

# The effects of small-scale turbulence on the ingestion rate of fathead minnow (*Pimephales promelas*) larvae

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**Abstract:** Small-scale turbulence increases encounter rates between planktonic predators and their prey. It has been hypothesized to lead to an increase in feeding by fish larvae, yet this has rarely been tested experimentally. We investigated the effects of turbulence on feeding by fathead minnow (*Pimephales promelas*) larvae to test the null hypothesis of no effect of turbulence on ingestion. In one experiment, larvae were exposed to four turbulent velocities from 0 to 2 cm·s<sup>-1</sup> at a single prey concentration. Data analysis led to a rejection of the null hypothesis. Moreover these data suggested a significant nonlinear response of ingestion to increasing turbulence. In a second experiment, we varied turbulence and prey concentrations (15, 50, and 500 prey/L) simultaneously. We rejected the null hypothesis of no effect of turbulence for all prey concentrations. Results differed among prey concentrations. We observed a negative linear response for the two lower prey concentrations, but a domed response at 500 prey/L. We conclude that turbulence does influence ingestion, but not as suggested by an extension of encounter models. Thus, turbulence may not always be beneficial in the field.

**Résumé :** Les turbulences à petite échelle accroissent la fréquence des contacts entre les prédateurs planctoniques et leurs proies. On a avancé que ce phénomène pouvait conduire à une alimentation plus intense chez les larves des poissons, mais cette hypothèse n'avait été testée expérimentalement que rarement. Nous l'avons fait en prenant des larves du tête-de-boule (*Pimephales promelas*) et en testant l'hypothèse principale, soit d'aucun effet des turbulences sur l'ingestion. Dans un cas, des larves ont été exposées à un flot turbulent qui s'écoulait à quatre vitesses différentes, de 0 à 2 cm·s<sup>-1</sup>, et à des proies à une seule concentration. L'analyse des données nous a conduits à rejeter l'hypothèse principale. De plus, les données semblaient indiquer l'existence d'une réponse non linéaire significative de l'ingestion à la turbulence accrue. Dans un autre cas, nous avons fait varier à la fois la turbulence et la concentration des proies (15, 50 et 500 proies/L). Nous avons rejeté l'hypothèse principale d'aucun effet de la turbulence à toutes les concentrations de proies. Les résultats différaient selon la concentration des proies. Nous avons observé une relation linéaire inverse dans le cas des deux concentrations les plus faibles, mais nous avons obtenu une courbe en forme de cloche à 500 proies/L. Nous parvenons à la conclusion que les turbulences influencent réellement l'ingestion, mais pas de la manière que le laisse prévoir une extension des modèles qui décrivent les contacts prédateur-proie. Sur le terrain, ces turbulences n'ont pas toujours un effet bénéfique.

[Traduit par la Rédaction]

## Introduction

Turbulence is a consistent hydrodynamic feature of all aquatic ecosystems (Thorpe 1985; Yamazaki and Osborn 1988). Typically, turbulence is confined to the surface or

mixed layers of aquatic environments, although tidal currents do also produce bottom layer turbulence (Tennekes and Lumley 1972). It occurs at spatial scales small enough to affect planktonic trophodynamics via influences on phytoplankton size distributions and production of primary and

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secondary producers (Oviatt 1981; Davis et al. 1991; Kjørboe 1993). For zooplankton, it has been shown to modify their behaviour (Costello et al. 1990; Haury et al. 1992; Saiz and Alcaraz 1992a), metabolism (Marrasé et al. 1990; Saiz and Alcaraz 1992b; Alcaraz et al. 1994), and growth rates (Alcaraz et al. 1988; Saiz and Alcaraz 1991; Saiz et al. 1992). Less is known of the effects of turbulence on larval fish (B.R. MacKenzie, Danish Institute for Fisheries and Marine Research, Charlottenlund Castle, Charlottenlund, DK-2920, Denmark, unpublished results).

