The effect of a lunar eclipse on the vertical migration behaviour of *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea

G.A.Tarling, F.Buchholz[1] and J.B.L.Matthews

The Scottish Association for Marine Science, PO Box 3, Oban, Argyll PA34 4AD, UK and [1]Biologische Anstalt Helgoland – AWI, Meeresstation, D-27483 Helgoland, Germany

Abstract. The vertical migration of a zooplankton community dominated by the euphausiid *Meganyctiphanes norvegica* was monitored between 16 and 23 September 1997 with a 153 kHz Acoustic Doppler Current Profiler (ADCP) and a MOCNESS net. The sampling period covered a phase in the lunar cycle when the rise of the moon (full moon) coincided initially with sunset and then became progressively later. On 16 September 1997, a lunar eclipse occurred 45 min after sunset, lasting for ~2 h. At dusk, the ADCP observed the upward vertical migration of two principal backscattering bands ~10 min apart with vertical velocities of up to 7 cm s^{-1}. After a period at the surface, a more diffuse band subsequently sank at a slower rate (1–2 cm s^{-1}) to a depth of 75–100 m. Net samples showed that the earlier band consisted mainly of the pteropod *Cavolinia inflexa*, whilst the later band was mostly euphausiids, predominantly *M.norvegica*. This species was also the major constituent of the band that sank. The timing of upward migration was relatively constant over the sampling period, but there was an increasing delay of the secondary sinking until 21 September. This showed as a strong correlation between the onset of sinking and the time of moonrise. The lunar eclipse on 16 September perturbed this pattern, such that animals did not sink soon after their arrival at the surface, as occurred on 17 September, but remained at the surface until the end of the umbra. This suggests that *M.norvegica* can perceive moonlight and that this influences vertical migration. Evidence that the behaviour is not solely mediated by this exogenous factor, however, is seen in the pattern that emerged after 21 September, when midnight sinking occurred at a relatively constant time after sunset and before moonrise. These observations support the hypothesis that moonlight is a *Zeitgeber* for an endogenous rhythm that synchronizes secondary sinking behaviour with the lunar cycle.

Introduction

Light has long been recognized as being a stimulus that influences vertical migration in zooplankton. According to the original view of workers such as Esterley (1911, 1912) light was a cue to start upward or downward migration, a 'go–no go' type of stimulus (Longhurst, 1976). Michael (1911) put forward an alternative mechanism whereby the organisms followed an optimal isolume (layer of constant light) up and down the water column. Russell (1926) built on these later ideas when he proposed that migrating zooplankton were only able to perceive light at or above intensities that matched their experience during vertical migration. Commonly made observations of 'midnight sinking', where animals were seen to sink down a small distance after arriving at the surface at the end of their upward migration [e.g. *Euphausia pacifica* (Esterley, 1914), *Meganyctiphanes norvegica* (Jespersen, 1944) and *Sagitta elegans* (Pearre, 1973)], were thus explained as being a result of the level of light being below the threshold of perception, causing the animals to become inactive and sink. Any additional influence of moonlight on midnight sinking has received little consideration. Nevertheless, vertical migration behaviour is influenced by the moon. For instance,

zooplankton in a freshwater reservoir (Lake Calahora Bassa, Mozambique) were observed to have different night-time vertical positions in the water column depending on the relative timing of the moonrise and sunset (Gliwicz, 1986). Furthermore, various studies have shown that zooplankton and juvenile fish synchronize their vertical migration with the lunar tidal cycle in order to enter estuarine recruitment sites from the open sea (e.g. Blaxter *et al.*, 1989; Queiroga *et al.*, 1997).

The question of whether the lunar cycle is influential in producing midnight sinking may be investigated in the field by monitoring vertical migration over a period starting when the rise of the moon occurs just after sunset and continuing over a period of days while the interval between sunset and moonrise becomes greater. A relationship between midnight sinking and the phase of the moon would only be a possibility if the sinking behaviour became consistently later over this period. Nevertheless, what remains unclear from such a study is whether individuals are able to detect and respond directly to the moon's appearance or whether their behaviour is purely an endogenous rhythm synchronized with the lunar cycle. For example, Velsch and Champalbert (1994) found that *M.norvegica* exhibited regular cycles of activity and inactivity even when the animals were in complete darkness. Positive proof of a reaction to moonlight can only be obtained when it is known that endogenous rhythms are not simultaneously influencing the animal's behaviour.

A natural situation where such a differentiation can be made occurs during a lunar eclipse. Such eclipses occur less than once a year, rarely in the same geographical position, and last for ~1.75 h. They can only take place at full moon, which results in a dramatic reduction in the level of illumination as the moon suddenly becomes shaded when it should be at its brightest. If zooplankton can detect and respond to moonlight, such a dramatic change would be expected to evoke a strong response. Furthermore, it is unlikely that any such behavioural response could be influenced by endogenous rhythms, since the infrequency of such events makes them unpredictable within the lifetime of planktonic animals.

