Feeding behaviour of *Centropages typicus* in calm and turbulent conditions

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ABSTRACT: Feeding of the copepod *Centropages typicus* on the oligotrich ciliate *Strombidium sulcatum* was studied in the laboratory under controlled, measured conditions of grid generated small scale turbulence. High levels of turbulence, ε (kinetic energy dissipation rate) = 2.9×10^{-2} to 3×10^{-1} cm^2 s^{-3}, increased the clearance rate of *C. typicus* feeding on *S. sulcatum* by up to a factor of 4 in comparison to calm water values. At a level of turbulence of 4.4 cm^2 s^{-3}, we observed a drastic decrease in clearance rates to values equivalent to those in calm water. We suggest an explanation for the observed changes in predation rates with levels of turbulence. Video recorded observations of the behaviour of free swimming *C. typicus* conducted in calm conditions suggest that the copepod uses a cruising strategy to search and encounter *S. sulcatum*. In the presence of this ciliate, *C. typicus* increases the proportion of time spent swimming at a mean velocity of 3.5 mm s^{-1} from 49.5% in filtered seawater without ciliates to 79.5% in the presence of *S. sulcatum* (1 cell ml^{-1}). Furthermore, a qualitative change of the swimming behaviour is triggered by the presence of the ciliate, resulting in an increased proportion of time spent slow swimming in a 'helical' mode. Our results suggest that high levels of small scale turbulence substantially increase predation rates of cruising copepods.

KEY WORDS: Turbulence · Predation · Swimming Behaviour · *Strombidium sulcatum* · *Centropages typicus*

INTRODUCTION

The effects of small scale turbulence on zooplankton feeding ecology have become an active field of investigation over the last 10 yr. Despite the increasing body of literature concerning the theoretical aspects of this subject (Rothschild & Osborn 1988, Davis et al. 1991, MacKenzie & Leggett 1991, Yamazaki et al. 1991, Kiørboe & Saiz 1995, Caparroy & Carlotti 1996, Osborn 1996), only a few experimental or field studies have actually demonstrated that small scale turbulence could increase feeding rates of zooplanktonic predators (Sundby & Fossum 1990, Saiz et al. 1992, Landry et al. 1995, Saiz & Kiørboe 1995, Lough & Mountain 1996).

In a recent modelling study, Kiørboe & Saiz (1995) suggested that the potential effects of small scale turbulence

on copepod predation rates are highly dependent on the predator's swimming behaviour. Their theory predicts a major contribution of small scale turbulence to predator-prey encounter rates in the case of an ambush feeding strategy, whereas only a minor contribution could be expected for suspension feeding copepods.

The experimental validation of this hypothesis (Saiz & Kiørboe 1995) in the case of the calanoid copepod *Acartia tonsa*, when suspension feeding on the diatom *Thalassiosira weissflogii* or ambush feeding on the ciliate *Strombidium sulcatum*, has emphasised the necessity of combining descriptions of the feeding (swimming) behaviour with predation rate studies in order to understand the underlying mechanisms of predation and its potential sensitivity to the effects of small scale turbulence. This approach has already provided sound results for both copepods (Saiz 1994, Saiz & Kiørboe 1995, Kiørboe et al. 1996) and fish larvae (MacKenzie & Kiørboe 1995).

In this study we chose to examine the effect of turbulence on *Centropages typicus* feeding on *S. sulcatum*,

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because: (1) up to now the effects of small scale turbulence on copepod feeding rates have only been studied for species of the genus *Acartia*; (2) *C. typicus* displays a flexible behavioural repertoire which includes a raptorial component (Cowles & Strickler 1983) and the ability to passively sink in the water column (Tiselius & Jonsson 1990); and (3) the presence of motile prey such as *S. sulcatum* triggers a switch to ambush search mode in other copepods (e.g. *A. tonsa*: Jonsson & Tiselius 1990, Kiørboe et al. 1996).

These considerations lead to the suggestion that *Centropages typicus* could behave as an ambush predator in the presence of *Strombidium sulcatum*, and that its feeding rates could be substantially increased in turbulent versus calm conditions. Because the effect of turbulence on predator-prey encounter rates strongly depends on the predator searching behaviour, we also examined the free swimming behaviour of *C. typicus* in the presence of the oligotrich ciliate *S. sulcatum* in order to determine which searching strategy is triggered by the presence of this prey.

The goal of this study was to assess the magnitude of the effect of small scale turbulence on the feeding rates of *Centropages typicus*, an important calanoid copepod in Mediterranean waters, on the aloricate ciliate *Strombidium sulcatum*, and to use behavioural observations to interpret our feeding experiment results.

MATERIAL AND METHODS

Feeding experiments. *Generation and measurement of turbulence:* Small scale turbulence was generated by means of oscillating stainless steel grids (diameter 8.6 cm, mesh size 1 cm, open area ca 70%). The amplitude of the stroke (19 cm) covered approximately the entire volume of the experimental containers. A thyristor control permitted variation of the stroke frequency and consequently of the turbulence intensity. Turbulence was estimated for the different stroke frequencies through measurement of the kinetic energy dissipation rate: ε (cm^2 s^{-3}). Instantaneous fluid velocities (the vertical component u_z, and 1 horizontal component u_x) were measured with a 2-axis laser Doppler anemometer, using iriodin particles (equivalent spherical diameter 1.5 μm) as tracers of fluid motion.

