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Eclipse effects on field crops and marine zooplankton: the 29 March 2006 total solar eclipse

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Abstract. Some effects in the biosphere from the Total Solar Eclipse of 29 March 2006 were investigated in field crops and marine zooplankton. Taking into account the decisive role of light on plant life and productivity, measurements of photosynthesis and stomatal behaviour were conducted on seven important field-grown cereal and leguminous crops. A drop in photosynthetic rates, by more than a factor of 5 in some cases, was observed, and the minimum values of photosynthetic rates ranged between 3.13 and 10.13 μmol CO_2 m^{-2} s^{-1}. The drop in solar irradiance and the increase in mesophyll CO_2-concentration during the eclipse did not induce stomatal closure thus not blocking CO_2 uptake by plants. Light effects on the photochemical phase of photosynthesis may be responsible for the observed depression in photosynthetic rates. Field studies addressing the migratory responses of marine zooplankton (micro-zooplankton (ciliates), and meso-zooplankton) due to the rapid changes in underwater light intensity were also performed. The light intensity attenuation was simulated with the use of accurate underwater radiative transfer modeling techniques. Ciliates, responded to the rapid decrease in light intensity during the eclipse adopting night-time behaviour. From the meso-zooplankton assemblage, various vertical migratory behaviours were adopted by different species.

1 Introduction

On 29 March 2006, millions of people in the Northern Hemisphere had the opportunity to observe a total solar eclipse. In the Greek territory, the phenomenon had a maximum duration of 2 minutes and 58 s, at the small island of Kastelorizo, in the east-southern part of the country. The eclipse effects on the biosphere and on various atmospheric layers have been investigated during a combined field experiment over Greece. Information about the experimental campaigns, the measurement sites, eclipse path maps and eclipse local circumstances at each location, can be found in the overview paper by Gerasopoulos et al. (2007).

The effects of solar eclipses on the behaviour of living organisms have been the subject of many observations in the past. Plant behaviour was first studied by Deen and Bruner (1933), by following stomatal movements of the gray birch during the sun eclipse of 1932. Two Polish zoologists were the first to observe the behaviour of mammals, birds, and insects during seven eclipses between 1954 and 1975 (Zirker, 1995). More recent data have shown that birds behave as they normally do at sunset (Tramer, 2000), animals alter their behaviour (Jennings et al., 1998) and some planktonic crustacea are vertically redistributed (Vecchione et al., 1987; Giroud and Balvay, 1999).

In general, eclipse effects on plants are expected to be related to the light limitation experienced during the phenomenon. Although fluctuating light conditions are a common feature for natural habitats (e.g. through transitional light flecks in canopies, changing cloudiness, diurnal periods of light and dusk) (Schulze and Hall, 1982; Küppers et al., 1997); the sudden drop in solar irradiance during a solar

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eclipse provides a challenge for investigating its related impacts on plant behaviour. Observations have shown that a drop of sap flow velocity in a number of plants was related to solar eclipses (Ladefoged, 1963; Fernandez et al., 1996; Morecroft et al., 2000; Häberle et al., 2001). Developmental processes, such as transient aberrations in the chromosomal structure of root meristems and delayed seed germination, have been also ascribed to the impact of an eclipse (Sathaiah et al., 1984; Kumar et al., 1984). In addition, limited short-term effects on photosynthesis and evapotranspiration of crop plants, such as pigeon pea and bread wheat, were reported by Singh et al. (1992). In mature forest trees of *Picea abies*, *Fagus sylvatica* and *Quercus robur* photosynthesis was reduced to an extent that allowed net CO_2 evolution from leaves during an eclipse (Häberle et al., 2001).

Moreover, it is very interesting that this natural experiment takes place under particularly degraded conditions by means of air quality, which pose additional impact on plants. For instance, eastern Mediterranean experiences ozone levels that are year round above the EU phytotoxicity limit of 32 ppb/24 h (Kourtidis et al., 2002; Kouvarakis et al., 2002; Kondratyev and Varotsos, 2002; Gerasopoulos et al., 2005, 2006a), while enhanced particulate matter levels (Gerasopoulos et al., 2003, 2006b) do also influence the fraction of solar irradiance reaching the surface (Zerefos et al., 1998; Papayannis et al., 1998; Varotsos et al., 2001).

The effects of solar eclipses on marine ecosystems have been partially studied. Pepita (1955) reported an upward migration of free-swimming larvae of shrimps, clams, snails and barnacles, as well as of adult copepods during the period of maximum totality, in Sebastopol Bay. Skud (1967) observed a decrease in zooplankton volumes at surface waters in Maine, although he reported an upward migration of two copepod species (*Pseudocalanus minutus* and *Acartia longiremis*), during the time of darkness. Adult copepods moved upwards in the water column during an eclipse event observed in the region of Boothbay harbor, Maine, in March 1970 (Sherman and Honey, 1970). Similarly, Bright et al. (1972) found that certain species of copepods and euphausiaceans (e.g. *Nannocalanus minor, Scolecithrix danae* and *Undinula vulgaris*) in the Gulf of Mexico, responded to the noontime solar eclipse of March 1970 by migrating to the surface. Moreover, according to Bright et al. (1972), the response as reflected in the number of organisms captured at the surface, was larger than the respective response to a decrease in light intensity at night. Some studies of the movements of scattering layers during solar eclipses showed that layers started ascending at the beginning of the eclipse (Backus et al., 1965; Tont and Wick, 1973; Kampa, 1975), while in other cases the scattering layers did not respond at all (Franceschini et al., 1970).

The diurnal vertical migration of many zooplankters is a well known behavior, with some of the organisms migrating several hundred meters in the water column (Marshall and Orr, 1955; Longhurst, 1976). The factors controlling vertical migration in mesopelagic species, however, have not been intensively studied. It is generally accepted that down-welling irradiance plays an important role (Banse, 1964; Ringelberg, 1995), since most vertical migrations of plancton occur at sunrise and sunset. Although, most of the above studies concern mesozooplankton there is lack of information concerning other zooplankton organisms.

