) was consequently thought to be robust to variability. Near Cagliari, the etho-assays could be performed only on a naturally protected sandy bay on the left side of the port, Calamosca (39°11′12″N, 9°09′07″E, Fig. 1b) because on the other side of the port no talitrids were found (FS and CR, personal observations). Those beaches had been nourished with new sediments to favour recreation activities, while at Calamosca the pocket beach was stabilised by keeping the seagrass banquette on site. Near El Kantaoui a sandy beach was chosen next to the port (100 m) on its right side, protected by the port structures, Hannibal beach (35°53′29″N, 10°36′01″E, Fig. 1c), and an extended beach was chosen on the left side at 5200 m of the port, Chat Mariem beach (35°55′58″N, 10°33′56″E, Fig. 1c). On this side nearer to the port, it was not possible to find established talitrid populations (SG, ME and CR, personal observations). Near Heraklion two beaches were selected on the right side of the port, Tombrouk beach (35°19′55″N, 25°12′07″E; 5000 m, Fig. 1d), which was protected by a natural headland, and Arina beach (35°19′49″N, 25°14′10″E; 8000 m, Fig. 1d), a natural bay that did not present prominent structures. On the left side of the port no talitrids were found (LF, CR and DN, personal observations); the Heraklion airport is located immediately after the port, so that the beaches are on the right side of both the man-made infrastructures. At each experimental session a profile of the beach was drawn from the waterline to the base of the dune, using standard topographic methodology (measures of beach width, slope, and shoreline direction). Recreation and Conservation indices (RI and CI; McLachlan et al., 2013) were estimated for each beach through a consultation among the authors, who had visited the beaches. This consultation was performed independently of the analyses of orientation.

2.2. Orientation experiments

The orientation experiments (etho-assays) were performed on the beaches, using a Plexiglas arena with a 40 cm diameter, having 72 pitfall traps of 5° each at its rim; a transparent cylindrical screen covered the entire device. A white cardboard was placed around the arena circumference to screen off the landscape, so that sun orientation was observed, to be compared among the various localities. The arena was positioned horizontally on a small table at 1 m above the beach surface; pitfall trap 72 was oriented to the North. The talitrid samples for the etho-assays were collected randomly from the waterline to the base of the dune. Groups of about ten individuals were placed in the centre of the arena by means of a transparent tube vertically inserted through the cover of the arena; after one minute the tube was removed and the animals were free to hop or run in the preferred direction. Experimental series of 4–6 groups were repeated twice, in the morning and in the afternoon, using new individuals each time. This procedure was applied as the orientation of individuals tested in small groups can be considered independent (Scapini et al., 1981). More than four samples were tested when two sympatric talitrid species were present on the beach; the species were checked later in the laboratory, so that the individuals tested were not disturbed before the etho-assay. At each release the following immediate variables were registered: time of the release, air temperature (°C; electronic thermo–hygrometer), air humidity (%; electronic thermo–hygrometer), and sky cloudiness (0–8; visual appreciation), sun vision (visible, veiled, shape, not visible; visual appreciation). All individuals tested were kept in separate tubes with 75% alcohol for the measurement of intrinsic variables: morphometric measures (number of segments of the second antennae and cephalic length, proxy of age and size, respectively, of the tested individuals; Williams, 1987; Marques et al., 2003), species and sex. The samples are preserved at the Department of Biology, University of Florence, Italy.

2.3. Orientation data analysis

To estimate the precision of orientation toward the shoreline, the summary statistics for circular distributions were calculated (Fisher, 1993; S-Plus 6 Insightful with a library developed *ad hoc*; Marchetti and Scapini, 2003). For each angle distribution, it was calculated: the mean angle, the mean vector length (r) and the circular confidence interval around the mean angle; the Rayleigh test for uniformity was applied, to assess the null hypothesis of random orientation. Probability density functions were calculated and smoothed via the kernel method, and were double plotted in a Cartesian graph to visualise all the peaks of the circular distributions (Fisher, 1993).

