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## Observations of copepod feeding and vertical distribution under natural turbulent conditions in the North Sea

Received: 12 October 2000 / Accepted: 11 December 2000

**Abstract** We present results of simultaneous measurements of turbulent-dissipation rate, zooplankton vertical distribution and copepod gut pigments in the northern North Sea. Analysis shows that some, but not all, copepods (by species, sex and stage) exhibit significant dependence on turbulence in respect to vertical distribution and feeding rate. *Oithona similis* (female and copepodite stages) exhibits an avoidance of the surface layer when turbulence is strong there. For the range of turbulence ( $10^{-7}$  to  $10^{-3}$   $\text{m}^2 \text{s}^{-3}$ ) and ambient chlorophyll concentration ( $0.5\text{--}0.8$   $\mu\text{g l}^{-1}$ ) encountered, *Calanus* spp. and *Metridia lucens* exhibited a significant negative response in feeding-rate index with increasing turbulence. *Centropages typicus* and *Pseudocalanus* spp. also exhibited a negative response but of less significance.

### Introduction

Turbulence is a ubiquitous feature of the marine environment and has a substantial effect on the distribution

and interactions of planktonic biota. Rothschild and Osborn (1989) advanced the theory of turbulent-encounter rates in the plankton. That is, planktonic predators encounter more prey with increasing turbulence, all other things being equal. The magnitude of this positive effect of turbulence depends strongly on the feeding behaviour of the predator (Kiørboe and Saiz 1995) and only operates when the ambient food concentration is less than the saturation concentration of the functional response (Marrasé et al 1990; Saiz et al. 1992). However, turbulence also has a potentially negative influence on feeding. Specifically, beyond a certain level, turbulence may impair the copepod's rate of ingesting food by eroding the feeding current, interfering with the remote detection of prey, or by increasing the pursuit time (Kiørboe and Saiz 1995). Such negative effects have been demonstrated under laboratory conditions (Saiz and Kiørboe 1995) and, combined with the positive effects, result in a dome-shaped relationship between copepod feeding and turbulence, in a manner similar to that described for larval fish, both theoretically (MacKenzie et al. 1994) and experimentally (MacKenzie and Kiørboe 2000).

Superimposed on this general picture in a natural environment is the vertical distribution of turbulence (specifically turbulent-dissipation rate) and the ability of many zooplankton species to migrate vertically. For instance, many copepod species exhibit a diel vertical migration, avoiding the well-lit surface layers during daylight hours to reduce predation risk, and returning at dusk to feed (e.g. Lampert 1989). Furthermore, laboratory studies have shown that copepods change their swimming behaviour in response to turbulence (Saiz 1994; Caparroy et al. 1998). Typically, in a stratified continental-shelf sea, turbulence levels are high in the surface, owing to the wind stress, high near the bottom, owing to tidal and wave-induced bottom stresses, and low in the vicinity of the pycnocline where the vertical density gradient suppresses turbulent motion. The possibility therefore exists that vertical migratory behaviour can be used by zooplankton to seek out the depth of

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Communicated by L. Hagermann, Helsingør

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turbulence and food concentration that maximises feeding opportunities and/or minimises predation risk.

The measurement programme reported on in this work was specifically designed to test whether the theoretical and laboratory studies of copepod feeding translate into observable effects in nature, and/or whether the vertical migratory behaviour of copepods is modified by the effects of turbulence. To date, few field studies have investigated the role of turbulence in zooplankton interactions. A few studies have suggested that copepods migrate downwards during periods of strong turbulence (Mackas et al. 1993; Lagadeuc et al. 1997; Incze et al., in press), and a single study has demonstrated that *Calanus finmarchicus* feeding rates may decline with increasing turbulence (Irigoien et al. 2000). The present measurements were taken in the northern North Sea in October 1998. Detailed physical measurements, including turbulent-dissipation rate, were made. Concurrently, observations of zooplankton vertical distribution and gut pigment contents provided the biological data to test the influence of turbulence.

## Materials and methods

The study was conducted at an anchor station in the northern North Sea (1°0'E, 59°20'N) aboard the R.V. "Dana" during 16–25 October 1998. Water-column depth at this location was 120 m. The site was chosen so as to be well away from strong currents, and the timing to coincide with the breakdown of the seasonal stratification which triggers the autumnal bloom.

### Meteorology, hydrography and turbulence

Casts with a CTD (Seabird 911) equipped with an in situ fluorometer were made at each sampling occasion (6-h intervals). Wind speeds were monitored by the ship's meteorological station, and 12-s averages were recorded every 4 min. Microstructure data were provided by Adolf Stips (JRC, Ispra, Italy). Briefly, an MST (microstructure-turbulence) profiler was used to gather turbulent-dissipation-rate profiles (e.g. Prandke and Stips 1998). The profiler was equipped with standard CTD sensors, a microstructure temperature sensor and two microstructure shear sensors. The profiler was used in the free-fall mode, sinking at about  $0.8 \text{ m s}^{-1}$ . The cable was paid out at high speed so as to avoid interfering with the instrument's free fall. During the cruise, deployments were made every 2–3 h except for a period of ca. 24 h on 17–18 October when the sea state was considered too rough for safe deployment.

Water samples were collected with Niskin bottles mounted on a rosette sampler at 5-, 15-, 30-, and 60-m depths. Four-litre subsamples were filtered by Whatman GF/C glass-fibre filters that were extracted in 90% acetone for 24 h in the dark. The samples were then analysed spectrophotometrically for chlorophyll *a* (Lorenzen 1967) and used to calibrate the in situ fluorometer.

