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## Larval fish feeding and turbulence: A case for the downside

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### Abstract

Theory states that small-scale turbulence decreases pursuit success of planktonic predators by advecting the encountered prey from the reactive zone of the predator during the pursuit event. We tested the quantitative predictions of a previously published model describing this phenomenon in larval cod by videorecording particle motion and feeding behavior of larval cod (8.7–12.3 mm) preying on copepods in a laboratory tank. Fluid motion shared characteristics with that in the ocean, i.e., intermittent, logarithmically distributed, average particle–particle velocity difference proportional to separation distance<sup>1/3</sup>. Estimated bulk dissipation rates were  $0\text{--}2 \times 10^{-8} \text{ m}^2 \text{ s}^{-3}$  and similar to those commonly experienced by larval cod in nature (e.g., located at 30 m during winds of ca.  $7 \text{ m s}^{-1}$ ). Owing to the intermittent nature of turbulence, we related individual predation events to local, instantaneous relative velocities instead of bulk averages. Pursuit success decreased significantly with relative velocity and the observations approximated the predicted effect of turbulence on pursuit success. Nonlinear and counteracting effects of turbulence on pursuit success and encounter may partly explain the contradictory observations of how turbulence affects larval fish feeding, growth, and survival in the sea.

Turbulence in the sea influences both the food environment for larval fishes and their ability to feed successfully (Kiørboe 1993; Dower et al. 1997). These influences include the production of new prey, dispersion of patches of existing prey, increases in encounter rates between planktonic predators and prey (Rothschild and Osborn 1988), interference with prey perception capability (Kiørboe and Saiz 1995), and reductions in pursuit and capture ability of encountered prey (Granata and Dickey 1991).

In visual predators like larval fish, the primary negative effect of turbulence may be the advection of encountered prey out of the reactive zone faster than the predator can react to it (e.g., Sundby and Fossum 1990; Matsushita 1992). Thus, turbulence may reduce the pursuit success of larval fish. MacKenzie et al. (1994) modeled this effect for larval cod. The model was later slightly modified by Kiørboe and Saiz (1995). Predictions of the revised model suggest that

the effect of turbulence on pursuit success becomes significant at turbulent dissipation rates experienced by small larval cod in their ocean habitats (Kiørboe and MacKenzie 1995). In this study we provide an experimental test of the model using larval cod.

The pursuit success model requires as input estimates of dissipation rate or relative velocities, prey encounter (or reaction) distance, and duration of pursuit time. We therefore designed our experiments so that these parameters could be quantified and we then compared the predicted and modeled pursuit success. We demonstrate a significant negative effect of small scale turbulence on pursuit success, even at low-moderate dissipation rates, and a fair correspondance between the predicted and observed pursuit success.

### Materials and methods

*Experimental animals*—We conducted experiments with two size and age groups of cod larvae (average total lengths 8.7 mm at age 43–44 d and 12.3 mm at age 57 d). Cod larvae (*Gadus morhua*) were produced from artificially-fertilized eggs as described by Munk (1995) and were reared in tanks containing flowing turbulent water (see Munk and Kiørboe 1986 for details of tank design). Prey were nauplii and early stage copepodites of *Acartia tonsa*, which were reared as described by Støttrup et al. (1986). Water temperature during larval rearing and behavior experiments was 6–8°C.

Nauplii and copepodites of *A. tonsa* were also used as

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prey in behavior experiments. Since relative prey–predator size affects feeding success in fish larvae (e.g., Munk 1995), we used prey sizes (lengths) in our experiments that matched those shown by Munk (1995) to optimize feeding success in cod larvae. This prey size was approximately 3% of the larval body length.

*Experimental setup*—All experiments were conducted in a 19-liter cylindrical plexiglas tube (diameter 20 cm, height 61 cm) which contained 17.7-liter seawater. To reduce the effect of curvature of the cylindrical tank on video image quality, the cylindrical tank was placed in a seawater bath inside a rectangular plexiglas tank (25.5 × 25.5 × 50.8 cm). Illumination was provided by three fluorescent tubes situated behind the bath. A motor-driven grid (diameter 19 cm, bar width 1.8 mm, inter-bar distance 10.0 mm, ratio of open area to total area 0.70) was oscillated vertically (stroke amplitude 18 cm) in the upper 24 cm of the cylindrical tank to generate turbulence. A 250- $\mu\text{m}$  plankton mesh screen was inserted horizontally 3.5 cm below the lowest grid oscillation point to prevent cod larvae from becoming entrained into the upper grid oscillation region of the tank where they could be damaged by the oscillating grid. Turbulence in the tank was estimated quantitatively by particle motion analysis (see below for details).

On the day before an experiment was conducted, 10 larvae were transferred from the rearing tank to the experimental tank and held overnight (ca. 12–18 h) in calm water without food. Prey were added (concentration in tank  $\sim 100 \text{ L}^{-1}$ ) on the morning of the experiment and feeding behavior was observed and recorded first in calm water for a period of 10–15 min, after which grid oscillations began to generate turbulence. Additional observations in turbulent water were then recorded under two nominal levels of turbulence (first low, then high, corresponding to different grid oscillation frequencies) for comparisons with the calm treatment observations. Observations were made in the sequence calm, low turbulence, and high turbulence on each day. We recorded approximately 50 encounter and attack events for each condition (two larval sizes, three levels of turbulence).

In total, 318 pursuits and attacks were available for analysis. Individual pursuit events were classified visually according to whether they were successful or failures using definitions below. A random subset of 110 pursuits was used for detailed quantitative analysis of particle motions and predator–prey behaviors.

*Video-recording techniques*—Larval and prey behaviors were recorded in 2D on videotape. The video output signal from a color video camera was directed to a video monitor and to a super-VHS video cassette recorder (50 fields  $\text{s}^{-1}$ ). A time–date generator recorded experimental run-time directly onto video records at an interval of 0.01 s.