Measurements were made at a point located in the upper half of the beaker, midway between the wall and the shaft of the grid, where each component of the velocity was sampled for ca 20 min at 20 Hz. The cylindrical beaker was enclosed in a square acrylic plastic tank filled with seawater, in order to avoid velocity measurement errors due to refraction of the beam by the cylindrical wall. An incremental electronic counter

adjusted to the rotation axis of the motor driving the turbulent apparatus generated a coded signal at the beginning of each oscillating period. In the raw data files of velocity measurements, this coded signal permitted subdivision of the whole velocity time series into individual oscillation periods.

Turbulent kinetic energy, TKE (cm^2 s^{-2}), at time t during an oscillating period was computed as (Peters & Redondo 1997):

$$\text{TKE}(t) = \tfrac{1}{2}\left[\sigma^2 u_x(t) + \sigma^2 u_y(t) + \sigma^2 u_z(t)\right] \tag{1}$$

where $\sigma^2 u_i(t)$ is the variance of the velocities measured at time t in direction i. The y component of the velocity was considered equal to the x component, assuming horizontal isotropy of turbulence in the beaker. The passage of the grid through the measurement point resulted in a clear peak signature of the TKE time series (Fig. 1). ε was estimated from the exponential decay of TKE over time after the onset of a peak of kinetic energy (Saiz & Kiørboe 1995):

$$\text{TKE}(t) = a e^{-bt} \tag{2}$$

where t is the time since the peak of kinetic energy and a and b are constants.

The instantaneous dissipation rate $\varepsilon(t)$ is given by:

$$\varepsilon(t) = \left|\frac{d\text{TKE}(t)}{dt}\right| = abe^{-bt} \tag{3}$$

and a time averaged dissipation rate, $<\varepsilon>$, was computed as:

$$<\varepsilon> = \frac{1}{T}\int_0^T \varepsilon(t)dt = \frac{a}{T}(1 - e^{-bT}) \tag{4}$$

where T is the portion of the period following the passage of the grid that showed a trend of decreasing turbulent kinetic energy (Peters et al. 1996).

At each stroke frequency, 2 values of $<\varepsilon>$ were computed: 1 for the downward passage of the grid and 1 for the upward passage. The time average of these 2 values (ε_{av}) was retained as the estimated dissipation rate for the whole oscillation period, and was used in subsequent calculations. Three stroke frequencies were examined, and results of turbulence measurements are presented in Table 1.

Experimental design: We examined the effect of turbulence on feeding rates of *Centropages typicus* at ciliate concentrations comparable with coastal western Mediterranean waters (0.25 to 4 ciliates ml^{-1}).

The experimental design was similar to the one used by Saiz & Kiørboe (1995) and consisted of 1 experimental factor, turbulence intensity, tested at 3 levels and contrasted with a control situation (calm water conditions). The 2 lowest intensities of turbulence (Table 1) are representative of realistic values for coastal and shelf waters (MacKenzie & Leggett 1993),
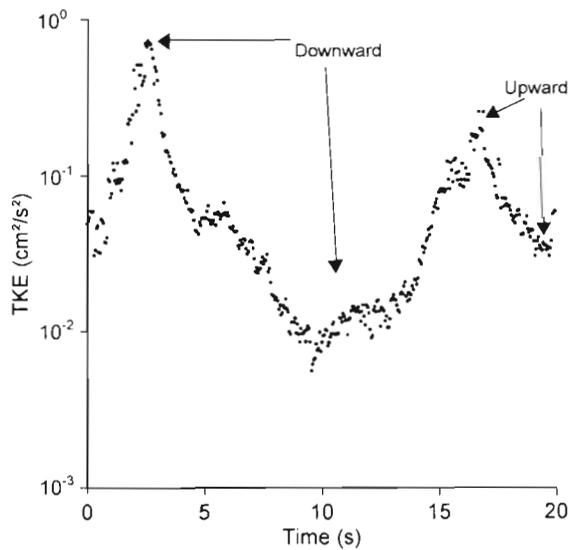
Fig. 1. Time series measurement of turbulent kinetic energy, TKE (cm² s⁻²), over a period of oscillation of the grid at 3 strokes min⁻¹. The 2 peaks of kinetic energy indicate the downward and upward passages of the grid during the oscillation period. Arrows indicate fractions of the oscillation period showing a decrease of TKE over time which are used to compute $<\varepsilon>$ (see text and Table 1 for further details)

whereas the highest intensity of turbulence is probably too high to be representative of field conditions.

Turbulent experiments were conducted in glass beakers (inner diameter 11.5 cm, effective volume 2.3 l), whereas calm conditions experiments were conducted in screw-cap bottles (2.3 l), with no air bubbles inside, incubated on a slowly rotating wheel (end-over-end; 0.2 rpm). Four independent experiments were conducted at each turbulence intensity. Each experiment consisted of 3 replicates in turbulence and 3 in still water. Three additional containers without copepods were run at each condition to correct for growth of prey.

The oligotrich ciliate *Strombidium sulcatum* was grown on live bacteria (in protease peptone medium; Oxoid Unpath, Inc.) in darkness at 17°C. Exponential growth phase ciliate cultures, 3 d post-transfer, were used in all experiments.

