

Grazing in a turbulent environment: Behavioral response of a calanoid copepod, *Centropages hamatus*

(encounter rate/feeding/functional response)

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ABSTRACT Models of marine ecosystem productivity rely on estimates of small-scale interactions, particularly those between copepods and their algal food sources. Rothschild and Osborn [Rothschild, B. J. & Osborn, T. R. (1988) *J. Plankton Res.* 10, 465–474], hypothesized that small-scale turbulence in aquatic systems increases the perceived abundance of prey to predators. We tested this hypothesis by exposing the planktonic copepod *Centropages hamatus* to turbulent and nonturbulent environments at different prey concentrations. Our results fell into two main categories. First, the response to turbulence was characterized by an initial period having a high number of escape reactions. This period was followed by one of increased foraging. *C. hamatus* responded to the higher encounter rates due to turbulence as if it were experiencing altered prey concentrations. Second, the termination of turbulence resulted in an increased foraging response, which was not directly related to the encounter rate. Functional response curves do not adequately explain this foraging response because the time course of the foraging response depends on prior encounter experience and foraging motivation.

Turbulence is a consistent hydrodynamic feature of all marine ecosystems, ranging from near-shore (1) through continental shelf (2) and open ocean (3) regions. Turbulence occurs on spatial scales small enough to affect planktonic trophic dynamics (4) and has been demonstrated to affect community interactions between zooplankton and algae (5, 6). However, the mechanisms through which the effects occur remain unresolved and, therefore, so are the outcomes of turbulent events influencing energy flow in marine food webs.

The importance of this issue has been underscored by recent research on predator–prey dynamics. Expanding on the encounter rate concept (7–9), Rothschild and Osborn (10) modeled the effect of turbulence on encounter rates of planktonic predators and their prey [see also Evans (11)]. They concluded that small-scale turbulence has the effect of increasing encounter rates between predators and prey and, therefore, from a predator's perspective, turbulence increases perceived prey abundance.

An important implication of this hypothesis is that trophic energy flow at the ecosystem level will be underestimated unless the influence of turbulence on transfer rates of planktonic systems is considered. If higher encounter rates translate to higher ingestion rates, grazing rates in a turbulent hydrodynamic regime should be significantly higher than would be predicted by relative grazer and algal concentrations. The elevation in grazing rate should then be a function of turbulent intensity.

Projections based on the Rothschild and Osborn model (10) are difficult to reconcile with empirical results from microcosm studies. Oviatt (5) and Alcaraz *et al.* (6) noted a decreased copepod biomass in mixed compared to unmixed microcosms. Oviatt (5) attributed this effect to disruption of copepod feeding in a turbulent flow. This contention was supported by studies demonstrating that calanoid copepods depend on detection of food items within their feeding currents (12–14). Disruption of feeding currents due to turbulent flow may interfere with effective feeding by causing deterioration of the copepod's perceptive field (15). In addition, Alcaraz *et al.* (6) suggest that decreased biomass of *Acartia italica* in turbulent compared to nonturbulent microcosms was due to increased metabolic stress caused by more frequent escape responses of copepods in turbulent microcosms. This argument is supported by data demonstrating that copepods respond to a variety of fluid deformations with escape responses (16–18) and that, during escapes at high speeds (350 body lengths per sec during escape vs. 1 body length per sec during slow swimming), they use 400 times more energy (19). If copepods incorrectly interpret the fluid deformations associated with turbulence as generated by other planktonic animals, then the copepod's reactions could preclude successful utilization of the increase in perceived [perceived equals "apparent" prey abundance of Rothschild and Osborn (10)] food abundance occurring during turbulence. In this case, a copepod might respond with continuous escape reactions to retreat from areas of high turbulence and would thereby lose the benefit of high encounter rates with food.

Based on these considerations, a central issue concerning the impact of turbulence on copepod–algae interactions is whether the advantages accrued through increased encounter rate exceed the disadvantages of the altered perceptive field.

