Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates

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Acknowledgments

We thank Howard Browman and François Landry for access to data, and Ian Jenkinson, Brian Sanderson and Svein Sundby for reviewing an earlier version of the manuscript. B.R.M. was supported by graduate and post-doctoral fellowships from the Natural Sciences and Engineering Research Council of Canada and from the Danish National Science Foundation. This work was supported, in part, by grants from OPEN (the Ocean Production Enhancement Network), one of 15 Networks of Centres of Excellence supported by the Government of Canada through the Natural Sciences and Engineering Research Council, to W.C.L., and from the Danish Science Research Council (#11-0420-1) to Thomas Kiørboe (DIFMAR, Charlottenlund, Denmark).
Abstract

Recent theoretical work suggests that small-scale turbulence enhances encounter rates between larval fishes and their prey. This finding has been extended to suggest that feeding rates will increase in turbulent environments. However, this extrapolation assumes that turbulence has no detrimental effects on post-encounter behaviours (e.g. pursuit success). We develop an analytical model to estimate the probability that larval fishes feeding in turbulent environments successfully pursue encountered prey. We show that the overall probability of feeding is a dome-shaped function of turbulent velocity, and that the height and location of the maxima depend on turbulence level and the behavioural characteristics of the predator and prey. Highly turbulent conditions (e.g. storms) will reduce feeding rates below those which occur during calmer conditions, and will affect the type of prey which larval fishes capture and ingest.
Recent theoretical, laboratory and field studies have demonstrated that small-scale turbulence affects plankton ecology through changes in plankton distributions (Haury et al. 1990), photosynthesis and coagulation rates of phytoplankton (Kiørboe 1993), encounter rates between predators and prey (Rothschild and Osborn 1988; Marrasé et al. 1990; Matsushita 1991), swimming behaviour of zooplankton (Saiz and Alcaraz 1992), and rates of development, growth and ingestion of zooplankton (Saiz et al. 1992) and ichthyoplankton (Sundby and Fossum 1990; MacKenzie et al. 1990; Landry et al, pers. comm.). However, our understanding of both the underlying turbulent processes (Nelkin 1992; Hill et al. 1992) and their effects on plankton communities (Rothschild 1992) is inadequate. In this paper, we explore the influence of turbulence on ingestion rates in planktonic animals, with particular reference to larval fish.

Feeding in fishes is often analyzed by considering its component processes - encounter, pursuit, attack and capture (Holling 1959). Rothschild and Osborn (1988) modelled the influence of small-scale turbulence on the encounter rate between planktonic predators and their prey. They showed that small-scale turbulence can increase the relative motion between predators and prey, thereby increasing encounter rates. These findings have been used to suggest that ingestion rates will be higher in more turbulent environments (Sundby and Fossum 1990; MacKenzie and Leggett 1991; Saiz et al. 1992). However, this extension of Rothschild and Osborn's model fails to recognize that encounter is a necessary, but not sufficient, condition for ingestion. A positive relationship between small-scale turbulence and ingestion requires the assumption that the post-encounter components of ingestion, namely pursuit, attack and capture are unaffected by turbulence. This assumption is unsubstantiated. Here, we investigate the effect of turbulence on the complete ingestion process by formulating a theoretical model of post-encounter processes.
that include the effects of turbulence. We then combine this model with existing encounter rate models to examine the overall effects of turbulence on ingestion.

**Theoretical development**

The probability of ingestion, \( P(\text{feed}) \) can be represented as the product of the probability that a prey is encountered, \( P(\text{enc}) \), and successfully pursued \( P(\text{sp}) \):

\[
P(\text{feed}) = P(\text{enc}) \times P(\text{sp})
\]

Thus successful pursuit, \( P(\text{sp}) \), includes the processes of approach, fixation and formation of attack posture (i.e. all behaviours from first encounter until initiation of the final attack strike), and the probability that the attack results in prey capture. Rothschild and Osborn (1988) have developed a model of the effect of turbulence on encounter. However, no framework exists to assess the effects of turbulence on the probability of successful pursuit. Therefore, to understand the effects of turbulence on ingestion, we must characterize the influence of turbulence on post-encounter processes.
To analyze the influence of turbulence on P(sp), we consider a larval fish, F and a prey, P encountered at a distance a from its eye (Fig. 1). We assume that the larva uses a cruise searching strategy and that it subsequently requires a minimum pursuit time, t, to identify, approach and fixate the prey, and enter into attack posture (e.g. Hunter 1972; Browman and O'Brien 1992). We assume that attacks occur only within the encounter sphere and that the larval swimming speed is greater than that of the prey, so that the prey cannot swim out of the encounter sphere by itself within the minimum pursuit.