Rothschild and Osborn (1988) have demonstrated theoretically that turbulence can enhance the rate of encounter between planktonic predators and their prey. This increased encounter rate has now been verified experimentally for zooplankton (Costello et al. 1990; Marrasé et al. 1990) and fish larvae (B.R. MacKenzie, unpublished results). The observed increases in encounter as a result of turbulence have been used to explain patterns of growth and survival of fish larvae in the field. For example, MacKenzie et al. (1990) suggested that turbulence-induced increases in feeding rates may resolve the paradox of the observation that prey concentrations in the field are often below those required to sustain fish larvae in the laboratory. Sundby and Fossum (1990) and Sundby et al. (1994) explained enhanced feeding in Arcto-Norwegian cod (*Gadus morhua*) observed during storms by invoking the beneficial effects of turbulence. Matsushita (1991) argued that the level of turbulence in the field was important in determining feeding success of Japanese anchovy (*Engraulis japonica*) and sardine (*Sardinops melanostictus*). Muelbert et al. (1994) also concluded that turbulence-related increases in feeding and growth were important factors affecting the distribution of herring larvae (*Clupea harengus*) off southwest Nova Scotia, Canada. Recently, F.E. Werner (Marine Sciences Program, University of North Carolina, College Box 3300, Chapel Hill, NC 27599-3300, U.S.A., unpublished results) has invoked turbulence to account for the growth and survival of cod and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank.

Although the link between turbulence, encounter, ingestion, growth, and survival is appealing, experimental tests of the linkages have yielded ambiguous results. Studies of copepods show evidence of beneficial effects of turbulence (Costello et al. 1990; Marrasé et al. 1990; Saiz and Alcaraz 1992a), but other studies have suggested detrimental effects (Oviatt 1981). For example, MacKenzie et al. (1994) predict that the effects of turbulence on feeding will be nonlinear. They predict peak levels of ingestion at intermediate levels of turbulence and lower levels of ingestion at high levels of turbulence. Furthermore, MacKenzie and Leggett (1991) and Saiz et al. (1992) suggest that the response to turbulence will be dependent on prey concentration. These authors suggest that feeding enhancement as a result of turbulence will be greatest at low prey concentrations. However, the hypothesis that the increases in encounter brought about by quantified levels of turbulence yield increases in ingestion and growth rates remains untested for fish larvae.

The objectives of our research were to determine the effects of turbulence on the ingestion rates of fish larvae. Specifically, we tested the null hypothesis that small-scale

turbulence does not influence ingestion rates of larval fish. The alternative hypotheses examined were that ingestion was either linearly or nonlinearly related to the level of turbulence. In a second experiment, we investigated the interaction between turbulence and prey concentration suggested by MacKenzie and Leggett (1991) and Saiz et al. (1992).