The scope of this study is to investigate some of the effects of the 29 March 2006 total solar eclipse on living organisms of two diverse ecosystems, terrestrial and marine. In the former case, the effects of eclipse on the carbon assimilation of field crops, whereas in the latter the migratory responses of marine zooplankton, will be examined. Evidently, the reaction of the organisms to the unexpected dark spell is expected to vary substantially between the two ecosystems, and there is great difficulty to associate them. Instead, more information concerning the mechanisms involved in the reaction of the organisms within each ecosystem will be extracted. In field crops, the effects of the reduced photon flux density on CO_2-uptake will be interpreted through simultaneous observations on stomatal behaviour and other parameters of the assimilatory pathways involved. As regards the migratory responses of marine zooplankton, field studies addressing this issue are scarce, primarily because of the difficulties associated with measuring rapid changes in underwater light intensity, simultaneously with changes in animal distributions. In this study, this has been overcome with the use of accurate underwater radiative transfer modeling.

2 Materials and methods

2.1 Photosynthesis and stomatal conductance in field crops

2.1.1 Study site

The study was carried out at the experimental field of the Agricultural University of Athens (37°59′ N, 23°32′ E), at an altitude of 30 m a.s.l. The site was located about 560 km from the central axis of the eclipse totality, with 84% sun obscuration. The crops have been growing in a slightly alkaline (pH 7.24) clay loam soil (35.9% sand, 35.9% silt and 29.8% clay) over an area of 400 m^2.

2.1.2 Plant material

Seven important field-grown cereal and leguminous crops were studied. In particular, the studied crops were: cereals [*Triticum durum* (durum wheat), *Tr. aestivum* (bread wheat), *Hordeum vulgare* (barley), *Avena sativa* (oat)] and legumes [*Lathyrus sativus* (grass pea), *Pisum sativum* (pea) and *Vicia faba* (faba bean)]. On 29 March 2006 all cereals were at the booting stage and the legumes at flower appearance. The measurements were taken on the third leaf from the top for the cereals and on the leaves at the middle of the stem for the legumes.

2.1.3 Measurements of photosynthesis and stomatal conductance

The chlorophyll fluorescence technique was used to measure the photosynthetic activity of leaves. Net photosynthesis (P_n), mesophyll CO_2-concentration (C_i) and stomatal conductance (g_s) were measured in the field, using a closed portable Infra-Red Gas Analysis system (IRGA, LI-COR, LI-6200 model). Each leaf was enclosed in a 4 l chamber connected to the IRGA, and the instrument was moved from crop to crop for consecutive measurements within less than one minute. Air flow rate into the IRGA system was 800 μmole s^{-1}. The Photosynthetically Active Radiation (PAR) measured with a quantum sensor connected to the chamber, was also recorded in parallel to P_n and g_s measurements. P_n and g_s calculation was based on the equations of Leuning and Sands (1989) and are expressed as μmol $CO_2\,m^{-2}\,s^{-1}$ and mole $H_2O\,m^{-2}\,s^{-1}$, respectively. Hourly measurements were carried out from 06:00–17:00 UTC, on 29 March 2006.

Additional meteorological and actinometric data monitored at Thission station (National Observatory of Athens, at a distance of about 2 km eastern of the experimental site) were used in this study. Information about the station characteristics and infrastructure used can be found in Founda et al. (2007).

2.2 Marine zooplankton

2.2.1 Study site and hydrographic measurements

One oceanographic cruise on board the R/V AEGAIO was carried out on 29 March 2006, at a fixed station close to Kastelorizo Island in the Eastern Mediterranean (36°08′ N, 29°34′ E). Downward surface global (200–850 nm) and direct (280–700 nm) irradiance spectra were measured during 09:00–13:00 UTC at a sampling frequency of 20 s and 8 s, respectively, using two diode-array spectrometers (Kazadzis et al., 2007; Blumthaler et al., 2006).

The water column structure was sampled before, during, and after the eclipse, at approximately 1 h intervals, during an 8 h period (Table 1). Vertical profiles of temperature and salinity were measured with a Seabird CTD System (911 plus) assembly. Phytoplankton fluorescence (Chl-*a*) was recorded with a Chelsea in situ fluorometer. Water samples were taken in the euphotic 0–100 m layer, using Niskin bottles with teflon-coated springs and O-rings. For micro-zooplankton, 7 replicate samples were taken hourly, at steps of 10 m in the water column, whereas for mesozooplankton, 6 replicates of samples were collected hourly at discrete layers (0–10 m, 10–20 m, 20–50 m, 50–100 m, 100–200 m).

2.2.2 Zooplankton measurements

Five hundred ml micro-zooplankton samples were preserved with borax-buffered formalin (final concentration 2% formaldehyde) and stored at 4°C in the dark. Before examination, samples were left to settle in their bottles in the dark at 4°C and after 48 h, the top 400 ml of the sample was slowly siphoned off. The bottom 100 ml of the sample was transferred into sedimentation chambers, was allowed to settle for 24 h (Utermohl, 1958) and was finally examined by means of an inverted microscope OLYMPUS IX 70.

Table 1. Micro-zooplankton and meso-zooplankton samplings before, during and after the total solar eclipse at Kastelorizo marine station (max depth 290 m).

Cast	Time (UTC)	Zooplankton Measurements Micro-	 Meso-
K1	7:52	+	+
K2	9:00		+
K3	9:40	+	+
K4	10:20	+	+
K5	11:20	+	+
K6	12:50	+	+
K7	14:15	+	

Meso-zooplankton was sampled by vertical hauls of a WP-2 net (200 μm mesh size). Samples were fixed immediately after collection and preserved in a 4% borax buffered-formaldehyde seawater solution. In the laboratory the samples were split using a folsom splitter. The first half was used to get information on the taxonomic level of order or species and counted under an OLYMPUS stereoscope.

2.2.3 Underwater radiative transfer modeling

Measured changes in above water light intensity and underwater composition during the solar eclipse, were used as input to the extensively validated Hydrolight Radiative Transfer Program (Mobley, 1988), to estimate changes in underwater radiation fields. In the absence of in situ underwater radiometric measurements, the model calculations allowed us to estimate the changes in light levels (e.g. PAR) at specific depths in the water column, where changes in micro- and meso-zooplankton concentrations were observed during the solar eclipse event. Mobley (1994) has given a detailed description of the physical assumptions and mathematical calculations in the Hydrolight Model. Tzortziou et al. (2006) recently reported very good agreement (differences less than 10%) between in situ measurements of water leaving radiance and Hydrolight results, over a wide range of conditions in the bio-optically complex estuarine waters of the Chesapeake Bay, and demonstrated very good optical closure between independently measured quantities.