An opportunity to investigate the response of zooplankton to a lunar eclipse occurred during a cruise to the Ligurian Sea in September 1997, which formed part of the MAST III 'PEP' Project (see Acknowledgements) investigating the adaptability of the euphausiid *M.norvegica* (Northern krill) to a climatic gradient. *Meganyctiphanes norvegica* shows a pronounced vertical migration pattern in the central zone of the Ligurian Sea, moving from daytime depths in excess of 600 m (400 in winter, 800 in summer) to the surface at night (Casanova, 1974; Sardou and Andersen, 1993; Sardou *et al.*, 1996; Velsch, 1997). It usually occurs in swarms, which makes it detectable by non-invasive acoustic devices and allows the migratory behaviour to be monitored continuously. In this respect, this study benefited from the information gathered by an Acoustic Doppler Current Profiler (ADCP), which has been used successfully in a number of previous studies of euphausiid vertical migration (e.g. Cochrane and Sameoto, 1994; Zhou *et al.*, 1994; Buchholz *et al.*, 1995; Tarling *et al.*, 1998). The ADCP is able to detect individual particles and the size of zooplankton, and determine their horizontal and vertical velocities through measuring Doppler shift (see Woodward and Appell,

1986; Flagg and Smith, 1989; Pleuddemann and Pinkel, 1989). Its use in this study, combined with a ground-truthing multinet, allowed a fine-scale analysis of the upward vertical migration and subsequent midnight sinking of *M.norvegica* in relation to the lunar cycle, starting when the moon was eclipsed just after sunset on 16 September 1997.

Method

Sampling was carried out between 16 and 23 September 1997 in the central zone of the Ligurian Sea in the Mediterranean Sea (~43°18′N, 7°52′E) on board R/V 'Heincke'. During this period, sunset was between 18.35 and 18.30 h local time [Universal Time Coordinated (UTC) + 2 h] and moonrise was from 18.34 h on 16 September to 23.30 h on 23 September. A lunar eclipse occurred on 16 September, the moon entering the penumbra (partial eclipse) at 19.08 h and leaving at 22.25 h. The umbra (total eclipse) started at 20.15 h and ended at 21.18 h. The moon was full on 16 September (100% illuminance) and waned to half-moon on 23 September when its illuminance was only some 10% due to the low angle of reflection at the moon's surface. Cloud cover varied mostly between 0 and 2/8, although levels above 4/8 did occur during 22 September. The water was relatively clear with a Secchi depth of 28 m.

A 153 kHz narrow-band ADCP (RD Instruments, San Diego, CA) was deployed through the oceanographic well of the ship during the period of this study. The ADCP was set to collect signals in 128 'depth bins', each of 8 m, but good signals were rarely received from below a maximum depth of 320 m. Raw velocity data were collected every second and these were averaged over periods of 6 min to reduce the standard deviation to an acceptable level (± 0.83 cm s^{-1}). Processed data were obtained for horizontal and vertical velocities (cm s^{-1}) and relative backscatter (dB).

The acoustic data were compared with samples taken with a 1 m^2 MOCNESS net system using nets with 300 μm and 2 mm mesh size (see Wiebe *et al.*, 1985) with flowmeter, temperature and salinity sensors. Forty-three deployments were made over the 8 day period, sampling between 0 and 200 m with a maximum depth interval of 20 m in the upper layers, mostly at night-time between dusk and dawn. Animals were identified and counted immediately after capture, and then frozen for any further analysis.

Results

Figure 1 shows the temperature profile at 43°18′N, 7°52′E on 21 September. The water column below 70 m was relatively stable at around 13°C. Above 70 m, there was a strong thermocline with temperatures increasing to 15°C at 40 m and then to a maximum of 22.5°C between 15 m and the surface.

Figure 2 illustrates the relative backscatter observed during the early night-time on four nights which were representative of the general patterns observed between 16 and 22 September, with the lunar eclipse occurring on the first of these nights. During each of the nights, there was the same general increase in
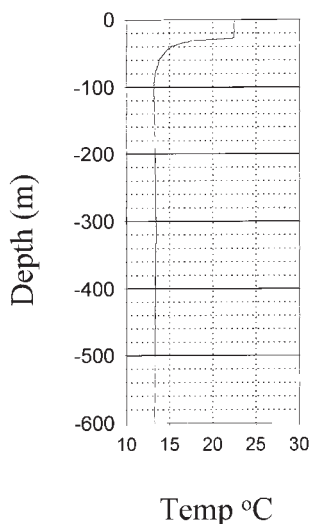
Fig. 1. Temperature profile in the Ligurian Sea at 43°18′N, 7°52′E on 21 September 1997.

relative backscatter at all depths after ~19.00 h following the upward movement of three bands of high relative backscatter (RB1, RB2 and RB3). RB1 was relatively diffuse, originating at 240 m around 18:35 h, and following a relatively gradual upward trajectory until arriving at 32 m between 20:00 and 20:15 h. RB2 was more distinct than the first, appearing at 300 m around 19:05 h, and showing a relatively steep upward trajectory between 240 and 80 m before converging with the first band. RB3 was also distinct and did not appear at 300 m until around 19:20 h. It exhibited the steepest upward trajectory of the three bands which resulted in it converging with Band 2 above 144 m and with Band 1 above 80 m. During some evenings (e.g. 17 and 19 September), there was a further zone of relatively high backscatter immediately behind RB3. This zone was much less distinct on other evenings (e.g. 16 and 22 September). The arrival of these bands near the surface produced a dramatic increase in the level of backscatter that persisted for at least 2 h on each of the four nights (Zone A). Below this, there was a deeper layer of high backscatter that gradually sank from the surface to between 50 and 120 m by midnight (Zone B). During this period of sinking, the backscatter in the surface layer decreased correspondingly.