## Methods

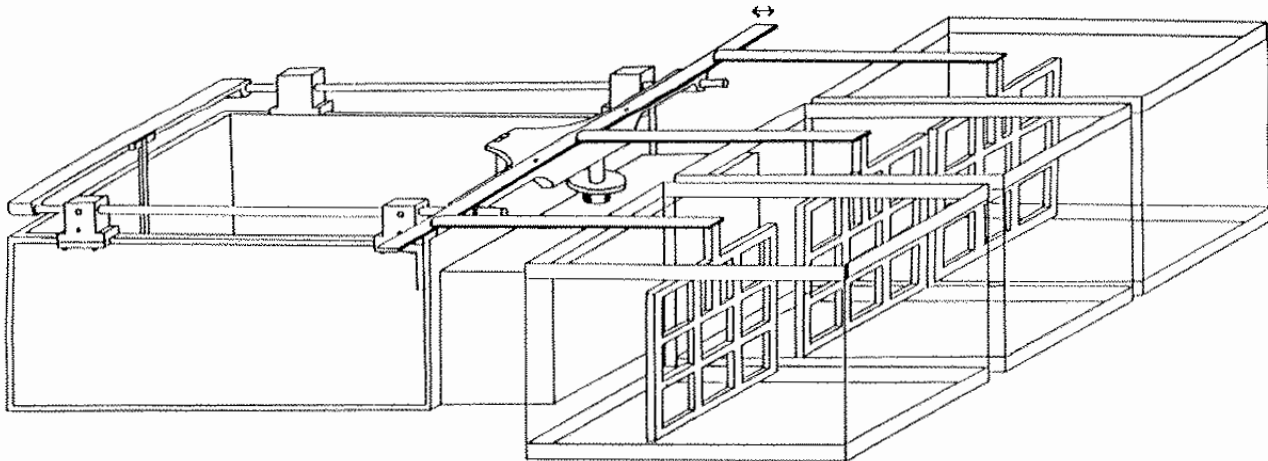
We conducted experiments using fathead minnow (*Pimephales promelas*) larvae. Fathead minnow is an intermittent, multiple spawning freshwater species that is easy to culture (Gale and Buynak 1982). Larvae hatch at approximately 5 mm total length. Five mating pairs of adults provided a continuous supply of larvae for the experiments. Each pair was reared in a 20-L aquarium at 25°C under a 16 h light : 8 h dark cycle. Spawning was induced by alterations in the temperature and light environments (Denny 1987). A polyvinyl chloride (PVC) pipe, cut in half longitudinally, served as a spawning substrate (Denny 1987). Once the eggs were laid, the substrate was removed to a brood tank, and hatching occurred after 4 days. Larvae began feeding on the day of hatching. They were fed brine shrimp (*Artemia* sp. San Francisco strain) nauplii ad libitum. This prey is within the size range of natural food for these larvae (Norberg and Mount 1985). We used 6-day-old larvae (average total length 6.5 mm) in the experiments to ensure sufficient time for conditioning to feeding, and to enable us to identify which larvae had successfully initiated feeding.

The first experiment, conducted to evaluate the effect of turbulence on feeding rate in fathead minnow larvae, involved four levels of turbulence in a gradient treatment, at a single prey concentration (30 prey/L). This concentration was chosen because Miller et al.'s (1992) data suggest this should be a nonsaturating prey concentration. The experiment was conducted in eight complete blocks. Mean number of prey per gut was the response variable. Data were analyzed as a one-way analysis of variance with turbulence and squared turbulence as covariates. We incorporated a second-order polynomial to differentiate between the competing alternative hypotheses.

Trials were conducted in 20-L aquaria (40 × 20 × 25 cm) in complete blocks. Each aquarium held ten 6-day-old larvae. Twenty hours prior to a trial, larvae were transferred to each experimental tank by gently spooning them from stock tanks. This period ensured full gut clearance prior to the trial. Each trial allowed the larvae to feed for a period of 15 min while being exposed to a level of turbulence. At the end of the trial, the larvae were immediately removed from each tank using a small dip net and killed in a chilled solution of MS-222 prior to final preservation in a 70% ethanol solution. A visual check was made to ensure no regurgitation occurred prior to preservation. Subsequently, larvae were individually dissected under a dissecting microscope to count the *Artemia* sp. in their stomachs.

To obtain the prey concentration required in the tanks for each trial, we added a prescribed volume of a known concentration of nauplii. The actual prey concentration in each tank was sampled during each trial by lowering three PVC

**Fig. 1.** Scale diagram of the oscillating grid apparatus. The grids were made out of 1-cm square stock Plexiglas. The grid was  $19 \times 19$  cm and had a mesh opening of 5 cm. The oscillating motion was generated by an American Optical (model 02156) shaking water bath. The stroke of the oscillation was 2.8 cm. The arrow indicating the oscillation is drawn to scale. The distance from the midpoint of the grid's stroke to the centre of the tank was 3.6 cm. Three 20-L aquaria were filled with 17 L of water.



tubes (4 cm diameter) over stoppers placed randomly on the bottom of each tank. These samples were taken 3 min after the prey were added. The volume of each sample was measured (~175 mL) and the sample was then poured through a 64- $\mu$ m mesh sieve to retain the *Artemia* sp. for later enumeration.