### Zooplankton abundance and vertical distribution

Zooplankton abundance was measured using a submersible pump fitted with a plankton-net bag (mesh size  $40 \mu\text{m}$ ). Samples were collected every 6 h – weather permitting – at depths of 5, 10, 20, 30, 40, 50, 60 and 80 m and the pumping time at each depth was 3–5 min. Samples were immediately fixed in a buffered formalin-seawater solution (4% vol/vol). Servicing of the pump during the

cruise led to an increased pumping rate from 0.2 to  $1.2 \text{ m}^3 \text{ min}^{-1}$ , on 21 October and, owing to technical problems, samples were only collected in the upper 40–50 m of the water column after 23 October.

Zooplankton was counted by species, stage and sex in subsamples, and at least 100 individuals – or the entire sample – of each of the five most abundant species were enumerated in each sample. During the cruise, two *Calanus* species, *C. finmarchicus* and *C. helgolandicus*, were present. These were not differentiated and are reported as *Calanus* spp. here.

To examine the possible influence of turbulence on the vertical distribution, we introduce a parameter,  $\xi$ , defined as the ratio of the integrated abundance,  $C(z)$ , over the upper 25 m to the total integrated abundance.

$$\xi = \frac{\int_0^{25\text{m}} C(z)dz}{\int_0^{80\text{m}} C(z)dz}$$

The 25-m depth horizon was chosen as roughly the level below which turbulence variations are relatively weak. Further, we divided the observations into day and night. We examined the effect of turbulence on the vertical distribution by a regression model:

$$\arcsin\left(\sqrt{\xi}\right) = c + m \log_{10}(\bar{\epsilon})$$

where  $c$  and  $m$  are the intercept and the slope of the linear regression, respectively, and  $\bar{\epsilon}$  is the averaged turbulent-dissipation rate in the upper 25 m. The arcsin transformation is appropriate to normalise the distribution of a proportion or percentage (Sokal and Rohlf 1998). Negative values of  $m$  suggest that there are relatively fewer copepods present in the surface layer when turbulent intensity is high.

In addition to this partitioning ratio, we also examined the depth of centre of mass of the vertical distribution as suggested by Lagadeuc et al. (1997). Specifically, we have  $N$  observations at depths ( $z_1, z_2 \dots z_N$ ) and can define

$$\xi_i = \frac{\int_{z_i}^{z_{i+1}} C(z)dz}{\int_0^{80\text{m}} C(z)dz} \quad \text{for } i = 1, N-1$$

That is, the series  $\xi_i$  gives the frequency distribution of copepods with prescribed depth bins. The centre of mass of the vertical distribution is given by

$$z_c = \sum_{i=1}^{N-1} \xi_i (z_i + z_{i+1}) / 2$$

An increase in  $z_c$  with increasing  $\bar{\epsilon}$  would indicate a downward displacement (either active or passive) of copepods in response to surface turbulence.

### Copepod gut fluorescence and diurnal feeding

Copepods were collected at 6-h intervals in vertical hauls from 40 m using a WP-2 net ( $200 \mu\text{m}$ ). Samples were immediately filtered on nylon-mesh filters (mesh size  $200 \mu\text{m}$ ), frozen in a plastic petri dish using freeze spray, and stored in the dark in a deep freezer ( $-70 \text{ }^\circ\text{C}$ ). On return to the laboratory, dominant copepods, identified to species, stage and sex under a dissecting microscope, were picked for gut fluorescence analysis. During sorting, samples were kept chilled. Sorted animals were rinsed with filtered seawater and transferred to 5 ml 90% acetone for pigment extraction. The samples were kept in the dark at  $4 \text{ }^\circ\text{C}$  for 24 h and fluorescence was measured for chlorophyll pigments using a Turner 111 fluorometer (Holm-Hansen et al. 1965). The fluorescence was calibrated using a chlorophyll-*a* standard (Sigma). To get significant signals, 10–30 specimens were used for each extraction. For most species and stages, 3–10 replicates were measured at each station.

To examine the dependence of gut fluorescence on environmental factors, we first corrected for the variation in gut content due to ambient chlorophyll by computing a filtering-rate index ( $f$ ,  $\text{ml ind}^{-1}$ )

$$f = G/\text{Chl}$$

where  $G$  is gut pigment contents ( $\text{ng chlorophyll-equivalent pigment ind.}^{-1}$ ) and  $\text{Chl}$  is average chlorophyll- $a$  concentration ( $\text{ng chl-}a \text{ ml}^{-1}$ ) in the surface layer (5-, 15- and 30-m depth). We next extracted the diel component of the filtering-rate index by Fourier analysis. The diel component consists of the Fourier coefficients,  $A_o$  and  $B_o$ , of the observations,  $f_i$ , at the diurnal frequency,  $\omega = 2\pi/24 \text{ h}$ . That is:

$$A_o = \frac{2}{N} \sum_{i=1}^N f_i \sin(\omega t_i)$$

$$B_o = \frac{2}{N} \sum_{i=1}^N f_i \cos(\omega t_i)$$

where  $t_i$  is the time of observation in hours from the beginning of the cruise. The amplitude of the diel signal is given by  $f_{\text{amp}} = (A_o^2 + B_o^2)^{1/2}$ . The filtering index residuals,

$$f' = f_i - \bar{f} - A_o \sin(\omega t_i) - B_o \cos(\omega t_i)$$

where  $\bar{f}$  is the mean filtering index, were then calculated and used as the independent variable in analyses of feeding rate versus environmental factors.

## Results

### The physical environment

The sampling period was notably punctuated by frequent and protracted strong wind events (wind speeds over  $15 \text{ m s}^{-1}$ ) separated by short periods of calm (wind speed under  $5 \text{ m s}^{-1}$ ). The time-series for power,  $P$  ( $\text{W m}^{-2}$ ) supplied by the surface wind stress on the water column is plotted in Fig. 1. In this we note that the drag coefficient  $C_d$  is dependent on the wind speed  $w$  ( $\text{m s}^{-1}$ ) as

$$C_d(w) = 0.0063 + 0.000066w$$

(Smith and Banke 1975). The power per unit surface area,  $P$  ( $\text{W m}^{-2}$ ) is then given by

$$P = \rho_a C_d(w) w^3$$

where  $\rho_a$  is the density of air ( $1.22 \text{ kg m}^{-3}$ ). Also plotted in Fig. 1 are the measured dissipation rates at 25-m depth ( $\epsilon_{25}$ ,  $\text{m}^2 \text{ s}^{-3}$ ). These follow the wind power reasonably well, indicating that local wind is a dominant input of turbulent kinetic energy. No significant diurnal variation was found in the dissipation-rate measurements.