Measurements of downward surface irradiance spectra, $E_s(\lambda)$, and chl-*a* vertical profiles were used as inputs to perform the model calculations. The water was modeled by three components: pure water, pigmented particles and covarying colored dissolved organic matter (CDOM). We

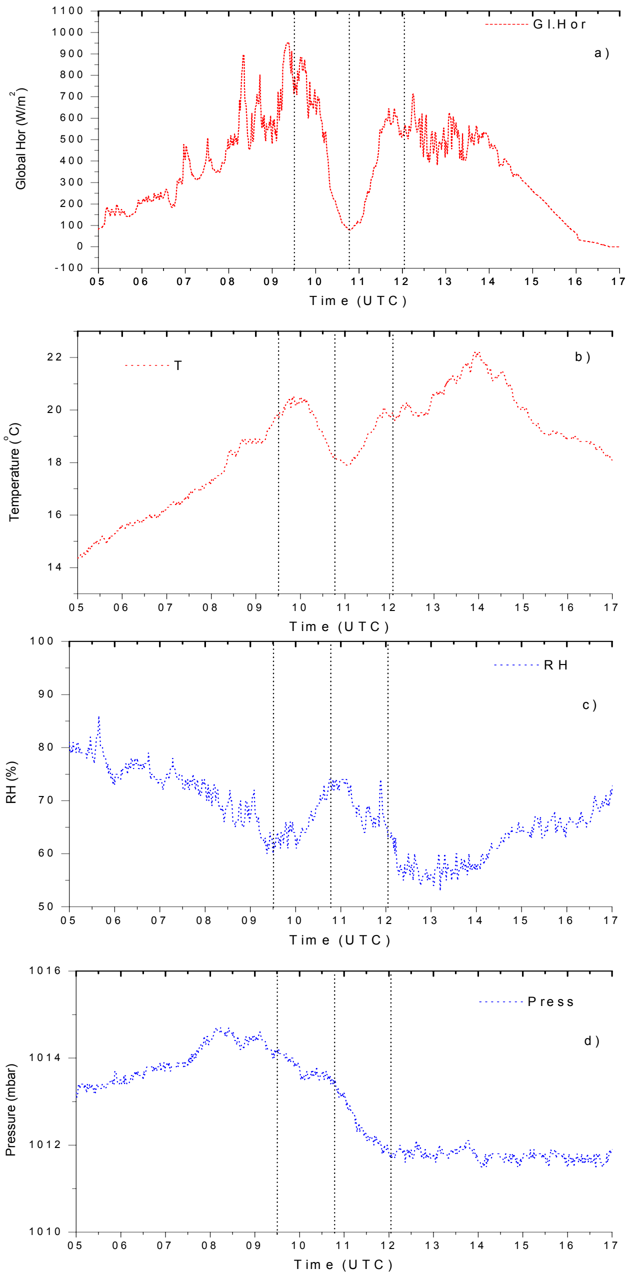

Fig. 1. The diurnal course of meteorological parameters **(a)** Global Horizontal Irradiance, **(b)** Temperature, **(c)** Relative Humidity and **(d)** Pressure, during 29 March 2006, at Thission station, Athens (National Observatory of Athens).

assumed that mineral concentrations were negligible in the very clear, oligotrophic waters at the Kastelorizo site.

The Pope and Fry (1997) absorption values for pure water and the seawater scattering coefficients of Morel (1974) as retabulated by Smith and Baker (1981), were used in our model simulations. Particle absorption at depth z and wavelength λ, $a_p(z,\lambda)$, was estimated using the Morel (1991) model and the chlorophyll-specific absorption coefficients given in Prieur and Sathyendranath (1981). Absorption by CDOM, $a_{\mathrm{CDOM}}(z,\lambda)$, was assumed to covary with particle absorption according to $a_{\mathrm{CDOM}}(z,\lambda)=0.2\cdot a_p(z,440)\cdot \exp[-0.014\cdot(\lambda-440)]$ (Mobley and Sundman, 2000). Particulate scattering was estimated using the Gordon and Morel (1983) model, while CDOM was assumed to be non-scattering. Since measurements of particulate backscattering were not available, a backscattering fraction of 0.044 was used in our calculations based on previous studies for clear waters (e.g. Mobley, 1994; Stramski et al., 2004). Raman scattering and CDOM and chlorophyll-a fluorescence were included in all model runs using the Hydrolight default assumptions for fluorescence efficiency and wavelength redistribution functions for fluorescence by chlorophyll (Mobley, 1994) and CDOM (Hawes, 1992).

Water surface roughness was estimated assuming that the slope probability distribution of the capillary waves follows the Cox and Munk (1954) wind-direction independent distribution. A wind speed of 5 m s^{-1} was used in the simulations based on local meteorological observations. The water column was assumed to be infinitely deep below the greatest depth of interest (ca. 250 m). Model results included underwater vertical profiles of photosynthetically active radiation, PAR (in μmol phot m^{-2} s^{-1}), estimated according to Mobley (1994) from underwater scalar irradiance, $E_o(z,\lambda)$, and integrated over the spectral region 400–700 nm.

3 Results and discussion

3.1 The effect of the solar eclipse on photosynthesis and stomatal conductance

The diurnal course of meteorological parameters during 29 March 2006 is shown in Fig. 1. Solar global irradiance (Fig. 1a) displayed a sharp decline of 796 W m^{-2} during the eclipse, in comparison with the pre-eclipse maximum. A decline was also exhibited in air temperature (2.2°C, Fig. 1b) and atmospheric pressure (0.7 hPa, Fig. 1d). On the other hand, relative humidity increased by about 10% (Fig. 1c). More details on the meteorological response of the atmosphere during the March 2006 eclipse is given by Founda et al. (2007). The combination of light "switch off" and increased humidity, together with the decreased temperature during eclipses has been previously shown to have an impact on forest trees (e.g. Steppe et al., 2002). The rate of solar irradiance change during the eclipse has been calculated and compared to the corresponding rates during other frequent illumination changes such as dusk, dawn and clouds. This way eclipse conditions are put into context with more familiar illumination changes. During the eclipse, and excluding periods around first and last contact and near totality, the rate of irradiance change varies between 10–15 Watt m^{-2} min^{-1},

