Effects of small-scale turbulence on copepods: The case of *Oithona davisae*

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Abstract

We report the effects of small-scale turbulence on the feeding rates of the marine copepod *Oithona davisae*. Laboratory experiments were conducted under a range of turbulence dissipation rates between 10^{-4} and 10^1 cm^2 s^{-3}. Net enhancements of feeding were observed only at the lowest, whereas negative net effects appeared only at the highest, turbulence intensities. These results contrast with expectations from an encounter-based model for this copepod species that predicted positive feeding enhancements at all turbulence intensities. This disagreement suggests the presence of detrimental effects at moderate and high turbulence intensities, very likely driven by either a lower mechanosensor perception capability or lower capture success. In comparison to other ambush copepods, *O. davisae* appears much more sensitive to the presence of turbulence, which might be the result of its strict ambush behavior, whereas copepods like *Acartia tonsa* or *Centropages typicus,* which can switch into different feeding modes, appear to benefit more from turbulence. The response of *O. davisae* feeding to turbulence in our experiments agrees with recent field observations on changes in the vertical distribution of *Oithona* as a function of wind-driven turbulence events. Hence, *O. davisae* seems to choose those depths where small-scale turbulence favors feeding.

Although there was some early evidence suggesting that small-scale turbulence could affect zooplankton behavior and feeding (e.g., Singarajah 1975; Alcaraz et al. 1989), the seminal theoretical work of Rothschild and Osborn (1988) stimulated an intensified effort at quantifying this interaction (e.g., Sundby and Fossum 1990; MacKenzie and Leggett 1991; Saiz et al. 1992). In the last 15 yr, both laboratory experimentation (e.g., Saiz 1994; Landry et al. 1995; Caparroy et al. 1998) and modeling exercises (e.g., Kiørboe and Saiz 1995; Visser and MacKenzie 1998) have demonstrated that the increase in particle contact rates from turbulence affects such processes as aggregate formation and planktonic trophic interactions. Theoretically, the (root mean square) turbulence velocity adds to the particle relative motion, enhancing encounter as an inverse function of the velocity difference between particles (Rothschild and Osborn 1988; Kiørboe and Saiz 1995). In the case of zooplankton, the translation of this enhancement in encounter into higher ingestion rates depends on the feeding behavior of the predator (and very likely on the prey response to turbulence). Suspension-feeding and cruising zooplankton seem to benefit less by turbulence than ambush and pause-and-travel predators (Kiørboe and MacKenzie 1995; Kiørboe and Saiz 1995). Furthermore, turbulence effects depend on the turbulence dissipation rate (ε). While higher turbulence intensities could shift the Kolmogorov scale down into smaller

scales and influence the encounter rate of smaller sized predators, higher turbulence intensities can begin to interfere with their detection and capture mechanisms (MacKenzie et al. 1994; Kiørboe and Saiz 1995), resulting in a trade-off between benefits and detriments. Thus, a few studies have observed negative effects on the feeding of both fish larvae (Landry et al. 1995; MacKenzie and Kiørboe 2000) and copepods (Saiz and Kiørboe 1995; Caparroy et al. 1998) at relatively high levels of turbulence ($\varepsilon > 10^{-1}$–10^0 cm^2 s^{-3}), exhibiting a dome-shaped feeding response to turbulence intensity.

In the case of copepods, it might be incorrect to make extensive, general conclusions about the effects of turbulence on their feeding because of the range of body sizes and the diversity of feeding behaviors they display. Presently, direct empirical evidence has been demonstrated for only two similarly sized, related genera of copepods—*Acartia* (e.g., Saiz et al. 1992; Saiz and Kiørboe 1995) and *Centropages* (Caparroy et al. 1998)—which responded similarly to turbulence. On the contrary, Lagadeuc et al. (1997) reported that the vertical distribution of several copepod species was affected differently by mixing, suggesting species-specific responses to turbulence.

In this last decade, there has been significantly more interest in the role of small copepods in the oceans, particularly the genus *Oithona*. This genus is spread in waters all over the world (Gallienne and Robins 2001), from polar to equatorial, in coastal as well as oceanic areas, and very likely experiences a wide range of turbulence intensities. In the Atlantic, the genus *Oithona* is often one of the dominant groups of copepods, represented in very high numbers and being a significant contributor to secondary production (Nielsen and Sabatini 1996; Calbet and Agustí 1999). Nevertheless, we lack direct evidence of the effects of turbulence on *Oithona*. On the basis of its ambush behavior (feeding on motile prey or sinking pellets, Kiørboe and Visser 1999), one can predict a large enhancement of its feeding rates under turbulence. However, recent field studies (Incze et al. 2001; Visser et al. 2001) that couple fine-scale copepod dis-

tribution with small-scale measurements of turbulence indicate that *Oithona* can avoid high turbulence levels by going to deeper, calmer waters, which suggests a detrimental effect of turbulence on their performance. Evidence is inconclusive because of the dispersive effect of turbulence (Haury et al. 1990), which could explain the deepening of the average depth of their distribution. It is also in disagreement with the observations by Lagadeuc et al. (1997), who reported that *Oithona similis* exhibited the same vertical distribution in stratified and unstratified water columns.