The observation arena was considerably larger than the depth and field of view of the camera. Larval positions were, therefore, tracked in realtime by following individual larvae on the monitor as they swam or were moved by water currents. Tracking was accomplished by manually raising and lowering the camera on a tripod and adjusting its focus with a zoom lens. This enabled us to maintain an individual larva

in focus for several minutes regardless of its location within the tank and to observe sharp magnified (5–15 fold, depending on distance from the front of the tank) images of larval behaviors in real-time on the video monitor. The length of time that an individual larva could be followed depended on its behavior (e.g., whether it swam along a tank wall, was resting near a tank edge, or was actively feeding).

*Motion analysis*—The motion of prey particles recorded on the videotapes was used to estimate relative velocities between prey particles and between the larva and prey. The method employs tracking individual particle positions over short time intervals (1–5 s) as they are being advected by water motion (Saiz and Kiørboe 1995; Peters and Redondo 1997; Sanford 1997). These positions, together with the intervening time intervals, are then used to estimate velocities of prey particles relative to each other and to the fish larva. The scalars used in estimating distances were larval eye diameters and lengths. These were recorded from larvae retrieved from the tank at the end of a day's experiment and were highly correlated (Eye Diameter [ $\mu\text{m}$ ] =  $105 \times$  total larval length [mm] – 226;  $R^2 = 0.96$ ;  $N = 31$ ; length range 7.0–13.9 mm). Prey relative velocities are then used to derive an approximate estimate of the level of turbulence in the system.

Positions of larva (centre of eye) and prey were noted at time intervals of 0.1–0.5 s. Time intervals were adjusted so that durations of critical events (e.g., pursuit and attack time, prey escape behaviors) during the predation sequence could be determined accurately. This information was then used to derive interparticle (including larval-prey) distances and relative velocities. Each predation sequence contained several velocity estimates (median  $N$  per sequence = 25) based on all combinations of particle pairs that appeared in consecutive fields of view. A typical predation sequence lasted  $\sim 1$ –5 s depending on prey escape and predator pursuit and attack behavior (see results).

We calculated a mean relative velocity for each predation sequence. For these calculations, we excluded the positions of both the larva and the prey that was being pursued and attacked (target). Their behavior (e.g., escape attempts) would bias estimates of relative velocity that were otherwise due to the turbulence in the tank and behaviors unrelated to feeding or escape (i.e., normal swimming behavior). Prey–prey relative velocities as calculated here represent, therefore, the combined motion due to turbulence and non-escape swimming behavior of the copepods. We used the so calculated mean relative velocities for individual predation events as input to model calculations.

All distances and velocities were recorded in 2D and thus, underestimate true (3D) distances and velocities. By assuming isotropic water motion, average 3D velocities and distances were computed, where appropriate, by multiplying average 2D estimates with 1.225.

*Turbulent dissipation rate*—To achieve a crude estimate of turbulent dissipation rates in the tank we first separated observed average relative velocity ( $\Delta v$ ) into its prey swimming ( $v$ ) and water motion ( $w$ ) velocity components by noting that (Evans 1989)

$$\Delta v = (2v^2 + 2w^2)^{0.5}. \quad (1)$$

Average swimming velocity was estimated in the calm water treatment ( $w = 0$ ) from eq. 1, and this estimate was then used to estimate average  $w$  in each of the turbulent treatments, assuming that average swimming velocity is independent of turbulent intensity (turbulence may elicit rapid escape responses in copepods [Saiz and Alcaraz 1992; Saiz 1994], but only at turbulent intensities exceeding those applied here [Kiørboe et al. 1999]).

We next note that at spatial scales exceeding the Kolmogorov scale, relative particle-particle velocities ( $w$ ) are expected to vary with particle separation distance ( $d$ ) in a turbulent environment as (Sanford 1997)

$$w = 1.37(\epsilon d)^{1/3} \quad (2)$$

where  $\epsilon$  is the turbulent energy dissipation rate. Because of the intermittent nature of turbulence, both in the ocean and in our experimental tank, such a relation was not clearly evident when considering individual estimates of relative velocity, and separation distance. However, since dissipation rates and other microstructure quantities are related to kinetic energy inputs only after averaging over suitable spatial and temporal scales (Oakey 1985), we binned the data after conversion to 3D. Binning was accomplished by grouping separation distances in logarithmically-spaced intervals. The binning process used here is analogous to the data averaging techniques employed in the analysis of oceanic shear microstructure (Oakey 1985; Yamazaki and Lueck 1990; Stips et al. 1998). We then calculated geometric means of  $\Delta v$  within each binning interval and subsequently  $w$  from Eq. 1. Finally, Eq. 2 was fitted using nonlinear regression to the so binned and corrected data, and a dissipation rate ( $\epsilon$ ) estimated for each treatment. The regression analysis was weighted using the number of relative velocity estimates per separation distance interval (median = 132; range 19–299). These dissipation rate estimates allowed a comparison of fluid motion in the tank with that in the ocean and were not used as model inputs.

*Operational definitions of larval cod feeding behaviors*—The behavioral events that we investigated were encounters, pursuits, attacks, and captures. We used the following definitions of these events and the parameters used to quantify them in our analyses.

**Encounter:** perception of prey by the larva as elicited by changes in orientation of the larval body, eyes or head toward a food particle. In some cases, changes in swimming direction and body posture are also visible. The distance between predator and prey at the time of encounter is the *encounter distance*. Encounter initiates the predation sequence (Holling 1959; Gerritsen and Strickland 1977) and is followed immediately by a pursuit.

**Pursuit:** Pursuit is the event in which a larva swims toward an encountered prey, or waits until the prey is advected closer to its mouth. Pursuits begin immediately after encounter and can include time required to fixate the prey in the field of view prior to final attack. A given pursuit can include

repeated approaches of the larva to the prey if the prey displays escape maneuvers. The pursuit is terminated when any of the following events happen: (i) the larva opens its mouth and attacks the prey; (ii) the prey escapes and the larva does not follow; (iii) the prey is advected by water motion away from the larva and the larva does not (or cannot) follow the prey. The duration of the pursuit (*pursuit time*) is the time interval between encounter and either of (i)–(iii). Pursuits can be successful (case i) or unsuccessful (ii and iii), and *pursuit success probability* is the percentage of encounters that lead to attacks.