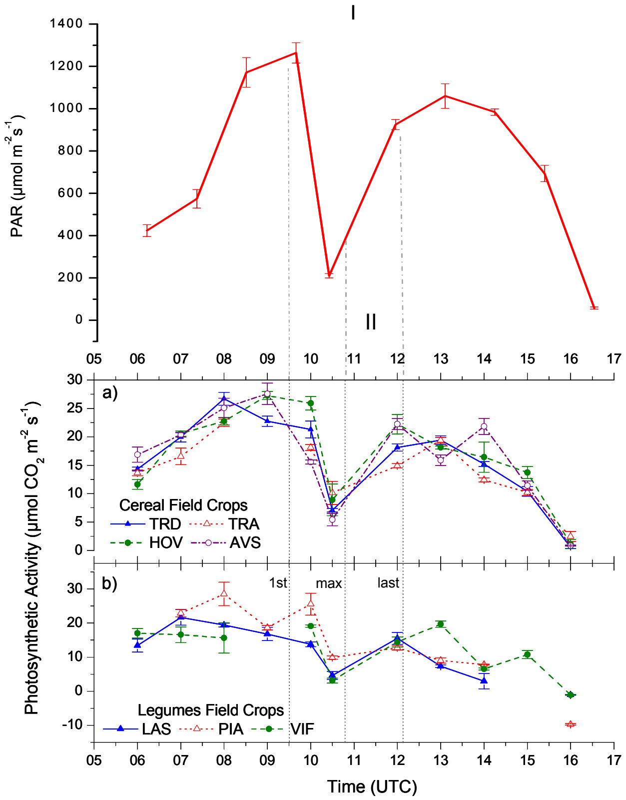

Fig. 2. (I) The course of PAR during the observations at the experimental site. (II) Diurnal changes in CO_2 assimilation rate (μmol CO_2 m^{-2} s^{-1}), of four cereals and three leguminous species during 29 March 2006 eclipse, at AUA experimental field (TRD – *Tr. durum*, TRA – *Tr. aestivum*, HOV – *H. vulgare*, AVS – *A. sativa*, LAS – *Lathurus* sativus, PIA – *P. arvense*, VIF – *V. faba*). The bars indicate the standard errors of the means.

within a period of about 2.5 h. The corresponding rates during dusk and dawn were calculated to be in the range 1–3 Watt m^{-2} min^{-1}. The situation is more complex for clouds depending on their type and thickness. Calculations on clouds appearing at the site the day after the eclipse, have shown rates of irradiance change varying between 5–30 Watt m^{-2} min^{-1} with a median of 15 Watt m^{-2} min^{-1}, but these changes are much quicker. Thus, during the eclipse the irradiance change rate appears to be much faster than during dusk and dawn, whereas clouds even though can disturb incoming light at similar rates, is not expected to be as sufficient due to shorter duration and the parallel effect of light scattering by atmospheric particles.

Table 2. Maximum photosynthetic rates observed before the beginning of the eclipse and minimum photosynthetic rates near totality, for the examined species. The minimum/maximum ratios are also shown.

Species	Photosynthetic rates μmol CO_2 m^{-2} s^{-1}		
	Max. before	Min. at totality	Min./Max.
Triticum durum	26.70	7.08	0.2651
Triticum aestivum	22.47	10.13	0.4508
Avena sativa	27.59	5.41	0.1961
Hordeum vulgare	27.26	8.89	0.3261
Lathyrus sativus	21.66	4.61	0.2128
Pisum sativum	28.52	9.87	0.3461
Vicia faba	19.12	3.13	0.1637

Figure 2I illustrates the course of PAR during the observations at the experimental site. A sharp decline from 1265 at 10:00 UTC to a minimum of 210 μmol photons m^{-2} $s^{-1}$was recorded during the eclipse. High values between 930 and 1060 μmol photons m^{-2} s^{-1}were recorded shortly after the termination of the phenomenon. Figure 2II shows the diurnal course of photosynthetic rate for the cereals (Fig. 2IIa) and legumes examined (Fig. 2IIb). A drop in photosynthetic rates, by more than a factor of 5 in some cases, was observed as a response to the variation in PAR during the eclipse. The minimum values of observed photosynthetic rates ranged between 3.13 (faba beans) and 10.13 μmol CO_2 m^{-2} s^{-1} (bread wheat). The relative reduction of photosynthesis during the eclipse varied among the different species (Table 2, Fig. 2II). Faba beans, oats and grass pea exhibited the more drastic reduction in photosynthesis. On the other end, bread wheat was the least affected species. In general, cereals were less influenced than legumes with average min/max ratios 0.31 and 0.24, respectively.

One-way ANOVA was applied, on three replicates for each species, in order to test the statistical significance of the diurnal fluctuations in stomatal conductance (g_s). Table 3 shows the values of g_s for the examined species. In all species except pea, g_s showed a decline at 10:00 UTC and at earlier eclipse stages, occasionally significant (e.g., in bread wheat, oats, and faba beans) in comparison with the preceding values. At 10:30 UTC, however, a time near the totality, g_s returned to values before the beginning of the eclipse, which were maintained throughout the rest of the day. Thus, the drop in g_s at 10:00 UTC is probably not eclipse-induced.

The results of Table 3 imply that the diurnal course of g_s in all species followed the typical pattern expected for mesophytes: higher values early in the day (06:00–07:00 UTC), steadily declining within the next two-three hours and remaining stable thereafter. It is also known that morning values of g_s are higher than those observed in the afternoon for similar values of PAR (Rochette et al., 1991). A midday temporary decrease in g_s is also a common phenomenon in dry environments, like the one of southern Greece. Accordingly, the drop in g_s observed at 10:00 UTC may simply reflect normal, "midday stomatal closure" (Miller, 1938; Meidner and Mansfield, 1968).

Stomatal movements are decisively influenced by environmental factors (Meidner and Mansfield, 1968). Light is considered amongst the most important factors determining

Table 3. Diurnal changes in stomatal conductance as least means (mmol g H_2O m^{-2} s^{-1}), of four cereals and three leguminous species during the 29 March 2006 eclipse, at AUA experimental field. Values followed by the same letter are not statistically significant at the 95% significance level.