In tests carried out under natural conditions several factors may influence orientation simultaneously and must be taken into consideration. A multiple regression analysis is recommended when the data are obtained under natural (changing) conditions (Underwood and Chapman, 1985), such as the set of etho-assays at the study sites to be compared. Multiple regression models were developed adapted to angular data (SPLM, Spherical Projected Linear Models; Scapini et al., 2002; Marchetti and Scapini, 2003) to point out the sources of variation; the significance of the recorded variables and factors to the orientation angles was estimated. First, additive baseline models were developed considering all the variables and factors; further models were developed considering the possible interactions of factors. Various models were compared, and the best model was chosen using the Akaike Information Criterion (AIC), i.e. the maximum likelihood with the least number of parameters. From the best model, the effects of single variables on the orientation angles were estimated using the Likelihood Ratio Test (LRT), by comparing the best model with nested models not containing the variable tested.

3. Results

3.1. Local stability, exposure and human use

The beaches differed for several features that may influence their stability: exposure, extension, slope and presence of wrack or seagrass banquette (*Posidonia*, Table 1). At all sites, the beach profiles differed between seasons and appeared more flat in September, after the touristic season (Fig. 2). Regarding the exposure to dominant winds, Calamosca was protected from the dominant WNW winds, but was exposed to the S winds, Chat Mariem and Hannibal were exposed to the dominant NNE and E winds, Arina and Tombrouk were exposed to the dominant NNW winds (Table 1; windfinder, 2014). Regarding the Conservation and Recreation indices (Table 2), the selected beaches fell within the same category (“C”, i.e. balanced use between recreation and conservation), except for Hannibal that was highly used for its proximity to the port and the hotels (assigned to category “B”, i.e. intensive recreation).

3.2. Talitrid populations

The smallest bays, Hannibal and Calamosca, presented a *Posidonia* banquette, in which two sympatric talitrid species *Orchestia stephenseni* and *Orchestia montagui* were found. In the other beaches only one talitrid species, *Talitrus saltator*, was found. The samples presented high percentages of juveniles at Arina and Tombrouk in May (Table 3). In both these beaches, as well as at Tombrouk in September and Hannibal in June, the sex ratio of the samples was male biased, while the sex ratio was considerably female biased at Chat Mariem (Table 3).

3.3. Orientation of talitrids

The orientation of talitrids resulted well adapted to the shoreline direction for all populations in both seasons and times of day, except for *T. saltator* at Chat Mariem beach. In this sole case, we recorded a scattered orientation toward several directions not linked to the shoreline direction, as shown by the density distributions for this population (Fig. 3) and the small value, close to 0, of the mean resultant length (r) obtained in May–June (Table 3). No apparent seasonal differences were observed in the mean directions, but the orientation after the touristic season was slightly less precise on all beaches, with smaller mean resultant lengths (compare the r values in Table 3), with again the different case represented by Chat Mariem. On this beach, the precision improved from June to September, reaching the significance to Rayleigh test, but with a mean angle of orientation deviating of about 80° from the shoreline direction (Fig. 3; Table 3).

From the multiple regression analysis a significant interaction was found of the factor beach with an intrinsic variable (the number of antennae articles), the month (before and after the touristic season) and sky conditions (cloudiness and time of the day) (M1, Table 4). Species, sex, air humidity and temperature were not significant factors in this model. In consideration of the significant interaction of the factor beach, we then calculated regression models for each beach separately. The best model with the least number of parameters was that obtained for Arina beach, in which only the cephalic length was retained as significant factor (M5, Table 4). In fact the smallest (cephalic length < 0.5 mm, $N = 50$) and medium size (1 mm > cephalic length > 0.5; $N = 103$) individuals were more concentrated ($r = 0.7563$ and $r = 0.7436$, respectively) than the biggest ones (cephalic length > 1 mm, $N = 52$; $r = 0.2453$). The model for Calamosca beach had environmental factors (sky conditions, sun azimuth and time of day) as significant factors (M2, Table 4); the model for Hannibal beach retained also the month as significant factor (M4, Table 4). The highest number of factors was retained in the models of Chat Mariem beach (M3, Table 4) and Tombrouk beach (M6, Table 4), reflecting the scatter shown by the distributions, at Chat Mariem in both seasons and at Tombrouk in September (Fig. 3; Table 3).