The studies mentioned above therefore question the assumption that, at common coastal and oceanic intensities of turbulence, the overall effect of turbulence on the feeding rates of planktonic copepods would be positive. Similarly, Irigoien et al. (2000) and Visser et al. (2001) have suggested that there would be detrimental effects of turbulence on copepod feeding. This idea is based on the observation of negative relationships between *Calanus* gut fluorescence and turbulence intensity. However, it is unclear whether these negative relationships actually indicate negative effects on feeding or a switch to nonpigmented prey, as Saiz and Kiørboe (1995) postulated. Hence, the effects of small-scale turbulence on zooplankton still remain an open matter that arouses controversy.

Here, we report the effects of small-scale turbulence on *Oithona davisae*. We have conducted laboratory experiments under controlled turbulence conditions in order to determine their effects on the feeding of *Oithona* and to substantiate field observations of the negative effects of turbulence on this genus. Data are also discussed in light of a recent encounter model for *Oithona* feeding behavior (Svensen and Kiørboe 2000). Finally, we compare our results to other studies on the direct effects of turbulence on copepod feeding.

Methods

O. davisae specimens came from a continuous culture kept in our laboratory since October 2000. The culture was created from zooplankton samples collected in the harbor of Barcelona, Spain, and has been fed with the heterotrophic dinoflagellate *Oxyrrhis marina* and the flagellate *Rhodomonas baltica,* the latter acting mainly as food for *O. marina.* Professor Shuhei Nishida, from the University of Tokyo, Japan, kindly identified our specimens as *O. davisae,* an oithonid previously reported only in the Pacific.

As prey for the feeding experiments, we used cultured *O. marina* grown on *R. baltica.* The *O. marina* were not fed the day before the experiment began in order to ensure that the dinoflagellate depleted all the *R. baltica* and that only *O. marina* was offered as prey to the copepods. The absence of *R. baltica* in experimental bottles was verified by checking occasionally with a Coulter Multisizer particle counter. Further experiments showed that *O. davisae* is unable to feed significantly on *R. baltica* (unpubl. data).

In order to examine the effect of turbulence on feeding rates, experiments must be conducted well below saturating food concentrations (Saiz et al. 1992). Thus, a preliminary experiment was carried out to determine the functional response of *O. davisae* feeding on *O. marina* in calm water.

This experiment was run over a broad range of food concentrations, ranging from ~5 to 800 cells ml^{-1}. Incubations took place in 74-ml screw-cap bottles, rotating on a plankton wheel (0.2 rpm, end over end) at 21°C in darkness. Four replicate bottles were prepared per food concentration: two with copepods (4–10 adult females each, inversely dependent on food concentration) and two without. Overall, the other experimental procedures were common to those followed for the turbulence experiments (*see below*).

The experimental design for the turbulence experiments was similar to that described in Saiz and Kiørboe (1995). Six independent feeding experiments were conducted, each consisting of a calm treatment (no turbulence) and a turbulent treatment (one of six turbulence intensities, *see below*). For the calm treatment, Pyrex screw-cap bottles (2.3 liters) were incubated on a plankton wheel at 0.2 rpm. Care was taken to avoid bubbles inside the rotating bottles. For the turbulence treatment, Plexiglas cylinders (14-cm inner diameter, effective volume 2.3 liters) were used as containers. Turbulence was generated with a setup identical to that used by Saiz and Kiørboe (1995). Inox grids (13.2 cm diameter, 1-cm mesh size, open area ~70%) were oscillated through the whole volume of the experimental container (amplitude of the stroke: 12 cm) at different speeds. Dissipation rates (ε) were estimated from stroke frequencies (freq, min^{-1}) by the equation provided by Saiz and Kiørboe (1995).

$$\varepsilon \ (cm^2 \ s^{-3}) = 8.5 \times 10^{-4} \times freq^{3.003} \qquad (1)$$

The grid frequencies used for the experiments were 0.9, 2.1, 4.5, 7, 10, and 25 strokes min^{-1}, which rendered dissipation rates of 6.2×10^{-4}, 7.9×10^{-3}, 7.8×10^{-2}, 2.9×10^{-1}, 8.6×10^{-1}, and 1.3×10^{1} cm^2 s^{-3}, respectively. The selected intensities of turbulence ranged from realistically low to high values for coastal and shelf waters (MacKenzie and Leggett 1991; Kiørboe and Saiz 1995; Visser et al. 2001) and included extreme values (10^1 cm^2 s^{-3}) only found occasionally in nature.

