

Visual ecology of talitrid amphipods from Mediterranean and Atlantic coasts

Ecología visual de anfípodos talítridos de las costas Mediterráneas y Atlánticas

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Palabras clave: Crustacea, Amphipoda, talítridos, orientación, ecología visual, estructura del ojo.

ABSTRACT

Eye morphology and responses to various visual stimuli were comparatively investigated in several populations of three species of talitrid amphipods: *Talitrus saltator*, *Orchestia gammarellus* and *Talorchestia spinifera* from Mediterranean and Atlantic coasts. The responses to a directional artificial light (phototaxis) and to a black boundary (scototaxis) appeared tuned to orient talitrids downshore or, alternatively, to shelters according to their activity phase. In addition, Mediterranean *T. saltator* showed a peak of spectral sensitivity to blue light, the most abundant wavelength in the sky over the sea (450 nm), and this appears to be an effective means to orient seaward. In *T. spinifera* the arrangement of a particular vesicular structure in the lenses of the ommatidia appears suited to amplify the perception of horizontal light reflection on the sea surface, thus achieving a similar orienting device on an anatomical rather than physiological basis as exhibited by *T. saltator*. In summary, the compound eyes of talitrid amphipods have a common basic structure, but show a variety of morphological and/or physiological features, each suited to optimize vision under different optical conditions and to adapt the animals to the environments they inhabit and behaviours they express.

RESUMEN

Se comparó la morfología del ojo y las respuestas a varios estímulos visuales en varias poblaciones de tres especies de anfípodos talitridos: *Talitrus saltator*, *Orchestia gammarellus* y *Talorchestia spinifera* procedentes de las costas Mediterráneas y Atlánticas. Las respuestas a luz dirigida artificial (fototaxis) y a oscuridad (escototaxis) parecen relacionarse con la orientación de los talitridos hacia la costa o, alternativamente, hacia zonas protegidas, según su fase de actividad. Además, *T. saltator* del Mediterráneo mostró un pico de sensibilidad espectral a la luz azul, la longitud de onda más abundante en el cielo sobre el mar (450 nm) y parece ser un medio efectivo de orientación. En *T. spinifera*, la disposición de una estructura vesicular en la estructura de las lentes de los ommatidia, parece adecuada para amplificar la percepción de la reflexión horizontal de la luz en la superficie del agua, reflejando una orientación de base más anatómica que fisiológica, como la que presenta *T. saltator*. En resumen, los ojos compuestos de anfípodos talitridos tienen una estructura básica común, pero muestran una variedad de rasgos morfológicos y fisiológicos, que optimizan la visión en diferentes condiciones ópticas para adaptar los animales a los ambientes donde viven y a los comportamientos que expresan.

INTRODUCTION

Talitrid amphipods represent a case study for zonal recovery behaviour. Several surveys show that they use many different cues to orient themselves on the beach. These cues include the sun, moon, local optic factors, magnetic field, shore slope and wind. Among all, visual cues play a hierarchically preeminent role (reviews in Pardi & Ercolini, 1986; Scapini & Mezzetti, 1993; Scapini, 2006).

We can easily observe that the environment inhabited by talitrid amphipods is optically inhomogeneous, showing a dichotomous difference between seaward and landward views. Seaward landscape is much brighter and richer in shorter wavelengths in the blue spectrum of light because of the reflecting surface of the open sea and the scattering of light by humidity in the air, while landward view is darker and richer in longer wavelengths because of light absorption by soil and vegetation (Fiocco *et al.*, 1984). As a consequence, it is reasonable to hypothesize, in agreement with Edwards & Naylor (1987), that responses to simple optic stimuli such as phototaxis, scototaxis and colour-specific responses may help the animals to orient landward or seaward during their diel foraging migrations on the beach. In this respect, different species of talitrid amphipods from Mediterranean and Atlantic coasts were studied.

The species involved in this survey are *Talitrus saltator* (Montagu, 1808) and *Orchestia gammarellus* (Pallas, 1766), both of which are common on Mediterranean and Atlantic coasts of Europe. In the morphological investigation, a third species, *Talorchestia spinifera* (Mateus, 1962), which inhabits Atlantic coasts from France to Morocco (Mateus, 1962; Marfin, 1983) was examined for comparative purposes.