	Crop species						
Time (UTC)	Bread wheat	Durum wheat	Oats	Barley	Grass pea	Pea	Faba beans
06:00	1.87 *a*	1.14 *a*	0.94 *a*	0.47 *ab*	2.10 *a*	1.58 *a*	0.90 *a*
07:00	0.80 *bc*	0.66 *b*	0.49 *c*	0.51 *a*	1.09 *b*	1.41 *a*	0.46 *b*
08:00	0.40 *d*	0.50 *c*	0.64 *b*	0.50 *ab*	0.52 *cd*	0.71 *b*	0.35 *cd*
09:00	1.08 *b*	0.31 *de*	0.35 *d*	0.33 *c*	0.42 *cd*	0.22 *c*	0.30 *de*
10:00	0.35 *d*	0.29 *e*	0.17 *g*	0.28 *cd*	0.27 *d*	0.41 *bc*	0.16 *f*
10:30	0.55 *cd*	0.38 *de*	0.25 *efg*	0.33 *c*	0.36 *cd*	0.38 *c*	0.34 *cd*
12:00	0.41 *d*	0.42 *cd*	0.29 *def*	0.43 *b*	0.62 *c*	0.30 *c*	0.22 *ef*
13:00	0.30 *d*	0.43 *cd*	0.20 *fg*	0.25 *de*	0.32 *cd*	0.20 *c*	0.35 *cd*
14:00	0.24 *d*	0.33 *de*	0.33 *de*	0.34 *c*	0.31 *cd*	0.25 *c*	0.24 *ef*
15:00	0.22 *d*	0.30 *e*	0.36 *d*	0.49 *ab*	–	–	0.40 *bc*
16:00	0.34 *d*	0.11 *f*	0.16 *g*	0.18 *e*	0.19 *d*	0.42 *bc*	0.21 *ef*

Table 4. Diurnal changes in the average intercellular CO_2-concentration (ppm) of the crop species examined during the 29 March 2006 eclipse. Values within a species followed by the same letter are not statistically significant at the 95% significance level.

	Crop species						
Time (UTC)	Bread wheat	Durum wheat	Oats	Barley	Pea	Grass pea	Faba beans
07:00	350.57 *a*	357.50 *a*	341.50 *a*	322.33 *c*	351.87 *c*	344.73 *b*	333.67 *b*
08:00	324.80 *b*	298.30 *b*	301.03 *b*	300.46 *c*	359.60 *c*	317.90 *c*	296.03 *b*
09:00	242.80 *d*	247.30 *c*	271.80 *c*	263.60 *cd*	298.70 *d*	282.40 *d*	271.53 *b*
10:00	254.96 *d*	215.06 *d*	207.46 *e*	212.63 *e*	208.,33 *e*	267.20 *e*	300.60 *b*
10:40	325.36 *b*	341,00 *a*	327,33 *a*	482,50 *a*	557,56 *a*	337,23 *b*	368,76 *a*
12:00	278.06 *c*	276.40 *c*	210.96 *e*	270.10 *c*	273.73 *d*	284.53 *d*	231.43 *c*
13:00	226.46 *d*	254.23 *c*	209.00 *e*	208.50 *e*	288.26 *d*	295.73 *d*	230.10 *c*
14:00	264.23 *c*	270.,93 *c*	235.86 *d*	276.40 *c*	300.53 *d*	339.93 *b*	320.03 *b*
15:00	232.76 *d*	296.23 *b*	296.06 *b*	300.63 *c*			305.30 *b*
16:00	361.90 *a*	372.66 *a*	353.80 *a*	358.86 *b*	454.63 *b*	380.70 *a*	376.26 *a*

the course of stomatal behaviour, although many interactions with other environmental (e.g. CO_2-concentration, vapour pressure deficit, temperature, etc.) and plant factors (plant water status, endogenous rhythms) exist to a considerable extent. Accordingly, the lack of a response of g_s to the dramatic fall in solar irradiance during the eclipse is surprising and could be attributed to an endogenous buffering reaction against the rapidly falling rate in the incoming radiant energy (0.177 W m^{-2} s^{-1}). The "normal" diurnal falling rate observed between 14:00 and 16:00 UTC on the same day, which was also associated with a fall in g_s for most of the examined species (Table 3), was much smaller (0.065 W m^{-2} s^{-1}). Judging from the course of the environmental variables during the eclipse (Fig. 1), no dramatic changes in plant water status, to an extent affecting stomatal movements, were likely to occur. In contrast to our findings, a moderate decline in g_s was observed in forest trees at total solar eclipse in Central Europe (Häberle et al., 2001).

Mesophyll CO_2-concentration (C_i) was significantly raised at totality for all the examined species (Table 4). The levels of C_i were equivalent (in bread and durum wheat, oats, grass pea, faba beans) or even higher (in barley and pea) than those observed at dawn or dusk. Such an increase in intercellular CO_2-evolution is usually observed after darkening leaves of C_3 plants photosynthesizing in air and can be attributed both to photorespiration and tricarboxylic acid (TCA) respiration ("post-illumination burst"; Lawlor, 2001). Evidently, these raised levels of C_i were not able to induce stomatal closure during the eclipse.

It is clear from the results of g_s that the observed fall in net photosynthesis cannot be attributed to stomatal closure and, hence, to a reduced CO_2-supply. Therefore, one could expect

Table 5. Diurnal changes in the average rate of CO_2–uptake (ppm) per intercepted photon (μmol $m^{-2}s^{-1}$) of the crop species examined during the March 29, 2006 eclipse. Values within a species followed by the same letter are not statistically significant at the 95% significance level.