The stock culture of ciliates was diluted to the desired concentration with 0.45 µm filtered seawater. Growth of the ciliates during the grazing experiments was sustained by adding planktonic bacteria to the experimental suspensions to a concentration of ca 10^6–10^7 bacteria ml⁻¹, and EDTA to a final concentration of 30 µM (Jonsson & Tiselius 1990).

Individuals of the copepod *Centropages typicus* were collected with a 'homogeneous plankton net' (280 µm mesh size) at Point B, a standard oceanographic station at the entrance of the bay of Villefranche, France. Specimens were diluted in buckets and transported to the laboratory. Adult females were sorted by pipette and acclimated for 24 h at 17°C. To ensure some homogeneity in the physiological condition of the copepods, the acclimation consisted of being held in 5 l beakers filled with 0.45 µm filtered seawater to which was added a suspension of the haptophycean *Hymenomonas elongata* to a final concentration of 10^4 cells ml⁻¹. At the start of each experiment, 8 to 10 acclimated copepods were placed in the experimental containers. Two initial 1 l samples were preserved in 2 % acid Lugol's solution.

Experiments were conducted in darkness, at 17°C, and lasted ca 18 h. At the end of the experiments, the whole experimental suspension was sieved (200 µm) and mortality of the copepods determined. Final 1 l samples were preserved in 2 % Lugol's solution for each experimental container.

Initial and final samples were filtered onto 5 µm membrane filters and counted under a microscope at 100× magnification. As a general procedure, the whole filter was counted and the filtered volume was chosen such that at least 100 cells were counted. Average food concentrations and clearance rates were computed as in Frost (1972).

Behavioural observations. The calm water behaviour of free swimming *Centropages typicus* feeding on *Strombidium sulcatum* was investigated by filming adult females in the absence (0.45 µm filtered seawater) or presence of ciliates (1 cell ml⁻¹). Two replicate tapes were recorded for each experimental condition. Copepods were filmed in a transparent Plexiglas aquarium (height 20 cm, width 10 cm, depth 10 cm, volume 2 l) using a black-and-white CCD camera (Hitachi KP-M1) equipped with a 108 mm macro lens. The video recorder (Sony EVO-9800P) gener-

Table 1. Measurements of kinetic energy dissipation rate ε_{av} (cm² s⁻³) for the 3 stroke frequencies (strokes min⁻¹) used in this study. For both upward and downward motions of the grid, the coefficients of the exponential model (a and b, Eq. 2) fitted to time series of TKE, the correlation coefficient of the fit (r), and the time averaged dissipation rate $<\varepsilon>$ (cm² s⁻³) are shown. ε_{av} (cm² s⁻³) is the time averaged dissipation rate for the whole oscillation period

Stroke frequency	Direction	a	b	r	$<\varepsilon>$	ε_{av}
3	Upward	0.117	0.586	0.94	2.7×10^{-2}	2.9×10^{-2}
	Downward	0.207	0.625	0.96	3.4×10^{-2}	
6	Upward	0.771	1.026	0.97	3.4×10^{-1}	3.0×10^{-1}
	Downward	1.333	0.967	0.96	2.9×10^{-1}	
12	Upward	8.920	2.634	0.97	7.4×10^{0}	4.4×10^{0}
	Downward	7.400	1.452	0.94	2.9×10^{0}	

ated a time code and provided a time resolution of 40 ms between frames (25 frames s^{-1}). A white light source filtered through a red filter provided illumination of the aquarium (3.4 µE m^{-2} s^{-1} measured with Biooptical QLS-100 sensor).

Copepods were subjected to an acclimation period identical to the one used for feeding experiments (see above). Ten adult females were placed in the aquarium and allowed to stay undisturbed for 1 h before recording started. All tapes were recorded in a temperature controlled room, at 17°C. Recording started at 15:00 h. Individuals were filmed for a period of ca 5 min, during which the operator kept them in focus through the turning of the camera on a tripod and manual focusing. If a copepod was lost or filmed for a sufficient amount of time, the operator searched for another copepod and started a new sequence. For each experiment a total of 50 to 60 min was recorded.

The videotapes were analysed at normal speed (25 frames s^{-1}) by the operator, with the assistance of a computer running a FORTRAN program. This program allowed the recording of both the type and duration of the different behavioural sequences by using the internal clock of the computer. Three types of behavioural sequences were considered following the nomenclature of Cowles & Strickler (1983): (1) jumps or fast swimming; (2) slow swimming; and (3) breaks or sinking events.

During slow swimming, the copepod performs rhythmic motions of the feeding appendages (second antennae, first maxillae and maxillipeds) which create a feeding current and propel the copepod forward in a gliding movement. Two modes of slow swimming were distinguished: rectilinear swimming mode (RS) in which the cephalic appendage motions propelled the copepod in a rectilinear path, and helical swimming mode (HS) in which the copepod performed 360° vertical turns (Tiselius & Jonsson 1990) using its urosome as a rudder. Direction of net displacement corresponded to the rotation axis of the helix. Sinking events are periods without any motion of the feeding appendages, which resulted in passive sinking of the copepod. Jumps or fast swimming were 2 to 4 bodylengths displacements in a short period of time (ca 3 to 4 frames).

Since we had chosen to film free swimming copepods for periods of several minutes, it was not possible to keep the copepod in clear focus at high magnification, and to clearly distinguish the motion of the feeding appendages at all times. Nevertheless, it was still easy for the operator to distinguish the

different behavioural sequences due to the slow swimming motion during feeding current generation, and the immediate passive sinking which follows the arrest of appendage motions. The velocity of *Centropages typicus* while making swimming bouts was estimated by tracking successive positions of the copepods on plastic sheets frame by frame.