**Attack:** Attacks occur when a larva opens its mouth in an attempt to capture and ingest a prey. The attack itself is sometimes accompanied by forward motion of the larva toward the prey. The *attack distance* is the distance between larva and prey at which this happens, and the *attack success probability* is the percentage of attacks (mouth-openings) resulting in prey capture.

## Results

The videotaping method produced clear color images of both larva and prey in the same field of view. The videotapes showed the positions of the larval eye and movements of the mouth, and fins, as well as larval pursuit and attack behaviors. In addition, some prey behaviors could be resolved, particularly escape attempts.

*Prey-prey separation distances, relative velocity, and turbulent intensity*—Prey-prey separation distances largely followed Poisson distributions and hence, suggest random distributions of prey in the tank (Fig. 1). The average 3D separation distances (*d-average*) varied between 11 and 14 mm, and were close to that expected for random distributions and a concentration ( $C$ ) of 100 prey  $L^{-1}$  (*d-average* =  $0.55C^{-1/3}$ ), 12 mm.

The distribution of relative velocities between prey particles in each of the three treatments (calm, low, and high turbulence) show a wide range of velocities (Fig. 1). The geometric mean of relative velocity (2D) was lowest in the calm treatment and higher in the low and high turbulence treatments. The average 3D relative velocities in the three treatments were 0.27, 0.57 and 1.12  $mm\ s^{-1}$ . From Eq. 1, this implies an average prey swimming velocity of 0.19  $mm\ s^{-1}$  and average turbulent velocities ( $w$ ) of 0.35 and 0.75  $mm\ s^{-1}$  at the average prey-separation distances at low and high turbulence, respectively.

Relative particle-particle velocity difference depended on separation distance largely as predicted by theory (Eq. 2; Fig. 2). This correspondence was strongest for the high turbulence treatment where the fitted parameters described a statistically significant relationship. In the low turbulence case, the fit was not statistically significant, and parameters based on this relationship are therefore less certain. The fitted relationships allow us to provide crude bulk estimates of  $\epsilon$  for the two levels of turbulence, i.e.,  $2 \times 10^{-8}\ m^2\ s^{-3}$  and  $2 \times 10^{-9}\ m^2\ s^{-3}$ . These values are similar to the turbulence that would be expected at 30 m depth within a surface mix-

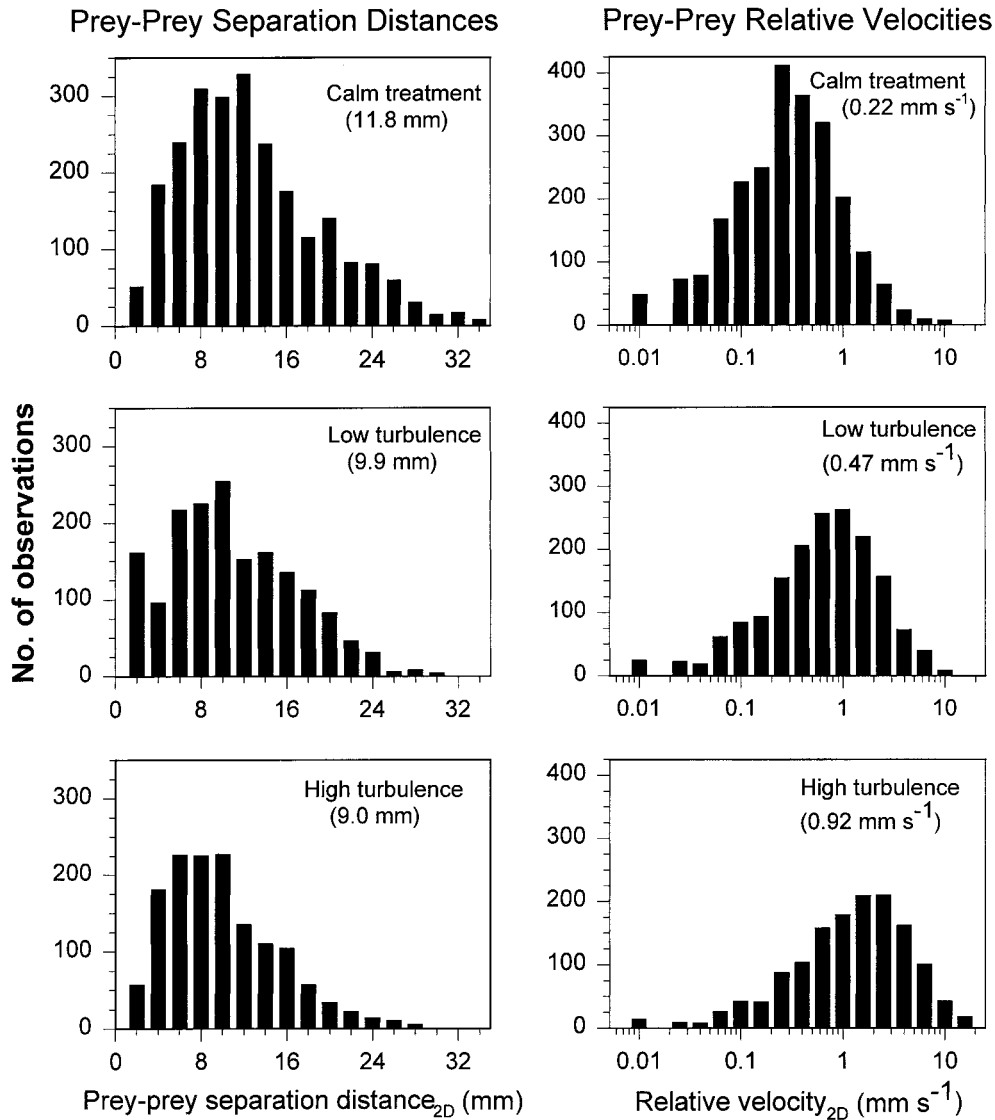


Fig. 1. Frequency distributions of separation distances, and relative velocities between food particles during individual pursuit events in calm, low turbulence, and high turbulence experimental treatments. For each pursuit event, several (10–50) measurements of separation distance, and relative velocity were available.

ing layer during winds of ca. 7 and 3 m s<sup>-1</sup> (MacKenzie and Leggett 1993, model 4).