Despite the strong winds, the water column remained stratified (Fig. 2a) with a 40–50 m surface mixed layer separated from a well-mixed bottom layer by a sharp pycnocline. Over the 8 days of observations, the surface temperature cooled slightly from  $11 \text{ }^\circ\text{C}$  to  $10 \text{ }^\circ\text{C}$ . The concentration of phytoplankton was relatively stable throughout, with low concentrations (chlorophyll  $< 0.1 \text{ } \mu\text{g l}^{-1}$ ) below the pycnocline and higher concentrations of  $0.5\text{--}0.8 \text{ } \mu\text{g l}^{-1}$  chlorophyll in the surface layer (Figs. 2b and 3).

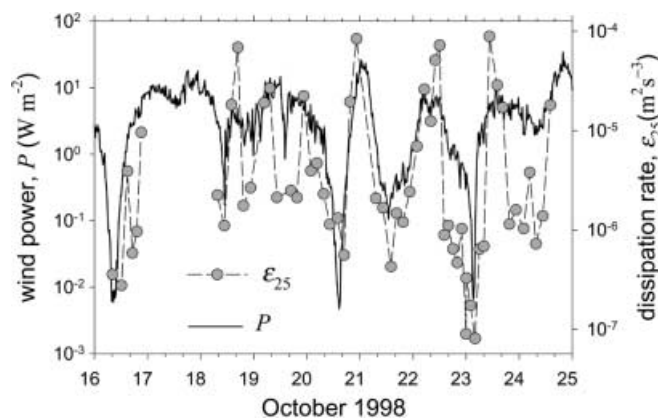
The vertical distribution of turbulent-dissipation rate (Fig. 2c) shows strong depth dependence, with high levels ( $> 10^{-5.5} \text{ m}^2 \text{ s}^{-3}$ ) in the upper 20 m. There was no evidence of a specific tidal signal near the bottom, which would appear at the quarter diurnal. However, somewhat elevated levels ( $> 10^{-6.5}$ ) of turbulence were observed there. These are likely due to bottom stress arising from a combination of tide, waves and wind-driven currents.

### Zooplankton species composition and abundance

Numerically, the copepod fauna was entirely dominated by *Oithona similis*, with a handful of other species occurring at concentrations 1–2 orders of magnitude less (Table 1). There were no consistent changes in the abundance or species composition of copepods in the course of the study period (Fig. 4).

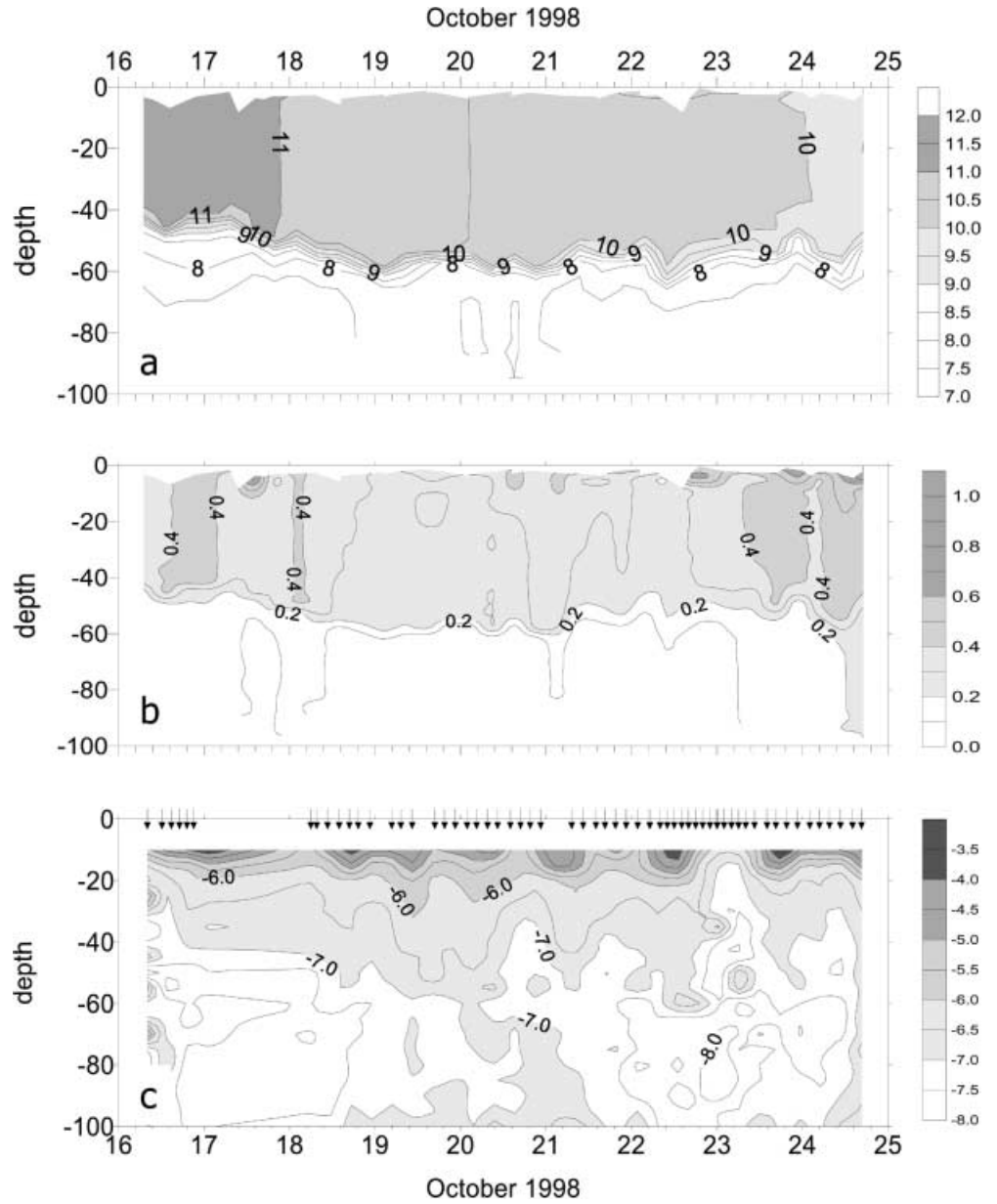
### Vertical distribution and diel migration