	Crop species						
Time (UTC)	Bread wheat	Durum wheat	Oats	Barley	Pea	Grass pea	Faba beans
07:00	0.0353 *a*	0.0586 *a*	0.0460 *a*	0.0336 *bc*	–	0.0273 *b*	0.0303 *a*
08:00	0.0286 *a*	0.0273 *c*	0.0503 *a*	0.0656 *a*	0.0256 *b*	0.0566 *a*	0.0230 *ab*
09:00	0.0136 *b*	0.0187 *d*	0.0261 *c*	0.0328 *bc*	0.0153 *c*	0.0146 *bc*	0.0168 *b*
10:00	0.0148 *b*	0.0178 *d*	0.0222 *c*	0.0228 *c*	0.0148 *c*	0.0162 *bc*	0.0121 *b*
10:40	0.0345 *a*	0.0388 *b*	0.0357 *b*	0.0408 *b*	0.0465 *a*	0.0199 *b*	0.0182 *b*
12:00	0.0167 *b*	0.0219 *d*	0.0209 *c*	0.0144 *cd*	0.0131 *c*	0.0200 *b*	0.0146 *b*
13:00	0.0203 *b*	0.0196 *d*	0.0126 *e*	0.0126 *cd*	0.0066 *c*	0.0133 *bc*	0.0153 *b*
14:00	0.0110 *bc*	0.0163 *de*	0.0230 *c*	0.0160 *cd*	0.0080 *c*	0.0030 *c*	0.0046 *c*
15:00	0.0140 *b*	0.0110 *f*	0.0190 *cd*	0.0200 *cd*	–	–	0.0210 *b*
16:00	0.0293 *a*	0.0070 *g*	0.0116 *e*	0.0140 *cd*	−0.2610 *d*	−0.5466 *d*	−0.0303 *d*

that the reduced photon flux density would affect mainly the photochemical pathway. Photosynthesis is inherently dependent on light. The three functions of the light harvesting apparatus (light capturing, energy transfer and electron transfer) are controlled by the physical and chemical characteristics of the plant pigments. Absence of light disrupts electron transport, leading to a decline of photosynthesis (Schreiber et al., 1995). An indirect way of checking this hypothesis is to compare the quantum yields (Φ), i.e. the rate of CO_2-uptake per intercepted photon, diurnally over all the examined species (Table 5). A significant increase in Φ was observed for most species at totality, in comparison to values during the other daylight hours. A marginal, non-significant, increase was exhibited only by faba bean and grass pea. Such an increase in quantum yield observed at totality may imply photoinhibitory effects at bright sunshine for the other crop species (Baker et al., 1994; Ögren, 1994) given that PAR-values at the experimental site were very high already at 09:00 UTC (Fig. 2I).

3.2 The effect of eclipse on marine zooplankton

The solar eclipse induced effects on ecosystems has been additionally investigated in the marine environment. These effects are mainly driven by the change of underwater irradiance that has been simulated via the Hydrolight Radiative Transfer Program for the case of Kastelorizo. Figure 3 shows the change with time in downward irradiance as measured above the water surface, E_s, during the eclipse event. Light intensity dropped dramatically with the onset of the eclipse, with E_s at 550 nm decreasing from ~1.35 W m^{-2} nm^{-1} at 09:35 UTC (1st contact) to below the range of the instrument's sensitivity during totality 10:53 UTC, increasing again to ~1.16 W m^{-2} nm^{-1} at 12:10 UTC (last contact). Model estimated photosynthetically active radiation (PAR) just below the water surface was ~2000 μmol phot m^{-2} s^{-1} just before the 1st contact, while the evolution of PAR at more depths (10 and 30 m) is also shown in Fig. 3.

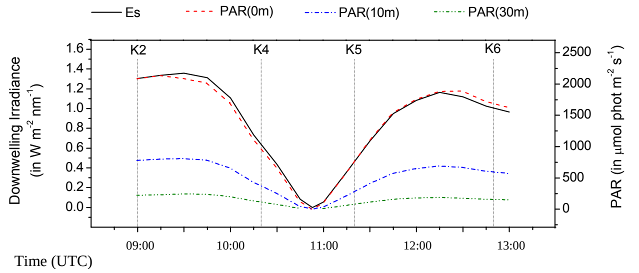

Fig. 3. (Left axis) Change in measured downward surface irradiance (in W m^{-2} nm^{-1}) at 550 nm during the eclipse event (solid line). (Right axis) Change in model estimated photosynthetically active radiation (PAR, in μmol phot m^{-2} s^{-1}) just below the water surface (z=0 m, dash line), at 10 m depth (dash-dot line), and at 30 m depth (dash dot dot line). The exact times of the casts K2, K4, K5 and K6 are shown as vertical dash lines.

The water column structure at the sampling station before, during and after the eclipse is described in Fig. 4. Temperature and salinity ranged from 16.2 to 17°C and from 39 to 39.2 psu, respectively, in the upper 200 m. Due to spring warming, the surface layer (from the surface down to 20–30 m) is warmer and saltier than the underlying waters, transported in the area by the Asia Minor current (POEM group, 1992). The water mass under the thermocline is the Levantine Intermediate water, with almost homogenous temperature and salinity extended down to 250 m. Temperature and salinity remained almost constant during the eclipse event. Chl-a concentration varied from 0.14 to 0.19 μg l^{-1}, with a small chlorophyll maximum between 40 and 60 m. No significant changes in chl-a vertical distribution were observed during the eclipse event.

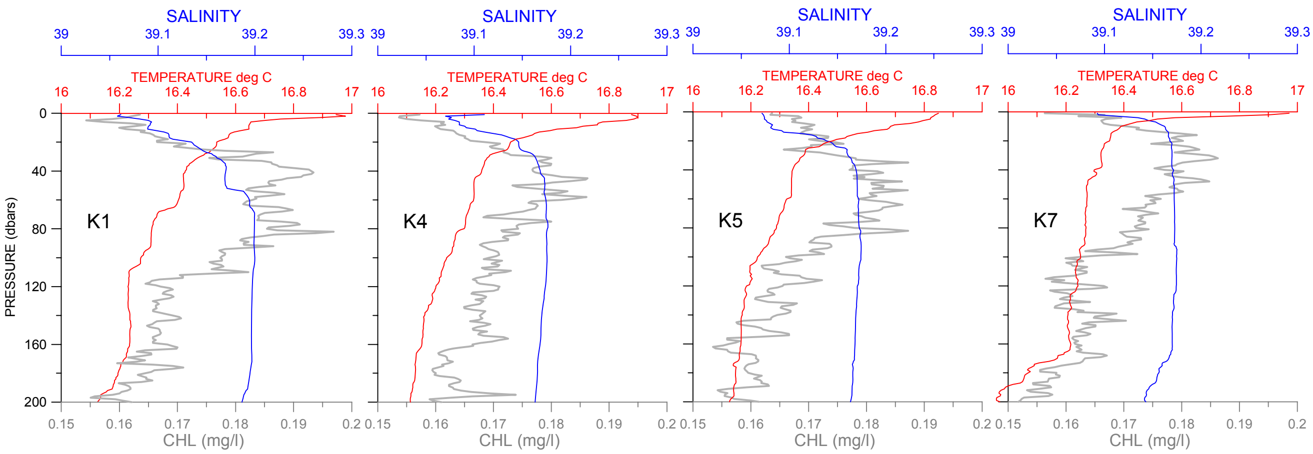

Fig. 4. Distribution of Temperature (red line), Salinity (blue line) and Chlorophyll-*a* (grey line) versus depth (down to 200 m). The profiles K1 and K7 represent the water column before the first contact and after the last contact, respectively. The profiles K4 and K5 are taken before and after the maximum of the eclipse.