We have performed experiments to determine the impact of a turbulent environment on copepod behavior. We chose *Centropages hamatus* as the experimental animal because it is locally abundant in an environment regularly experiencing wind and tidally forced turbulence, and because it is thought to be primarily a herbivorous feeder (20). In addition, behavior patterns of the genus *Centropages* have been well characterized (21, 22). The questions we asked were, first, what is the effect of turbulence on the copepod's behavior, and, second, does the copepod equate the apparent concentration occurring during turbulence with higher prey concentrations.

METHODS

Experimental Organisms and Equipment. *C. hamatus* were captured in surface net tows from Buzzards Bay, MA and

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transported to our laboratory at the Marine Biological Laboratory (Woods Hole, MA). Copepods were kept at 20°C for 2 days prior to the experiments. Experiments were also performed at 20°C. The algae, cultured *Gymnodinium* sp., were provided by S. Gallagher (Woods Hole Oceanographic Institution). *C. hamatus* males were tethered and their position was fixed according to Alcaraz *et al.* (23). The acclimation period was 3–4 hr prior to the experiment.

Activities of the copepods were observed by using a modified Schlieren optical pathway (16); video images were recorded with a Panasonic WV-1800 infrared-sensitive camera and a Panasonic NV-8500 video cassette recorder. A QSI frame counter was used for sequential numbering of each frame. The optical setup provided clear illumination of particles as well as their movements in relation to the copepod. Limb and body movements of the copepod were readily visible. The entire experiment was recorded onto videotape for analysis. Particle motions and copepod behavior were quantified by using frame by frame analysis of videotapes on a Panasonic NV-A500 editing controller regulating a Panasonic NV-8500 video cassette recorder.

Turbulence was introduced by vibration of a slender rod with three metal pins at its tip. The rod was attached to a small electric motor, which provided the vibration needed to generate turbulence in the experimental vessel. Turbulent energy dissipation rates ranged from 0.05 to 0.15 cm²·sec⁻³ [Marrase *et al.* (24)]. The vessel contained 4.7 liters of 0.22- μ m filtered seawater and either of two concentrations (low concentration, 70 cells per ml; high concentration, 350 cells per ml) of *Gymnodinium* sp. cells.

Experimental Design. Experiments began with an \approx 17-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 min of turbulence (turbulent period). The turbulent period was followed by a 17-min nonturbulent period (termed postturbulent period).

Two experiments were performed, each identical except for one experimental variable, algal concentration. 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 period. Preliminary experiments provided the ratio of encounter rates occurring during preturbulent and turbulent periods. This ratio was then used to determine the prey concentrations for low (70 cells per ml) and high (350 cells per ml) prey concentrations. After the first experiment (low concentration), the copepod was acclimated 30 min in a high concentration mixture before the start of the high concentration experiment.

Data Analysis. Experimental data comprised a complete behavioral record of a limited repertoire. Following the nomenclature of Cowles and Strickler (21), four behavioral categories were recorded: (i) slow swim, (ii) fast swim, (iii) break, and (iv) groom. Slow swimming is the only behavior during which feeding occurs (21). Fast swimming occurs during escape reactions and involves the use of the swimming legs for rapid acceleration (19). During breaks no appendage motion occurs. These periods are the sink phase of the "hop and sink" swimming pattern (22). Grooming is characterized by passage of the first antennae through the feeding appendages (25). While the experiments were replicated several times, only one set of experiments involving one copepod was analyzed in its entirety frame by frame. The rate at which copepods changed their behavior relative to the sample duration created a large behavioral sample size. All behaviors of the repertoire were sampled since the two most rapid events, grooming and fast swimming, occur in 100–160 msec and the temporal resolution of video is 33 msec.

Direct enumeration of encounter rate was based on the description of an encounter area (see capture area, figure 8 in ref. 15) surrounding the feeding appendages of a tethered *C. hamatus*. Particles entering the encounter area were tabulated in 33.3-sec (1000 frames) bins.

The combined experiments required examination of 180,326 frames and resulted in 5097 behavioral events. Calculation of kinematic graphs describing time budgets and transition frequencies followed the methods of Sustare (26).