Night-time net catches were dominated by two zooplankton groups: the euphausiids (typically between 1000 and 2000 mg dry weight m^{-2}) and the pteropods (typically between 100 and 1000 mg dry weight m^{-2}). Integrated biomass levels for the third most dominant group, the copepods, were an order of magnitude less than for the previous two groups (between 50 and 100 mg dry weight m^{-2}). The euphausiid community was made up of 10 species, of which *M.norvegica* constituted between 60 and 85% of the night-time biomass between 0 and 500 m, and *Nematoscelis megalops* between 15 and 30%. During daytime, *N.megalops* made up between 45 and 50%, whilst *M.norvegica* made up around
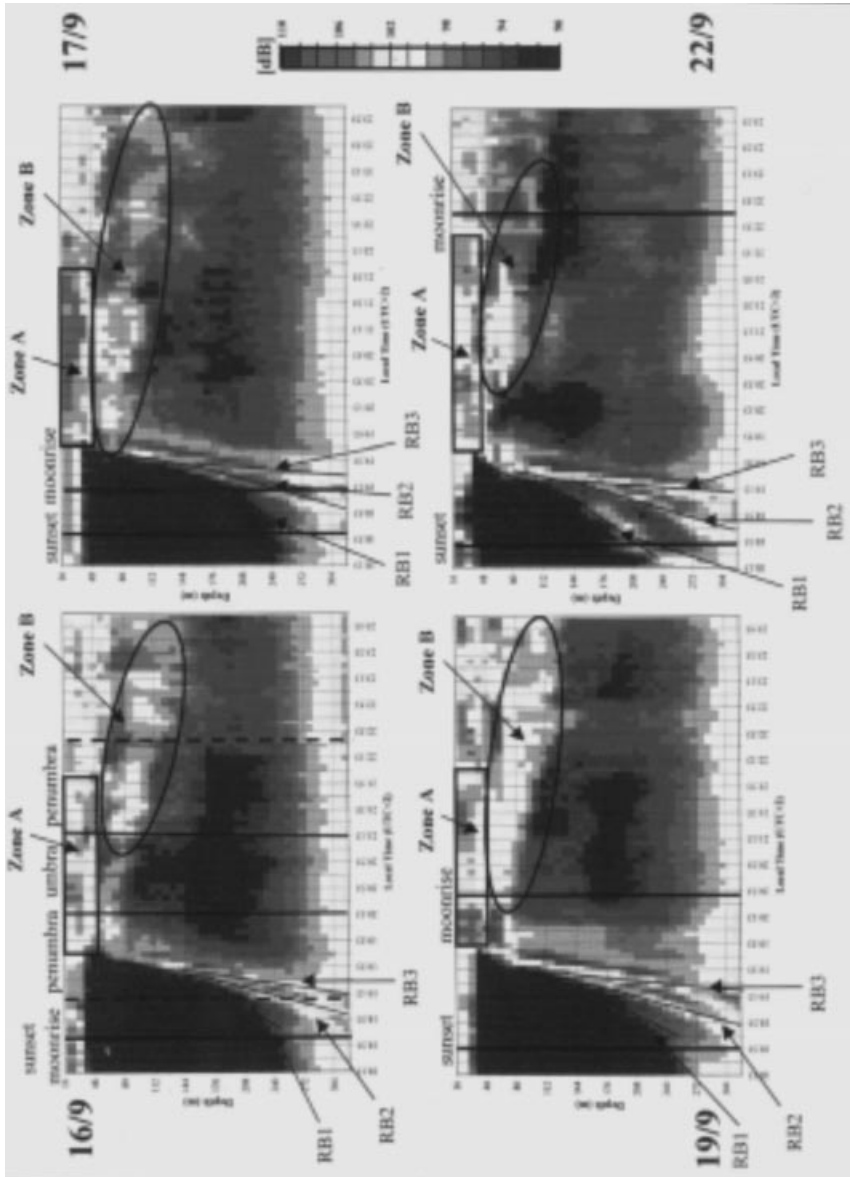
Fig. 2. ADCP relative backscatter (dB) between 18.00 and 24.00 h on 16, 17, 19 and 22 September 1997, indicating the bands and zones described in the text in relation to solar and lunar events.
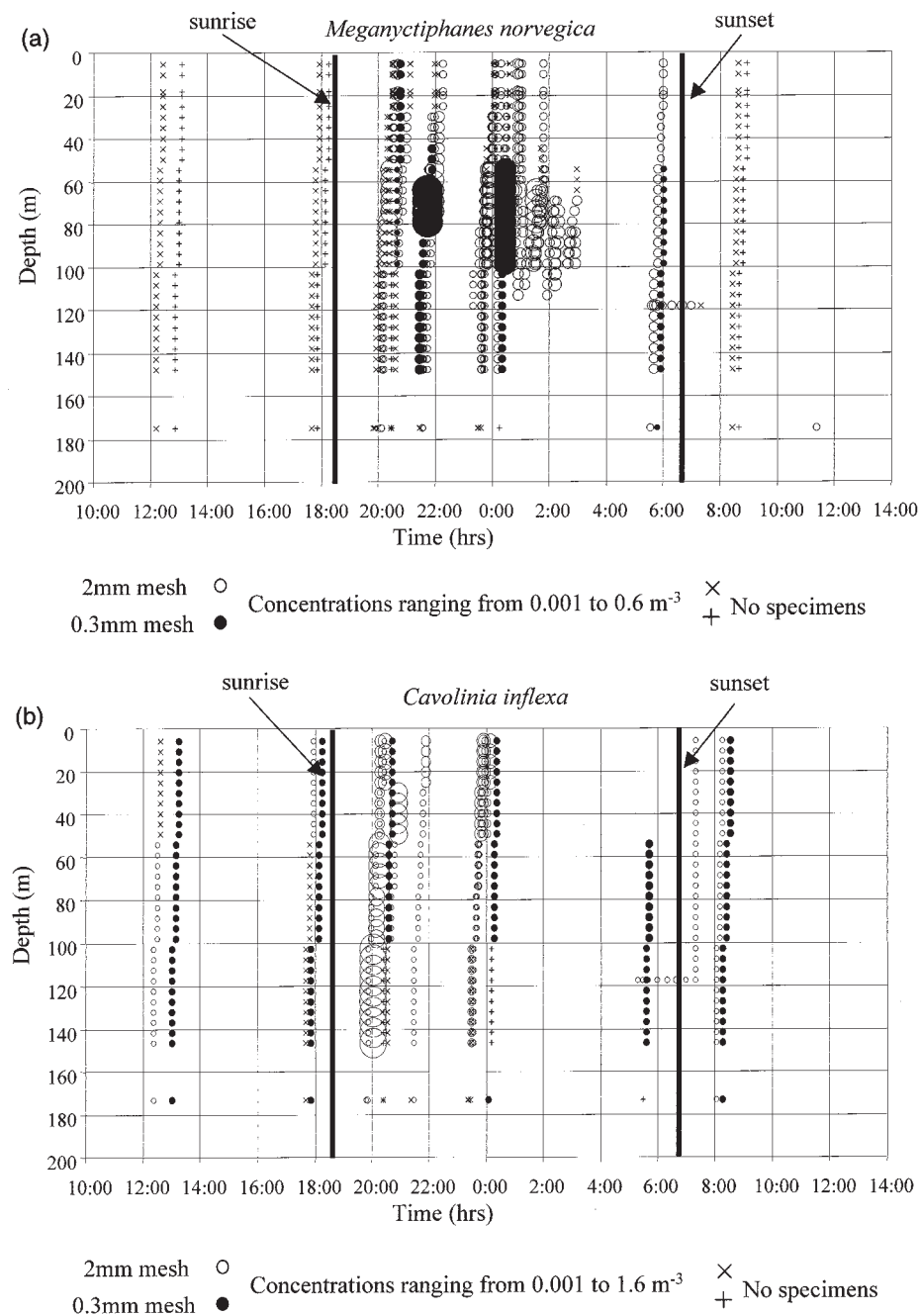
Fig. 3. Abundance of (**a**) *M.norvegica* and (**b**) *C.inflexa* in all MOCNESS deployments in relation to depth between 16 and 23 September 1997, plotted on a 24 h time scale.