4. Discussion

4.1. Talitrid behavioural adaptation to beaches in relation to human uses

The beaches considered in this study represented a set of different distances from touristic ports and of ecological conditions, with the exception of the estimated Conservation and Recreation indices (CI and RI) which did not differ much among sites. The only beach assigned to a different category was Hannibal beach, located very close to hotel structures. Regarding the other beaches, the presence of developed dunes at Chat Mariem, Tombrouk and, in lower measure, Arina suggests that these beaches are also suitable for protection, however unlikely in the long term, due to the proximity of touristic facilities. They all were assigned to a mixed use category. From this study it can therefore not be tested the effect of touristic use of a beach on talitrid behavioural adaptation (alternative

Table 1
Beach features and meteorological factors during the orientation experiments.

	Italy		Tunisia				Greece			
	Calamosca		Chat Mariem		Hannibal		Arina		Tombrouk	
	May–June	Sept.	May–June	Sept.	May–June	Sept.	May–June	Sept.	May–June	Sept.
Annual dominant winds*	WNW, ESE, S		NNE, E, NNW				NNW, SSW			
Distance from port (m)	3500 (left)		5200 (left)		100 (right)		8000 (right)		5000 (right)	
Extension (m)	150		11,000		450		800		2000	
Wrack	*Posidonia*		*Posidonia*		*Posidonia*		No		No	
Seaward direction (°)	190	181	58	60	69	99	2	351	348	349
Beach width (m)	22	20	22	21	24	20	20	29	20	26
Mean beach slope(°)	1.1	2.0	2.5	1.9	2.3	0.8	3.0	0.8	3.4	3.4
Slope confidence interval (°)	±3.1	±2.0	±5.0	±3.7	±2.2	±2.4	±1.8	±3.8	±1.7	±4.6
Temperature range (°C)	26–33	26–31	27–29	29–34	27–32	31–34	24–30	27–32	20–28	28–33
Air humidity range (%)	28–54	48–66	60–66	55–72	57–68	53–63	34–46	40–63	38–60	37–48
Cloudiness (0–8)	1–4	0-8	2–3	2–7	0	2–6	2–3	1–4	4–7	0–1

* Calamosca data from Cagliari port, Tunisia data from Sousse, Greece data from Heraklion port; winds in order of prevalence. (windfinder, 2014).