RESULTS AND DISCUSSION

Behavior Prior to Turbulence. At low food concentrations prior to turbulence (Fig. 1a), relatively little time was spent slow swimming (31%) and breaks dominated the time budget (68%). Grooming occupied a small proportion of the time budget and no fast swimming occurred. Thus, the animal did not spend much time maintaining a feeding current at low food concentration. Reduced feeding at low food concentrations has been observed for other calanoid copepods (21, 22, 27–34), particularly for near-shore species living in environments of high particle concentration (35). Because of the general occurrence of this pattern, we have termed the period of low feeding activity at low food concentration the "stand-by mode." It will be the goal of future research to determine the critical concentration at which *C. hamatus* and individuals from other species switched from standby mode to higher levels of activity and vice versa.

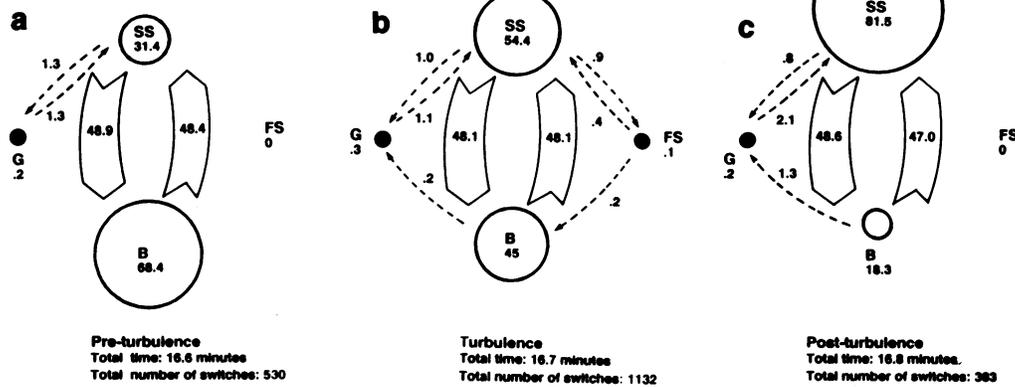
At high food concentrations prior to turbulence (Fig. 1d), a greater proportion of time was spent slow swimming (60.7%) and less time was spent breaking (38.7%). Increased foraging at high food concentrations agrees with other direct observations (21, 34, 35) and classical zooplankton grazing techniques (28–31, 33). Data of this type are the basis for viewing copepod grazing in terms of Holling's (8) functional response curves (27–31) and optimal foraging strategies (36).

Behavior During Turbulence. Time budgets demonstrate that the behavioral response of *C. hamatus* to turbulence was similar in both high and low food concentrations. In both cases, the percentage of time allocated to slow swimming dominated the time budgets. Fast swimming increased significantly during turbulence relative to preturbulence (Wilcoxon test, $P < 0.05$). However, because these events are so rapid, their increase is better shown by the number of times they occur (behavioral transition frequencies) rather than their portion of the overall time budget (Fig. 1b and e). At low food concentrations, fast swimming occurred only during the turbulent period, while during the high food concentration turbulent period, fast swimming accounted for a large fraction (31%) of the behavioral transitions.

The answer to our first research question is that the behavioral response of *C. hamatus* to turbulence consisted of an increased frequency of fast swimming and, at low food concentration, an increased allocation of time to slow swimming.

In answer to our second research question, *C. hamatus* responded to the higher encounter rates due to turbulence as if it were experiencing altered prey concentrations. At low food concentrations, *C. hamatus* allocated significantly more time to slow swimming during the turbulent period than the preturbulent period (Wilcoxon test, $P < 0.05$). However, the data do not support the contention that *C. hamatus* equates apparent prey concentrations occurring during turbulence with those of higher actual prey concentrations. The low food concentration, turbulent period and the high food concentration, preturbulent period had different turbulence regimes but similar encounter rates. Average control encounter rates for these periods were almost equal [low concentration turbulent, $x = 68.8$ encounters per 1000 frames, $SD = \pm 11.3$; high concentration preturbulent, $x = 69.1$ encounters per