Statistical analysis. The effects of turbulence intensity on maximum clearance rates and ciliate presence/absence on behavioural variables (time budgets and behavioural frequencies) were analysed by using unpaired Student's 2-tailed (t_2) or 1-tailed (t_1) t-tests when the assumption of homoscedasticity was fulfilled. When this was not possible, Mann-Whitney U-tests (U_t) were used.

RESULTS

Effect of turbulence on *Centropages typicus* clearance rates

The effect of turbulence on the functional response of *Centropages typicus* was studied at ciliate densities less than 4 cells ml^{-1}. In calm conditions, clearance was in-
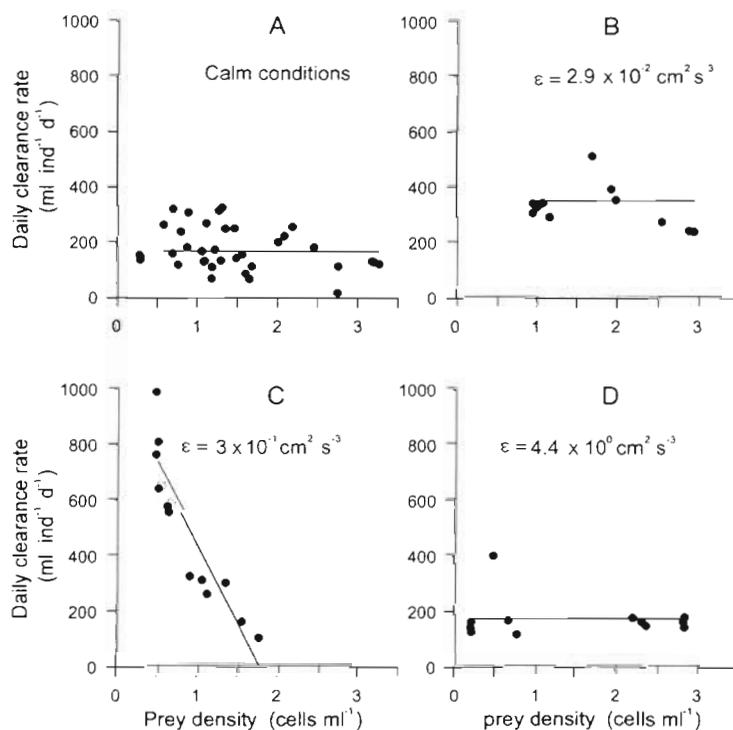

Fig. 2. Clearance rate (F; mean: $<F>$) of *Centropages typicus* feeding on *Strombidium sulcatum* in calm and turbulent conditions at concentrations ($<C>$) <4 cells ml^{-1} (A) Calm water conditions, $<F>$ = 170 ± 81 (SD) ml cop.$^{-1}$ d^{-1} (B) 3 strokes min^{-1}: $<F>$ = 354 ± 64 (SD) ml cop.$^{-1}$ d^{-1} (C) 6 strokes min^{-1} F = 1011 – 564 $<C>$, R^2 = 0.8, regression line shown. (D) 12 strokes min^{-1} $<F>$ = 177 ± 74 (SD) ml cop.$^{-1}$ d^{-1} Solid line in A, B and D· $<F>$

Table 2. Clearance rates of *Centropages typicus* feeding on *Strombidium sulcatum* at different turbulent intensities. Maximum clearance rate at the optimal level of turbulence ($\varepsilon = 3 \times 10^{-1}$ cm^2 s^{-3}) is estimated as the predicted clearance rate at a ciliate concentration of 0.5 cells ml^{-1} from a fitted linear regression (see text and Fig. 2 for further details)

Dissipation rate (cm^2 s^{-3})	Clearance rate (± SD) (ml cop.$^{-1}$ d^{-1})
0	170 ± 81
2.9×10^{-2}	354 ± 64
3×10^{-1}	732 ± 114[a]
4.4×10^{0}	177 ± 74

[a]Maximum clearance rate ±95 % confidence intervals

dependent of ciliate concentration (Fig. 2A; $R^2 = 0.13$, p > 0.05) and averaged 170 ± 81 (SD) ml cop.$^{-1}$ d^{-1} (Table 2)

Variations in clearance rate with ciliate densities for the 3 levels of turbulence examined are presented in Fig. 2B, C and D. Different patterns were observed depending on the level of turbulence considered. At the lowest value of dissipation rate ($\varepsilon = 2.9 \times 10^{-2}$ cm^2 s^{-3}), clearance rate was independent of prey density (Fig. 2B; $R^2 = 0.1$, p > 0.8) and averaged 354 ± 64 (SD) ml cop.$^{-1}$ d^{-1} (significantly higher than calm water estimate: t_1, p < 0.001). The same trend was observed for the highest level of turbulence tested ($\varepsilon = 4.4$ cm^2 s^{-3}), for which clearance rate averaged 177 ± 74 (SD) ml cop.$^{-1}$ d^{-1} (Fig 2D: $R^2 = 0.025$, p > 0.6) and was not significantly different from calm water estimate (t_2, p > 0.8).