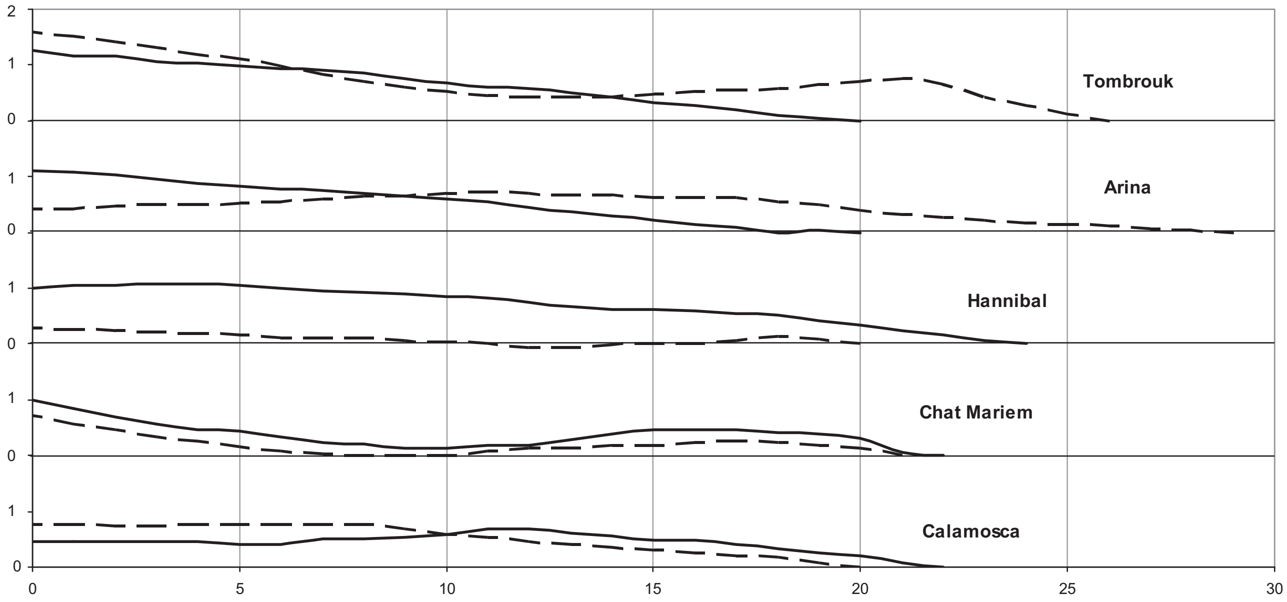

Fig. 2. Profiles of the five beaches (Calamosca, Sardinia, Italy; Chat Mariem and Hannibal, El Kantaoui, Tunisia; Arina and Tombrouk, Crete, Greece) at the times of the orientation experiments (May–June 2012: bold lines; September 2012: dashed lines). On the horizontal axis distances (metres) from the basis of the foredune (0) to the shoreline are shown; on the vertical axis the heights (metres) above sea level (0) are shown.

hypothesis 1, see Introduction). However, the indirect indication can be taken that beaches in the vicinity of touristic infrastructures are unlikely to be designated to protection *sensu stricto*.

Despite the differences among beaches, all local talitrid populations were found capable of sun compass orientation, except for Chat Mariem population. The use of sun compass as orientation mechanism can be inferred by the fact that the orientation tendency seawards was the same at different times of the day (morning and afternoon) compensating the azimuthal displacement.

The proximity to a port was found not to have a negative impact on the precision of seawards orientation, with beaches closer to ports (like Hannibal beach) hosting precisely oriented populations. As a consequence, the hypothesis of talitrid orientation being negatively affected by the proximity of a port (alternative hypothesis

Table 2
Beach characteristics: Conservation (CI) and Recreation (RI) indices (McLachlan et al., 2013), as estimated by the authors independently from the orientation analysis.

	Heraklion		Cagliari	El Kantaoui	
	Arina	Tombrouk	Calamosca	Hannibal	Chat Mariem
Type	**C** (Multiple use)	**C** (Multiple use)	**C** (Multiple use)	**B** (Intensive recreation)	**C** (Multiple use)
CI	**2** (1 dunes, 1 macrobenthos)	**2** (2 dunes, 0 macrobenthos)	**1** (0 dunes, 0 endangered and iconic species, 1 intermediate macrobenthos)	**1/2** (0 dune, 0 endangered and iconic species, 1/2 benthos)	**3/4** (2 dunes, 0 endangered and iconic species, 1/2 macrobenthos)
RI	**5** (2 infrastructures, 2 safety and health, 1 carrying capacity)	**5** (2 infrastructures, 2 safety and health, 1 carrying capacity)	**4/5** (2 infrastructures, 2/3 safety and health, 0 carrying capacity)	**7** (4 infrastructures, 2 safety and health, 1 carrying capacity)	**5** (2 infrastructures, 2 safety and health, 1 carrying capacity)

Table 3
Population traits and summary statistics of talitrid sun orientation.