Low Food Density



High Food Density

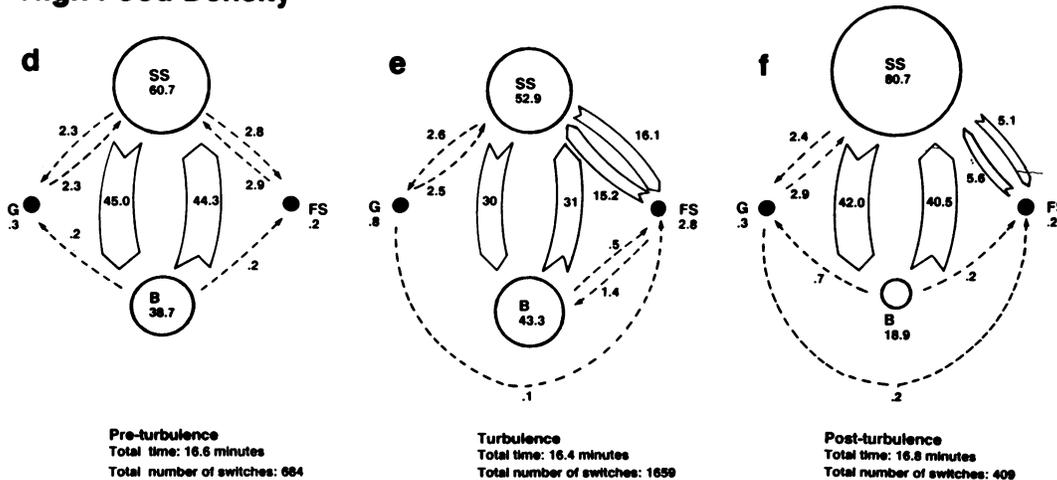


FIG. 1. Time budget and behavioral transition data for the low food concentration (70 *Gymnodinium* sp. per ml) experiment. (a) Nonturbulent period prior to turbulence. (b) Turbulent period. (c) Nonturbulent period after turbulence, and for the high food concentration (350 *Gymnodinium* sp. per ml) experiment. (d) Nonturbulent period prior to turbulence. (e) Turbulent period. (f) Nonturbulent period following turbulence. Behaviors are abbreviated as SS (slow swimming), B (breaking), FS (fast swimming), and G (grooming). Each behavior is represented by a circle; the diameter of the circle is proportional to the percentage of total time spent performing that behavior, with the actual percentage as listed. Solid circles represent behaviors occupying too low a percentage of the total time to be represented at the scale of the figure. Arrows represent transitions between behaviors. The direction of the arrow indicates the direction of the behavioral transition; the width of the arrow is proportional to the fraction that particular type of transition represents among all the behavioral transitions. This percentage is also listed as numbers associated with the arrows. Dotted arrows represent transition frequencies too low to be accurately represented on the scale of the figure.

1000 frames, $SD = \pm 15.1$. See Marrase *et al.* (24) for further description of encounter rates]. Therefore, the two treatments represented similar apparent prey concentrations. While the overall time budgets and transition frequencies appear similar (Fig. 1 b and d), the distribution of time allocation to slow swimming was significantly different between the two treatments (Wilcoxon test, $P < 0.05$). These results demonstrate that the response to turbulence was dynamic and time allocation averages need to be qualified by examination of time series data, as in Fig. 2. The results also indicate that although encounter rates play an important role in the behavior of *C. hamatus*, the response to turbulence is more complex than can be explained solely as a function of apparent prey concentration.

Behavior After Turbulence. The postturbulent periods most clearly demonstrated the complex nature of the foraging response of copepods in response to changes in encounter rate. After the cessation of turbulence, the copepod kept slow swimming at levels much greater than would be expected based solely on encounter rates. This response occurred at the termination of turbulence in both low and high food concentration treatments and was reflected in the overall

time budgets (Fig. 1 c and f, respectively). The same pattern was observed in preliminary experiments and in experiments performed after those described here.