The ecology of Atlantic and Mediterranean coasts is very different. Atlantic shores are characterized by wide tidal excursions, thus littoral amphipods dig their shelters in the upper shore to avoid submersion; they stay in their burrows during the day, and migrate seaward to forage on the shore at night. By contrast, Mediterranean shores are characterized by narrow tidal excursions and relatively high temperatures also during the night from late spring to the beginning of autumn. As a consequence, for Mediterranean talitrids dehydration is the main risk.

The Mediterranean *T. saltator* dig shelters in the moist sand near the sea and migrate landward to forage on the dune at night, showing the reversed behaviour with respect to Atlantic populations (Scapini *et al.*, 1992, 1997).

On Mediterranean shores, *O. gammarellus* take shelter at the basis of *Juncus acutus* bushes in the dune slack during the day to avoid dehydration, and forage on decaying leaves and roots. During the night they spread around to other bushes (Gagnarli, 2009).

MATERIAL AND METHODS

Orientation tests were carried out using an arena device as described by Scapini & Pardi (1979), consisting of a circular Plexiglas arena of 40 cm diameter, with 72 pitfall traps each covering a 5° arc at its rim. For scototaxis tests, a black boundary was provided by a vertical black cardboard, which extended over an arc of 60° under a homogeneous illumination, while for phototaxis tests the light stimulus was provided by a slide projector, equipped with coloured filters and/or neutral filters to control quality and intensity of light. Statistical analysis of the circular distributions of orientation angles was performed according to Batschelet (1981). The mean vectors were calculated and the significance of orientation was estimated by the Rayleigh's test.

Specimens of *T. saltator* were collected on the Atlantic shore at Grand Crohot, Bordeaux, France, and on the Tyrrhenian beach at Burano, Grosseto, Italy, and specimens of *O. gammarellus* were collected on a tidal beach near Menai Bridge, North Wales, U.K. (Mezzetti *et al.*, 1994), and on the Tyrrhenian shore in the Maremma Regional Park, Grosseto, Italy.

For the electroretinographic experiments, specimens from the Tyrrhenian population of San Rossore, Pisa, Italy, were used (Mezzetti & Scapini, 1995).

For the morphological investigation, specimens of *T. spinifera* from Asilah, Morocco, Atlantic coast; *T. saltator* from Oued Laou, Morocco, Mediterranean coast; Maremma Regional Park, Grosseto, Italy, Tyrrhenian coast, and Palizzi Marina, Italy, Ionic coast, and *O. gammarellus* from Maremma Regional Park were compared. Observations were performed utilizing a SEM Philips 515 or Zeiss EVO MA 15 implemented by an image digitization device in the MEMA laboratory (Centro Interdipartimentale di Microscopia Elettronica e Microanalisi), University of Florence (Mezzetti *et al.*, 2010).

RESULTS

Edwards & Naylor (1987) demonstrated that Atlantic *Talitrus saltator* show positive scototaxis during the day while they are indifferent to a black boundary during the night. In addition, Mezzetti *et al.* (1994) demonstrated that these amphipods are indifferent to a light stimulus during the day, while they show positive phototaxis during the night (Fig. 1A, left).

By contrast, Mediterranean *T. saltator* always show positive phototaxis, while they are indifferent to a black boundary during the day and show negative scototaxis at night (Fig. 1A, right).

Similar differences were highlighted for *Orchestia gammarellus* from Atlantic and Mediterranean coasts. Atlantic specimens show a reversal of their phototactic response from negative during the day to positive during the night; we have no data yet for scototaxis. Mediterranean specimens always show a positive scototaxis, while they respond to light only at night with a positive phototaxis (Fig. 1B).