	Italy		Tunisia				Greece			
	Calamosca		Chat Mariem		Hannibal		Arina		Tombrouk	
	May–June	Sept.	May–June	Sept.	May–June	Sept.	May–June	Sept.	May–June	Sept.
Species	*Orchestia spp.*		*Talitrus saltator*		*Orchestia spp.*		*Talitrus saltator*		*Talitrus saltator*	
Sex ratio	0.733	0.909	0.349	0.574	1.423	0.886	3.400	0.723	1.400	1.857
Percentage of juveniles (%)	7.1	0.0	1.2	1.2	0.0	0.0	63.3	4.7	25.0	4.8
Mean cephalic length (mm)	0.9	1.1	1.1	1.1	1.2	1.1	0.7	0.9	0.9	1.1
Confidence interval	±0.2	±0.1	±0.1	±0.1	±0.2	±0.2	±0.3	±0.2	±0.3	±0.3
Mean n. of antennae articles	16.1	18.8	20.9	22.8	18.5	18.5	13	19.1	17.6	21.8
Confidence interval	±2.9	±1.7	±2.8	±4.3	±2.2	±1.9	±6.7	±4.1	±5.2	±5.5
N	84	84	86	86	126	84	120	85	96	63
Orientation mean angle (°)	159.8	209.1	88.5	345.4	80.9	122.1	341.4	351.8	336.5	350.0
Or. confidence interval (°)	±14.2	±19.8	NA	±22.3	±9.0	±15.0	±8.0	±12.6	±14.3	±25.0
Deviation from seaward dir. (°)	−30.2	+28.1	+30.5	−74.6	+11.9	+23.1	−20.6	+0.8	−11.5	+1.0
Mean resultant length (*r*)	0.5602	0.4329	0.080	0.3757	0.6688	0.5301	0.6548	0.5759	0.4911	0.3664
Rayleigh test (*p*)	<0.001	<0.001	n.s.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 4
Multiple regression models (SPLM) developed from the total dataset (M0, M1) and each beach (M2-M6). AIC, Akaike Information Criterion; Likelihood Ratio Test for the factors: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

M0 Starting additive model	angle ~ month + beach + posidonia + morning/afternoon + azimuth + air temperature + air humidity + sun + sky cloudiness + sex + cephalic length + number of articles of second antennae	Likelihood = 2737.6287 AIC = 2809.6287 Number of parameters = 36 Degrees of freedom = 878
M1 Total dataset–Best model	angle ~ beach*** × (number of articles of second antennae*** + sky cloudiness*** + month*** + morning/afternoon***)	Likelihood = 2638.0302 AIC = 2738.0302 Number of parameters = 50 Degrees of freedom = 864
M2 Best model for Calamosca	angle ~ sky cloudiness*** + azimuth*** + morning/afternoon**	Likelihood = 484.3845 AIC = 500.3845 Number of parameters = 8 Degrees of freedom = 160
M3 Best model for Chat Mariem	angle ~ morning/afternoon*** + azimuth*** + number of articles of second antennae** + air temperature + month	Likelihood = 564.112 AIC = 588.112 Number of parameters = 12 Degrees of freedom = 160
M4 Best model for Hannibal	angle ~ morning/afternoon*** + month*** + sky cloudiness**	Likelihood = 571.1465 AIC = 587.1465 Number of parameters = 8 Degrees of freedom = 202
M5 Best model for Arina	angle ~ cephalic length***	Likelihood = 541.6541 AIC = 549.6541 Number of parameters = 4 Degrees of freedom = 201
M6 Best model for Tombrouk	angle ~ cephalic length*** + morning/afternoon*** + air humidity* + sky cloudiness* + air temperature* + month	Likelihood = 457.7448 AIC = 485.7448 Number of parameters = 14 Degrees of freedom = 145

Likelihood Ratio Test for the factors:

[*] $p < 0.05$.

[**] $p < 0.01$.

[***] $p < 0.001$.

2, see Introduction) was not supported by the results of the etho-assays.

4.2. Talitrid orientation with relation to sedimentary dynamics and beach extension

The remaining hypotheses (3: extension of a beach and 4: local ecological stability, see Introduction) suggest that talitrids can cope with anthropogenic impacts (port structures and touristic pressure) when the local sedimentary dynamics allows for shoreline stability.