**Encounter distance**—Average apparent (2D) encounter distance varied significantly between the two larval size groups (mean  $\pm$  95% CL: 6.55  $\pm$  1.08; 9.17  $\pm$  1.64 mm for small and large larvae; Mann–Whitney Rank Sum test,  $P = 0.016$ ), but was unrelated to relative velocity at the time of encounter ( $R^2 = 0.001$  and 0.003). Assuming random orientation of the predator–prey axis relative to the camera, average 3D distances are about 8.0 and 11.2 mm. This is roughly equivalent to one body length, as reported for many larval fish (Miller et al. 1988), including larval cod (MacKenzie and Kjørboe 1995).

**Pursuit time**—The duration of pursuits was invariant with larval size ( $t$ -test,  $P = 0.22$ ), but was on average longer for successful than for failed pursuits (Fig. 3A). In addition, pursuit time declined significantly as relative velocity during pursuit events increased (Fig. 4). When pursuits were successful, relative velocity was significantly slower than during failed pursuits (Fig. 3B).

**Pursuit success probability**—Average pursuit success among all 318 pursuits exhibited by both size groups of larvae was relatively high (77%) regardless of the relative velocity in the three turbulence treatments (Fig. 5A). The larger larvae were generally more successful (94%) than the smaller larvae (71%). When pursuit success was grouped according to the three turbulence treatments, a decrease in pursuit

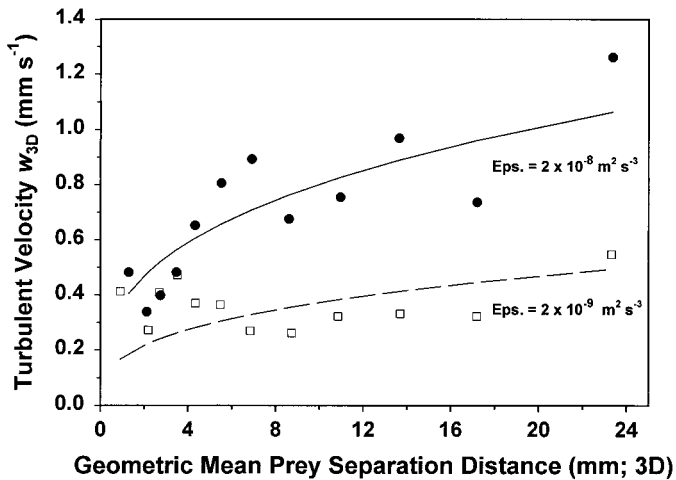


Fig. 2. The influence of prey separation distance on relative velocity between prey pairs for two levels of turbulence during individual larval cod pursuit sequences. All velocity measurements exclude larval and prey target motions. Relative velocity estimates (i.e.,  $w$ ) also exclude the contribution of non-target prey swimming behavior according to details in text. Solid line, and filled dots: high turbulence case; dashed lines, and open squares: low turbulence case. The fitted line for the high turbulence case is statistically significant ( $R^2 = 0.70$ ;  $P = 0.0004$ ; RMSE/mean rel. vel. = 10%), but that for the low turbulence cases is not ( $P = 0.8$ ). Regression analyses were conducted nonlinearly using mean values in each relative velocity and distance interval, and were weighted for the number of relative velocity estimates per distance interval.

success was evident in the high turbulence treatments. This decrease was significant for the small group of larvae and when both groups of larvae were combined (chi-square tests:  $P < 0.001$ ), but was not significant for the large group ( $P = 0.224$ ).

Pursuit success probability was then considered for the random subset of pursuit events for which local and instantaneous relative velocity measurements were available. The relative velocities during these pursuits for both size groups were grouped into intervals and the number of successful pursuits relative to the total number of pursuits was determined for each velocity category. In these comparisons, relative velocity represents the total relative velocity and therefore includes motion due to both the input of mechanical energy by the oscillating grid and behavior of non-target nauplii and copepodites. Pursuit success probability was generally high (94%) at relative velocities  $< 0.65 \text{ mm s}^{-1}$ , but decreased significantly at higher relative velocities, particularly among the smaller larvae (Table 1).

This pattern suggests a nonlinear relationship of pursuit success probability with relative velocity. Overall, the negative relationship between pursuit success probability and relative velocity was statistically significant and sigmoid regression models (using untransformed data), and linear regression models (using transformed data) explained up to 71% of the variance in observed pursuit success probability (Table 2, Fig. 6).

*Comparison of observations with theory*—The analyses above demonstrate statistically significant empirical relation-