For the intermediate (but high) level of turbulence ($\varepsilon = 3 \times 10^{-1}$ cm^2 s^{-3}), clearance rate decreased sharply with increasing ciliate densities (from 0.5 to 2 cells ml^{-1}). This trend can be explained by a turbulence enhanced apparent prey density, resulting in saturated ingestion rates at low ciliate concentration. Maximal clearance rate was estimated as the predicted clearance rate at a ciliate concentration of 0.5 cells ml^{-1}, from a fitted linear regression (Fig. 2C): $\beta = 732 \pm 114$ (95 % confidence intervals) ml cop.$^{-1}$ d^{-1}. Due to the modification of *Centropages typicus* functional re-

sponse at this particular level of turbulence, maximum clearance rate is the best estimate of β (ml cop.$^{-1}$ d^{-1}), the encounter rate kernel or capture rate volume (Saiz & Kiørboe 1995), which includes the kinetic contribution of small scale turbulence to predator-prey relative velocity.

For the 2 lowest levels of turbulence (Table 2), estimated capture rate volumes were higher than the one observed in calm water conditions. We observed then a dome shaped effect of turbulence on estimated capture rate volumes. Maximal effect was observed at 6 strokes min^{-1}, at which β reached a value nearly 4 times higher than that in calm water conditions, and decreased at both higher and lower levels of turbulence.

Swimming behaviour of *Centropages typicus* in calm conditions

In filtered seawater, *Centropages typicus* spent equal amounts of time between swimming activity [49.5 ± 7.1 (SD) %; Table 3] and breaks [50.4 ± 7.1 (SD) %]. In the presence of ciliates, *C. typicus* altered its behaviour. The percentage of time spent swimming significantly increased up to 79.5 ± 4.2 (SD) % (t_1, p < 0.02), whereas the percentage of time spent in breaks decreased significantly to 20.5 ± 4.2 (SD) % (t_1, p < 0.02). Jumping behaviour was not considered in the computation of the time budget, because it represented, at most, 0.2 % of the total time of observation.

No changes in the duration of breaks were observed between the 2 food conditions (U_t: p > 0.08); the average break durations were 2.78 ± 0.13 (SE) s (range: 0.16 to 23 s) and 2.78 ± 0.06 (SE) s (range: 0.16 to 26 s) in the presence and absence of *Strombidium sulcatum* respectively.

A more striking result was that the contribution of swimming bout length to *Centropages* swimming time changed in the presence of *Strombidium sulcatum*, due to a major contribution of long swimming bouts. In filtered seawater, the average swimming bout duration was 2.06 ± 0.1 (SE) s (range: 0.11 to 69.7 s), whereas it

Table 3. *Centropages typicus*. Total time of observation (s) and percentage of observation time spent slow swimming, in helical (HS) and rectilinear (RS) swimming modes, and in breaks (passive sinking). Both replicates (rep1 and rep2) are shown and data are classified according to absence (0.45 µm filtered seawater) or presence (1 cell ml^{-1}) of *Strombidium sulcatum*

Food conditions		Time	% slow swimming	% HS	% RS	% breaks
Filtered	Rep1	2421	54.6	16.6	38.0	45.4
seawater	Rep2	3402	44.5	10.0	34.5	55.5
	Average ± SD		49.5 ± 7.1	13.3 ± 4.6	36.2 ± 2.4	50.4 ± 7.1
Strombidium	Rep1	3034	82.5	76.2	6.30	17.5
sulcatum	Rep2	3226	76.5	65.6	10.9	23.5
(1 cell ml^{-1})	Average ± SD		79.5 ± 4.2	70.9 ± 7.4	8.6 ± 3.2	20.5 ± 4.2

increased to 6.44 ± 0.46 (SE) s (range: 0.11 to 143 s) in the presence of ciliates. In the presence of ciliates, swimming bout length was significantly higher (U_t: p < 0.0001).

This trend was a result of a change in the relative contribution of the 2 kinds of swimming modes, rectilinear swimming (RS) and helical swimming (HS), to the total swimming time. Fig. 3 shows a decomposition of the cumulative distribution of % of total time spent swimming in these 2 modes.

The major difference in behaviour between food conditions was due to a larger contribution of HS bouts in the presence of ciliates. The proportion of swimming time spent in HS mode increased on average from 26.85 ± 6.2 (SD) % in filtered seawater to 89.2 ± 4.5 (SD) % in the presence of ciliates (t_1: p < 0.01), and consequently the proportion of swimming time spent in RS mode decreased. HS bouts were significantly longer than RS bouts (U_t: p < 0.0001) and bout duration for these swimming modes averaged 14.1 ± 0.8 (SE) s (range: 0.43 to 143 s) and 1.48 ± 0.05 (SE) s (range: 0.1 to 69 s) respectively. The actual length of both RS and HS bout durations was unaffected by the presence of ciliates (U_t: RS, p > 0.1; HS, p > 0.4).

Both breaks and RS frequencies decreased in the presence of ciliates (Table 4; t_1: RS, p < 0.01; breaks, p < 0.001) whereas HS frequency increased (t_1: p < 0.01).

Jumping frequency was unaffected by the presence of ciliates (Table 4; t_2: p > 0.5) and averaged 2.5 ± 1 (SD) jumps min^{-1}. The swimming velocity of Centropages typicus, determined from the videotapes, was 0.35 ± 0.09 (SD) cm s^{-1} (n = 45).