Regarding the alternative hypothesis related to beach extension (hypothesis 3) it was found that the extension of the beach negatively affected orientation. The populations from more extended beaches (Chat Mariem and Tombrouk) were more scattered, while those from small bay-beaches were more precisely oriented to the shoreline (Arina, Calamosca and Hannibal). It is worth noting that talitrid populations from small bays, protected by natural or artificial headlands presented a sun orientation well adapted to the shoreline direction of the bay, despite the spatial variation of the general coast. The best behavioural adaptation of talitrids (*T. saltator*) was observed on the Arina beach in Crete. Also Calamosca in Sardinia (a pocket beach protected by natural headlands) and Hannibal in Tunisia (protected by artificial groynes) had well oriented talitrid populations (*O. montagui* and *O. stephenseni*). On the other hand, the most extended beaches, Chat Mariem (11,000 m of extension) had talitrids (*T. saltator*) with a more scattered orientation (measured by the mean resultant length, Table 3). Tombrouk (2000 m of extension) presented an intermediate situation.

Significant differences were not observed in the orientation among species, confirming the finding by Fanini et al. (2012) on talitrids from Moroccan Atlantic beaches, and in line with the paradigm that biota on sandy beaches is physically driven (McLachlan and Brown, 2006). On the other hand, the significant