Each experiment consisted of three replicates for each turbulence and calm treatment. Adult female *O. davisae* (130–150) were placed into each container previously filled with a suspension of *O. marina* in filtered seawater (~12–16 cells ml^{-1}, below saturation according to functional response data—*see Results*). Three additional containers without copepods were run at each treatment to correct for growth of prey. Experiments were run for ~24 h in darkness at 20.6–21.5°C. No previous acclimation was conducted. At the end of the experiments, the water from all containers (either with or without copepods) was filtered through a 60-μm submerged sieve, and the copepods were checked for activity and then preserved for later sizing. Mortality was always negligible, with occasionally one or two dead animals (not considered for calculations) found. Initial (two 200-ml subsamples from the bulk suspension) and final (one 200-ml subsample per container after sieving) water samples were preserved in 1% acid Lugols solution for *O. marina* quantification. Three to seven aliquots were filtered onto 25-mm-diameter, 0.45-μm pore size cellulose filters, and the *O. marina* present in the whole filter were counted under the microscope. The volume of the aliquots was adjusted to render 200–400 cells per filter.

The carbon content of *O. marina* was obtained from cell volume estimates with a conversion factor (0.123 pg C μm^{-3}) provided by Pelegrí et al. (1999) for this species. In the case of final samples, the cell volume of *O. marina* (*n* = 120) was estimated assuming ellipsoidal shape by measuring cell linear dimensions on digital pictures with National Institutes of Health (NIH) software. For initial samples, cell volume was estimated by Coulter Multisizer counts of the stock cultures used. A preliminary comparison indicated that cell volume estimates by either procedure did not differ (Multisizer: geometric mean = 2,192 μm^3, 95% confidence intervals = 2,122–2,264 μm^3, *n* = 8 samples; microscope: geometric mean = 2,148 μm^3, 95% confidence intervals = 1,962–2,352 μm^3, *n* = 66 cells).

The carbon content (*B*) of adult female *O. davisae* was estimated by the carbon-size relationship provided by Uye and Sano (1998) for the same species.

$$B \ (\mu g \ C) = 1.83 \times 10^{-6} \times PL^{2.05} \tag{2}$$

PL is the prosome length of the copepod (μm). Video pictures of the preserved copepods were taken under a stereomicroscope, and after digitization, their prosome length was measured using the NIH software. Average prosome size of *O. davisae* varied between 288 and 323 μm among the turbulence experiments.

Average food concentrations and clearance and ingestion rates were computed as in Frost (1972). Comparison between treatment means was done by one-way analysis of variance after checking for homoscedasticity using the Levene and Brown-Forsythe tests.

Previous to clearance computations, the significance of *O. marina* reduction in the grazing bottles was tested by one-way analysis of variance, comparing the apparent growth coefficient of grazing bottles with the intrinsic growth rate for the corresponding control bottles (*k* and μ, respectively; Frost 1972). In all cases, growth in grazing bottles (*k*) was much lower than in control bottles (μ); differences were usually of high statistical significance (8 of 10 comparisons: one-tailed $p < 0.01$; one case: one-tailed $p < 0.044$), except for the turbulence treatment in the 10 strokes min^{-1} experiment, where in spite of an average *k*-value lower than the average μ-value, variability between replicates reduced the significance (one-tailed $p < 0.063$). In this last case, we conservatively computed the clearance rates (which were all positive) instead of attributing these rates to an absolute lack of feeding (i.e., clearance rate = 0).