Turbulence was generated by an oscillating grid. The grid design was based upon one used in two previous studies (Thompson and Turner 1975; Hopfinger and Toly 1976). We used shaking water baths to oscillate a Plexiglas mesh grid (Fig. 1). Each water bath generated turbulence in three experimental chambers. Owing to both the size of the chamber and the apparatus used, turbulence was not uniform throughout the tank. We characterized the level of turbulence in the tank as the turbulent velocity ( $u$ , in  $\text{cm}\cdot\text{s}^{-1}$ ) present in the centre of the tank by applying Hopfinger and Toly's (1976) equation to our system, so that

$$[1] \quad u = C \cdot f \cdot S^{1.5} \cdot M^{0.5} \cdot z^{-1}$$

where  $C$  is a constant of proportionality equal to  $2.5 \times 10^{-1}$ ,  $f$  is the frequency of the oscillating grid,  $S$  is the stroke (2.8 cm),  $M$  is the mesh size (5.0 cm), and  $z$  is the distance from the midpoint of the grid's stroke to the center of the tank (3.6 cm). The stroke used in the trials, 2.8 cm, reduced the probability of the larvae hitting the grid. We used four different frequencies of oscillation (0, 0.9, 1.8, and 2.7 Hz), which generated calculated turbulent velocities of 0, 0.65, 1.31, and 1.96  $\text{cm}\cdot\text{s}^{-1}$  in the middle of the tank. Turbulence is usually reported in the literature as the energy dissipation rate ( $\epsilon$ ) in  $\text{cm}^2\cdot\text{s}^{-3}$ . A typical value of  $\epsilon$ , reported to be beneficial to ingestion in fish larvae, is  $10^{-3} \text{ cm}^2\cdot\text{s}^{-3}$  (Marrasé et al. 1990). Using this value in Rothschild and Osborn's (1988) turbulent velocity equation (their eq. 4), and an estimated larval reactive distance of 0.65 cm, the approximate equivalent turbulent velocity is  $0.2 \text{ cm}\cdot\text{s}^{-1}$ .

The second experiment investigated the effects of turbulence and prey concentration simultaneously. The experiment employed a randomized complete block design

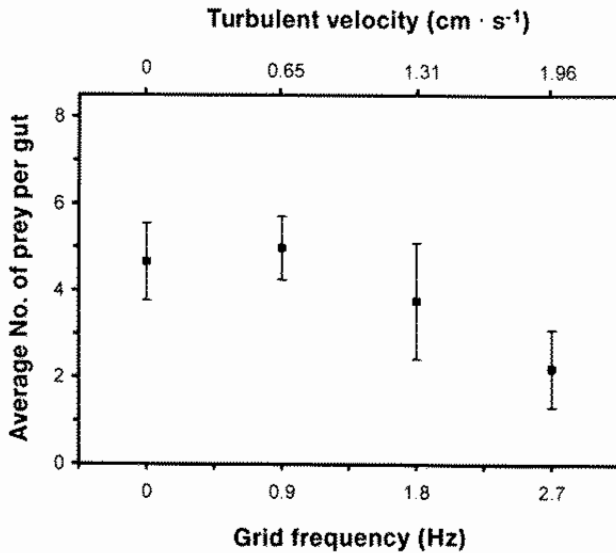
replicated eight times. We used the same four levels of turbulence in a gradient treatment design as in the first experiment. Prey concentration (15, 50, and 500 prey/L) was considered a factorial treatment. We hypothesized that we would see no influence of turbulence if we exposed larvae to a prey concentration that permitted them to feed at a maximal rate and thus we chose three prey concentrations to ensure that we would bracket both a nonsaturating and a saturating prey concentration. We chose 15 and 50 prey/L to ensure that the prey concentration differences would be sufficiently large that we could maintain them during trials. Thus, 15 prey/L may have been anywhere from 10 to 20 but never overlapped with the 50 prey/L concentration. The prey concentrations we employed were typical of those found in the field (Pace 1984, 1986; Wu and Culver 1991). Experimental procedures were the same as in the first experiment. The data were analyzed as a two-way analysis of variance with turbulence and squared turbulence as covariates.