Time Course of the Behavioral Response to Turbulence. Encounter rates increased sharply at the onset of turbulence, remained high during the turbulent period, and declined during the postturbulent period. This pattern was consistent for both algal concentrations (Fig. 2 a and e).

Examination of the time course of the three main behavior patterns—grooming, fast swimming, and slow swimming—revealed different response patterns for each behavior. The fourth behavior, breaking, was essentially the inverse of slow swimming because these two behaviors occupied the majority of the time budget.

Only grooming appeared to directly track the abrupt rise and decline in encounter rate at the beginning and end of turbulent periods. Grooming showed little variation with turbulence at low food concentration (Fig. 2b) but increased significantly at the outset and declined at the termination of turbulence at the high food concentration (Wilcoxon test, $P < 0.05$; Fig. 2f). The occurrence of grooming in all experimental conditions reflects the necessity of cleaning the va-

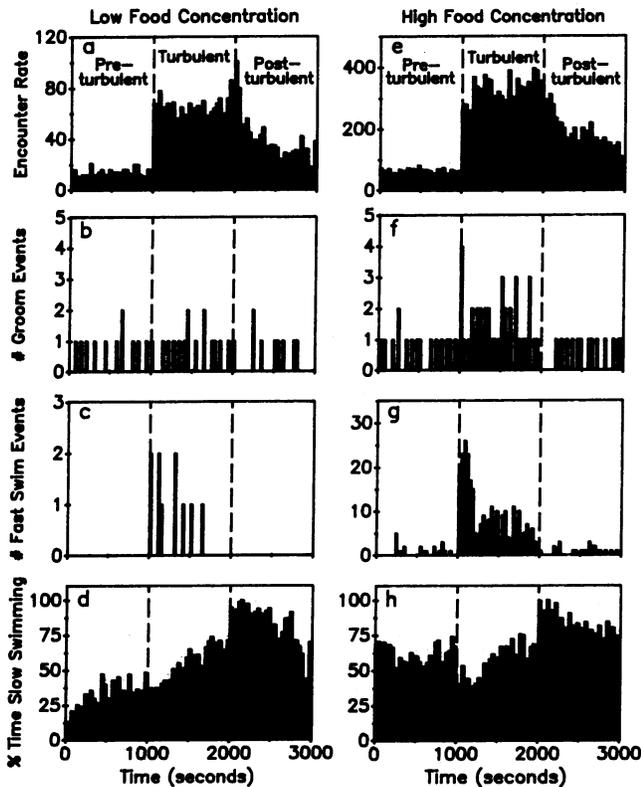


FIG. 2. Time course for changes of encounter rate (a and e) and three associated behaviors (b-d and f-h) during the low (a-d) and high (e-h) food concentration experiments. The behaviors shown are the number of grooms, number of fast swims, and the percentage of time spent slow swimming. Each variable is tabulated over 1000 video frame periods (33.33 sec). Note different y-axis scales for a and e as well as for c and g.

riety of chemo- and mechanoreceptors found on the first antennae and other body parts (16, 37) to maintain sensory performance (25).

Fast swimming events increased significantly during turbulence, particularly during the high food concentration treatment (Wilcoxon test, $P < 0.05$; Fig. 2g). However, fast swimming decreased markedly after 3-4 min, indicating habituation of the response to turbulence. This might be expected because fast swimming is an escape response; escape responses of other crustaceans have been found to habituate rapidly under conditions of rapid, repeated stimulation (38-41).

Slow swimming did not directly track variations in encounter rate (Fig. 2d and h). Instead, the percentage of time spent slow swimming lagged behind increases in encounter rate. The changes in slow swimming during the time course of the turbulent period were not significantly different between low (Fig. 2d) and high (Fig. 2h) food concentrations. Similarly, postturbulent slow swimming frequencies were not significantly different for low and high food concentrations (Fig. 2d and h). These patterns indicate a similar response to the onset and cessation of turbulence by *C. hamatus* at both high and low food concentrations.