Clearance rates were compared to the expected encounter rates under calm and turbulent treatments predicted from a modified version of an encounter model proposed by Svensen and Kiørboe (2000) for *Oithona similis*. Their encounter model predicts the instantaneous rate of prey encounter, β (i.e., the maximum clearance rate at low food concentrations), as

$$\beta = \left(\frac{4}{\pi}Rd + 4R^2\right)(v_x^2 + v_s^2)^{0.5} \tag{3}$$

where *R* is the reaction distance, *d* is the span of *Oithona* antennae, v_x is the prey (transport) velocity, and v_s is the *Oithona* sinking velocity. The first term of the equation is
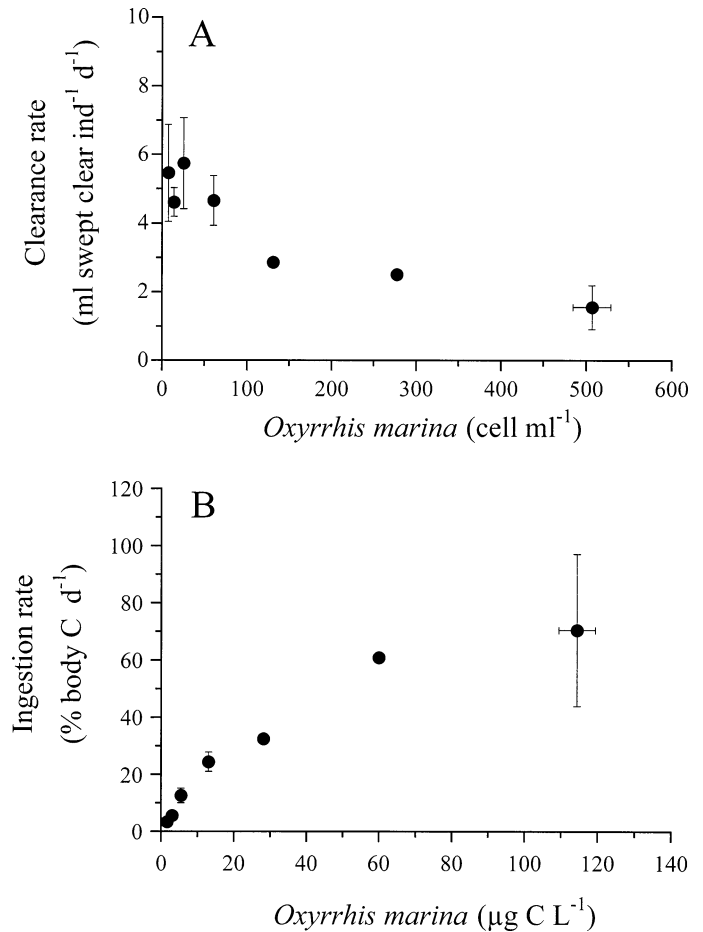

Fig. 1. Functional response experiment. (A) Clearance and (B) ingestion rates of *Oithona davisae* fed on the dinoflagellate *Oxyrrhis marina*. Error bars: ±1 SE.

the cross-sectional area of the *Oithona* perceptive volume around the first antenna (defined by the reaction distance *R*) perpendicular to the arrival direction of the prey. The second term is the velocity difference between predator and prey. This model can be implemented so that the effects of small-scale turbulence in encounter rate are also included (Kiørboe and Saiz 1995). In this case, the velocity difference between predator and prey uses the additive component of the root mean square turbulent velocity ω_ε (Evans 1989), where ω_ε is estimated from the equation provided by Kiørboe and Saiz (1995).

$$\omega_\varepsilon = 1.37(\varepsilon R)^{1/3} \tag{4}$$

The expected clearance rate under turbulence β_ε is computed as

$$\beta_\varepsilon = \left(\frac{4}{\pi}Rd + 4R^2\right)(v_x^2 + v_s^2 + 2\omega_\varepsilon^2)^{0.5} \tag{5}$$

Results

Figure 1 shows the functional response of *O. davisae* clearance and ingestion rates to the concentration of the di-

noflagellate *O. marina.* The clearance rates of *O. davisae* at the lowest food concentrations of *O. marina* ranged between 4 and 6 ml individual^{-1} d^{-1} (Fig. 1A). Although variability was high at the highest food concentration, a tendency toward saturation appears at concentrations >100 μg C L^{-1} (~450 cells ml^{-1}), with food rations of up to 70% of body carbon ingested per day (Fig. 1B). In consideration of these data, the turbulence experiments were conducted at starting concentrations of 12–16 *O. marina* ml^{-1} (well below any symptoms of saturation in the functional response).

Comparison of calm and turbulence treatments in the feeding experiments took into consideration the effects of turbulence on size and growth of *O. marina.* Because the direct effects of turbulence on feeding deal with encounter and capture of prey particles, clearance rates were based on prey number concentration. However, in order not to exclude changes in prey size between treatments (*see below*), ingestion rates were computed on a prey biomass basis. Pairwise comparisons were necessary (parallel calm and turbulence treatments conducted in the same day) because of significant differences in the ingestion rate of *O. davisae* under calm conditions between experiments conducted on different days.