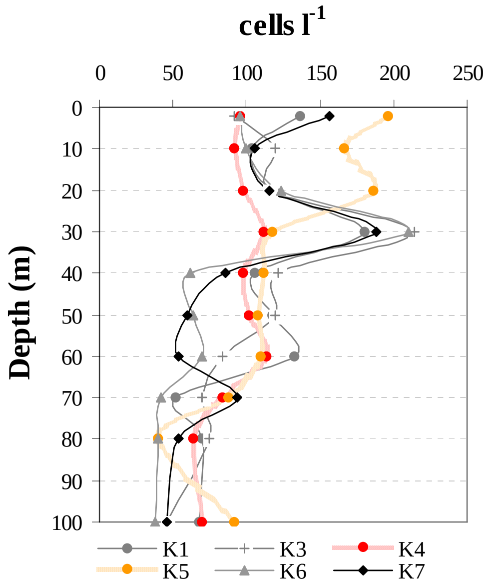

Fig. 5. Vertical distribution (abundance l^{-1}) of ciliates during different sampling hours. K1 and K7 correspond to the first contact and the last contact respectively. K4 and K5 are taken before and after the maximum of the eclipse.

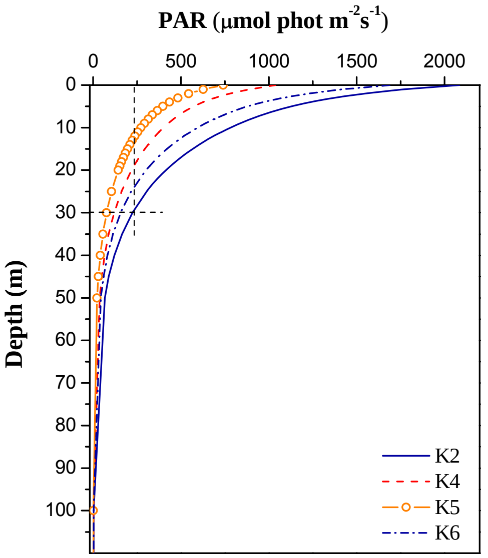

Fig. 6. Vertical profiles of PAR during different sampling hours. The exact time of casts K2, K4, K5 and K6 is shown in Fig. 3.

3.2.1 Ciliates

The ciliate community included members of the orders Choreotrichida (*Strobilidium* spp, *Lohmaniella* spp), Tintinnida, Oligotrichida (*Strombidium* spp, *Tontonia* spp and *Laboea* spp). Cell numbers were dominated by small oligotrichs 20–30 μm (35–75%).

From the vertical abundance profiles (Fig. 5, K1 and K3) it was clear that before the eclipse ciliates showed a non-random distribution and tended to accumulate at 30 m depth, where they showed a distinct peak in cell numbers (up to 212 cells l^{-1}). At this depth, PAR was ∼11% of its surface value (cast K2 in Fig. 6).

However, at 10:20 UTC (cast K4), one hour after the 1st contact and 30 min before totality, we observed a vertical homogenous spreading of the ciliates in the water column. At this time, surface PAR had already decreased by ∼50%. It seemed like ciliates responded to the rapid decrease in light intensity during the eclipse, adopting a night-time behavior. At 11:20 UTC (cast K5), almost 30 min after totality, when surface PAR was ∼35% of its initial value before the eclipse, ciliates were found in greater numbers within the first 20 m from the surface. Two hours after totality (cast K6 at 12:50 UTC), the notable peak at 30 m was re-established.

Ciliate diel cycles have been surprisingly little studied before. Jonsson (1989) reported that ciliates often accumulate around the pycnocline, mainly due to the effect of negative geotaxis. Chemokinetic and photokinetic responses have been shown to influence the vertical distributions in some ciliates in lake environments (Finlay et al., 1987). Interactions between sinking velocity, swimming velocity, tumbling rate and shape or density asymmetry of the cell have also been suggested to explain the vertical distribution of planktonic ciliates in natural waters (Jonsson, 1989). Perhaps the ciliate community tried to stay within its optimal photo-environment during the unusually rapid decrease in light intensity due to the eclipse. Vertical migration could also be governed by other factors, such as predation. Ciliates could move downwards in order to avoid predation pressure from zooplankton, accumulated near the surface layers at night. Perez et al. (2000) found in a study at the Western Mediterranean sea, that chlorophyll containing ciliates were mainly concentrated at the chl-a maximum depth, however heterotrophic ciliates often migrated from 20–30 m depth during the day to the surface at night or in the early morning. Measurements by Stoecker et al. (1989) across Georges Bank (Northwest Atlantic) revealed that oligotrichous ciliates with chloroplasts were usually located in the upper half of the euphotic zone during the day, showing diel changes in their distribution pattern. For example, *Laboea strobila* was concentrated near the surface just before sunrise and early in the morning, but had a subsurface maximum at noon.

3.2.2 Mesozooplankton

The mesozooplankton assemblage was made up 39–74% by copepods, showing an increasing relative abundance with depth. Copepodites of *Clausocalanus*, *Paracalanus*, *Oithona* and *Ctenocalanus* dominated the copepod assemblage (up to 40, 42, 19 and 15% respectively). Less important were *Clausocalanus paululus*, *Ctenocalanus vanus*, *Oithona plumifera* and *Oncea media* (up to 8–10%). The non-copepod zooplankton made a significant contribution to the total abundance represented, by 5 taxa: Appendicullaria, Doliolidae, Chaetognatha, Medusae and Pteropoda.

