Grazing in a turbulent environment: Energy dissipation, encounter rates, and efficacy of feeding currents in *Centropages hamatus*

(zooplankton/copepod/turbulence/energetics/physical–biological interactions)

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ABSTRACT The creation of feeding currents by calanoid copepods increases encounter rates of copepods with their food and provides an advantage in dilute nutritional environments. Small-scale turbulence has also been hypothesized to increase the encounter rate between planktonic predators and their food. *Centropages hamatus* was exposed to turbulent and nonturbulent environments at two prey concentrations to quantify the influence of turbulence on feeding current efficacy. Turbulent energy dissipation rates used in the experiment were in the range of 0.05–0.15 cm²·sec^{−3}. In the nonturbulent environments, feeding currents increased the encounter rates of *C. hamatus* 3–5 times that of control encounter areas. In turbulent environments, encounter rates were not increased by feeding currents, yet *C. hamatus* continued to create feeding currents. Energetic calculations indicate a tradeoff in the value of turbulence to a copepod feeding on phytoplankton. While turbulence is probably beneficial at low food concentrations, it may be deleterious at high food concentrations.

Predictions of oceanic productivity are universally sensitive to the energy transfer between phytoplankton and zooplankton (1–4). The accuracy of these predictions depends on realistic estimates of species-specific feeding rates. However, these rates show large variations. For example, within the most widely studied copepod genus, *Calanus*, grazing rates differ significantly between investigators as well as within the results of individual investigators (5). Feeding rates of other calanoid copepods are less well described despite the importance these other species play in planktonic food webs (6–9).

Resolution of the structure and dynamics of complex processes often depends on systematic analyses of the component parts of the processes. In the case of copepod feeding, this requires identifying the underlying principles governing the entire feeding process. Fundamentally, capture and ingestion of food items by calanoid copepods, as well as other zooplankton grazers, begin with an encounter event. Attack, capture, and ingestion are conditional events that follow a successful encounter (10, 11). While not equivalent to ingestion, the encounter event can be the limiting step in the conditional sequence leading to ingestion.

Several models have been developed that investigate the role encounter rates play in zooplankton feeding. Cushing (2) modeled copepod encounter rates with algae as a function of copepod velocity through the water (v) and “contact surface” (Fig. 1a). The contact surface (A) was defined by dimensions of the sensory apparatus of the copepod’s first antennae. Thus, the number of algae encountered by a copepod per unit time was the product $v \times A \times$ algal concentration. Algal velocity (u) was assumed to be negligible.

Cushing’s viewpoint was modified by Strickler (12), who presented data on feeding currents utilized by most copepods. Due to the low Reynolds number (Re) of water at the length of scale of a copepod ($Re < 5$; ref. 13), viscosity plays

FIG. 1. Two-dimensional theoretical encounter patterns for Cushing (2) (a), Strickler (12) (b), and Rothschild and Osborn (19) models (c). A, the sensory horizon; v and u , copepod and algal velocity, respectively.

an important role in animal and water movements. To swim, a copepod must draw water, and therefore algal particles, past its appendages. The appendages used for swimming are also used for food capture. This combination results in the creation of feeding currents during swimming. Feeding currents cause an increased passage of water and algae by the copepod during swimming. This affects the copepod’s encounter rate with algae in two ways. First, algal velocity (u) is increased. Second, the copepod’s sensory horizon (A) is increased because the feeding current pulls a cone rather than a cylinder of water toward the animal (Fig. 1b). In addition, feeding currents allow (i) sensing of algae from a distance (13–16) and (ii) reorientation of particles as they approach the copepod (17, 18). The encounter rate is also dependent on the sensory physiology and behavior of the copepod. Strickler’s description increased estimates of the volume searched by a copepod. These estimates depend on the value of $V \times A$, where V combines the velocity of the copepod (v) and the algal velocity (u) and A is several times larger than Cushing’s contact surface (Fig. 1b).

Rothschild and Osborn (19) recently presented a model [further modified by Evans (20)] that included the effects of small-scale turbulence. In this case, both animal (v) and algae (u) velocities may be increased due to the kinetic energy of turbulent eddies. Their conclusion was that copepod encounter rates could be increased in a turbulent environment (Fig. 1c). Therefore, the importance of turbulence in copepod feeding depends on the magnitude of feeding current velocities relative to turbulent eddy velocities at the size scales of the copepods and their algal food.