DISCUSSION

Clearance rates and free swimming behaviour of Centropages typicus in the presence of Strombidium sulcatum in calm conditions

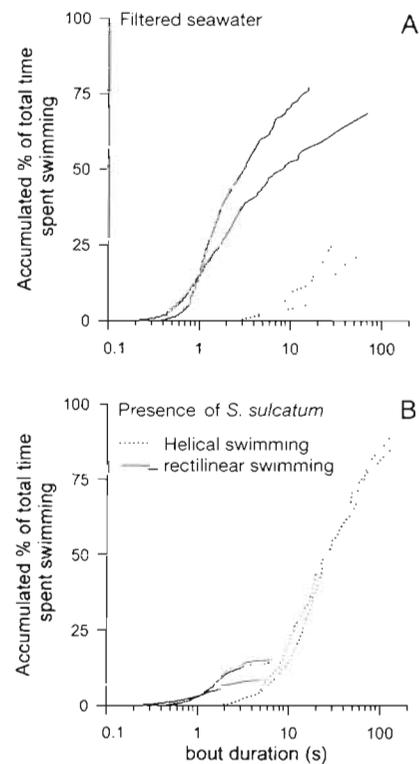Our estimations of Centropages typicus clearance rates on Strombidium sulcatum obtained in calm con-

Fig. 3. Centropages typicus. Cumulative distributions of the proportion of total time spent swimming in rectilinear mode or helical mode in (A) filtered seawater and (B) the presence of Strombidium sulcatum. Data shown for both replicates

ditions were comparable to previous results concerning species of the genus Centropages (Table 5). Clearance rates for C. hamatus and C. abdominalis feeding on the same range of ciliate concentrations were between 11.0 and 170.4 ml cop.$^{-1}$ d^{-1}.

The highest clearance rates measured at low ciliate concentrations were those of Wiadnyana & Rassoulzadegan (1989), and concerned Centropages typicus. Although their study was conducted in the presence of an alternative prey, the dinoflagellate Prorocentrum micans, their results can be compared with our observations due to the net preference of C. typicus

Table 4. Centropages typicus. Total time of observation (s) and frequency (min^{-1}) of jumps (fast swimming), HS, RS and breaks. Both replicates (Rep1 and Rep2) are shown and data are classified according to absence (0.45 μm filtered seawater) or presence (1 cell ml^{-1}) of Strombidium sulcatum

Food conditions		Time	Jumps	HS	RS	Breaks
Filtered	Rep1	2421	4.2	0.9	14.2	11.0
seawater	Rep2	3402	1.8	0.4	13.0	11.0
	Average ± SD		3.0 ± 1.7	0.6 ± 0.3	13.6 ± 0.8	11.0 ± 0.0
Strombidium	Rep1	3034	1.8	2.9	4.1	4 6
sulcatum	Rep2	3226	2.2	2.9	4.8	4.9
(1 cell ml^{-1})	Average ± SD		2.0 ± 0.27	2.9 ± 0.0	4.4 ± 0.4	4.7 ± 0.2

Table 5. Clearance rates (F, ml cop.$^{-1}$ d^{-1}) of *Centropages* species feeding at low ciliate concentrations ($<C>$, cells ml^{-1})

Copepod species	Ciliate prey	$<C>$	F	Source
Centropages hamatus	Natural assemblage	0.20–0.80	32.3–125.0	Tiselius (1989)
	Natural assemblage	1.73	11.0–19.4	Turner & Granéli (1992)
C. abdominalis	Natural assemblage	1.2–2.2	28.8–170.4	Fessenden & Cowles (1994)
C. typicus	*Strombidium sulcatum*	0.7–1.7	349–1221	Wiadnyana & Rassoulzadegan (1989)

for *S. sulcatum*, which represented 80% of its reported daily ration in these experiments. Within a range of ciliate concentrations similar to our experiments (<3 cells ml^{-1}), these authors observed clearance rates varying from 349 to 1221 ml cop.$^{-1}$ d^{-1}. These results are in the range of our observed clearance rates for the 2 lowest levels of turbulence (see Fig. 2). Furthermore, it should be noted that Wiadnyana & Rassoulzadegan's experiments were performed on a Ferris wheel rotating at 12 rpm with air bubbles inside the incubating bottles. So most probably their experiments were performed at an unquantified level of turbulent conditions. This emphasises the necessity of controlling the state of fluid motion in zooplankton feeding experiments in order to obtain accurate estimates of feeding rates.

Our behavioural study in calm conditions indicated that in the presence of *Strombidium sulcatum Centropages typicus* increases its foraging effort in the form of an increased proportion of time spent in swimming activity. Similarly, Cowles & Strickler (1983) observed that at low concentrations of *Gymnodinium nelsonii, C. typicus* increased the proportion of time spent swimming compared to filtered seawater conditions.

We found that the amount of time spent slow swimming in the presence of *Strombidium sulcatum* [79.5 ± 4.2 (SD) %] is somewhat higher than previous results for the same species. Tiselius & Jonsson (1990) reported swimming activity of 58 ± 6 (SD) % at comparable low light levels. However, their experiments were performed in natural seawater at unquantified levels of naturally occurring prey.

A more important difference with previous observations of the swimming behaviour of *Centropages typicus* is that the presence of ciliates stimulated a qualitative change in the swimming behaviour of the copepod. This change resulted in an increased contribution of long swimming bouts performed in the helical swimming mode (see Fig. 3).