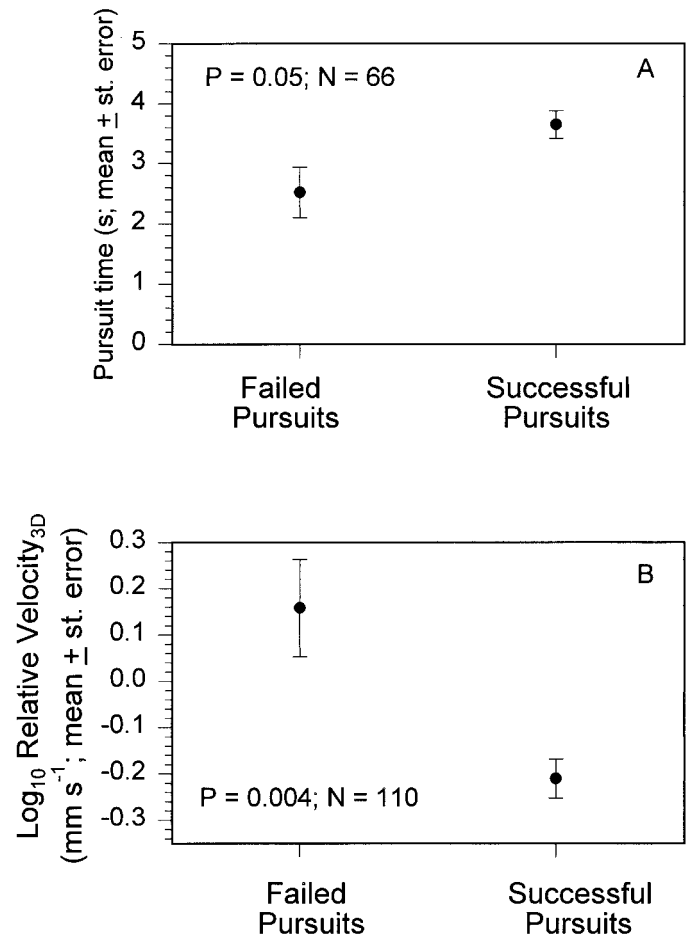


Fig. 3. (A) Duration of pursuit time (= time elapsed between encounter of an individual prey item and attack) for failed (mean  $\pm$  st. error:  $2.5 \pm 0.42 \text{ s}$ , and successful pursuits (mean  $\pm$  SE:  $3.6 \pm 0.23$ ) of prey by larval cod (mean size = 10.5 mm). The difference is almost statistically significant ( $t$ -test:  $P = 0.053$ ). (B) Relative velocities during failed and successful pursuit of prey by larval cod (mean size = 10.5 mm); the difference is statistically significant ( $t$ -test:  $P = 0.004$ ). Prey were live *Acartia tonsa* nauplii and copepodites.

ships between pursuit success probability and relative velocity. Since theoretical models also predict a decline in pursuit success with increasing relative velocity (MacKenzie et al. 1994; Kjørboe and Saiz 1995), we compared our pursuit success probabilities with these theoretical estimates.

Because reactive distances differed between size groups, we used size-specific inputs for the model. Pursuit times did not vary between larval sizes and were therefore assumed common for both size groups. However, pursuit time varied with relative velocity during pursuits (Fig. 4) and differed between failed and successful pursuits. These two observations suggest that larvae may require a specific amount of time to pursue, approach, and fixate an encountered prey before initiating attack. We therefore assumed that the total amount of time required to execute these maneuvers is equivalent to the time used to pursue prey in calm or low velocity situations. Pursuit times used as model inputs were, therefore, derived from the relationship between pursuit time

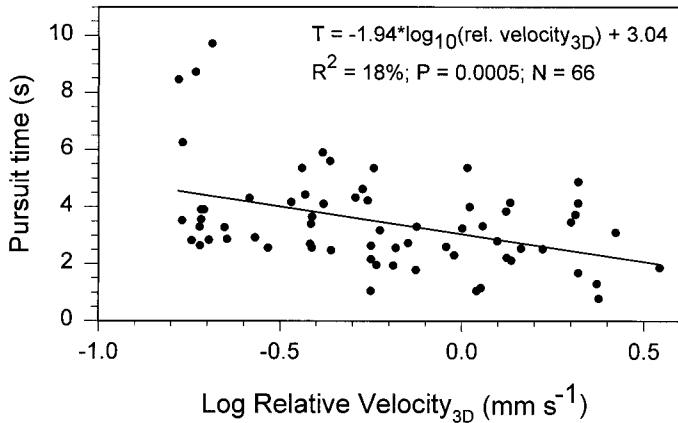


Fig. 4. The influence of ( $\log_{10}$ ) relative velocity between food particles during individual pursuit events on the duration of pursuit time for larval cod (mean size = 10.5 mm) preying on live *A. tonsa* nauplii, and copepodites. Each dot represents one pursuit event.

and log relative velocity during the individual pursuit (Fig. 4); in this relationship we used the slowest relative velocity to estimate pursuit time. However, to test the validity of this assumption and to allow for the possibility that larvae actively adjusted their pursuit behavior under higher turbu-

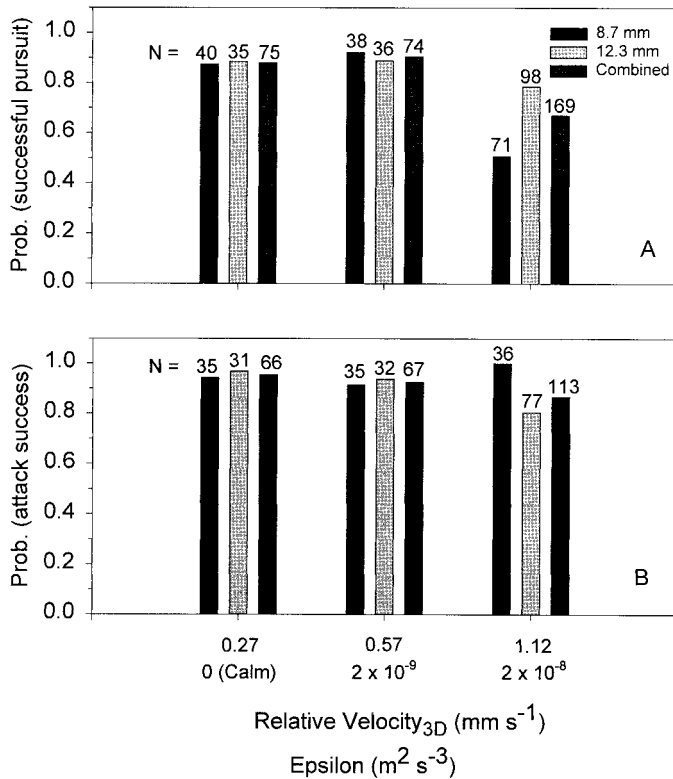


Fig. 5. Probability of successful pursuit (A), and attack (B) by two size groups of cod larvae preying on live *A. tonsa* nauplii and copepodites in three levels of turbulence. Numbers above each bar represent number of pursuits or attacks. Relative velocities and turbulent dissipation rates are bulk averages, and therefore may not be indicative of the turbulence levels experienced by the larvae during individual pursuit and attack events.