Abbreviation: VTD, vertical turbulent diffusion.

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The Rothschild and Osborn (19) model emphasized the coupling of small-scale physics with biological properties of planktonic grazers. Mesocosm experiments (at undefined levels of turbulent kinetic energy) have indicated that copepods may not respond favorably to turbulent environments (21, 22). These studies suggest that turbulence may interfere with food capture either by disrupting feeding currents (15, 21) or by inducing shifts in behavior patterns that are detrimental to feeding performance (22).

We have conducted a series of experiments to investigate the coupling of physical and biological parameters governing calanoid copepod grazing rates. We subjected a coastal copepod, *Centropages hamatus*, to two levels of turbulence (none and $\epsilon = 0.05\text{--}0.15\text{ cm}^2\text{sec}^{-3}$) and two food levels (70 and 350 cells per ml) and observed the animals' reactions, the encounter rate, and the trajectories of the algae.

In another contribution (23), we reported our findings about the animals' behavioral responses under these conditions. Here we address two questions: (i) can we estimate turbulent energy simultaneously to, and without interfering with, the animals' movements; and (ii) does the increased encounter rate due to turbulence render feeding currents ineffective.

METHODS

Experimental Organisms and Design. *C. hamatus* were captured in surface net tows from Buzzards Bay, Massachusetts, and transported to our laboratory at the Marine Biological Laboratories (Woods Hole, MA). The algae of *Gymnodinium* sp. (diameter, 20 μm) were cultured and donated by S. Gallagher (Woods Hole Oceanographic Institution).

Experiments began with an $\approx 17\text{-min}$ period during which no mechanical mixing occurred in the experimental vessel other than the flow generated by the copepod's feeding current (preturbulent period). This period was followed by $\approx 17\text{ min}$ of turbulence (turbulent period).

Two experiments involving algae were performed. The two algal concentrations were selected with the specific goal of equating encounter rates in the low concentration turbulent period with that of the high concentration preturbulent (static) period. Preliminary experiments provided the ratio of encounter rates occurring during preturbulent and turbulent periods. This ratio was then used to determine the food concentrations for low (70 cells per ml) and high (350 cells per ml) food concentrations. The copepod was acclimated for 30 min in each of the food concentrations prior to experimentation. Water temperature during the experiment was 20°C.

Continuous video recordings of a tethered copepod (24) and particle movements were made with a modified Schlieren optic pathway (25). The position of each algal cell within the observation area of $9 \times 7\text{ mm}$ was determined by using video image analysis software (Image-Pro, Media Cybernetics, Takoma Park, MD). The depth of focus was kept at 1 mm. Methodology for the subsequent behavioral analysis of the videotapes is described in Costello *et al.* (23). All calculations were made with Lotus 1-2-3 software.

Calculation of Particle Kinetic Energy. Calculation of the particle mean kinetic energy followed the approach of Dickey and Mellor (26). The x and z coordinates of 1500 particles at two successive times ($x_{t1}, z_{t1}; x_{t2}, z_{t2}; \Delta t = 0.1\text{ sec}$) were used to calculate instantaneous velocities in the x (horizontal) and z (vertical) dimensions.

The x component of instantaneous velocity (u) was calculated as follows:

$$u = (x_{t2} - x_{t1})/t,$$

and the z component of instantaneous velocity (w):

$$w = (z_{t2} - z_{t1})/t.$$

The observational area was divided in 63 cells (9 columns and 7 rows) where i designates the column and k designates the row of the cell. Each cell corresponded to a $1 \times 1\text{ mm}$ real area. In each cell, we calculated the x and the z components of the instantaneous velocity vectors $[(u_{ik})_n$ and $(w_{ik})_n$, respectively]. The number of particles (N) followed within a cell varied from 8 to 30. The x component of the fluctuating velocity (u'_{ik}) was calculated as follows:

$$(u'_{ik})_n = (u_{ik})_n - U_{ik}, \quad [1]$$

where U_{ik} was the mean of the x component of the instantaneous velocities within the cell ik .

$$U_{ik} = \Sigma(u_{ik})_n/N. \quad [2]$$

We repeated the same calculations for z component and determine the $(w'_{ik})_n$ and W_{ik} values.