Comparable qualitative changes in bout duration were observed in *Acartia tonsa* (Saiz 1994). At low concentrations of the diatom *Thalassiosira weissflogii*, an increase of the proportion of time spent in long swimming bouts (>3 s) clearly explained the shape of the reported Holling type III functional response of the

copepod. Nevertheless, it is noteworthy that no comparable plasticity in swimming mode has been previously described in any *Centropages* species.

Cowles & Strickler (1983) observed swimming bout duration ranging between 0.1 and 10 s, but their study concerned tethered adult females of *Centropages typicus* feeding on dinoflagellates. Tiselius & Jonsson (1990) reported an average feeding bout duration of 4 ± 0.3 (SD) s.

We observed much longer swimming bouts (up to 143 s). Over the 1778 sequences of RS bouts recorded, only 16 were higher than 10 s. During these long bouts, the copepod performed tightened turns between periods of strict linear slow swimming. The rest of the RS bouts described the 'hop' phase of the typical 'hop and sink' motion.

Swimming bouts >10 s were mainly composed of the HS mode or looping behaviour described by Tiselius & Jonsson (1990). The major difference between our results and previous measurements of *Centropages typicus* feeding bout length is due to the observation of these long helical swimming bouts.

Vertical looping behaviour has been described in the freshwater cyclopoid copepod *Mesocyclops edax* (Williamson 1981), and was considered as an adaptation in order to remain in patches of high food density. However, our experiments were conducted at low ciliate densities, and HS swimming behaviour was observed at all depths in the aquarium, excluding a hypothetical effect of vertical patchiness in ciliate distribution. A more general advantage of the HS mode may be to increase the copepod searching efficiency through higher 'realised encounter volume' (Bundy et al. 1993).

Four types of feeding strategies have been described for calanoid copepods (Greene 1988, Tiselius & Jonsson 1990): (1) motionless sinking ambush strategy combined with short jumps (*Acartia clausi* and *A. tonsa*); (2) slow moving or stationary suspension feeding strategy (*Temora longicornis, Eucalanus crassus*); (3) fast swimming continuously cruising strategy (*Euchaeta elongata*); and (4) cruising strategy interrupted by sinking periods or 'cruise and sink behaviour' (Greene 1988).

Centropages species such as *C. hamatus, C. typicus,* and *C. velificatus* have been classified in the fourth category by different authors (Strickler 1985, Tiselius & Jonsson 1990, Paffenhöfer et al. 1996), and our results are in agreement with this classification.

Furthermore, as the presence of ciliates stimulates an increase in time spent swimming and a decrease in proportion of time spent in passive sinking, we conclude that this latter behavioural sequence is not implied in the predation process and that the searching strategy triggered by the presence of *Strombidium sulcatum* is the cruising mode.

Although predation on microzooplanktonic prey has been supposed to be mainly performed in the ambush mode by most calanoid predators, including *Centropages typicus* (Tiselius & Jonsson 1990, Kiørboe & Saiz 1995), our results suggest that *C. typicus* preferentially uses the cruising strategy to search for *Strombidium sulcatum.* This type of swimming behaviour has different implications for the subsequent processes of encounter and capture.

From their theoretical study, Gerritsen & Strickler (1977) concluded that cruising behaviour was the optimal searching strategy to encounter slow moving prey. Tiselius & Jonsson (1990) further suggested that cruising copepods such as *Centropages typicus* and *C. hamatus* may reduce the rate of fluid deformation ahead using this strategy, and thus approach prey in a hydrodynamically quieter way than stationary suspension feeders. Considering that the maximum swimming velocity of *Strombidium sulcatum* at bacterial concentrations similar to those of our experiments is less than 0.2 mm s^{-1} (Fenchel & Jonsson 1988), the much higher swimming velocity of *C. typicus* (3.5 mm s^{-1}) appears adapted to maximise encounter rate with *S. sulcatum.* Furthermore, during its swimming cruising motion, *C. typicus* uses its cephalic appendages to simultaneously generate propulsive forces as well as a double shear field associated with the feeding currents (Cowles & Strickler 1983, Tiselius & Jonsson 1990). These feeding currents allow the searching copepod to explore an additional dimension as water is displaced from a different direction than the one in which it swims. The flow field generated by *C. typicus* while swimming appears adapted to capture *S. sulcatum.* We did not manage to obtain more than 2 clear sequences of *S. sulcatum* entrained in the feeding currents of *C. typicus,* and we cannot support this statement with hard data. Nevertheless, this is not a novel aspect of our work, and the inability of *S. reticulatum* (a species similar in size and swimming velocity to *S. sulcatum*) to escape from the feeding currents of *Acartia tonsa* has been already observed by Jonsson & Tiselius (1990). This hypothesis appears also to be supported by the results of Kiørboe et al. (1996), who observed that clearance rates of *A. tonsa* feeding on *S. sulcatum* were

independent of the type of searching behaviour (passive sinking or feeding current generation) adopted. As *C. typicus* creates stronger feeding currents than the intermittent flow field of the smaller *A. tonsa* (Tiselius & Jonsson 1990), it appears reasonable to hypothesise that *S. sulcatum* is not able to escape from the feeding currents of *C. typicus.*

The velocity field of *Centropages typicus* feeding currents cannot be assessed from our films. Changes in feeding current flow field velocity and shear, resulting from changes in body orientation during swimming activity, have been observed in the congeneric species *C. velificatus* (Bundy & Paffenhöfer 1996). Similarly, the helical swimming mode of *C. typicus* might cause regular changes in the contribution of drag and gravity to the balance of forces which control the geometry and the velocity of the feeding currents' flow field (Strickler 1982). It can thus be suspected that this particular swimming behaviour, which appears associated with predation on *Strombidium sulcatum,* coinfers particular properties on the *C. typicus* feeding current flow field, but more detailed cinematographic studies are needed to determine accurately its contribution to the predator-prey relative velocity.