Most of the abundant copepods present during the measurement period showed only weak diel migration. The notable exception was *Metridia lucens* females (Fig. 5a) which showed distinct day–night differences in vertical distribution with higher concentrations in the surface layer at night and below the pycnocline during the day. *O. similis* females in comparison (Fig. 5b) maintained high concentrations in the surface layer throughout, with a local concentration maximum at the pycnocline. This local maximum was also evident in *O. similis* copepodite stages. The pattern exhibited by *Calanus* spp. females (Fig. 5c), with no apparent diel migration and high concentration in the surface, was typical of other copepod species and stages.



**Fig. 1** Time-series of wind power per unit sea-surface area,  $P$  ( $\text{W m}^{-2}$ ), during the observation period in October 1998; also shown is the turbulent dissipation rate,  $\epsilon$  ( $\text{m}^2 \text{ s}^{-3}$ ) measured by the MST profiler at 25-m depth

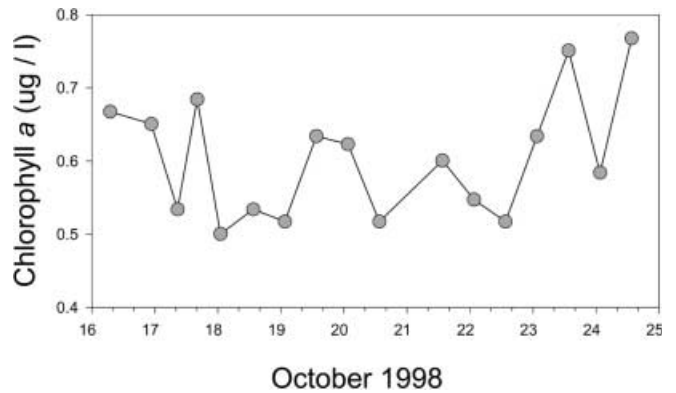
**Fig. 2** The vertical structure of temperature (°C) (a), fluorescence ( $\mu\text{g chlorophyll l}^{-1}$ ) (b), and turbulent dissipation rate [ $\log_{10}(\epsilon \text{ m}^2 \text{ s}^{-3})$ ] (c) during October 1998. Arrows indicate the times at which dissipation rate was measured



**Turbulence and vertical distribution**

We examined the response to turbulence of males, females and all copepodite stages combined in terms of vertical distribution during the day and the during night in the seven most abundant copepod species (Table 2). Our data only allow us to examine bulk properties of vertical distribution. Very few categories showed a statistically significant response in the partitioning ratio ( $\xi$ ) However, estimates of  $m$  were negative in 31 cases and positive in 11 cases. This is significantly different from a 1:1 distribution ( $\chi^2$  test,  $P < 0.01$ ) and suggests that, overall, copepods descended in the water column during periods of strong turbulence.

Data for *O. similis* allow a slightly more detailed analysis (because of better count statistics and/or a

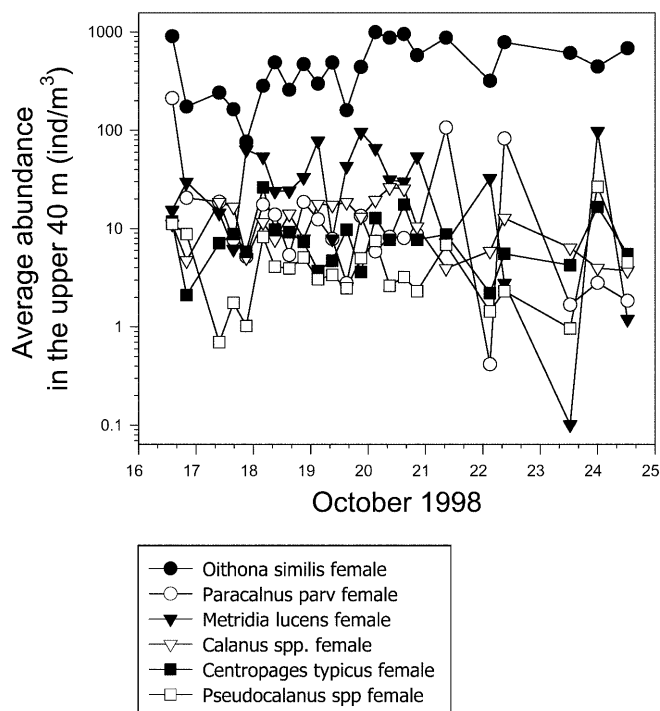


**Fig. 3** Time-series of chlorophyll-a ( $\mu\text{g l}^{-1}$ ) in the surface layer; these are the average of discrete measurements at 5-, 15- and 30-m depth

**Table 1** The mean and standard deviation (in brackets) of the abundance in the upper 40 m ( $\text{ind m}^{-3}$ ) of the dominant copepods by species, sex and stage; *Calanus* spp. includes *C. finmarchicus* and