As far as colour sensitivity is concerned, Mediterranean *T. saltator* show a net peak of sensitivity in the blue light around 450 nm, corresponding to the “sky colour over the sea” (Mezzetti & Scapini, 1995; Fiocco *et al.*, 1984), but during the night, sensitivity to blue light further increases (Mezzetti *et al.*, 1994). In this amphipod a selective adaptation to a blue background light markedly depresses the electroretinographic response to the shorter wavelengths of the visible spectrum, with only a weak effect on the longer wavelengths (Mezzetti & Scapini, 1995; Ugolini *et al.*, 1996). Just the reverse can be observed with a yellow background light.

We examined the morphology of the eyes of the three species, *Talorchestia spinifera*, *T. saltator* and *O. gammarellus* (Mezzetti *et al.*, 2010). These all have compound eyes, but structurally there appears to be differences (Fig. 2a-c). External SEM micrography reveals that there is no relief on the

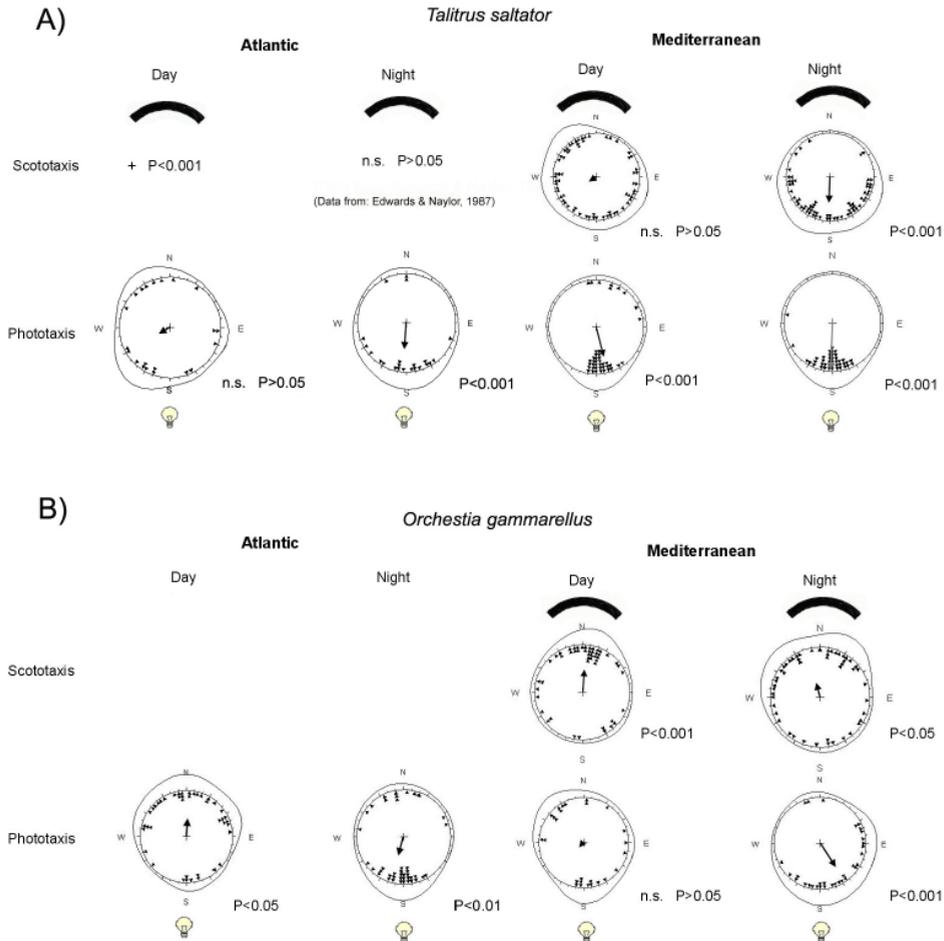


Fig. 1.—Night/day changes in response to a black shape and to light in A) Atlantic and Mediterranean *Talitrus saltator* (Montagu) and in B) Atlantic and Mediterranean *Orchestia gammarellus* (Pallas). Points, orientation angles of individuals; arrows, mean vectors; P, Raileigh's test.