Table 1 shows the clearance and ingestion rates of *O. davisae* in the turbulence experiments, as well as the corresponding size, carbon content, and concentration of *O. marina.* The average *O. marina* concentrations during the turbulence experiments ranged between 14 and 28 cells ml^{-1}. Statistically significant differences in clearance rate were found only at both extremes of the turbulence range tested, with no net effect of turbulence at intensities between 10^{-3} and 10^{-1} cm^2 s^{-3} (one-way ANOVA, $p > 0.2$; Table 1). At the lowest turbulence intensity (0.7 strokes min^{-1}, $\varepsilon \approx 10^{-4}$ cm^2 s^{-3}), clearance rates were 80% higher than under calm conditions ($p < 0.002$). Negative net effects were achieved only at the highest turbulence intensities (10 and 25 strokes min^{-1}, $\varepsilon = 10^0$–10^1 cm^2 s^{-3}), clearance rates being depressed respectively 67% ($p < 0.015$) and 58% ($p < 0.002$) with respect to calm conditions.

We observed a significant decrease in the size of the heterotrophic dinoflagellate *O. marina* under turbulence (Table 1; paired *t*-test, two-tailed $p < 0.001$), in association with a higher rate of cell number increase (on average, 22% higher μ under turbulence, data not shown). Although the differences in *O. marina* size between treatments decreased the magnitude of the treatment effect on ingestion rates, the pattern observed was identical to that found for clearance rates. Thus, ingestion rates (as a percentage of body carbon ingested per day, Table 1) were significantly higher at the lowest turbulence intensity (0.7 strokes min^{-1}; one-way ANOVA test after arcsine transformation, $p < 0.019$) and lower at the highest turbulence intensity (10 and 25 strokes min^{-1}, $p < 0.022$ and $p < 0.001$, respectively), whereas no significant difference appeared for the intermediate intensities ($p > 0.2$).

The model of Svensen and Kiørboe (2000) was applied to *O. davisae* with values of 0.038 cm s^{-1} for *O. marina* velocity (v_x; $n = 27$, data not shown) and 0.054 cm for the spread between the tips of *O. davisae* first antennae (d; live measurements, $n = 7$) and assuming a similar sinking velocity ($v_s = 0.009$ cm s^{-1}) and reaction distance to dinofla-

Table 1. Clearance and ingestion rates (mean ± 1 SE, $n = 3$) of the copepod *Oithona davisae* in the six turbulence experiments, including the corresponding paired calm treatments. Size and carbon content of *Oxyrrhis marina*, as well as average cell concentrations (±1 SE, $n = 3$), are also given.

Experiment	Turbulence (strokes min^{-1})	ε (cm^2 s^{-3})	Treatment	Prey size (μm^3 cell^{-1})	Prey carbon content (pg C cell^{-1})	Average prey concentration (cell ml^{-1})	Clearance rate (ml ind^{-1} d^{-1})	Ingestion rate (% body C d^{-1})
1	0.9	6.2×10^{-4}	Turbulence	1,753	216	22±0.2	12±0.3**	28±0.4*
			Calm	2,408	296	21±0.4	7±0.6	21±1.6
2	2.1	7.9×10^{-3}	Turbulence	1,844	227	20±1.7	6±2.8 ns	13±4.4 ns
			Calm	2,178	268	17±0.2	7±0.5	13±0.8
3	4.5	7.8×10^{-2}	Turbulence	1,600	197	28±0.9	4±0.9 ns	10±1.9 ns
			Calm	1,868	230	25±0.7	4±0.9	12±2.2
4	7	2.9×10^{-1}	Turbulence	1,780	219	22±1.1	7±1.7 ns	15±2.8 ns
			Calm	2,219	273	20±0.3	5±0.5	12±0.9
5	10	8.6×10^{-1}	Turbulence	1,565	192	26±0.8	2±1.2*	6±2.5*
			Calm	2,066	254	20±0.2	8±0.3	18±0.5
6	25	1.3×10^{1}	Turbulence	1,553	191	17±0.3	3±0.5**	4±0.6**
			Calm	2,269	279	14±0.1	8±0.3	11±0.3

Paired calm treatments significant at * $P < 0.022$ and ** $P < 0.002$. ns, not significant at the $P = 0.2$ level.

gellates ($R = 0.014$ cm) as to *O. similis* (Svensen and Kiørboe 2000). The predicted maximum clearance rates (β) under calm conditions (6 ml ind^{-1} d^{-1}) were similar to the clearance rates empirically determined at low food concentrations in the functional response experiments (Fig. 1).