The different response patterns of each behavior indicate that, following the onset of turbulence, the attention of *C. hamatus* shifts from predator avoidance (initial period characterized by a high number of escape responses) to foraging (increased slow swimming during the time course of turbulence). The attention pattern shift may reflect the dynamics of coping with the selective pressures of the copepod's environment. For example, in an environment experiencing frequent turbulence, the expectation state of the neural

system (42) associated with escape reactions may be different than that for a low-turbulence environment. Therefore, the escape response of copepods inhabiting a high-turbulence environment may habituate much more rapidly than those of a copepod in a low-turbulence environment. In the low-turbulence environment, turbulence would more reliably indicate predators and the attention shift from predator avoidance to foraging would require a longer time period. In this case, interspecific variations in response patterns of copepods would influence ability of different species to utilize the changes in apparent prey concentration caused by turbulence. These patterns can be quantified in the time allocation and transition frequency patterns of different copepod species.

It is important to distinguish the copepod's response to variations in encounter rate from those due to alterations in turbulent energy alone. How would *C. hamatus* respond to turbulence in particle-free water? An additional experiment was run under conditions similar to those previously described with the exception that the copepod was held in 0.22- μm filtered seawater and the level of turbulence was not quantitatively defined. Prior to turbulence (Fig. 3a), *C. hamatus* spent the predominant portion of its time resting (92%) and very little time slow swimming (7%). Grooming and fast swimming occupied low proportions of the time budget. This activity pattern is characteristic of the standby mode. Initiation of turbulence (Fig. 3b) resulted in a greater amount of time spent slow swimming (18%); however, the predominant activity was still resting (81%). Increased grooming and fast swimming also accompanied turbulence. The most dramatic shift in behavior occurred during the postturbulent period. The cessation of turbulence (Fig. 3c) was accompanied by increased slow swimming (54%). This reaction was similar, although less pronounced, to that found for *C. hamatus* held in the algae-containing treatments and suggests that the cessation of turbulence caused a motivational shift in the copepod, which resulted in increased foraging.

The behavior of the copepod in filtered seawater indicated that although the overall behavioral repertoire was influenced by encounter rates with food items, there was a reaction to alterations in turbulent energy alone, particularly the decline of turbulence. The response pattern to turbulent events was characteristic and repeatable and occurred even when no prey were encountered. Thus, both encounter rate history and alterations in turbulent kinetic energy interact to influence the behavior of *C. hamatus*. The synergistic nature of this relationship is central to understanding copepod feeding in environments of variable turbulent energies.

Critique of the Use of the Functional Response Paradigm. As previously noted, the time spent slow swimming (foraging) did not respond directly to the increased encounter rate

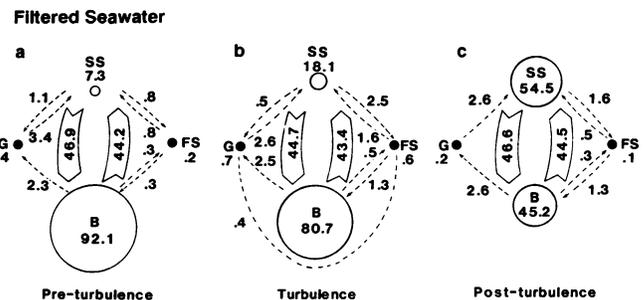


FIG. 3. Time budget and behavioral transition data for the additional experiment with 0.22- μm filtered seawater. (a) Nonturbulent period prior to turbulence. (b) Turbulent period. (c) Nonturbulent period after turbulence. Graphic conventions are identical to those in Fig. 1.

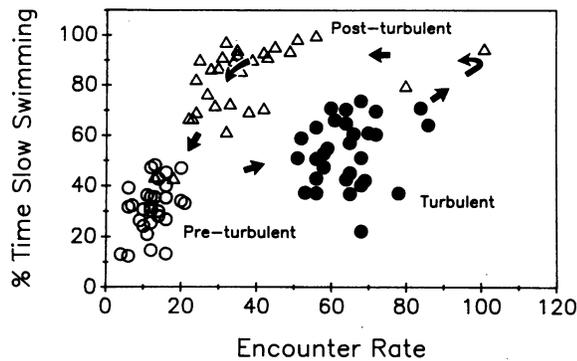


FIG. 4. Effect of motivation on the relationship between encounter rate (encounters per 1000 video frames) and the percentage of time spent slow swimming for the low food concentration treatment. The axes of this figure are analogous to food concentration (x axis) and clearance rate (y axis) typical of functional response curves. ○, Preturbulence; ●, turbulence; △, postturbulence.