	Female	Male	CI	CII	CIII	CIV	CV
<i>Oithona similis</i>	502 (285)	24 (27)	84 (61)	231 (152)	261 (172)	294 (186)	178 (98)
<i>Paracalanus parvus</i>	25.3 (48.0)	4.8 (13.2)	0.0 (0.1)	35.9 (68.1)	40.6 (67.2)	39.0 (61.7)	30.6 (65.9)
<i>Metridia lucens</i>	35.2 (29.2)	3.4 (4.9)	1.1 (2.4)	5.4 (7.2)	9.8 (11.4)	18.2 (17.4)	33.1 (32.5)
<i>Calanus</i> spp.	12.3 (6.8)	0.2 (0.6)	0.4 (1.1)	6.3 (3.6)	33.9 (13.5)	33.1 (11.1)	0.6 (1.3)
<i>Centropages typicus</i>	8.6 (5.6)	6.6 (5.7)	0.2 (0.7)	3.2 (2.4)	3.5 (3.2)	3.1 (3.5)	1.1 (1.9)
<i>Pseudocalanus</i> spp.	5.1 (5.5)	0.5 (0.8)	0.0 (0.0)	4.7 (14.2)	8.0 (10.8)	4.5 (4.9)	0.4 (0.8)
<i>Microcalanus pusillus</i>	3.0 (4.9)	0.2 (0.3)	0.0 (0.0)	0.8 (2.0)	1.0 (1.7)	3.3 (4.4)	0.7 (1.7)
<i>Candacia armata</i>	0.5 (0.6)	0.4 (0.4)	0.1 (0.2)	0.2 (0.7)	0.4 (0.5)	0.1 (0.1)	5.9 (4.6)

stronger response). For this species, none of the stages showed a significant response during daytime, and most of the  $m$  values were in fact positive. In contrast, all individual adult and copepodite stages except CV and males had significantly negative  $m$  values during night-time. The depth of the centre of mass,  $z_c$ , for *O. similis* females and copepodites varied in a similar manner (Fig. 6a) between 12- and 35-m depth. While a small element of this variation may be due to a diurnal migration (Fig. 5b), night-time depth of centre of mass correlated significantly with dissipation rate for *O. similis* females and copepodites (Fig. 6b). Thus, apparently, *O. similis* responds to turbulence by descending in the water column only during the night.



**Fig. 4** Time-series of the vertically averaged abundance of copepods ( $\text{ind m}^{-3}$ ) in the upper 40 m of the water column

*C. helgolandicus*, which were not distinguished. *Pseudocalanus* spp. is mostly *P. elongatus*, but may include other species

### Gut pigment, diel variation, and turbulence

All the copepods examined exhibited a diel feeding rhythm to a greater or lesser extent (Fig. 7, Table 3). The most pronounced diel pattern was that exhibited by *M. lucens* (female and CV) with the highest relative amplitude in gut contents, and the least obvious one, that by *Centropages typicus* (female and male). The diel variation in feeding was well described by a sine function (Fig. 8a).

Because gut pigments were very low in several species during daytime, we used only the night-time levels to examine the relation between copepod feeding and external factors. First, we found no significant relation between gut pigment and ambient chlorophyll in any of the species, probably because the variation in ambient chlorophyll level was very modest ( $0.5\text{--}0.8 \mu\text{g l}^{-1}$ , Fig. 3).

The influence of turbulence on the feeding activity of the copepods was then examined by looking at the residuals of the diel fit at and around midnight. The filtering-rate-index residuals were computed for observations made within 4 h of midnight and regressed against average turbulent-dissipation rate in the upper 25 m. Figure 8 illustrates the method for the example of *Calanus* spp. females.

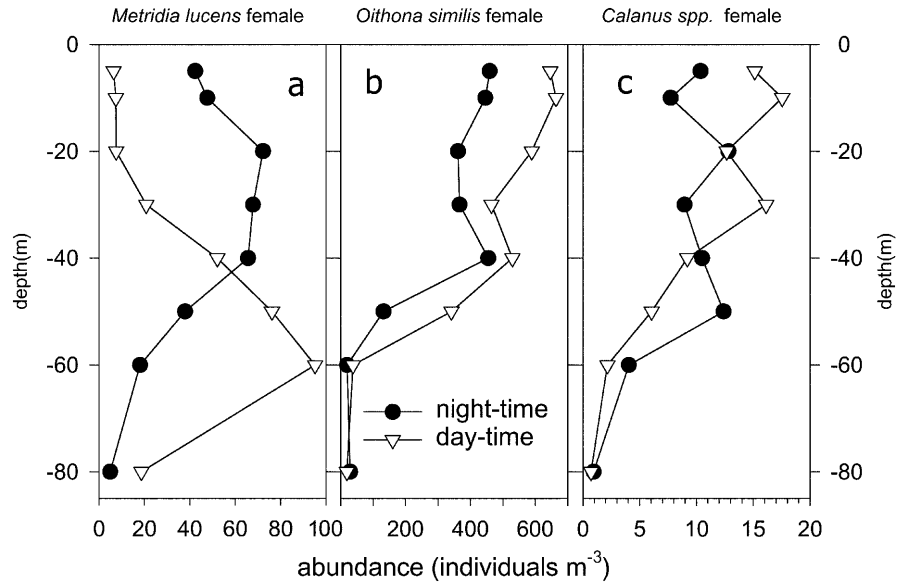
In all eight copepod categories (species, stage, sex) examined, the filtering-rate index declined with increasing turbulence (Fig. 8b and Table 3). This trend was quite significant ( $P < 0.05$ ) for *Calanus* spp. females, CV and CIV, and for *M. lucens* females and CV. The regression is less significant ( $P < 0.1$ ) for *C. typicus* and *Pseudocalanus* spp. Thus, over the range encountered during these observations, turbulence appears to have a negative effect on the rates at which copepods feed on phytoplankton.