30% of the euphausiid biomass between 0 and 500 m, indicating that *M.norvegica* constituted the majority of the migrating euphausiid biomass. The pteropod community almost exclusively consisted of *Cavolinia inflexa* and, like *M.norvegica*, this species also had considerably lower biomass levels between 0 and 500 m during daytime compared with night-time.

Figure 3 combines all the net catches to show the concentrations of the two dominant vertically migrating species, (a) *M.norvegica* and (b) *C.inflexa*, above 200 m between 16 and 22 September. Both species became abundant in this depth interval soon after 19:00 h and so are considered to have been the major contributors to the observed increase in backscatter. Closer examination of the catches shows that the two species performed temporally distinct vertical migrations. *Cavolinia inflexa* appeared in large numbers between 100 and 75 m by 20:00 h, but *M.norvegica* was not observed at these depths for at least another 10 min. This difference continued up to the time when both groups reached the surface layer (above 25 m), which was at 20:00 h for *C.inflexa* and around 20:15 h for *M.norvegica*. Comparison of catches later in the evening shows that there was depth discrimination between the two species, with the main distribution of *C.inflexa* being in the top 50 m after 21:00 h, whilst *M.norvegica* was most abundant between 50 and 120 m after this same time. Comparison of the backscatter traces with net catches indicates that the two species were responsible for different bands: RB1 and RB2 containing *C.inflexa*, and RB3 containing *M.norvegica* (see Figure 2). After a short phase when they merged in the upper layers (Zone A), the two species separated once more, with *M.norvegica* sinking to a depth of 50–120 m (Zone B) and *C.inflexa* remaining above this layer.

Of particular interest is the timing of the onset of sinking by *M.norvegica*. In general, there was a progressive delay from 17 to 22 September. On 17 September (Figure 2b), when the moon had risen before the start of the ascent, the region of high backscatter started to sink to below 50 m almost immediately after its arrival at the surface. On 19 September (Figure 2c), no major movement from the surface to depths below 50 m was observed until 30 min after the arrival of the backscattering bands at the surface, which coincided with moonrise. By 22 September (Figure 2d), the interval between the arrival of backscattering bands at the surface and the occurrence of high backscatter below 50 m was around 60 min, although moonrise was not for another 2 h after this time. The pattern observed on the night of the lunar eclipse was similar to that observed on 22 September in that both exhibited high backscatter at the surface for 1 h and then high backscatter below 50 m after this period. The period of high backscatter in the surface coincided almost exactly with the umbra period of the lunar eclipse, and high backscatter below 50 m did not occur until the start of the penumbra period, when the level of lunar illumination started to increase gradually, but was still very low at the beginning.