Table 1. Results of chi-square test of the null hypothesis that pursuit success probability does not differ for pursuits made during relative velocities less than and greater than  $0.65 \text{ mm s}^{-1}$  for two size groups of cod larvae preying on *A. tonsa* nauplii and copepodites. Analyses used pursuits ( $n = 110$ ) for which relative velocities were estimated directly during individual pursuits.

Size (mm)	$<0.65 \text{ mm s}^{-1}$	$>0.65 \text{ mm s}^{-1}$	$P$
8.7	1.00	0.50	$<0.001$
12.3	0.875	0.88	$>0.99$
All	0.94	0.76	$0.005 < P < 0.01$

lence, we also calculated theoretical pursuit success probabilities using variable pursuit times (i.e., mean pursuit time for a given relative velocity).

The model also requires estimates of relative velocity at the spatial scale at which pursuit begins (i.e., encounter or reactive distance). We assumed that the relative velocity measured during each pursuit event represent these velocities (see Discussion) and used this as input to the model. The calculations used total relative velocity (i.e.,  $[2v^2 + 2w^2]^{0.5}$ ), because these velocities represent the motion actually experienced by the larva. Given these inputs and assumptions, theoretical predictions of pursuit success probability were calculated, and compared with the observations.

The observed pursuit success probabilities agreed reasonably with theoretical predictions when both size groups were used in the comparison (Fig. 7). The agreement is more satisfactory if the analysis is made separately for each size group, where the smaller group conformed better to the theory than the larger size group. The deviations from the pre-

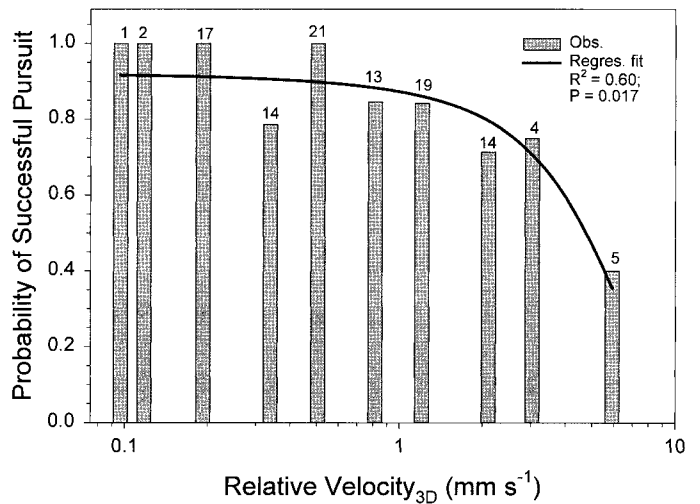


Fig. 6. Probability of successful pursuit in relation to relative velocity of prey during individual pursuit events for cod larvae (mean size = 10.5 mm) preying on live *A. tonsa* nauplii, and copepodites. The fitted line is described by the statistically significant weighted sigmoid regression model for both size groups of larvae (Table 2). Regression calculations were conducted using untransformed data, although for purposes of presentation, the pursuit success data are shown relative to  $\log_{10}$ -transformed relative velocities. Sample sizes indicated above each vertical bar.

Table 2. Fitted weighted regression models for describing the influence of relative velocity on pursuit success probability in different size groups of larval cod preying on *A. tonsa* nauplii and copepodites. Note that for the linear regression models, the fitted dependent variable is the arcsin-square root transformed value (Sokal and Rohlf 1981) of pursuit success probability and the independent variable was  $\log_{10}$  transformed. Weights used in regression analyses were the number of pursuits per relative velocity interval (see Fig. 7 for sample sizes).

Size (mm)	Sigmoid	$R^2$	$P$	Linear	$R^2$	$P$
8.7	$y = 1/(1 + e^{-(x-1.76)/-0.5})$	0.71	0.0099	$y = -0.73 \cdot \log x + 1.136$	0.69	0.0035
12.3	$y = 0.91/(1 + e^{-(x-4.95)/-0.17})$	0.34	0.1201	$y = -0.02 \cdot \log x + 1.344$	0	0.94
All	$y = 1/(1 + e^{-(x-4.75)/-1.95})$	0.60	0.0169	$y = -0.48 \cdot \log x + 1.185$	0.56	0.0080