The ensemble average of the x fluctuating component σu_{ik} (equivalent to the standard deviation of x component of the instantaneous velocities) was computed as

$$\sigma u_{ik} = [\Sigma(u'_{ik})_n^2/N]^{1/2}. \quad [3]$$

The three component turbulent velocity Q (square root of twice the turbulent kinetic energy) was calculated for each ik element assuming that the dissipation in x and y directions was similar

$$Q_{ik} = \{2[(\sigma u_{ik})^2] + (\sigma w_{ik})^2\}^{1/2}. \quad [4]$$

Calculations for the three-component turbulent velocity (Q) and turbulent energy dissipation rates (ϵ) utilized the fluctuating components of the particle velocities. Therefore, turbulence calculations are independent of contributions to particle velocity from mean flow characteristics such as currents within the experimental vessel.

Vertical Turbulent Diffusion (VTD). The VTD is a triple product of particle velocities for each spatial dimension. Therefore, errors in the vector calculations are increased at a cubed rate. The area of each element was quadrupled to reduce the possible error. We recalculated the fluctuating components of the velocities as in Eqs. 1 and 3 for the 16 elements of a $2 \times 2\text{ mm}$ real space. The VTD for each row was then calculated as follows:

$$\text{VTD}_k = \Sigma\{[\Sigma(w'_{ik})_n(u'_{ik})_n + (w'_{ik})_n^3]/N\}/C, \quad [5]$$

where C is the number of columns, and the turbulent energy dissipation rate (ϵ) is

$$\epsilon = d\text{VTD}/dz. \quad [6]$$

Behavioral Analysis. Experimental data comprised a complete behavioral record of a limited repertoire. Following the nomenclature of Cowles and Strickler (27), four behavioral categories were recorded: (i) slow swim, (ii) fast swim, (iii) break, and (iv) groom. The methods of behavior classification and enumeration have been described in Costello *et al.* (23).

Encounter Rates. We defined an encounter as the entrance of an algal cell into the copepod capture area (15). The capture area was $0.7 \times 1.35\text{ mm}$ in size (Fig. 2). In addition, two control encounter areas (Fig. 2) were established to distinguish effects on encounter rate due to copepod feeding currents from those due to the general flow field. The control areas were of the same dimensions as the capture area of the copepod but were located outside the influence of the copepod's feeding current. The "animal encounter rate" included both the effects of limb movement and kinetic energy on encounter rate while the "control encounter rate" was influenced solely by turbulent kinetic energy.

FIG. 2. Typical trajectories of particles during the slow-swimming movement of the copepod in a nonturbulent condition (*b*) and a turbulent condition (*a*). The boxes in *b* indicate the location of the capture area used to calculate the animal and the control encounter rates (AER and CER).

RESULTS AND DISCUSSION

Physical Description of the Environment. The three component turbulent velocities for each of the 63 cells comprising the experimental area decreased with depth. The three component turbulent velocities (Q ; Fig. 3) ranged from 0.8 to 0.2 $\text{cm} \cdot \text{sec}^{-1}$ (top to bottom, respectively). While the fluctuating component of particle velocities showed a decrease with depth, the instantaneous velocities increased in the left corner of the experimental grid, indicating an ascendent current in that region.

The spatial distribution of turbulent velocity (Q), VTD, and turbulent energy dissipation rate (ϵ) is shown in Fig. 3. Dissipation rates varied between 0.15 to 0.05 $\text{cm}^2 \cdot \text{sec}^{-3}$ (top to bottom, respectively). Dissipation rates of the same order of magnitude are reported for turbulent areas above the thermocline in oceanic systems as well as for shelf and coastal regions (Table 1). Thus, the turbulence generated during these experiments was comparable in scale to turbulence encountered in a variety of areas in the copepod's natural environment.

Encounter Rates and Feeding Current Efficacy. Control encounter rates increased during turbulent periods for both high and low food concentrations (Fig. 4 *a* and *d*), supporting the contention that turbulent kinetic energy at scales found in

FIG. 3. Two-dimensional spatial variability of turbulent velocities (Q_{ik} , cm/sec). Left axis, dissipation rate (ϵ , $\text{cm}^2 \cdot \text{sec}^{-3}$); right axis, vertical variability of VTD ($\text{cm}^3 \cdot \text{sec}^{-3}$). Highlighted square is 1 mm^2 .

nature can increase encounter rates between zooplankton and their algal prey. During nonturbulent periods, animal encounter rates were consistently higher than control rates. This was due principally to the production of feeding currents by the copepod. During turbulent periods, animal encounter rates were similar to control encounter rates (Fig. 4 *a* and *d*). We determined a feeding efficacy index to evaluate efficacy of the feeding current in turbulent and nonturbulent periods,

feeding efficacy index =

$$\text{feeding encounter rate/control encounter rate, [7]}$$

where feeding encounter rate was the number of particles passing through the capture area by unit time of slow swimming.