Further detail can be added by examination of the corresponding vertical velocity plots (Figure 4). In all plots, it is evident that there were two main bands of strong upward velocities. VV(A) showed velocities of the order of 2–5 cm s^{-1}, and was temporally and spatially coincident with RB2 in the relative backscatter plots (see Figure 2) which consisted mainly of *C.inflexa*. VV(B) contained slightly
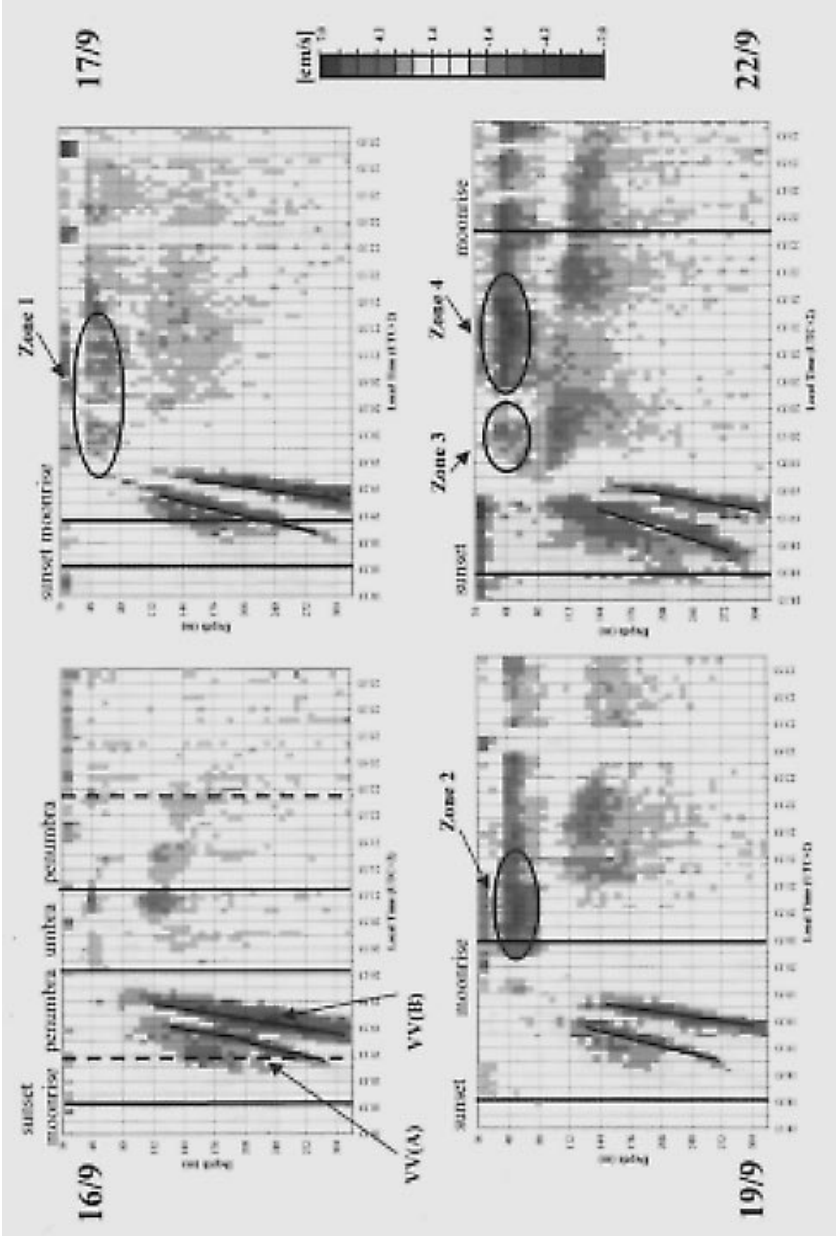
Fig. 4. ADCP vertical velocity measurements (cm s⁻¹) between 18.00 and 24.00 h on 16, 17, 19 and 22 September 1997, indicating the bands and zones described in the text in relation to solar and lunar events.

higher velocities reaching up to 7 cm s⁻¹ and corresponds to RB3 in the relative backscatter plots which consisted of *M.norvegica*. As with the backscatter bands, the timing and trajectories of the upward-velocity bands varied little during the period of observation, but major differences between nights were observed immediately after the upward phase. On 17 September, downward-velocity signals between 1 and 2 cm s⁻¹ were frequent between 50 and 100 m, immediately after the upward phase (Zone 1). On 19 September, even stronger downward velocities between 2 and 5 cm s⁻¹ (Zone 2) occurred after the upward phase, but this time there was a delay of ~30 min between the end of upward movement and the start of downward movement. On 22 September, the situation was a bit more complex with two zones of downward velocities, the first (Zone 3) occurring immediately after the upward phase and containing relatively weak velocities (1–2 cm s⁻¹) and the second ~1 h after the upward phase (Zone 4) which contained higher downward velocities (2–5 cm s⁻¹). Comparison with net catches indicated that the latter zone comprised mainly *M.norvegica*. The night of the eclipse (16 September) was very different from the subsequent nights in that there was no clear zone of downward movement after the upward phase.