caused by turbulence. When plotted in relation to encounter rate, the percentage of time spent slow swimming clusters into three distinct groups representing preturbulent, turbulent, and postturbulent periods (Fig. 4). While the increased slow-swimming rates occurring during turbulence were a response to the increased apparent prey abundance during turbulence, the postturbulent slow-swimming rates cannot be similarly explained because the initial postturbulent rates were high despite a decline in apparent prey abundance. Instead, the postturbulent period rates are best explained by a motivational shift following turbulence. The result is a hysteresis-like effect. The experience of high apparent prey concentrations during the turbulent period may have caused a residual encounter rate expectation level, which resulted in the initially elevated slow-swimming rates during the postturbulent period. The hysteric response indicates that energy expenditure by *C. hamatus* is influenced by the copepod's history of apparent prey concentration (whether determined by turbulence or prey patch dynamics) and hydrodynamic regime. Therefore, the efficiency with which *C. hamatus* responds to food depends on the copepod's recent feeding environment.

These observations and interpretations do not support the "automatic" response to food concentration as implied in the functional response paradigm (9). Zooplankton populations will respond to prey concentration in a species-specific pattern depending on temporal and spatial prey distributions, the intensity spectrum of turbulent eddies, and feeding history. Considering the prevalence of the functional response paradigm in leading papers (43) and textbooks (44, 45) that describe ocean productivity, it appears pertinent to us to further study the factors influencing response patterns at the temporal and spatial scales of the individual animal.

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- Grant, H. L., Steward, R. W. & Moillet, A. (1962) *J. Fluid Mech.* **12**, 241–263.
- Oakey, N. S. & Elliot, J. A. (1982) *J. Phys. Oceanogr.* **12**, 171–185.
- Lueck, R. G. & Osborn, T. R. (1982) *Report 80* (Department of Oceanography, Univ. of British Columbia, Vancouver).
- Dickey, T. D. (1990) in *Patterns, Processes and Yields of Large Marine Ecosystems*, ed. Sherman, K. (AAAS, Washington, DC), in press.
- Oviatt, C. A. (1981) *Mar. Ecol. Prog. Ser.* **4**, 57–67.
- Alcaraz, M., Saiz, E., Marrase, C. & Vaque, D. (1988) *Mar. Ecol. Prog. Ser.* **49**, 117–125.