Results for the different treatments are illustrated in Fig. 4 *b* and *e*. Feeding encounter rates were 3–9 times higher than control rates in nonturbulent conditions while approximately equal in turbulent conditions. The similarity of animal and control encounter rates during turbulence indicates that feeding current production during turbulence did not increase encounter rates of the copepod with food items. These results suggest that feeding current maintenance during turbulence may be an unproductive use of the animal's energy.

Feeding current generation can be modulated (12). The animal can alter its time allocation to different behavior patterns. Costello *et al.* (23) observed a significant shift in allocation by *C. hamatus* to slow and fast swimming during turbulence. Behavioral adaptation during turbulence may change the encounter rate. To estimate the amount of encounters that could result in captures, encounter rate data were combined with the behavioral data of Costello *et al.* (23). This combination was important because particle capture by *Centropages* can occur only during periods of feeding current generation termed slow swimming (27).

We calculated a third type of encounter rate, the "effective encounter rate," to estimate only the encounters that occurred during the time that the copepod was slow swimming (Fig. 4). Despite the fact that turbulence decreased the efficacy of feeding currents, absolute increases in encounter

Table 1. Dissipation rates and Kolmogorov eddies in different typical locations

Typical location	Dissipation, $\text{cm}^2 \cdot \text{sec}^{-3}$	Length, mm
Oceanic (28, 29)	10^{-6} – 10^{-2}	10–1
Shelf (30)	10^{-3} – 10^{-2}	2–1
Coastal (31)	10^{-3} –1	2–0.3

FIG. 4. Time course of animal and mimic encounter rates and feeding efficacy index under the four experimental conditions.

rates during turbulence, accompanied by high proportions of time spent slow swimming, resulted in significantly higher effective encounter rates in turbulent compared to nonturbulent flows for the low food concentration (Wilcoxon test, $P < 0.05$). However, effective encounter rates were not significantly different between turbulent and nonturbulent conditions at the high food concentration. Thus, the effect of turbulence on effective encounter rates depended on food concentration. The increase in effective encounter rate at low food concentrations was not exclusively based on the theoretical model of Rothschild and Osborn (19) but was also influenced by behavioral adaptation of the copepod (23). This finding indicates that encounter rate predictions that neglect flow conditions and animal behavior may seriously underestimate the effective encounter rates that animals experience under natural conditions.

"Apparent Prey Concentration" and Effective Encounter Rate. Rothschild and Osborn (19) use the term "apparent prey concentration" to describe the prey concentration perceived by a grazer. Both turbulent energy and actual algal concentration affect the apparent algal concentration perceived by a copepod. Our experiments were designed to create similar apparent algal concentrations in the low food concentration, turbulent treatment and in the high food, nonturbulent treatment. Control encounter rates, which were not influenced by the copepod's behavior, confirmed that apparent algal concentrations were similar for low food concentration, turbulent conditions and high food concentration, nonturbulent conditions (Fig. 4). Time budgets of behavior patterns also showed great similarity (23). How-

ever, the effective encounter rates were very different; $3.95 (\pm 1.12)$ encounters per sec for high food, nonturbulent versus $1.11 (\pm 0.28)$ encounters per sec for low food, turbulent. The disparity in effective encounter rates between the two conditions is due to the efficacy of the feeding current at generating encounters in nonturbulent conditions relative to turbulent conditions.

These results indicate that a given amount of time spent slow swimming in nonturbulent, high concentration conditions yields more encounters than the same time slow swimming in a turbulent, low concentration environment. Thus, what has been termed apparent prey concentration (19) may accurately reflect encounter rates for inanimate objects, such as the control encounter areas, but is of limited value in predicting actual encounter rates of copepods possessing complex behavior patterns.