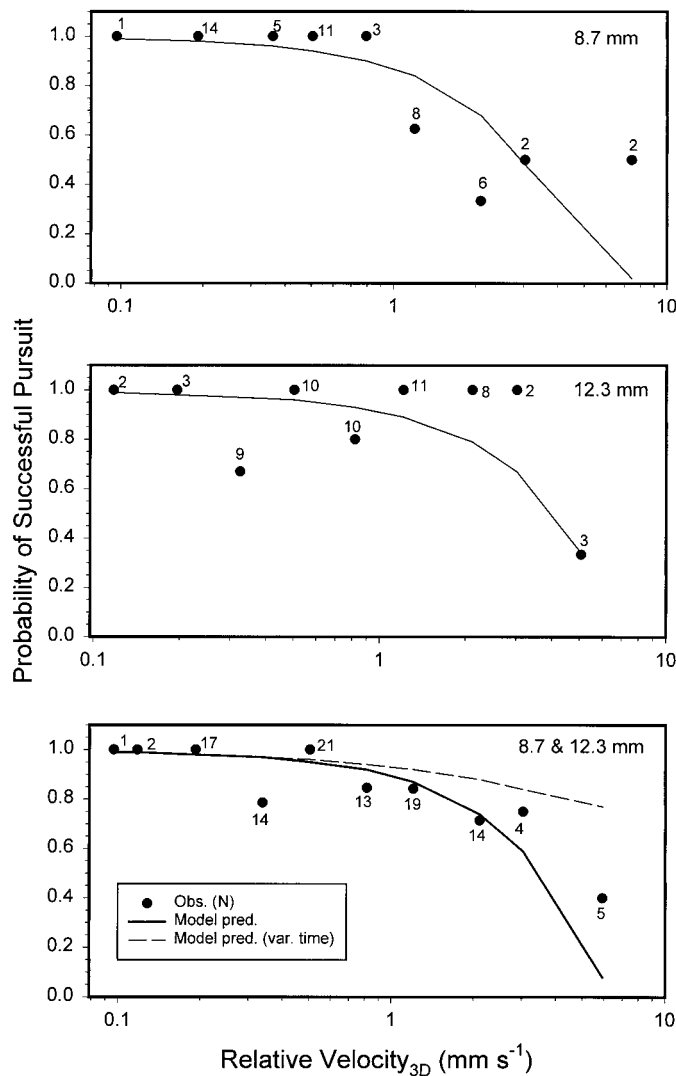


Fig. 7. Theoretical predictions of pursuit success probability compared with observations for cod larvae preying on live *A. tonsa* nauplii, and copepodites. Model calculations based on MacKenzie et al. (1994), and Kiørboe and Saiz (1995). Model inputs: reactive distance 8.0, 11.2 and 9.6 mm for the small, large, and combined size groups of larvae; pursuit time = 4.6 s for both size groups, except for panel C (dashed line) where pursuit time input was a function of relative velocity during the pursuit (see Fig. 5). Relative velocities are those measured during individual pursuit events, and are assumed to represent those at the spatial scale of one reactive distance.

dictions may be due in part to small sample sizes, particularly for the size-specific analyses at high relative velocities where turbulence will have most effect on pursuit success. When the analysis was conducted by allowing pursuit time to vary with relative velocity, theoretical pursuit success probability increased but this did not appear to improve the comparison with the observations.

**Attack behavior**—A total of 246 attacks were available for estimating attack success (Fig. 5B). These attacks were highly successful (91%) regardless of larval size or turbulence treatment (Fig. 5B; chi-square test:  $P > 0.05$ ). Attack success also varied independently of relative velocity among the subset of attacks for which detailed motion analysis records were available (Fig. 8;  $P > 0.05$ ).

Most attacks were conducted when prey were located very close to the larval mouth; average (3D) attack distances were 1.6 and 2.2 mm for small and large larvae, and were ca. 20% of the prey encounter distance. Attacks were much faster than pursuits and were usually 0.1–0.2 s in duration (mean, SD,  $n = 0.16, 0.08, 65$ ). Attack duration varied independently of relative velocity during the immediately preceding pursuit ( $P > 0.05$ ).

## Discussion

**Larval predation behavior and turbulence**—These are the first series of experiments to report direct videotaped obser-

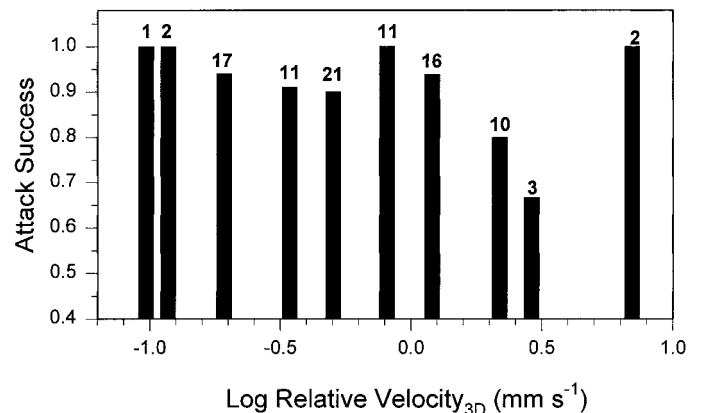


Fig. 8. The probability of successful attack of prey by larval cod (mean size = 10.5 mm) as influenced by relative velocity of prey particles during individual pursuit events. Sample sizes indicated above each vertical bar.

vations of feeding behavior of larval fish in turbulent water. We have found that turbulent water motion reduces the probability that larvae can successfully pursue their encountered prey. This finding is consistent with several theoretical predictions of larval fish feeding success in turbulent situations (Matsushita 1991; MacKenzie et al. 1994; Kiørboe and Saiz 1995; Jenkinson 1995), and is the first experimental evidence to support the conceptual basis associated with these predictions. These models are also supported by some field evidence: Dower et al. (1998) observed that the numbers of prey in guts of wild fish larvae decreased on turbulent days despite no measurable change in prey concentration.

Pursuit success probability was sensitive to turbulence over a range of relative velocities which is common in the sea. While relative velocities are difficult to measure directly in nature, turbulent dissipation rates, which are directly related to relative velocities, are now routinely measurable (e.g., Dewey et al. 1987; Simpson et al. 1997; Stips et al. 1998). The range of relative velocities (3–7 mm s<sup>-1</sup>) associated with the steepest decline in pursuit success probability for our larvae (Figs. 6, 7) corresponds to a range of dissipation rates of  $\sim 1 \times 10^{-6}$ – $1.3 \times 10^{-5}$  m<sup>2</sup> s<sup>-3</sup>, assuming a separation distance spatial scale of 10 mm ( $\sim 1$  larval reactive distance). Dissipation rates of this magnitude (and higher) occur in larval habitats (e.g., surface mixing layers during storms, tidal fronts; MacKenzie and Leggett 1993; Horne et al. 1996; Simpson et al. 1997), and suggest that larvae may become exposed to sufficiently turbulent situations that would impair their ability to feed on encountered prey. Owing to the intermittent nature of turbulence, even lower bulk dissipation rates would intermittently produce detrimental relative velocities. We note that one of the few attempts to directly measure relative particle velocities in the sea showed that relative velocities between copepods at natural concentrations were 5–25 mm s<sup>-1</sup> (Matsushita 1992). The higher end of this range implies significantly reduced pursuit success. Moreover, pursuit success is likely to be lowest among smallest larvae that are slow swimmers, and are unable to react quickly to fast-moving prey. In our experiments, which used relatively large and old larvae (compared with post-yolksac larvae whose size, and age are ca. 4.6 mm and 8 d; Solberg and Tilseth 1984), the smaller group showed a steeper decline of pursuit success than the larger group. Had we used smaller larvae, the range of relative velocities that might detrimentally affect pursuit success might have been slower.