Predicted maximum clearance rates under turbulence (β_ε) were 8, 15, 31, 47, 67, and 168 ml ind^{-1} d^{-1} for dissipation rates of 6.2×10^{-4}, 7.9×10^{-3}, 7.8×10^{-2}, 2.9×10^{-1}, 8.6×10^{-1}, and 1.3×10^1 cm^2 s^{-3}, respectively. Model predictions under turbulent conditions clearly disagreed with the clearance rates observed in the turbulence experiments (Table 1).

Discussion

In this study, we have observed that small-scale turbulence affects the feeding of the ambush copepod *O. davisae.* Positive net effects on feeding were evident only at the lowest turbulence intensity tested (10^{-4} cm^2 s^{-3}), which is comparable to values found in low-energy marine environments; at higher intensities, no net effect or impairment of feeding was observed. These results, as discussed below, are consistent with field observations of *Oithona,* which appear to avoid high turbulence layers.

The direct effects of small-scale turbulence on copepod feeding include not only positive effects like enhanced encounter rate, which would reflect on higher feeding rates, but negative effects as well (Saiz et al. 1992; Saiz and Kiørboe 1995). The absence of either sensorial or behavioral components that take into account these negative effects explains the failure of mechanistic encounter models to predict feeding rates of *O. davisae* under turbulence. Although predicted encounter rates under turbulence increase monotonically and would anticipate larger feeding enhancements at higher turbulence intensities, our study has shown quite a different pattern for *O. davisae*: from positive enhancement at low turbulence intensities and the absence of net effect at intermediate intensities to the presence of pernicious net effects at the highest turbulence intensities. A similar pattern of turbulence-dependent feeding response has been observed previously in other ambush copepods (Saiz et al. 1992; Saiz and Kiørboe 1995; Caparroy et al. 1998) and in fish larvae (Landry et al. 1995; Dower et al. 1998). It seems to be the result of enhanced encounter and the action of, above certain threshold turbulence intensities ($\varepsilon > 10^{-3}$ cm^2 s^{-3} for *O. davisae*), offsetting detrimental effects on feeding, such as lower perceptive performance or a lower capture success (Saiz and Kiørboe 1995), which would impair the ability of the copepod to detect, attack, and ingest encountered prey. However, in contrast to the other ambush copepods studied, as we will see below, *O. davisae* appears to be much more impaired by turbulence.

Figure 2 compares previous reports on the direct effects of turbulence on feeding rates of copepods (*Acartia tonsa,* Saiz and Kiørboe 1995; *Centropages typicus,* Caparroy et al. 1998) with our study on *O. davisae.* The figure also incorporates some unpublished experiments on the feeding rates under turbulence of the suspension-feeding copepod *Temora stylifera* fed on the diatom *Thalassiosira weissflogii* (~13.6-
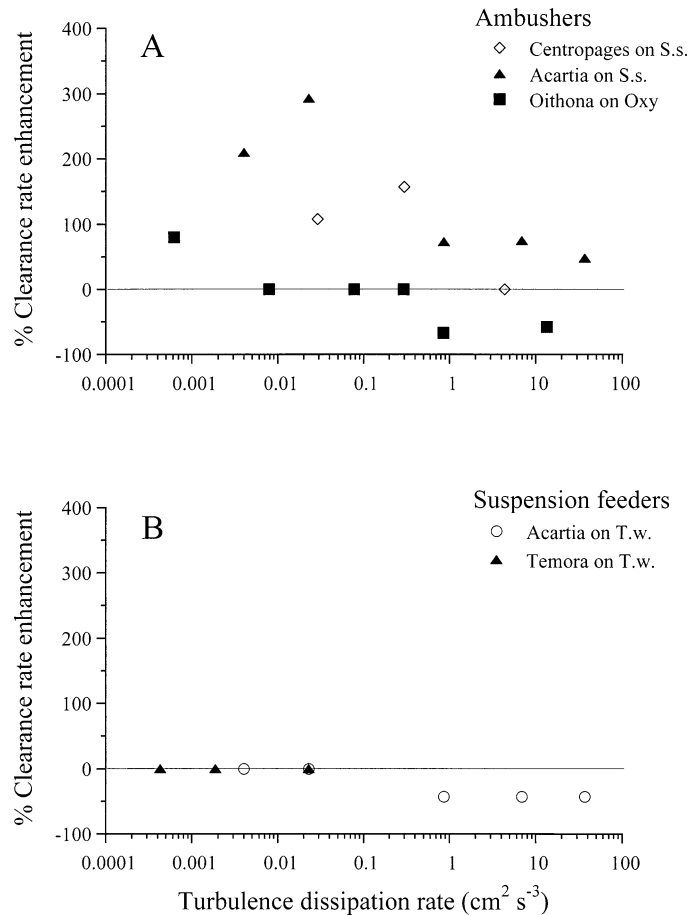