We consider the approach and fixation periods (i.e. pursuit time) of the larval feeding sequence to be most sensitive to detrimental effects of small-scale turbulence. Direct observations of larval fishes feeding on live mobile prey show that prior to making the final attack, larvae require time to orient and manoeuvre themselves into optimal attack positions and postures (Hunter 1972; Browman and O'Brien 1992).
Drost 1987; Browman and O'Brien 1992). Pursuit time therefore includes both the time required by the larva to approach and orient toward the prey, and to maintain the most effective attack position (fixation time; Wanzenböck 1992) prior to making the final strike and/or initiating suction of water containing fixated prey (Hunter 1972; Drost 1987).

We assume that the probability of capture (i.e. attack success; Munk and Kjørboe 1985; also known as catch success; Drost 1987) is constant and not altered by turbulence. This is reasonable because the final attack takes place only when the prey is separated from the larvae by a very short distance and after the predator has manoeuvred into position so that the prey is focussed within its field of view (Hunter 1972; Drost 1987; Browman and O'Brien 1992). The distance to which larvae approach their prey prior to final attack is small (7 - 10 % of larval body length: Hunter 1972, Miller 1990; 1 - 3 mm: Browman and O'Brien 1992), and depends partly on the distance at which the larva can approach the prey without being detected (Wanzenböck 1992; Heath 1993). At these spatial scales, turbulent velocities become extremely small (or are completely dampened by viscosity; Rothschild and Osborn 1988; Hill et al. 1992), especially when compared either with attack swimming speeds (Miller et al. 1988; Browman and O'Brien 1992; Wanzenböck 1992) or attack suction velocities (Drost 1987). As a consequence, the effect of turbulence on aiming success and capture is likely to be small.

To incorporate a turbulent velocity, \( \mathbf{v} \), into the interaction between a larval fish predator and its prey, we define a coordinate system centred on the larva's eye. We consider turbulence acts to induce relative motion between the fish and its prey. From this perspective, the larva may be considered fixed in space. At the distances at which larvae typically encounter and pursue their prey, we assume turbulence to be locally isotropic (Nelkin 1992). Therefore, the area in which
the prey can be moved by turbulent motion is defined by a sphere of radius \( ? \), centred on the original position of the prey. We term this sphere the prey excursion sphere (Fig. 1).

To evaluate the effects of turbulence on the probability of successful pursuit, we must define the probability that, when in a turbulent regime, the prey will remain within the larva's encounter sphere for an interval of at least the minimum pursuit time. Thus for a larva having reactive distance \( R \), locating a prey at a distance \( a \), the probability of successful pursuit can be expressed by ratio of the volume of overlap between the prey excursion sphere and the predator encounter sphere (the shaded region of Fig. 1) to the total volume of the prey excursion sphere. Hence,

\[
P(sp) = \frac{V_{\text{overlap}}}{V_{\text{prey}}} \tag{2}
\]

We now solve equation 2 for all values of \( a \), \( R \), \( ? \), and \( t \). To calculate the required volume, we assume that the two spheres intersect at \( x' \) (Fig 1), and integrate the region of overlap to yield the volume by,

\[
V_{\text{overlap}} = \int_{a \& t}^{x'} m \frac{dV}{x} \tag{3}
\]

Substituting for the two spheres gives,

\[
V_{\text{overlap}} = \int_{a \& t}^{x'} \frac{p(?, t)^2 \delta(x-a)^2}{m} \frac{dV}{x'} \tag{4}
\]

Noting that,
\[ x' = \left( \frac{R^2 \& (\frac{\Delta t}{t})^2 \% a^2}{2} \right) \]  

(5)

We integrate eq. 4 and substitute into eq. 2 to yield,

\[ P(s+P) = \frac{1}{2} (\frac{\% a}{a}) \frac{\% a}{4} (a^2 \& 1) \& \frac{3}{16} (\frac{\% a}{a})^2 \]  

(6)

It is convenient to let \( \frac{a}{\% t} = a \) and \( \frac{R}{\% t} = \). Substituting these identities into eq. 6 and simplifying yields,

\[ P(s+P) = \frac{3}{4} \frac{a}{\% t} \left( \frac{R^2 \& (\frac{\Delta t}{t})^2 \% a^2}{2} \right) \& \frac{3}{4} \frac{a}{\% t} \frac{1}{4} \left( \frac{2\% a}{\% a} \right)^3 \]  

(7)

This is the general solution to Eq. 2 and has four domains. We summarize the solution
Figure 2 The non-dimensional solution of Eq. 7. The solid circles represent encounter spheres, and the dotted circles represent excursion spheres. The solution has four domains, labeled A-D, only three of which are valid. Domain A is not a valid solution as captures can only occur under the constraint that an encounter must have occurred, that is a $\# R$. Thus only solutions within the area below the line $a=R$, in which the predator encounters the prey, are valid.