Fig. 1.—Variaciones noche/día en la respuesta a la oscuridad y a la luz, en A) *Talitrus saltator* (Montagu) del Atlántico y del Mediterráneo, y B) *Orchestia gammarellus* del Atlántico y del Mediterráneo. Puntos, ángulos de orientación de los individuos; flechas, vectores principales; P, test de Raileigh.

head in correspondence of the eye cuticle. In internal views, *T. spinifera* shows numerous ommatidia which appear well separated from each other by connective tissue (Fig 2d). *T. saltator* has numerous ommatidia as well, but these are in direct contact with each other (Fig. 2e). By comparison, ommatidia are fewer and grouped together instead of arranged in rows in

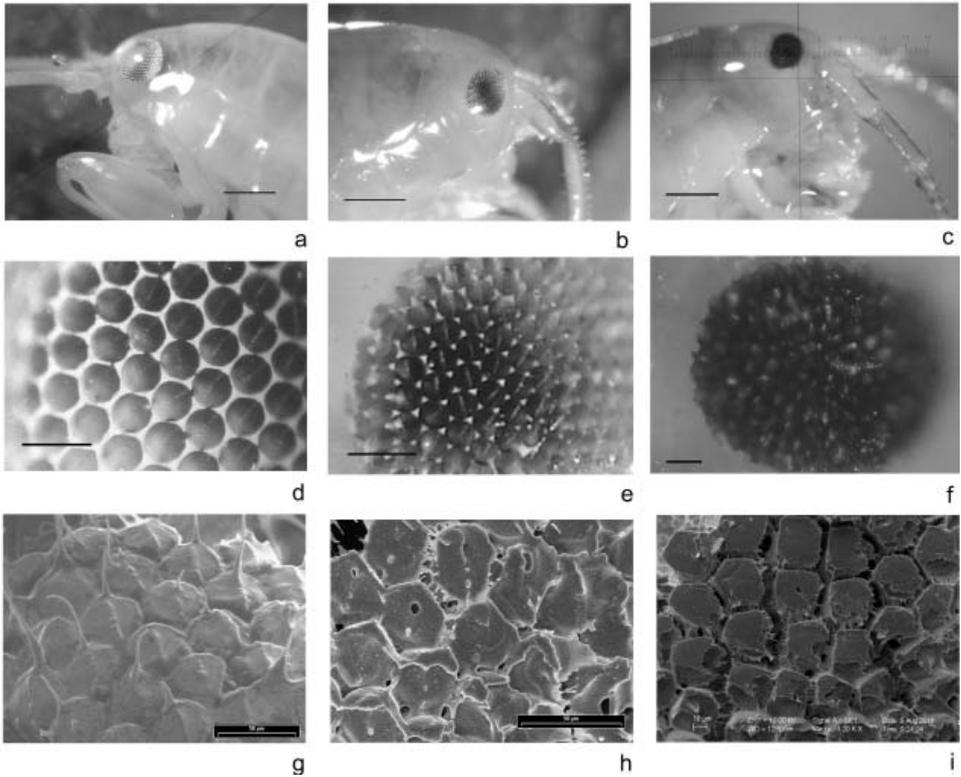


Fig. 2.—Compared eye morphology; in a, d and g *Talorchestia spinifera* (Mateus), in b, e and h *Talitrus saltator* (Montagu) and in c, f and i *Orchestia gammarellus* (Pallas). From a to f: optic micrographies, scale bar: 1mm in a, b and c; 0.1 mm in d, e and f. From g to i: SEM micrographies, scale bar: 50 μ m in g and h; 10 μ m in i.

Fig. 2.—Morfología comparada del ojo; en a, d y g *Talorchestia spinifera* (Mateus), en b, e y h *Talitrus saltator* (Montagu) y en c, f e i *Orchestia gammarellus* (Pallas). De la a hasta la f: microfografías ópticas, escala: 1mm en a, b y c; 0.1 mm en d, e y f. De la g hasta la i: fotografías al SEM, escala: 50 μ m en g y h; 10 μ m en i.

O. gammarellus (Fig. 2f). Furthermore, *T. spinifera* and *T. saltator* have vesicles across the facets of each ommatidium, but in the former species the vesicles are aligned horizontally, while in the latter they are arranged in arches. Instead, *O. gammarellus* has no rows of vesicles (Fig. 2d-i).