## Discussion

### Feeding rate and turbulence

The expected (positive and negative) effects of turbulence on feeding rates depend strongly on the behaviour

**Fig. 5** Depth profiles of averaged abundances (night-time and day-time) (ind m<sup>-3</sup>) for *Metridia lucens* females (a), *Oithona similis* females (b) and *Calanus* spp. females (c)



of the copepod (Kjørboe and Saiz 1995). For example, prey-encounter rates scale with the predator-prey velocity difference. If the behavioural component of this velocity difference is low compared to the turbulent velocity, as in an ambush predator, then turbulence may significantly enhance encounter rates. Conversely, if the behavioural component of the velocity difference is significant, as in copepods that gather food via feeding currents, then the positive effect of turbulence may be small. We here looked at in situ phytoplankton feeding rates in a number of copepods. Several of the examined species may use both an ambush and a feeding-current food-collection strategy (e.g. *Centropages typicus*; Jonsson and Tiselius 1990), but typically, phytoplankton

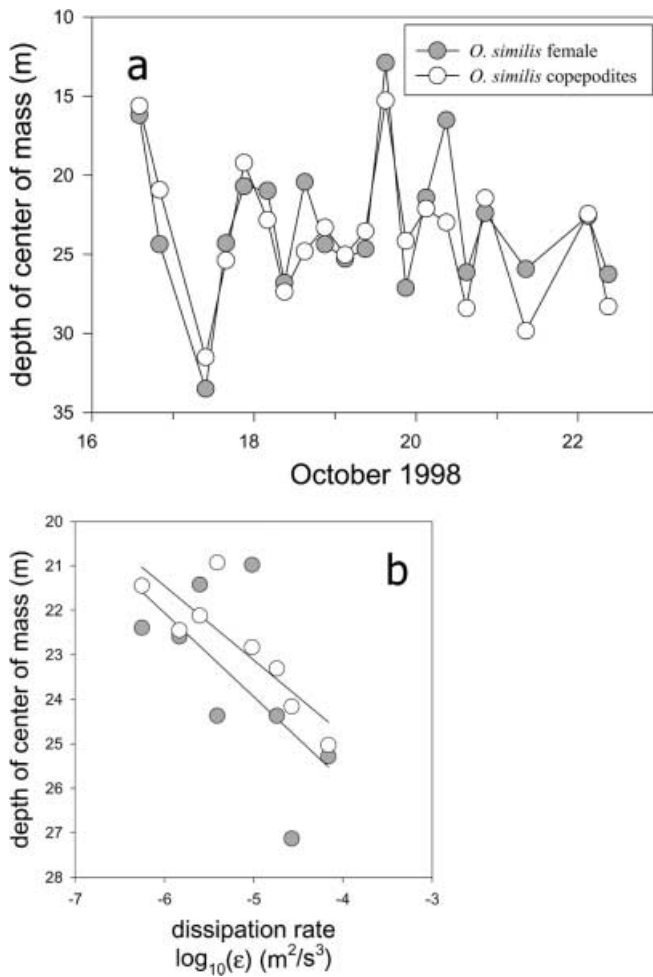
cells are collected in the suspension-feeding mode (Kjørboe et al. 1996). It is relevant, then, to compare feeding-current velocities with turbulence velocities. Perception distance of phytoplankton prey arriving in the feeding current is 1 mm or less, and typical feeding-current velocities at this distance are 0.5–1 cm s<sup>-1</sup> (Strickler 1982; ; Jonsson and Tiselius 1990; Paffenhöfer and Lewis 1990). The velocity difference due to turbulence can be estimated from Delichatsios and Probst's (1975) equation:

$$\omega = 1.37(\epsilon d)^{1/3}$$

where *d* is the separation distance (perception distance). For a typical dissipation rate of 10<sup>-6</sup> m<sup>2</sup> s<sup>-3</sup>,

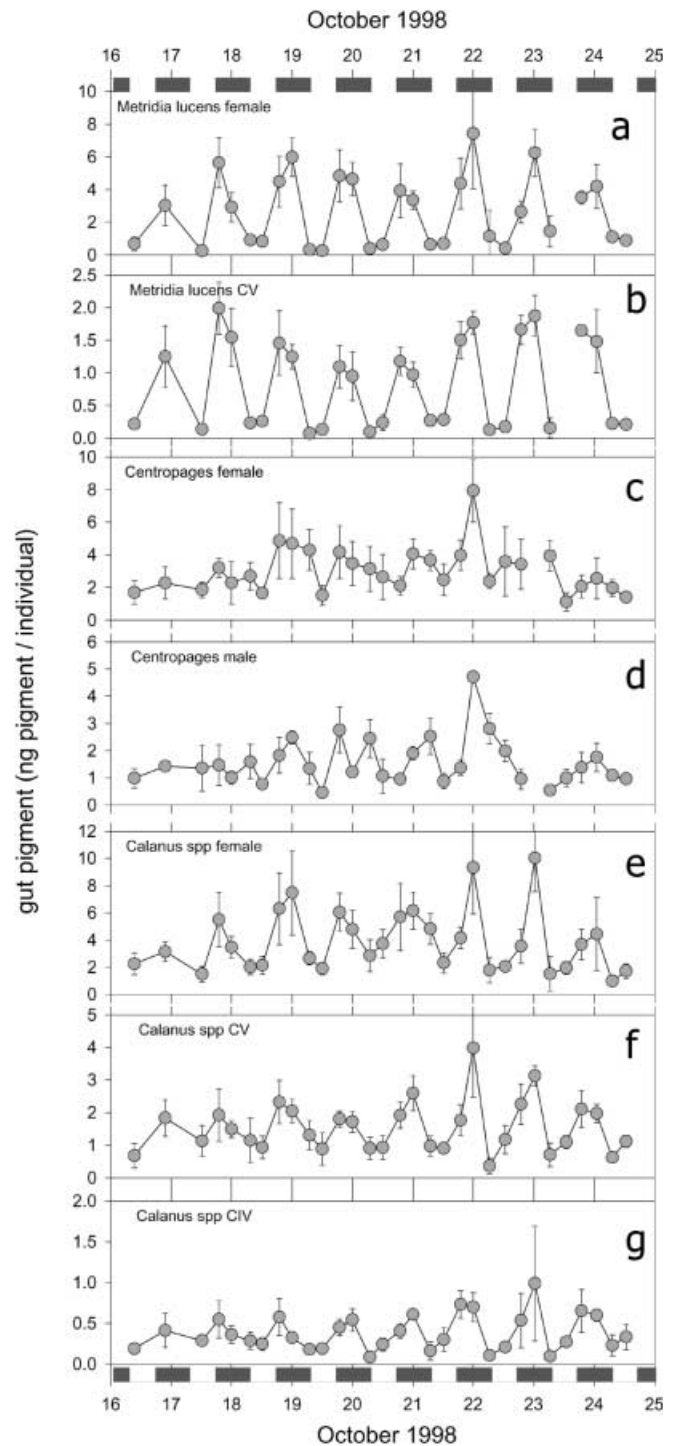
**Table 2** Regression coefficients (slopes) and significance levels for turbulence vs vertical distribution. The model is  $\arcsin(\xi^{1/2}) = c + m \log_{10}(\epsilon)$  where  $\xi$  is the integrated abundance in the upper 25 m to the total integrated abundance, and  $\epsilon$  is the average turbulent-dissipation rate in the upper 25 m. Coefficients that are significant at the 5% level are indicated in boldface. In each case, the number of data points was *n* = 8 for night and *n* = 11 for day