## Results

There were few subjective differences between the behaviour of larvae in the nonturbulent and turbulent aquaria. Larval swimming speeds and patterns appeared similar in the two cases. Larvae did avoid the area of the tank directly in the path of the grid in turbulent trials. However, because the area of the tank that was directly affected by the motion of the grid was small, this did not appear to restrict the overall movements of larvae in the turbulent environment.

The first experiment was designed to test the null hypothesis of no effect of turbulence on ingestion. The average number of prey eaten was affected by turbulence (Fig. 2). Overall the model was significant ( $F_{19,221} = 21.56$ ,  $p < 0.001$ ) with  $R^2 = 0.90$  (Table 1). Therefore, we rejected our null hypothesis and concluded that turbulence did influence ingestion rate. Furthermore, the parameter estimate for squared turbulence was also significant ( $turb^2$ ,  $F_{1,221} =$

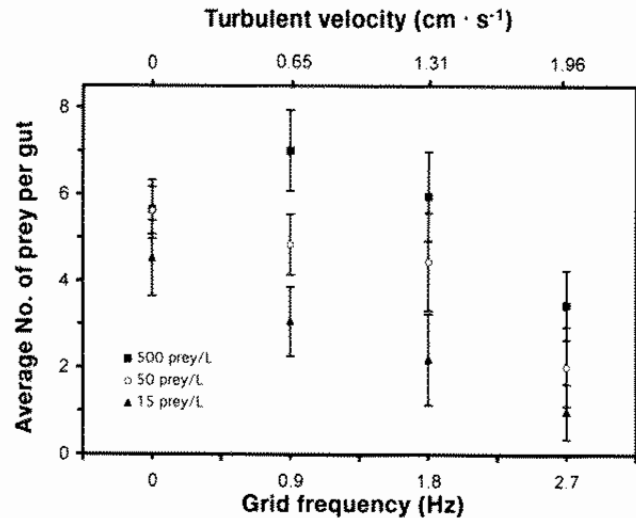
**Fig. 2.** Relationship between feeding rate of fathead minnow larvae and turbulence. Data are given as means  $\pm$  SE from eight replicates in which each replicate contained 10 larvae for each level of turbulence. The larvae were exposed for 15 min to a single concentration (30 prey/L) of *Artemia* sp. prey. Turbulence values are given as grid frequency (Hz) and turbulent velocity ( $\text{cm}\cdot\text{s}^{-1}$ ), which are estimated values for the center of the tank (see eq. 1).



5.91,  $p < 0.03$ ). Moreover, the quadratic term was negative, indicative of a nonlinear response of feeding rate to increasing turbulence. Single degree of freedom contrasts suggested a nonsignificant enhancement of feeding at low turbulence (0.9 Hz), and a significant reduction in feeding at the highest level (2.7 Hz) employed (Fig. 2).