Figure 7 shows the results of copepod vertical distribution at the surface down to 100 m. Copepods exhibited the greatest density between 10–20 m depth. At K4 10:20 UTC when surface PAR was ∼50 % (Fig. 6) of that before the eclipse, copepods showed higher abundance close to the surface which can be explained by a possible migrating behaviour. *Calanus* and *Clausocalanus* copepodites seemed to be synchronized with the exogenous changes of light due to the eclipse. Individuals of these species showed a vertical migratory movement towards the surface. Among the other copepodites, *Paracalanus* mainly localized at 0–10 m increased their abundance in this layer before totality. *Oithona plumifera* collected mostly in the 10–20 m tows appeared in greater abundance in the 0–10 m layer, as well as *Oncea media* concentration increased at the surface layers. The other copepodites, male and female copepods displayed no significant differences in distribution and apparent response to the eclipse.

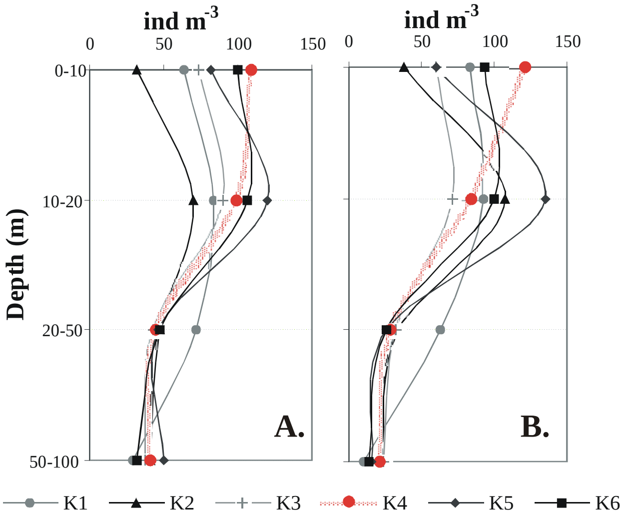

Fig. 7. Vertical distribution (abundance m^{-3}) of **(a)** copepods and **(b)** other mesozooplankton taxa during different sampling hours. K4 is taken before the maximum of the eclipse.

Similarly, the other zooplankton taxa were distributed high in the water column (10–20 m), whereas the fall of light intensity resulted in a migration upwards to the surface It seems that appendicullaria (*Oikopleura dioica*), meduses and doliolids responded to light changes and did move up in the water column towards the surface. Pteropods that maintained themselves mainly at 0–10 m increased their abundance before totality, while chaetognaths did not respond to light changes during the eclipse.

Avoidance of light by zooplankton has been demonstrated by many studies with a remarked preference for the surface layers during dawn and dusk (Conover et al., 1988; Hays et al., 1994). Earlier reports for *Pseudocalanus* and *Calanus* species (Runge and Ingram, 1991; Hattori and Saito, 1997), showed that medium to large calanoids exhibited a normal diel vertical migration moving upward into the surface layer sometime between 19:00 and midnight. *Calanus* is a fast swimmer moving in short bursts of about 15–66 m h^{-1} (Marshall and Orr, 1955). In a study of the diurnal vertical movements of chaetognaths and appendicularia, Schmidt (1973) reported that these animal groups during daytime avoid the upper layers, although around sunset and sunrise they tend to accumulate above 25 m. Consistent with our results are Sherman and Honey (1970) data, reporting that chaetognaths showed little change in vertical distribution during the eclipse. However the strong responses reported by Pepita (1955) for chaetognaths and decapod larvae differed from our results, probably due to species composition of the zooplankton.

4 Summary and conclusions

The solar eclipse of 29 March 2006 had very important effects on ecosystems, both on plants and marine zoo-plankton, which have been investigated in a parallel field experiment.

The diurnal course of photosynthetic rate for the seven important field-grown cereal and leguminous crops studied here, indicated a dramatic drop during the total phase of the eclipse. The minimum values of observed photosynthetic rates varied among the different species and ranged between 3.13 (faba beans) and 10.13 μmol CO_2 m^{-2} s^{-1} (bread wheat). In general, cereals were less influenced than legumes; in particular, faba beans, oats and grass pea were the most intensely affected species. Thus, they may be used as potential indices for future investigations of shading effects on field crops.

The fluctuations observed in the diurnal cycle of stomatal conductance (g_s) for the examined species could not be attributed to the solar eclipse. Thus, since stomatal closure could not be associated either with solar irradiance or the increased levels of the mesophyll CO_2-concentration, effects on the photochemical pathway of photosynthesis may have been responsible for the observed fall in photosynthetic rates. The observations on the quantum yield of photosynthesis before and during eclipse have revealed possible photoinhibitory effects in most species during the hours of bright sunshine. These findings have to be taken under serious consideration for planning solar eclipse related experiments in the future.

The solar eclipse induced effects on the marine environment were mainly driven by the change of underwater irradiance. Model estimated photosynthetically active radiation (PAR) just below the water surface was $\sim$2000 μmol phot m^{-2} s^{-1}just before the 1st contact. Temperature and salinity remained almost constant during the eclipse event. Chl-a concentration varied from 0.14 to 0.19 μg l^{-1}. No significant changes in chl-a vertical distribution were observed during the eclipse event.

The behavior of marine populations has been investigated, separately for micro-zooplankton (ciliates) and mesozooplankton. Ciliates, tending to accumulate at 30 m depth, responded to the rapid decrease in light intensity during the eclipse and adopting night-time behaviour showed a vertical homogenous spreading in the water column. At this time, surface PAR had already decreased by $\sim$50%. From the mesozooplankton assemblage, *Calanus* and *Clausocalanus* copepodites having been synchronized with the exogenous changes, showed a vertical migratory movement towards the surface. Among the other copepodites, *Paracalanus*, *Oithona plumifera* as well as *Oncea media* increased their abundance in the surface layer before totality. The other copepodites, male and female copepods displayed no significant differences in distribution and apparent response to the eclipse. Similarly, the other zooplankton taxa such as appendicullaria (*Oikopleura dioica*), meduses and doliolids responded to light changes moving up towards the surface.

Overall, given the biodiversity of the Greek territory we seized the opportunity of the March 2006 Total Solar Eclipse to investigate the sensitivity of various species in the biosphere. The different responses ascertained between various species both in field crops and marine zoo-plankton, provide an indication that future climate changes influencing the amount of radiation that reaches the earth's surface, may disturb the stability of the ecosystems, with direct and indirect impacts on crop productivity and in some cases on food chain it self.

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