Turbulence and Zooplankton Energetics. Although turbulence may cause increased encounter rates with food items, mesocosm studies (21, 22) have demonstrated that copepod biomass decreased in mixed relative to unmixed mesocosms. Can microscale observations of individual animals such as those of the present study help resolve this apparent contradiction? We believe that a solution lies in delineating the boundary conditions for which a copepod can experience an energetic advantage while grazing in a turbulent environment.

We have approached this problem from an energetic perspective. The relative energetic advantages of the interactions between turbulence and food concentration can be estimated by simple energetic comparisons between our experimental conditions. We made such comparisons based on effective encounter rates, time budgets described in Costello *et al.* (23), and literature estimates of relative energetic costs of swimming. Several assumptions were required. The energy utilized during break periods was assigned a value of 1. Energy expenditure during slow swimming and grooming were assumed to be 1–1.25 times greater than during breaks (32). Energy use during fast swimming was assigned values ranging from 40 to 400 times greater than during breaks (25, 33, 34). In addition, we assumed that the nutritional value of food items, as well as the ratio of effective encounters to captures, remained constant for all experimental conditions.

Based on the ratio of effective encounters and the behavioral responses of the copepod, *C. hamatus* always spent more energy in turbulent than nonturbulent conditions (1.04–1.42 times greater in low concentration, 1.82–6.78 times greater in high concentration; Table 2). The increased energy expenditure in turbulent regimes was due principally to increased escape reactions.

The overall energetic value of feeding during turbulence was dependent on food concentration. Energy expenditure during the low food concentration, turbulent period was a maximum of 1.42 times that of the nonturbulent treatment. During the same time, based on our previous estimates of effective encounter rates, the copepod could experience a maximum energy gain of 3 times. This result indicates a potential energetic gain for the copepod in turbulent versus nonturbulent conditions at low food concentrations. However, at high food concentrations, there was no significant

Table 2. Energy costs for behaviors of *C. hamatus* and ratios of energy spent

Cost value	Break	Groom	Slow swimming	Fast swimming	LDT/LD	HDT/HD	HD/LDT
High	1	1	1	40	1.04	1.82	1.04
Low	1	1.25	1.25	400	1.42	6.78	1.27

Energy cost values are relative and include a high and a low value. Ratios of energy spent between different experimental conditions are based on energy costs for the different activities. LDT, low concentration, turbulent; LD, low concentration, preturbulent; HDT, high concentration, turbulent; HD, high concentration, preturbulent.

increase in effective encounter rate during the turbulent treatment while the energy expenditure is between 1.82 and 6.78 times that of the nonturbulent period. Therefore, at high food concentrations, the costs of feeding and escape responses were much greater than the advantage of increased encounter rate. The result is a potential energy loss in high food concentration, turbulent environments.

Thus, based on our work, the advantages accrued through increased encounter rates in turbulent environments depend on the level of turbulence, the prey concentration, and the behavioral responses of the zooplankton. No previous research exploring the effects of turbulence on zooplankton feeding has simultaneously quantified more than one of these variables. Results from mesocosm studies indicating that turbulence is detrimental to zooplankton production most probably reflect the turbulent scales and an "unfortunate" set of parameters (higher food concentration than our experiments, species of grazers) used in the experimental designs. It remains to be determined how variable levels of turbulence will affect zooplankton energetics.

Further Considerations and Limitations. Research on zooplankton grazing in environments of varied turbulent energies is a relatively new topic in biological oceanography and initial studies have produced widely polarized results. While it is clear that turbulence can increase encounter rates (19), it is also clear that models simplifying predator-prey interactions to intersections of inanimate particles are insufficient to describe grazing by animate zooplankters with complex behaviors. Neither have mesocosm studies at undefined levels of turbulence (21, 22) described the full effects of turbulence on plankton. The interactions between zooplankton and their physical environment are complex; this complexity needs to be quantified for models to possess predictive power. The work we describe here and in Costello *et al.* (23) is a beginning in this direction. However, as with previous studies, our results must be viewed with caution because (i) there was no intra- or interspecific replication, (ii) we used only two levels of turbulence and food concentration, and (iii) the copepod was tethered. Due to the widespread nature of turbulence in most marine and freshwater environments, further research with a variety of zooplankton species at various turbulent energies is mandatory. The impact of turbulence may have important implications for plankton patch formation and dynamics as well as plankton biogeography and productivity.

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