The results from the second experiment yielded significant differences between prey concentrations (Fig. 3). Exposure to the highest level of turbulence led to a decline in ingestion at all prey concentrations, as in the first experiment. This led to a rejection of the null hypothesis of no effect of turbulence on ingestion. However, in contrast to the first experiment, enhanced feeding at low levels of turbulence was only observed at the high prey concentration. At 500 prey/L we documented a 1.24-fold increase in feeding from zero turbulence to the next level (0.9 Hz). However, at 15 and 50 prey/L, feeding rates declined as turbulence increased without any statistically significant evidence of nonlinearity as seen in the earlier experiment. Thus, we could not distinguish between the competing alternative hypotheses. Analysis indicated that both prey concentration and turbulence had significant effects (prey:  $F_{[2,84]} = 10.87$ ,  $p < 0.001$ ; turbulence:  $F_{[3,84]} = 8.01$ ,  $p < 0.001$ ; Table 2) on the feeding rate of the fathead minnow larvae. There was no significant interaction effect ( $F_{[6,84]} = 0.65$ ,  $p < 0.69$ ; Table 2). Thus, while prey concentration was clearly a factor that affected the relationship between ingestion and turbulence, we could not determine the nature of its effects from these data. There was a significant negative linear relationship for the lowest prey concentration and a significant nonlinear relationship for the highest

**Fig. 3.** Relationship between mean gut content per tank with turbulence as a function of prey concentration. Data are given as means  $\pm$  SE of eight replicates in which each replicate contained 10 larvae for each level of turbulence. The larvae were exposed for 15 min to a single concentration of *Artemia* sp. prey. The prey concentrations were 15, 50, and 500 prey/L. Turbulence values are estimates for the centre of the tank (see eq. 1).



**Table 1.** Parameter estimates for the effects of turbulence on feeding rate at a prey concentration of 30 prey/L.

	Intercept	Linear	Quadratic	$R^2$
$t$ statistic	5.12**	0.91	-2.43*	0.90
Parameter estimate	3.243	0.610	-0.579	
SE	0.63	0.67	0.24	

**Note:** The experiment was conducted in eight complete blocks involving four levels of turbulence (0, 0.9, 1.8, and 2.7 Hz). Each block used four tanks, each containing 10 larvae. Analyses were conducted on mean gut contents per tank using an analysis of variance (ANOVA). The overall ANOVA was significant ( $F_{[9,22]} = 21.56$ ,  $p < 0.001$ ). Tests of significance for the overall regression are based upon 32 observations, and individual parameter significance levels are based on a  $t$  test with 1 degree of freedom.

\*Significant at  $0.01 < p < 0.05$ .

\*\*Significant at  $p < 0.01$ .

prey concentration (Table 2). However, within the 50 prey/L trial, because of the larger variability in the results we were unable to distinguish between the null hypothesis and the alternatives.

## Discussion

Our data suggest that the effects of small-scale turbulence on feeding rate in fish larvae are complex. For the four prey concentrations we tested, we were able to reject our null hypothesis of no effect of turbulence on ingestion in three instances, yet we could not distinguish clearly between the alternative hypotheses of linear and nonlinear effects. However, our findings indicate that while encounter rates may

**Table 2.** Parameter estimates for the effect of turbulence on feeding rate at a three prey concentrations.

	Intercept	Linear	Quadratic	R <sup>2</sup>
15 prey/L				
<i>t</i> statistic	8.07**	-2.10*	0.32	0.86
Parameter estimate	5.439	-1.495	0.081	
SE	0.67	0.71	0.25	
50 prey/L				
<i>t</i> statistic	6.60**	0.14	-1.51	0.76
Parameter estimate	5.943	0.131	-0.509	
SE	0.90	0.95	0.34	
500 prey/L				
<i>t</i> statistic	8.66**	3.29**	-4.65**	0.86
Parameter estimate	5.929	2.379	-1.196	
SE	0.68	0.72	0.26	

**Note:** The experiment was a 4 by 3 factorial design replicated eight times. Overall, both turbulence ( $F_{[3,84]} = 8.01$ ,  $p < 0.001$ ) and prey concentration ( $F_{[2,84]} = 10.87$ ,  $p < 0.001$ ) were significant. Analyses were then conducted treating turbulence as a gradient treatment design. Analyses were conducted on mean gut contents per tank.  $R^2$  values for each regression are based upon 32 observations, and individual parameter significance levels are based on a *t* test with 1 degree of freedom.