On the whole, the vertical velocity plots correspond well with the relative backscatter data. On 17 September, backscatter continued to be apparent below 50 m and there were only weak downward velocities after the upward phase, which suggests that many *M.norvegica* did not reach the surface and so did not move strongly downwards later. On 19 September, moonrise coincided with a reduction of backscatter at the surface and an increase below 50 m, and also with the start
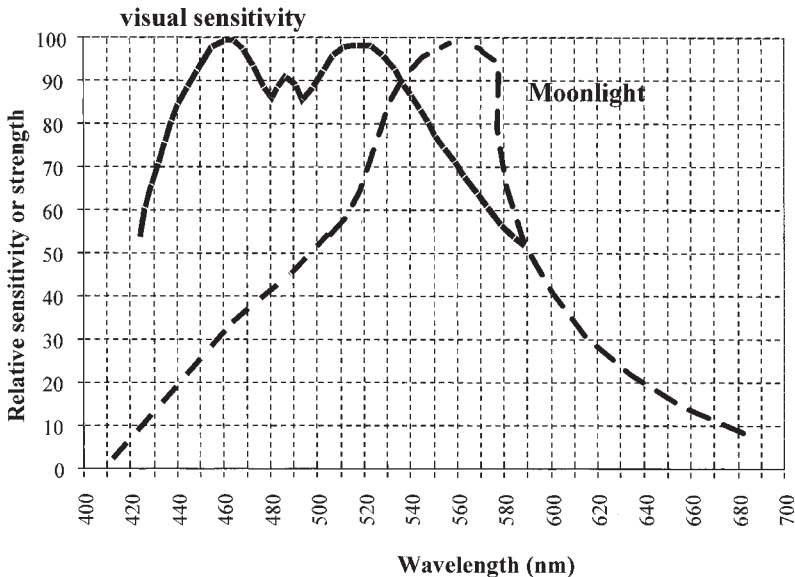

Fig. 5. The emission spectrum of moonlight (broken line), after Hobson *et al.* (1981), and the optical sensitivity spectrum of *M.norvegica* (solid line), after Kay (1965).

of strong downward velocities. Vertical velocity and relative backscatter data both showed strong downward movement ~1 h after the backscattering bands arrived at the surface. However, although the pattern of relative backscatter on 22 September was almost the same as on the night of the lunar eclipse (16 September), there was no corresponding sign of strong downward velocities on 16 September, but instead a period of slow downward movement extending over the 3 h after the arrival of the backscattering bands at the surface. This suggests that the behaviour of the animals, if not their distribution, differed on these two nights.

Discussion

One of the main observations from this study is that the behaviour and distribution of *M.norvegica* can change over the week after a full moon, with increasing numbers of animals reaching the surface and exhibiting midnight sinking progressively later day by day. Although these observations suggest that midnight sinking is synchronized with the lunar cycle, at least close to full moon, the possibility of an endogenous rhythm controlling such behaviour cannot be discounted at this stage. The mechanism behind this behaviour may be examined further, however, by comparing the distributions on the night of the lunar eclipse (16 September), when krill did reach the surface and did not reappear in large numbers below 50 m until an hour later, with the following night, when few krill reached the surface and most remained below 50 m all the time. If an endogenous rhythm controlled the sinking behaviour and the animals were not able to perceive moonlight, the same behaviour should have been observed on both nights. The fact that it differed is evidence of krill detecting and responding to moonlight.

That zooplankton can perceive moonlight is not obvious from the physiological perspective since the underwater spectrum of moonlight and the sensitivity maxima of zooplankton eyes are not identical (see the review by Forward, 1988). In daylight, the quantal spectrum in air shows a constant level of photons between 450 and 700 nm (Dartnall, 1975), but this changes at twilight and in moonlight. During twilight, the spectrum in air shows a maximum in the blue-green region (450–525 nm), a suppression between 540 and 625 nm, and another maximum at longer wavelengths (Munz and McFarland, 1973). In moonlight, the spectrum shows a maximum between 545 and 575 nm; this decreases rapidly above 600 nm, but more gradually toward the lower end to ~50% of the maximum value at 500 nm (Hobson *et al.*, 1981). Figure 5 compares the visual sensitivity of *M.norvegica* as measured by Kay (1965) with the quantal spectrum of moonlight in air (Hobson *et al.*, 1981). The sensitivity spectrum of *M.norvegica* consists of two peaks: one at 460 nm and the other at 520 nm. The first peak corresponds with the absorption characteristics of visual pigment (euphausiopsin), as identified by Kampa (1955) in *E.pacifica*. Mauchline and Fisher (1969) reported the discovery of another form of rhodopsin in *M.norvegica* by D.J.Pritchard with an absorption maximum of 528 nm, corresponding closely with the second peak. Both of these peaks are below the peak wavelengths of moonlight, so the light perception of krill eyes is definitely not optimized for moonlight. Nevertheless,

there is some overlap between the upper end of the second sensitivity peak and the lower end of the moonlight peak. Furthermore, the underwater spectrum of moonlight will be closer to the sensitivity peaks of krill eyes because longer wavelengths are preferentially filtered out as light penetrates the sea.

The behavioural evidence in this study that krill can perceive moonlight is further supported by experiments carried out by Velsch (1997) which showed that *M.norvegica* was negatively phototactic at values of light intensity $>3 \times 10^{-5}$ µW cm^{-2}. On a bright moonlit evening in the Mediterranean, this light level would typically occur between 25 and 50 m depth (Velsch, 1997), a depth below which krill normally sank during the present study. Given that potential fish predators have eyes with similar sensitivity spectra to those of euphausiids (see Munz and MacFarland, 1973; Hobson *et al.*, 1981), it may be presumed that the choice of deeper layers by krill during bright moonlit nights is a mechanism to avoid visual predators. This is supported by a study where zooplankton, which did not respond to moonlight in the upper layers at night, were subjected to higher predation levels by sardines during the full-moon period (Gliwicz, 1986).