- Koopman, B. O. (1956) *Oper. Res.* **4**, 324–531.
- Holling, C. S. (1965) *Mem. Entomol. Soc. Can.* **45**, 3–60.
- Gerritsen, J. & Strickler, J. R. (1977) *J. Fish. Res. Board Can.* **34**, 73–82.
- Rothschild, B. J. & Osborn, T. R. (1988) *J. Plankton Res.* **10**, 465–474.
- Evans, G. T. (1989) *J. Plankton Res.* **11**, 415–417.
- Strickler, J. R. (1982) *Science* **218**, 158–160.
- Andrews, J. C. (1983) *Can. J. Fish. Aquat. Sci.* **40**, 1293–1302.
- Legier-Visser, M. F., Mitchell, J. G., Okubo, A. & Fuhrman, J. A. (1986) *Mar. Biol.* **90**, 529–535.
- Strickler, J. R. (1985) in *Physiological Adaptions of Marine Animals*, ed. Laverack, M. S. (The Company of Biologists Limited, Cambridge, MA), pp. 459–485.
- Strickler, J. R. (1975) *Verh.-Int. Ver. Theor. Angew. Limnol.* **19**, 2951–2958.
- Haurly, L. R., Kenyon, D. E. & Brooks, J. R. (1980) *J. Plankton Res.* **2**, 187–202.
- Zaret, T. M. (1980) in *Evolution and Ecology of Zooplankton Communities*, ed. Kerfoot, W. C. (Univ. Press of N. Engl., Hanover, NH), pp. 594–603.
- Strickler, J. R. (1974) in *Swimming and Flying in Nature*, eds. Wu, T. Y.-T., Brokaw, C. J. & Brennen, C. (Plenum, New York), pp. 599–613.
- Conley, W. J. & Turner, J. T. (1985) *Mar. Ecol. Prog. Ser.* **21**, 113–120.
- Cowles, T. J. & Strickler, J. R. (1983) *Limnol. Oceanogr.* **28**, 106–115.
- Cowles, T. J. (1983) *Mar. Biol.* **78**, 53–57.
- Alcaraz, M., Paffenhofer, G.-A. & Strickler, J. R. (1980) in *Evolution and Ecology of Zooplankton Communities*, ed. Kerfoot, W. C. (Univ. Press of N. Engl., Hanover, NH), pp. 241–248.
- Marrasé, C. M., Costello, J. H., Granata, T. & Strickler, J. R. (1990) *Proc. Natl. Acad. Sci. USA* **87**, 1653–1657.
- Strickler, J. R. (1984) in *Trophic Interactions Within Aquatic Ecosystems*, eds. Meyers, D. G. & Strickler, J. R. (Westview, Boulder, CO), pp. 187–239.
- Sustare, B. D. (1978) in *Quantitative Ethology*, ed. Colgan, P. W. (Wiley, New York), pp. 275–311.
- Parsons, T. R., LeBrasseur, R. J., Fulton, J. D. & Kennedy, O. D. (1969) *J. Exp. Mar. Biol. Ecol.* **3**, 39–50.
- Frost, B. W. (1972) *Limnol. Oceanogr.* **17**, 805–815.
- Frost, B. W. (1975) *Limnol. Oceanogr.* **20**, 263–266.
- Mullin, M. M. & Brooks, E. R. (1976) *Limnol. Oceanogr.* **21**, 784–796.
- Reeve, M. R. & Walter, M. A. (1977) *J. Exp. Mar. Biol. Ecol.* **29**, 211–221.
- Lam, R. K. & Frost, B. W. (1976) *Limnol. Oceanogr.* **21**, 490–500.
- Houde, S. E. L. & Roman, M. R. (1987) *Mar. Ecol. Prog. Ser.* **40**, 69–77.
- Poulet, S. A. & Gill, C. W. (1988) *Mar. Ecol. Prog. Ser.* **43**, 259–267.
- Paffenhofer, G.-A. & Stearns, D. E. (1988) *Mar. Ecol. Prog. Ser.* **42**, 33–38.
- Lehman, J. T. (1976) *Limnol. Oceanogr.* **21**, 501–516.
- Strickler, J. R. & Bal, A. K. (1973) *Proc. Natl. Acad. Sci. USA* **70**, 2656–2659.
- Krasne, F. B. (1969) *J. Exp. Biol.* **50**, 29–46.
- Zucker, R. J. (1972) *J. Neurophysiol.* **35**, 621–637.
- Wine, J. J., Krasne, F. B. & Chen, L. (1975) *J. Exp. Biol.* **62**, 771–782.
- Wine, J. J. & Krasne, F. B. (1982) in *The Biology of Crustacea—Neural Integration and Behavior*, eds. Sandeman, D. C. & Atwood, H. L. (Academic, New York), pp. 242–299.
- Bullock, T. H. (1988) in *Sensory Biology of Aquatic Animals*, eds. Atema, J., Fay, R. R., Popper, A. N. & Tavolga, W. N. (Springer, New York), pp. 269–284.
- Steele, J. H. & Frost, B. W. (1977) *Philos. Trans. R. Soc. London Ser. B* **280**, 485–534.
- Parsons, T. R., Takahashi, M. & Hargrave, B. (1977) *Biological Oceanographic Processes* (Pergamon, Oxford, U.K.), 2nd Ed.
- Valiela, I. (1984) *Marine Ecological Processes* (Springer, New York).