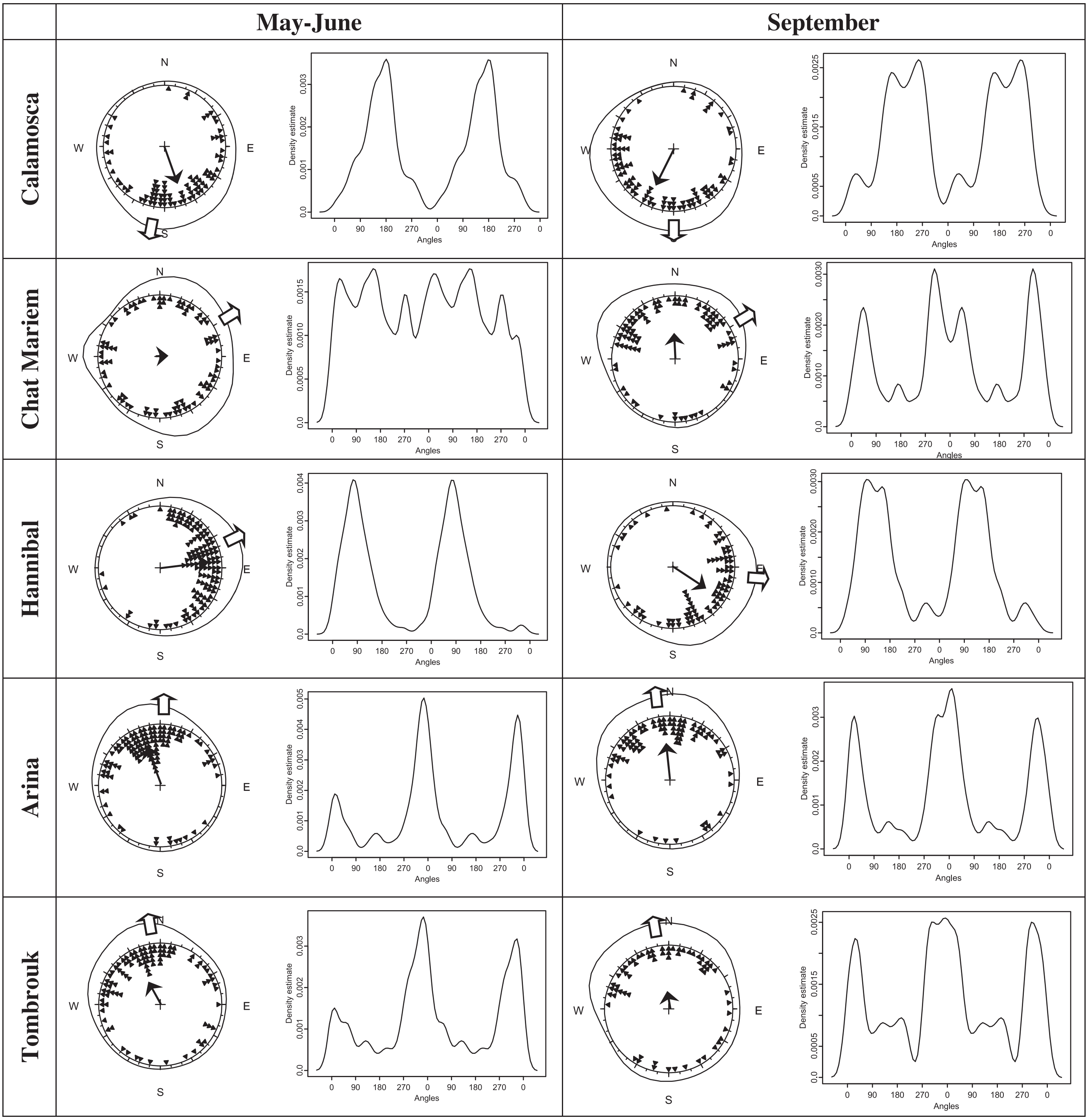

Fig. 3. Talitrid orientation on the five selected beaches in the two seasons (May–June and September 2012, at the beginning and end of the touristic season, respectively). Small triangles inside the circles, individual directions; arrows inside the circles, mean vectors; arrows outside the circles, sea direction at the test sites; the smooth lines outside the circles represent kernel density estimates; the kernel density estimates are double plotted in the Cartesian graphs on the right to highlight all the peaks. Summary statistics are shown in Table 3.

orientation observed in the etho-assays (with the exception of Chat Mariem in June) and the factors retained by the multiple regression models developed from the angular distributions further explain such fine population-ecosystem relationship. The Arina talitrids were the least dependent on environmental factors (best model with the least number of parameters, four), while the models for Tombrouk and Chat Mariem had 14 and 12 parameters, respectively (Table 4). The multiple regression models based on behavioural data confirm that the scattered distributions observed at Tombrouk and particularly at Chat Mariem were influenced by various environmental factors, while the model for the best oriented populations (Arina) retained only one intrinsic factor, related to the size of the animals tested. This means that the Arina population mainly relies on the sun compass to orient to an adaptive direction (the shoreline), coherently across all the replicates (seasons and times of day). The factors species or sex did not affect orientation, while size or age was retained by the models for Chat Mariem, Tombrouk and Arina. This was expected due to the high juvenile rate in the samples, being juveniles more likely stressed by dry air conditions and consequently orienting seawards in a more precise way (Scapini and Dugan, 2008).

A well-adapted seaward orientation of talitrids is expected when the shoreline is stable throughout the time, as this behaviour may be inherited or learned with experience on the natural environment (Scapini, 2014). The concept of "shoreline stability" has been debated in sandy beach ecology and management, as "littoral drift is not a constant phenomenon at any given site" (McLachlan and Brown, 2006, p. 319). Talitrids dwelling the intertidal and supratidal zones may be impacted by longshore littoral sediment drift and, in case of changes of shoreline direction or human induced interruptions on the sandy beach, the resident macrofauna populations may not find the conditions for behavioural adaptation to be fixed (Dugan and Hubbard, 2010; Dugan et al., 2013).

Barsanti et al. (2011) have described the longshore transport along the Italian coasts and proposed a conceptual model for the definition of coastal units of littoral transport. According to this model, the Italian beach Calamosca is a pocket beach with no apparent littoral transport. This fact may explain the behavioural adaptation of talitrids observed at Calamosca. The two beaches in Crete (Arina and Tombrouk) differed for extension and exposure, with Tombrouk more than twice extended than Arina and more exposed to the prevailing NNW winds. According to the biological model proposed by Scapini et al. (1995) for Italian beaches that populations from more stable shorelines have a better orientation than populations from changing shorelines, the talitrids at Arina were better oriented seawards than the same species at Tombrouk (Fig. 3). The two Tunisian beaches at the two sides of the artificial port of El Kantaoui offered more extreme conditions: Hannibal beach is an artificial pocket beach, while Chat Mariem is an extended beach backed by natural dunes. On the former beach the talitrids were well oriented seawards, whereas on the latter they were scattered, likely as a consequence of sand movements, both natural (due to winds and currents) and induced by works occurring on that beach (ME, personal observations).