\*Significant at  $0.01 < p < 0.05$ .

\*\*Significant at  $p < 0.01$ .

increase in turbulent environments, the extension to assuming that ingestion will similarly increase is unwarranted. In all cases, we document a decrease in ingestion at the highest level of turbulence. Furthermore, in two instances, we show evidence for a nonlinear response in ingestion. However, as the instances of nonlinearity we report were not consistent among food concentrations, caution must be exercised in interpreting these results. We suggest that the potential nonlinear response of ingestion rate by larval fish to increases in turbulence requires further study.

Despite the conflicting data with regard to the exact form of the relationship, our results clearly demonstrate negative effects on ingestion at high levels of turbulence. MacKenzie and Leggett (1991) suggested that small-scale turbulence associated with frontal and upwelling regions may increase larval ingestion rates. The assumption made in deriving this hypothesis was that turbulence-induced increases in encounter would translate into increases in ingestion. Our results suggest that if increases in ingestion in such regions are observed, they may more reasonably reflect hydrodynamically induced increases in prey abundance than turbulence-induced increases in ingestion. However, MacKenzie and Leggett's hypothesis may still hold if the nonlinear response that occurred in two instances in our study is typical. Under these conditions, frontal and upwelling regions may well provide the double benefit of increased prey abundance and increased ingestion probability.

The negative effect of turbulence observed in this experiment can be explained by several mechanisms. Generally prey are patchily distributed. Turbulence may act to disrupt local food concentrations; this would lead to a perceived reduction in prey concentration and thus reduced ingestion rates (Peterman and Bradford 1987; Wroblewski and

Richman 1987). The impact of turbulence may be related to larval reaction times. If larvae are too slow to respond to prey whose relative velocities are increased by small-scale turbulence, ingestion rates may decrease (Drost et al. 1988; Matsushita 1991). Finally, as suggested by MacKenzie et al. (1994), the energy in the turbulent eddies may be too high, such that even if the fish responds, its rate of successful capture and hence ingestion rate will decrease.

Other studies provide support for the nonlinear relationship between feeding rate and turbulence suggested in two instances by our data. Recently, MacKenzie et al. (1994) predicted, theoretically, a nonlinear response of ingestion to increasing turbulence for fish larvae. They suggested that this response occurs because, while encounter increases with turbulence, the probability of successful pursuit decreases as turbulence increases. In a similar theoretical development Matsushita (1991) also predicted a nonlinear response of ingestion to turbulence for fish larvae. Empirical evidence from copepods also suggests a nonlinear response. Saiz et al. (1992) reported an enhancement of feeding for *Acartia* sp. at low intensities of turbulence and a decrease in feeding at higher intensities of turbulence. The authors suggested that higher intensities of turbulence caused a detrimental effect on the feeding currents created by the copepod's appendages. Similarly Marrasé et al. (1990) showed a dome-shaped response of ingestion to turbulence in *Centropages hamatus*. In this case, the energetic cost of feeding in a turbulent regime was suggested as the mechanism causing the nonlinearity. Less direct empirical evidence for a nonlinear response to turbulence comes from studies on recruitment patterns in fishes. Cury and Roy (1989) reported that high levels of turbulence induced by upwelling were detrimental to recruitment of North African pelagic marine fishes, and that recruitment was highest at intermediate levels of wind stress. Subsequently, Ware and Thomson (1991) found similar patterns in recruitment time-series data for Pacific sardine (*Sardinops sagax*).

In summary, we have documented negative effects of turbulence on feeding rates in larval fish in a series of laboratory experiments. Our results suggest that the effect of turbulence may be nonlinear at certain prey concentrations. Although it is difficult to transfer these results directly to the field situation, our findings do suggest that the assumption that because turbulence increases encounter rates feeding rates will also increase may be inaccurate. We suggest that the influence of turbulence on feeding, growth, and distribution of fish is complicated, largely unknown, and warrants further study.

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