The observation that the krill started to move down before moonrise at a later stage in the lunar cycle, when moonrise was more than 3 h after sunset (i.e. 21, 22 and 23 September), indicates that midnight sinking is not just a response to moonlight, but a behaviour that is influenced by a number of factors. Pearre (1973, 1979) suggested that midnight sinking might be the result of satiated individuals leaving the surface and descending to deeper layers. This was indeed observed in both *M.norvegica* and *Thysanoessa raschii* by Simmard *et al.* (1986) in the St Lawrence estuary, where the animals moved into the surface waters at night to gather food before rapidly returning to below the thermocline. Simmard *et al.* (1986) hypothesized that such a movement below the thermocline was in order to minimize energy respiration loss, as suggested by McLaren (1963, 1974). The temperature profile taken in the central zone of the Ligurian Sea at the time of the study showed a strong thermocline above 70 m where the temperature increased from 13 to 22.5°C. Movement from the surface to waters below 60 m would confer a metabolic advantage given the strong positive relationship between temperature and metabolic rate in zooplankton (see Ikeda, 1985). Nevertheless, the value of this metabolic advantage has been contested by modelling studies, such as Ohman (1990), where decreasing predation risk was predicted to be a stronger inducement for satiated animals to sink below the thermocline.

Satiation is not the principal cue for midnight sinking during periods of the lunar cycle when moonrise is close to sunset. On 19 September, for instance, *M.norvegica* reached the surface layers ~10 min before moonrise and sank immediately after moonrise. One would expect some delay between arrival at the surface and midnight sinking if satiation were the most important cue since some feeding would need to take place. During this part of the lunar cycle, therefore, *M.norvegica* sinks as a direct response to predator avoidance, independent of its level of satiation.

What is becoming apparent from the available information is that through the lunar cycle there is a sequence of alternative actions available to *M.norvegica* which determine its behaviour when nearing the surface at the end of the upward

migration. It seems that when the moon is bright, the krill will stay in a deeper position in the water column regardless of any other factor such as their state of hunger or the location of food; when the moon is dim or has not yet risen in the early part of the night, the krill will rise above 50 m for ~1 h and then migrate to depths below 50 m. What remains a puzzle, however, is the difference in behaviour between the night of the lunar eclipse (16 September) and the night of 22 September. The timing of the moon's appearance was superficially similar on these nights because of the eclipse effect. Although krill could be seen to be collecting below 50 m ~1 h after their ascent on both nights, there was no simultaneous sign of downward velocities on 16 September, as was seen on 22 September. If the krill simply fed at the surface in the absence of strong moonlight, then sank, one would expect a synchronous downward movement on both nights. The velocity data on the night of the eclipse indicated, however, that the krill did not move synchronously but were slowly sinking for an hour to between 50 and 120 m. This behaviour is characteristic of the 'disorientation' described by Michael (1911) as being the principal cause of midnight sinking. The fact that this type of behaviour was not observed on any other night indicates that it is not normal, and suggests that an anticipatory mechanism may operate. The following scenario would be one explanation of the course of events: the night before the eclipse (15 September), the moon was almost full and had risen before the ascent of the krill, so the krill would have encountered an isolume of 3×10^{-5} µW cm^{-2} between 25 and 50 m (see earlier discussion), at which point their upward migration would have stopped; on the night of the lunar eclipse, the krill 'anticipated' similar light conditions, but did not detect the same isolume when they reached 25–50 m; they continued swimming to the surface where they still failed to detect the appropriate level of light, became disorientated and slowly sank.

An anticipatory mechanism of this sort can be brought about by the setting of an endogenous rhythm by an exogenous cue (a *Zeitgeber*). For example, diurnal vertical migration cycles in zooplankton have been widely reported to be set by some aspect of the light/dark cycle [see the review by Forward (1988)]. In *M.norvegica*, Velsch and Champalbert (1994) found that individuals kept in constant darkness performed a free-running cycle of higher and lower activity on a 23 h basis, but when exposed to natural light levels, their cycle of activity became synchronized with the 24 h cycle. Since the daytime depth of *M.norvegica* in the Mediterranean at the time of year of this study is between 500 and 700 m (G.Tarling, unpublished data; Sardou *et al.*, 1996) and light levels are too low to produce a phototactic response (Velsch, 1997), it seems likely that the animals phase their endogenous circadian rhythm from the light of the setting or the rising sun and moon when they are in the upper layers. They then commence their upward migration from between 500 and 700 m the following evening in accordance with their endogenous rhythm rather than in response to an exogenous cue.

References

Blaxter,J.H.S., Gamble,J.C. and Westerhagen,H. (eds) (1989) *The Early Life History of Fish*. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer*, **191**.

Buchholz,F., Buchholz,C., Reppin,J. and Fisher,J. (1995) Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat: Comparison of net catches and measurements with Acoustic Doppler Current Profilers. *Helgol. Wiss. Meeresunters.*, **49**, 849–866.

Casanova,B. (1974) Les Euphausiacées de Mediteranée. Thèse de Doctorat des Sciences Naturelles, University of Provence, Marseille, 380 pp.

Cochrane,N.A. and Sameoto,D.D. (1994) Temporal variability of euphausiid concentrations in a Nova Scotia shelf basin using a bottom-mounted acoustic Doppler current profiler. *Mar. Ecol. Prog. Ser.*, **107**, 55–66.

Dartnall,H.J.A. (1975) Assessing the fitness of visual pigments for their photic environments. In Ali,M.A. (ed.), *Vision in Fish*. Plenum Press, New York, pp. 543–563.

Esterley,C.O. (1911) Diurnal migration of *Calanus finmarchicus* in the San Diego region during 1909. *Int. Rev. Hydrobiol.*, **4**, 140–151.