DISCUSSION

The differences observed in responsiveness to light and a black boundary among populations of Atlantic and Mediterranean talitrids can be explained

by considering their different ecology. On tidal Atlantic shores talitrids recover shelters over the high tide mark during the day and migrate seaward at night to forage. A positive scototaxis during the day enables Atlantic *T. saltator* to correctly orient toward the dune for shelter recovering at day (Edwards & Naylor, 1987), while a positive phototaxis during the night guides the animals toward the sea to their foraging areas (Fig. 1A, left). Similarly, Atlantic *O. gammarellus* show a reversal of phototaxis from day to night that helps the animals to correctly orient landward during the day (negative phototaxis) and seaward at night (positive phototaxis, Fig. 1B, left).

By contrast, a positive phototaxis both at night and day enables Mediterranean *T. saltator* to rapidly recover the humid zone near the sea at any time to avoid dehydration, while a negative scototaxis at night brings the animals out of their shelters at the onset of their period of activity (Fig. 1A, Mezzetti *et al.*, 1994).

On Mediterranean shores *O. gammarellus* take shelter at the basis of the bushes in the dune slack during the day and wander about at night (Gagnarli, 2009). A positive scototaxis throughout the 24h enables the animals to recover shelters landward at any time, while the arousal of a positive phototaxis at night signs the beginning of their period of major activity. Thus, Mediterranean *O. gammarellus* show a reversed set of responses with respect to *T. saltator*, which inhabit the same shores, but in a different ecological niche nearer to the sea (Fig. 1B, right).

The fact that Mediterranean *T. saltator* exhibit a high sensitivity to blue light, which increases during the night, means that talitrids see the marine horizon much brighter than the rest of landscape at any other time, thereby improving orientation along a sea-land axis even in dim light. The results of the electroretinographic tests under a coloured background light, reveal the presence of at least two different photoreceptors in the eye of *T. saltator*. Besides the main peak at 450 nm (Mezzetti & Scapini, 1995), Ugolini *et al.* (1996) found a second peak of spectral sensitivity in the yellow light around 525 nm, probably corresponding to a second group of photoreceptors. This is the physiological basis for colour discrimination.

The lack of any relief on the head of the animals corresponding to the eye cuticle is a clear adaptation to burrowing behaviour; a smooth surface offers less friction against sand when the amphipod is burrowing.

We suggest that the vesicles observed in the eyes of *T. spinifera* and *T. saltator* (Mezzetti *et al.*, 2010) may work as POL-breakers, i.e. disruptors of light polarization. This device turns polarized light into non-polarized light. The latter is more effective to stimulate the whole retinular receptors that, for their intrinsic structure, are sensitive to light polarization. In this respect, the horizontal alignment of the vesicles observed in the eyes of *T.*

spinifera may enable these amphipods to fully perceive the brightness of sea reflection, which is horizontally polarized. This may be a cue for seaward orientation. By comparison, the arched arrangement of similar vesicles in the eyes of *T. saltator* may disrupt the sky-light polarization, enabling the amphipod to better evaluate the brightness of the sky light in all directions. This may help talitrids to detect the position of the sun in the sky, when they orient by sun compass, or the major quantity of blue radiation in the sky over the sea. In both species, the information about the absolute intensity of light is probably integrated by e-vector perception.

Mediterranean *O. gammarellus* lives on the upper shore, as compared to the other two species and shows a lower phototaxis, always orienting toward a black boundary or the darker part of the horizon, and this could explain the simpler structure of its eye. In fact, in this amphipod, the eye seems to have the only task to detect the direction of provenience of the light, to drive a simple response toward/away from the light source.

CONCLUSION

We can infer that talitrid amphipods actually use basic responses (phototaxis and/or scototaxis) to visual stimuli to improve their orientation on the beach in relation to their ecology and rhythmicity.

In particular, for Mediterranean *T. saltator* we can suggest that a high sensitivity for blue light and colour discrimination capability may help the animals to correctly orient seaward at any time of the diel cycle.

In summary we can assess that responsiveness to visual stimuli and eye morphology are both inter- and intra-specifically adapted to the ecology of talitrids.

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