		Night		Day	
		<i>m</i>	<i>P</i>	<i>m</i>	<i>P</i>
<i>Oithona similis</i>	Male	-0.01	0.45	0.02	0.40
	Female	<b>-0.06</b>	<b>0.01</b>	0.07	0.17
	Copepodites	<b>-0.06</b>	<b>0.01</b>	0.02	0.38
<i>Paracalanus parvus</i>	Male	-0.02	0.45	0.13	0.28
	Female	-0.05	0.16	-0.07	0.24
<i>Metridia lucens</i>	Copepodites	-0.03	0.19	-0.05	0.29
	Male	-0.03	0.22	-0.06	0.17
	Female	-0.02	0.10	-0.06	0.21
<i>Microcalanus pusillus</i>	Copepodites	-0.03	0.07	-0.08	0.13
	Male	<b>0.211</b>	<b>0.04</b>	<b>-0.13</b>	<b>0.00</b>
	Female	-0.08	0.08	-0.04	0.36
<i>Calanus</i> spp.	Copepodites	-0.04	0.21	-0.00	0.49
	Male	-	-	<b>-0.78</b>	<b>0.01</b>
	Female	0.02	0.47	-0.17	0.12
<i>Centropages typicus</i>	Copepodites	<b>0.05</b>	<b>0.05</b>	<b>-0.12</b>	<b>0.03</b>
	Male	-0.04	0.43	-0.08	0.22
	Female	0.00	0.39	-0.15	0.12
<i>Pseudocalanus</i> spp.	Copepodites	0.02	0.08	-0.09	0.20
	Male	0.03	0.28	<b>-0.06</b>	<b>0.03</b>
	Female	0.01	0.49	-0.04	0.39
	Copepodites	-0.03	0.26	-0.09	0.18



**Fig. 6a, b** Vertical distribution of *Oithona similis*. **a** Time-series of depth of centre of mass, and **b** night-time depth of centre of mass versus turbulent-dissipation rate; the coefficients of determination for the regressions in **b** are  $R^2 = 0.40$  ( $P < 0.05$ ) for females and  $R^2 = 0.73$  ( $P < 0.01$ ) for copepodites of *O. similis*

$\omega \sim 0.1 \text{ cm s}^{-1}$  during our study, which is one tenth of the feeding-current velocity. Thus, we would expect at most a 10% enhancement in feeding rate, which is too small to be detected, owing to sampling variation. Even at the highest dissipation rates measured,  $\sim 10^{-4} \text{ m}^2 \text{ s}^{-3}$ , turbulent velocities approach the feeding-current velocity at the perception distance; hence, with a potential for doubling the feeding rate. However, when the turbulent velocity at the scale of the perception distance approaches the feeding-current velocity, the feeding current may become significantly eroded and thus affect feeding rate negatively. Therefore, the expectation is that turbulence has a negative rather than a positive effect on food acquisition in suspension-feeding copepods. Phytoplankton feeding rates in all the species and stages examined here were in fact negatively influenced by turbulence. This finding is consistent with the field observation of Irigoien et al. (2000) for *Calanus finmarchicus* and with the experimental results on *Acartia tonsa* of Saiz and Kiørboe (1995).



**Fig. 7a–g** Time-series of gut pigment ( $\text{ng pigment ind}^{-1}$ ) over the observational period in October 1998. **a** *Metridia lucens* female, **b** *M. lucens* CV, **c** *Centropages typicus* females, **d** *C. typicus* males, **e** *Calanus* spp. females, **f** *Calanus* spp. CV, **g** *Calanus* spp. CIV. Grey-shaded areas along the  $x$  axes indicate hours of darkness