Effect of small scale turbulence on *Centropages typicus* clearance rates

The maximum increase in *Centropages typicus* clearance rate measured in this study (up to 330% for a value of $\varepsilon = 3 \times 10^{-1}$ cm^2 s^{-3}) is comparable to the maximum increase in *Acartia tonsa* clearance rate observed by Saiz & Kiørboe (1995). However, in our study this effect was observed at a higher level of turbulence compared with the one which maximised *A. tonsa* clearance rates on *Strombidium sulcatum.* At a level of turbulence of $\varepsilon = 2.3 \times 10^{-2}$ cm^2 s^{-3}, Saiz & Kiørboe (1995) observed a 293% enhancement of *A. tonsa* capture rate volume, whereas we estimate only a 96% enhancement of *C. typicus* feeding rates at a comparable level of turbulence ($\varepsilon = 2.9 \times 10^{-2}$ cm^2 s^{-3}).

At moderate intensities of turbulence, *Centropages typicus* appears to obtain less benefit than *Acartia tonsa* from the kinetic effect which affects the prey encounter process. This trend is qualitatively consistent with the fact that *C. typicus* displays a much higher swimming velocity (3.5 mm s^{-1}) compared to the sinking velocity of ambush feeding *A. tonsa* (0.69 mm s^{-1}; Jonsson & Tiselius 1990). However, because we do not have precise estimates of perceptive/reactive distance (Kiørboe & Saiz 1995) and searching activity in turbulent conditions (Costello et al. 1990) for *C. typicus,* we can only speculate on this differential effect with existing encounter rate models.

From both their experimental and modelling studies, Saiz & Kiørboe (1995) concluded that small scale turbulence would preferentially increase feeding rates of ambush feeding copepods compared to suspension feeders and cruising predators. Our results are not contradictory to this conclusion when compared with the clearance rates of *Acartia tonsa* ambush feeding on *Strombidium sulcatum* at comparable levels of turbulence. Nevertheless, previous results concerning feeding rates of suspension feeding copepods in turbulent conditions (Saiz et al. 1992) revealed only a slight increase in clearance rates (ca 26% for *A. tonsa* suspension feeding on *Thalassiosira weissflogii* at $\varepsilon > 10^{-1}$ cm^2 s^{-3}), whereas our study indicates that *Centropages typicus* can benefit from an important turbulence induced increase in feeding rates (by a factor 2 to 4) while searching for *S. sulcatum* in a cruising mode.

This result underlines the necessity extending studies of the feeding behaviour performed under controlled levels of turbulence to other copepod species and developmental stages.

Negative effect of turbulence on *Centropages typicus* clearance rates

At the highest level of turbulence tested in our experiments, the capture rate volume was drastically depressed compared to lower levels of turbulence. Different explanations can be proposed for this effect.

Assuming that *Centropages typicus* uses its feeding currents to search and capture *Strombidium sulcatum* in highly turbulent conditions, the shear rate due to turbulence might be strong enough to erode the shear field generated by the feeding currents at a distance related to the reaction distance of the copepod (Saiz & Kiørboe 1995). It is also possible that in highly turbulent conditions, *C. typicus* alters its swimming behaviour and reduces the time spent slow swimming (i.e. searching for prey). This would also result in a decreased capture rate volume.

Turbulence mediated changes in prey behaviour might also contribute to this effect. Although no jumping abilities have been described for *Strombidium sulcatum* in calm conditions (Fenchel & Jonsson 1988), if some critical turbulent shear rate value is susceptible of stimulating this behaviour as observed for copepods (Fields & Yen 1997) and rotifers (Kirk & Gilbert 1988), this could contribute to a decrease in capture efficiency for *Centropages typicus*, but also to an increase in encounter rate.

Nevertheless, this effect is presently of little interest, because we observed it at a level of turbulence ($\varepsilon = 4.4$ cm^2 s^{-3}) which is unlikely to occur in the sea.

Conclusion

The present study confirms previous observations of the effect of small scale turbulence on zooplankton predation rates and reinforces the concept of a differential effect of turbulence on prey encounter in co-existing predators with different feeding strategies. Predators such as *Centropages typicus*, which due to their swimming behaviour generate large velocities relative to their prey, will be affected by higher levels of turbulence compared to ambush predators such as *Acartia tonsa* (Saiz & Kiørboe 1995). *A. tonsa* and *C. typicus* have identical clearance rates (ca 180 ml cop.$^{-1}$ d^{-1}) on *Strombidium sulcatum* in calm conditions while using opposite feeding strategies. Thus, partitioning of prey resources in such copepod species appears to be potentially controlled by the level of turbulence. This comparative result corroborates the hypothesis initially proposed by Strickler (1985), who suggested that the state of small scale fluid motion could be viewed as a mechanism for niche separation in sympatric species of calanoid copepods.

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