Fig. 2. Review of the effects of turbulence dissipation rate on feeding rates of marine copepods: (A) ambushers, (B) suspension feeders. The effect on feeding is expressed as a percentage of turbulence enhancement on clearance rates with respect to calm (no turbulence) conditions. For simplicity, when effects were not statistically significant, they were plotted on the zero line. Centropages on S.s., *Centropages typicus* feeding on the ciliate *Strombidium sulcatum* (Caparroy et al. 1998); Acartia on S.s., *Acartia tonsa* feeding on the ciliate *Strombidium sulcatum* (Saiz and Kiørboe 1995); Oithona on Oxy, *Oithona davisae* feeding on *Oxyrrhis marina* (this work); Acartia on T.w., *Acartia tonsa* feeding on the diatom *Thalassiosira weissflogii* (Saiz and Kiørboe 1995); Temora on T.w., *Temora stylifera* feeding on *Thalassiosira weissflogii* (unpubl. data).

μm equivalent spherical diameter [ESD]; 380–530 cells ml^{-1}). The results on *T. stylifera,* together with the data from different studies presented in Fig. 2, were obtained by an identical device for turbulence generation in the laboratory and with the same calibration equation to estimate turbulence dissipation rates. This methodological homogeneity ensures that the variability in response is due entirely to interspecific differences. Suspension feeders, as exemplified by *T. stylifera* and *A. tonsa* fed on diatoms, seem to obtain little benefit from turbulence. On the other hand, *C. typicus* and *A. tonsa* feeding on ciliates and acting as ambush predators tend to obtain much larger benefits, and there appears to be a dome-shaped relationship with turbulence intensity. Overall, these observations agree with the theory provided by Kiørboe and Saiz (1995), which predicts a major effect of turbulence on

ambush copepods at low and moderate turbulence intensities and negligible effects on suspension feeders. Unexpectedly, our results for *O. davisae,* also an ambush predator, differed from the dome-shaped response exhibited by these other ambush copepods. In addition, *O. davisae* showed a modest response. At the same turbulence intensities in which the ambush predators *A. tonsa* and *C. typicus* show feeding enhancements of 150–300%, *O. davisae* displays no net effect. It appears that in the case of *O. davisae,* the dome-shaped relationship, if it exists, has shifted to much lower turbulence intensities, with positive net effects remaining only at the lowest turbulence intensity tested in our experiments.

A shift to lower turbulence intensities in the presumably dome-shaped response of *O. davisae* should be interpreted as much higher sensitivity to turbulence compared to the other copepod species studied. *O. davisae* is strictly an ambush, raptorial feeder, relying on mechanoreception for location of moving or large sinking prey (Kiørboe and Visser 1999; Svensen and Kiørboe 2000). Such a predator must have a well-developed mechanosensorial array and is potentially very sensitive to small-scale turbulence. The other ambush copepod species studied so far, *A. tonsa* and *C. typicus,* have the ability to create feeding currents as well, being able to switch into suspension feeding strategies if convenient (Saiz and Kiørboe 1995; Caparroy et al. 1998). Likely, such dual-mode foragers do not need to rely as much on their mechanosensory array; as a result, they should be able to cope with higher turbulence intensities. Whereas *A. tonsa* and *C. typicus* are able to feed efficiently at $\varepsilon > 10^0$ cm^2 s^{-3}, with associated fluid shear rates >10 s^{-1}, *O. davisae* exhibits statistically significant feeding detriment at such intensities.

In reconsidering the original goal of this work, it appears that this higher sensitivity of *O. davisae* feeding to turbulence would help explain the field observations of the deepening of *Oithona* vertical distribution under situations of high turbulence (Incze et al. 2001; Visser et al. 2001). Indeed, turbulence dissipation rates inducing such a deepening are on the order of 10^{-2}–10^0 cm^2 s^{-3} (Incze et al. 2001; Visser et al. 2001). In spite of expected differences in scale and measurement techniques, these values are of the same magnitude as the turbulence intensities that induce detrimental effects on feeding of *O. davisae* in the laboratory. Further support for a higher sensitivity to turbulence is suggested by the depths at which *Oithona* tend to occur in the field, under either quiescent conditions or strong winds, which have associated dissipation rates on the order of 10^{-4} cm^2 s^{-3} (Incze et al. 2001), a value at which feeding rates of *O. davisae* are enhanced in the laboratory.