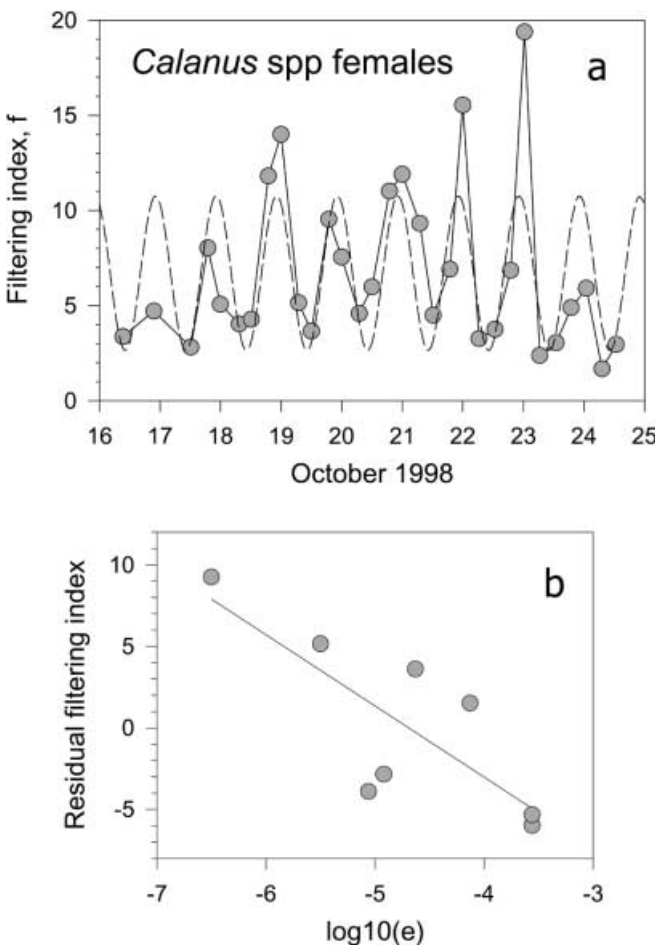
#### Turbulence and vertical distribution

If turbulence affects food acquisition in suspension-feeding copepods negatively, one might hypothesise that copepods would try to avoid the surface layer during

**Table 3** Filtering-rate index for various copepod species, sex and stage. Mean,  $\bar{f}$  and standard deviation  $\sigma_f$  of filtering-rate index; amplitude,  $f_{amp}$ , of the diel component; and regression of midnight

		Mean and standard deviation		Amplitude of diel component		Linear regression on residuals at midnight against turbulence		
		$\bar{f}$	$\sigma_f$	$f_{amp}$	$a$	$b$	$R^2$	$P$
<i>Calanus</i> spp.	Female	6.70	4.26	4.07	-20.5	-4.4	0.62	0.007
	C V	2.66	1.42	1.5	-5.7	-1.2	0.50	0.020
	C IV	0.65	0.38	0.41	-1.9	-0.4	0.70	0.003
<i>Metridia lucens</i>	Female	4.38	3.70	4.82	-14.3	-2.9	0.69	0.003
	C V	1.37	1.13	1.56	-3.1	-0.6	0.61	0.008
<i>Centropages typicus</i>	Female	5.25	2.50	0.94	-13.0	-3.0	0.37	0.064
	Male	2.70	1.53	0.46	-7.7	-1.8	0.37	0.066
<i>Pseudocalanus</i> spp.	Female	0.43	0.37	0.41	-0.9	-0.2	0.25	0.100

periods of strong turbulence, as has in fact been observed previously for some species (Mackas et al. 1993; Lagadeuc et al. 1997; Incze et al., in press). In our study, copepods in general had a vertical migration behaviour, which is consistent with this expectation: they descend in the water column during wind events.



**Fig. 8a, b** *Calanus* spp. females. Regression analysis of filtering index,  $f$ . **a** Time-series of observations (—•—) and Fourier fit at the diurnal frequency (---), **b** linear regression of residual-filtering index with turbulent-dissipation rate,  $\log_{10}(\epsilon \text{ m}^2 \text{ s}^{-3})$

residuals,  $f$ , from diel model on turbulent dissipation  $f = a + b \log_{10}(\epsilon)$ , where  $\epsilon$  is the average dissipation rate in the upper 25 m

The response is not very pronounced, however, and statistically significant only when all species are considered together. Our data for most of the species therefore do not allow us to decide whether this is due to an active response or caused by enhanced vertical mixing in the surface layer during wind events. The similarity in the response between day and night, despite major differences in feeding activity, might suggest that this is merely a passive response.

The response observed in *Oithona similis* was similar to that observed for most other species, even though *O. similis* is not a suspension feeder. However, it was also different, in that *O. similis* reacted to high turbulence by descending in the water column only at night, not during daytime. This suggests that the response was in fact active. Like other cyclopoid copepods, *O. similis* does not produce a feeding current (Paffenhöfer 1993), but is an ambush feeder that perceives swimming prey by the hydromechanical signals these produce (Svensen and Kiørboe 2000). While ambush-feeding copepods are expected to enjoy the largest benefit from ambient turbulence in terms of feeding rates, turbulence may interfere with hydromechanical prey perception, thus having a negative impact at high intensities (Kiørboe and Saiz 1995). Saiz and Kiørboe (1995) observed a dome-shaped relation between (ambush) feeding rate and turbulence in *Acartia tonsa* when it feeds on swimming ciliates that are perceived hydromechanically. Peak feeding rates were observed at a bulk turbulent-dissipation rate of about  $10^{-6} \text{ m}^2 \text{ s}^{-3}$  with lower feeding rates at higher and lower turbulence intensities. In the present study, bulk dissipation rates in the upper 25 m were mainly near or above  $10^{-6} \text{ m}^2 \text{ s}^{-3}$  and, hence, mainly on the downside of the dome-shaped relation for species like *A. tonsa*. Given the similarities in feeding behaviour between *O. similis* and *A. tonsa*, we interpret the avoidance of the highly turbulent surface layer by *O. similis* as a means of allowing continued remote detection of prey.

**Acknowledgements** This study was part of PROVESS (Processes of Vertical Exchange in Shelf Seas), an EU-funded project under the MAST III programme (contract number MAS3-CT97-0159). We acknowledge the field assistance of the captain and crew of the



R.V. "Dana". Dr. A. Stips is acknowledged for provision of dissipation rate data. The experiments comply with the current laws of the country in which they were conducted.

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