In comparison with pursuit success, attack success was very high for all levels of turbulence in our experiments. Cod larvae approached their prey to within a small distance which is only 20% of the encounter distance and at these spatial scales the relative motion between predator and prey is reduced on average by about 40% (Eq. 1). However, because of the intermittent nature of turbulence, even at these scales we observed relative velocities of several mm s<sup>-1</sup> (cf. Fig. 8). At such velocities we found a significant effect on pursuit success. However, the duration of an attack is negligible and advection of prey hence unimportant for attack success. The main reason for failed attacks is, therefore, likely the failure of larvae to approach close enough to the prey

without stimulating an escape response (Hunter 1972; Heath 1993).

*Water motion in the experimental tanks*—The intermittent nature of turbulence in our tank, as revealed by the variable relative velocities (Fig. 1), their approximately lognormal distribution (Fig. 1) and the fair correspondence between the theoretical and observed relation between relative velocity and separation distance (Fig. 2), particularly in the higher turbulence case, suggests that some essential features of ocean turbulence are replicated in our experimental tank. While our and other experimental setups used for investigating turbulence effects on marine systems cannot replicate the larger scales of turbulent motion, our system was able to produce relative motion at scales and magnitudes most relevant to the pursuit, and attack behaviour of individual fish larvae. The bulk estimates of turbulent dissipation rates in our two turbulence treatments are well within the range of turbulent intensities experienced by larval cod in their habitats; for example, they correspond approximately to the turbulence generated at 30 m depth in the surface mixing layer by winds from 3–7 m s<sup>-1</sup> (MacKenzie and Leggett 1993, model 4; Sanford 1997).

According to Hill et al. (1992), Eq. 2 was proposed by Delichatsios and Probst (1975) for separation distances ( $d$ ) only much larger than the Kolmogorov scale ( $\lambda = (v^3/\epsilon)^{0.25}$  where  $v$  is kinematic viscosity:  $10^{-6}$  m<sup>2</sup> s<sup>-1</sup>). However, Hill et al. (1992) demonstrated experimentally that Eq. 2 provides a good description even down to spatial scales near and slightly below  $\lambda$ . The Kolmogorov scale in our experiments was 5 and 3 mm for the low and high turbulence, respectively. Our data (Fig. 2) are consistent with the observation of Hill et al. (1992).

The intermittency of turbulence in our tanks and the consequently large variation in relative velocities, implies that a larva pursuing a prey in the low turbulence treatment during an individual pursuit event could have experienced a much higher relative velocity than a larva pursuing a prey in the high turbulence treatment. This makes the possibility of relating individual pursuit events to the relevant local and instantaneous relative velocity particularly advantageous.

The relative velocities measured in our experiments represent on average the relative velocity at a mean prey–prey separation distance given by the concentration of prey in our system (100 L<sup>-1</sup>). This distance, assuming prey are poisson distributed, is 12 mm and is nearly identical to the mean separation distance that we measured from the videotape particle-tracking procedure after conversion from 2D to 3D. In addition, this separation distance corresponds closely to the larval reactive distance (see Results). As a consequence, the relative velocities reported here, even though they are calculated from prey–prey separation distances, represent on average those at the scale of prey encounter (Evans 1989; Kiørboe and MacKenzie 1995; Visser and MacKenzie 1998), and therefore at the initiation of individual pursuits. Our computations are robust to deviations from equality of prey separation distance and larval reactive distance because the influence of spatial scale on relative velocity becomes weaker at such large scales (e.g., Eq. 2, Fig. 2).

Related to this point, in our comparisons of observed pur-



suit success with the theoretical model predictions (Fig. 7), we required an estimate of relative velocity at the scale of encounter (larval reactive distance) to generate predicted pursuit successes. The relative velocities we used were those measured from non-target prey-prey separation distances during the pursuits; because of the combination of larval sizes and prey concentration used in our experiments, the spatial scale associated with these relative velocities corresponds closely to both the mean larval reactive distance and the mean prey-prey separation distance. Hence, the *predicted* pursuit successes used relative velocities defined to start at the scale of the larval reactive distance.

*Ecological implications*—Our results indicate that turbulent water motion in the laboratory can be detrimental to the pursuit success of larval cod. Decreases in pursuit success at moderate-high levels of turbulence have been shown theoretically to fully offset (MacKenzie et al. 1994; Kiørboe and Saiz 1995; Kiørboe and MacKenzie 1995) the beneficial effects of turbulence on encounter rate (Rothschild and Osborn 1988). In these situations, ingestion rates become reduced relative to those in calmer conditions. Turbulence can therefore have an overall positive or negative effect on (hourly, daily) ingestion rates depending on its intensity and predator-prey behaviors.

However, it remains unclear how turbulence affects either larval feeding, or higher order processes such as growth or survival, in nature (Dower et al. 1997) where larvae are exposed to a wide and variable range of turbulence, prey species and escape behaviors and can adjust their vertical positions in the water column to variations in wind speed, turbulence, and light (e.g., Heath et al. 1988; Olla et al. 1996). As a result, various authors working with field populations have reported different and sometimes contradictory responses to turbulence (*see* review by Dower et al. 1997). The inconclusive nature of these results when considered as a whole is at least partly due to the positive effects of turbulence on other components of the predation sequence (encounter; Rothschild and Osborn 1988; MacKenzie and Kiørboe 1995), and the interference of extraneous processes on the measured response (feeding, growth, and survival). Such processes would include the redistribution and production of prey (Lasker 1975), larval behaviors not directly related to feeding (e.g., avoidance of turbulent layers of the water column), and various measurement errors (e.g., dissipation rates, food concentrations, larval feeding or growth rate indices).

In our experiments, we have avoided many of these confounding factors and have isolated as much as possible the treatment variable of concern. This approach and the direct measurements of relative velocity during individual pursuit events, has helped us via theoretical and empirical models to resolve how one component of the predation sequence (pursuit) is influenced by small-scale turbulence. In field situations, isolating such an effect is challenging. Nevertheless, when water masses in nature become turbulent, their contained ecosystems change radically (Kiørboe 1993; Marrasé et al. 1997; Sanford 1997). Our results show that one of these changes will be a reduction in the ability of larval fish to pursue encountered prey, thereby leading to reduced food

consumption rates in comparison with those expected assuming calm water pursuit abilities.

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