Although turbulence is a characteristic feature of aquatic systems, in just this last decade, its relevance to zooplankton ecology has been considered (*see* the extensive review in Yamazaki et al. 2002). Some patterns have begun to appear; however, our knowledge is still too limited to permit accurate predictions. Because of logistical, technical, and methodological difficulties, most evidence has come from the laboratory under conditions that might not fully reflect field conditions. The outcome of the direct effects of turbulence determined from laboratory experiments may not be easily interpreted into changes in feeding, growth, and recruitment

of zooplankton populations in the field. In the laboratory, containers ranging in size from one to some hundred liters are employed, and turbulence is commonly generated by stirring devices such as oscillating grids or shakers (Peters and Redondo 1997). In the case of our experiments, where oscillating grids and 2-liter containers were used, the incubations were conducted under conditions of homogeneous and nonstratified fluid, making the extension of the results valid only for those regions of the ocean where one can find such conditions of homogeneity (e.g., wind-driven mixed layers). The range of turbulence dissipation rates we applied is within the extent of values found in the mixed layer of natural systems, although only the smallest scales may be well represented in our containers. Obviously, the size of the container used ($\sim$14 cm) sets a limit to the largest scales that can be generated in our experiments and impairs any attempt to study the effects on copepods mediated by turbulence at larger scales (e.g., prey patch dispersion, ability to form swarms and stay in certain depths, etc.). However, one should keep in mind that the smallest scales are those that, at first instance, can directly affect the feeding performance of copepods with body sizes on the millimeter scale and spatial scales of their feeding bouts on the order of centimeters. In the case of *O. davisae,* total body length, from tip of antennae setae to tip of caudal setae, is close to 1 mm (we can also include the detection distance $R = 0.14$ mm in order to set a total length scale for the copepod). The lower bound to turbulence is the viscous length scale $\ell_\nu = 2\pi\eta$ (where η is the Kolmogorov scale), which depicts the limit at which inertial forces overcome viscous forces, and consequently sets the size of the smallest turbulent eddy (Gargett 1997). The values of ℓ_ν in our experiments varied between 13 mm at $\varepsilon = 10^{-4}$ cm^2 s^{-3}, 3–7 mm at intermediate turbulence intensities, and 1–2 mm at $\varepsilon = 10^0$–10^1 cm^2 s^{-3}. It is important to notice that copepods, with body sizes between ℓ_ν and η, actually experience turbulence in the near dissipation range, in which the fluid velocity varies linearly with distance (Jiménez 1997). However, it is still a challenge to understand what the instantaneous shear field surrounding a copepod is, and the subject needs further consideration (Gargett 1997; Yamazaki et al. 2002).

An additional proviso, which should be kept in mind in order to extend the laboratory experiments to the field, is that habitually the animal is exposed to relatively constant and uniform intensities of turbulence in the laboratory, with only the smallest scales being represented, whereas in nature, temporal and spatial variability at a range of scales allows for adaptive responses to suitable environments. For instance, foraging theory would predict that an optimal predator would attempt to be located at those turbulence intensities where the most benefit can be obtained, selecting best depth strata. The vertical distribution of *Oithona* in the studies of Incze et al. (2001) and Visser et al. (2001) appears to conform to this behavior (*but see* Lagadeuc et al. 1997), as our results indicate.

Other elements besides feeding can be crucial for determining the behavior and life history patterns of copepods in relation to turbulence. As MacKenzie (2000) pointed out, factors such as concurrent effects of turbulence on other components of pelagic food webs, the lack of understanding

of how relevant processes (e.g., prey patchiness, feeding behavior, growth, predation risk) are affected by turbulence, and unavoidable sampling artifacts can mask field observations. For example, ''optimal'' copepods might compromise their turbulence-mediated feeding enhancement by seeking to inhabit those depths in the water column where their predators, usually larger and more likely to take advantage of turbulence effects on encounter, would be less benefited by turbulence. Similarly, Franks (2001) suggested that strong swimmers like larval and juvenile fish might show higher feeding rates not directly driven by turbulence but by increased prey concentration because of prey turbulence avoidance. It appears, therefore, that the interactions between turbulence and zooplankton are much more complicated than those predicted by a simple application of the encounter theory and that further insights on the ecological role of turbulence in marine systems are still needed. As we have seen, laboratory experimentation is a valuable tool to study the effects on small-scale turbulence on the feeding of zooplankton, but its extrapolation to the field must be made cautiously and include higher order interactions. Fortunately, evidence from laboratory experiments and field studies is beginning to match and show a comprehensive picture of such interactions.

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