4.3. Talitrid adaptation and local ecological stability

Regarding the local ecological stability maintained by dunes and vegetation (Nordstrom, 2000), and *Posidonia* banquette (hypothesis 4, see Introduction), dunes and banquette appeared not to have the same ecological effect on talitrid adaptation. In this study the presence of dunes was not relevant for orientation, while the banquette had a positive impact on the orientation of talitrid populations both at Calamosca and Hannibal beaches. At Calamosca, the cleaning of this natural beach was regulated so that the *Posidonia* banquette would be kept on place to prevent sand erosion by the sea (FS and CR, personal communication by the bar-keeper on the beach). The Hannibal beach was periodically cleaned from wrack, however for a short season (ME, personal observation), but this action apparently had no negative impact on talitrid orientation. On the contrary, dunes were present in the more extended beaches (Chat Mariem, Arina and Tombrouk), favouring the presence of talitrid populations, but not a consistent behavioural adaptation.

Additional information may be found in the sample composition: the fitness of the talitrid populations may be inferred by the population structure and possibly by a balanced/unbalanced sex-ratio. In a population dynamics study carried out throughout the year on *T. saltator* from Mediterranean (Italy and Tunisia) and Atlantic (Portugal) coasts a varying sex-ratio was observed, with prevalence of males prior or during the recruitment and female-biased under stressful conditions in the warmest and coldest months (Marques et al., 2003). In the samples of the present study, the sex-ratio was strongly female-biased at Chat Mariem, where also the worst orientation was observed (Table 3). On the other hand, at Arina the largest number of juveniles was found, showing a high recruitment rate in this population, thus a fitness of the population in line with the results of the etho-assays (Table 3).

4.4. Behavioural adaptation as a bioindicator of shoreline stability

To sum up, this study showed the link of the behavioural adaptation of talitrids with beach geomorphology and sedimentology, through etho-assays. The results appear consistent with long term stability of shoreline in naturally and artificially protected headland-bay beaches, as from modelling of landforms over both Oceanic (Thomas et al., 2010; Hsu et al., 2010) and Mediterranean (Barsanti et al., 2011) coasts. The link between the behavioural adaptation of local populations strictly inhabiting sandy beaches, such as talitrids, and shoreline stability provided by natural and/or artificial headlands represent useful information for integrate (biotic and sedimentary) monitoring of coastal processes, and for the interpretation of species adaptation to changing environments. Other studies have proposed etho-assays (orientation tests) as indicators of environmental impacts, to monitor artificial coastline stabilisation both in the short- and medium-term (Fanini et al., 2007; Bessa et al., 2013; Nourisson et al., 2014) or as biomarker of metal pollution (Ungherese and Ugolini, 2009). The interest in using animal behaviour as ecological adaptation lies in the fact that behaviour integrates several driving forces at the level of individuals (that express the behaviour) and populations. This is shown by the results of the multiple regression analysis: the number of parameters in the models is least in those populations that are well adapted to the shoreline, reflecting the consistency of the behaviour throughout the day, seasons and with varying meteorological conditions, as well as among individuals of different sex and age. Also the statistics of angular distributions offer valid indices that may be proposed as bioindicators of change: the precision of the seaward orientation (expressed by the deviation from the seaward direction) and consistency of behaviour among individuals (expressed by the length r of the mean vector that varies from 0 – no orientation – to 1 – perfect orientation of the sample). In this study beaches across the Mediterranean were compared, subject to similar impacts, heavy tourism pressure and the vicinity of port structures. Despite the geographic distance and geomorphologic differences of the compared beaches, the sedimentary dynamics resulted to be the main factor of disturbance for talitrid orientation. Conversely, talitrid orientation may be proposed as bioindicator or etho-assay for the impact of sedimentary changing dynamics on the sandy beach natural ecosystem.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.01.012.

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