Esterley,C.O. (1912) The occurrence and vertical distribution of the copepoda of the San Diego region with particular reference to nineteen species. *Univ. Calif. Publ. Zool.*, **9**, 253–340.

Esterley,C.O. (1914) The vertical distribution and movements of the Schizopoda of the San Diego region. *Univ. Calif. Publ. Zool.*, **13**, 1–20.

Flagg,C.N. and Smith,S.L. (1989) On the use of acoustic Doppler current profiler to measure zooplankton abundance. *Deep-Sea Res.*, **36**, 455–474.

Forward,R.B. (1988) Diel vertical migration: zooplankton photobiology and behaviour. *Oceanogr. Mar. Biol. Annu. Rev.*, **26**, 361–393.

Gliwicz,Z.M. (1986) A lunar cycle in zooplankton. *Ecology*, **67**, 883–897.

Hobson,E.S., McFarland,W.N. and Chess,J.R. (1981) Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fish. Bull.*, **79**, 1–30.

Ikeda,T. (1985) Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* **85**, 1–11.

Jespersen,P. (1944) Investigation on the food of the herring and the macroplankton in the waters around the Faroes. *Medd. Kommn Damn. Fisk. Havunders. Ser. Plankton*, **3**, 1–44.

Kampa,E.M. (1955) Euphausiopsin, a new photosensitive pigment from the eyes of euphausiid crustaceans. *Nature*, **175**, 996–998.

Kay,R.H. (1965) Light-stimulated and light inhibited bioluminescence of the euphausiid *Meganyctiphanes norvegica* (G.O. Sars). *Proc. R. Soc. B*, **162**, 365–386.

Longhurst,A.R. (1976) Vertical migration. In Cushing,D.H. and Walsh,J.J (eds), *The Ecology of the Seas.* Blackwell Scientific, Oxford, pp. 116–137.

Mauchline,J. and Fisher,L.R. (1969) The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.

McLaren,I.A. (1963) Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Board Can.*, **20**, 685–727.

McLaren,I.A. (1974) Demographic strategy of vertical migration in a marine copepod. *Am. Nat.*, **108**, 91–102.

Michael,E.L. (1911) Classification and vertical distribution of the Chaetognatha of the San Diego region. *Univ. Calif. Publ. Zool.*, **8**, 21 pp.

Munz,F.W. and McFarland,W.N. (1973) The significance of spectral position in the rhodopsins of tropical marine fishes. *Vis. Res.*, **13**, 1829–1874.

Ohman,M.D. (1990) The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.*, **60**, 257–281.

Pearre,S.J. (1973) Vertical migration and feeding in *Sagitta elegans* (Verrill). *Ecology*, **54**, 300–314.

Pearre,S. (1979) Problems of detection and interpretation of vertical migration. *J. Plankton Res.*, **1**, 20–44.

Pleuddemann,A.J. and Pinkel,R. (1989) Characterization of the patterns of diel migration using a Doppler sonar. *Deep-Sea Res.*, **36**, 509–530.

Quieroga,H., Costlow,J.D. and Moreira,M.H. (1997) Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: implications for tidal stream transport. *Mar. Ecol. Prog. Ser.*, **149**, 121–132.

Russell,F.S. (1926) The vertical distribution of marine macroplankton. An observation on diurnal changes. *J. Mar. Biol. Assoc. UK*, **13**, 769–809.

Sardou,J. and Andersen,V. (1993) Micronecton et macroplancton en mer Ligure (Méditeranée): migrations nycthémérales et distributions verticales. *Oceanol. Acta*, **16**, 381–392.

Sardou,J., Etienne,M. and Andersen,V. (1996) Seasonal abundance and vertical distributions of macroplankton and micronekton in the northwestern Mediterranean Sea. *Oceanol. Acta*, **19**, 645–656.

Simmard,Y., Lacroix,G. and Legendre,L. (1986) Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in strati-fied surface waters. *Mar. Biol.*, **91**, 93–105.

Tarling,G.A., Matthews,J.B.L., Sabarowski,R. and Buchholz,F. (1998) Vertical migratory behaviour of the euphausiid *Meganyctiphanes norvegica* and its dispersion in the Kattegat Channel. *Hydro-biologia*, **375/376**, 331–341.

Velsch,J.-P. (1997) Dynamique de population et migrations verticales journalières de *Meganyc-tiphanes norvegica* (Crustaces: Euphausiaces) en Mediterranée Nord-Occidentale. Thèse de Doctorat des Sciences Naturelles, Centre d'Océanologie, Universitée de la Mediterranée Aix Marseille II, Marseille, 132 pp.

Velsch,J.-P. and Champalbert,G. (1994) Rythmes d'activité natatoire chez *Meganyctiphanes norvegica* (Crustacea, Euphausiacea). *C. R. Acad. Sci. Paris/Life Sci.*, **317**, 857–862.

Wiebe,P.H., Morton,A.W., Bradley,A.M., Backus,R.H., Craddock,J.E., Barber,V., Cowles,T.J. and Flierl,G.R. (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar. Biol.*, **87**, 313–323.

Woodward,W.E. and Appell,G.F. (1986) Current velocity measurements using acoustic Doppler backscatter: a review. *IEEE J. Ocean. Eng.*, **OE-11**, 3–6.

Zhou,M., Nordhausen,W. and Huntley,M. (1994) ADCP measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter. *Deep-Sea Res.*, **41**, 1425–1445.