In domain B, the predator pursuit sphere completely includes the prey excursion sphere, and $P(sp) = 1$, i.e., turbulence is incapable of moving the prey beyond the predators' ability to pursue it. This domain is represented by area to the right of the line $a=R-? t$. In domain C, the predators encounter sphere is totally contained within the prey excursion sphere, and $P(sp)$ is the ratio of the volumes of the two spheres [i.e. $P(sp) = (R/? t)^3$]. This domain is represented by the area below the line $a= ? t - R$. In the final domain, D, the two spheres overlap partially, and $P(sp)$ will be a function of $a$, $?$, $t$ and $R$, given by Eq. 6.

nondimensionally in Fig. 2.
We calculate the expected $P(sp)$ over the three valid domains,

$$P(sp)_{t < R} = \frac{1}{R} \int_{R}^{R+\epsilon} \int_{0}^{R} \frac{1}{m} \frac{R}{m} P(sp) \, da$$  \hspace{1cm} (8a)$$

$$P(sp)_{R < t < 2R} = \frac{1}{R} \int_{R}^{2R} \int_{0}^{R} \frac{R^3}{m (t - \epsilon)^3} \frac{R}{m} P(sp) \, da$$  \hspace{1cm} (8b)$$

$$P(sp)_{t > 2R} = \frac{1}{R} \int_{2R}^{\infty} \int_{0}^{R} \frac{R^3}{m (t - \epsilon)^3} \, da$$  \hspace{1cm} (8c)$$

where $P(sp)$ is given by Eq. 6, using a symbolic processor.

Finally, to calculate $P(feed)$ for a specific level of turbulence $\epsilon$, we evaluate both $P(enc)$ and $P(sp)$ for the particular level of turbulence. Thus,

$$P(feed) = P(enc) \ast \frac{Q}{P(sp)}$$  \hspace{1cm} (9)$$

where $P(enc)Q$ is given by Rothschild and Osborn (1988).

We use the model to consider general larval fish predator-prey interactions in turbulent environments. We assumed that the larva and prey were located at depth 20 m within a surface mixed layer. This assumption enabled us to convert turbulent velocities to equivalent wind speeds by assuming that dissipation rates at depth can be approximated by a boundary layer model of turbulent dissipation. A simplified version of this model is

$$g' = \frac{5.82 \times 10^6}{Z} (\bar{W}^3)$$  \hspace{1cm} (10)$$
where $e$ is the dissipation rate of turbulent kinetic energy ($m^2 s^{-3}$), $W$ is wind speed ($m s^{-1}$), and $Z$ is depth ($m$ - MacKenzie and Leggett 1993). To account for the different scales at which encounter and pursuit occur, we must define two turbulent velocities. We define $\nu_e$ as the turbulent velocity at the scale of the encounter process. The turbulent velocity ($m s^{-1}$) for encounter at 20 m that would be developed by wind stress can be estimated as

$$\nu_e^2 = 3.615(e@^{0.667})$$

(11)

where $r$ is separation distance (m) between predator and prey (Rothschild and Osborn 1988). In addition we also define $\nu_{sp}$, the turbulent velocity at the scale of the pursuit process. This velocity is given by Eq. 11 when the separation distance $r$ is replaced by the reactive distance $R$. Eq. 11 is traditionally considered to be valid when the predator-prey separation distance exceeds the Kolmogorov scale (e.g. Rothschild and Osborn 1988). However, recent evidence shows that velocities at scales similar to, and slightly smaller than, the Kolmogorov scale are considerably larger than those predicted by sub-Kolmogorov scale theory (Hill et al. 1992). We assume for our purposes that Eq. 11 gives reasonable estimates of the turbulent velocities appropriate for the spatial scales of larval fish encounter, pursuit and attack behaviors.

Results

The relationships between the components of ingestion and turbulent velocity for a larval
fish predator and its copepod nauplius prey are presented in Fig 3. In these simulations we use larval and prey swimming speeds, (Sundby and Fossum 1990), reactive distances and mean pursuit times (H. I. Browman pers. comm.) estimated for Atlantic cod (Gadus morhua) larvae.

Encounter, expressed relative to the non-turbulent condition, increases as turbulent velocity increases (Fig. 3A). This relationship, which does not include post-encounter predatory behaviours (e. g. pursuit and capture), reflects the current perception of how ingestion varies with turbulence. However, for realistic estimates of pursuit time the relationship between the probability of successful pursuit, P(sp), and turbulent velocity is negative and sigmoidal (Fig 3B). The product of these two functions is the relative ingestion rate and is shown in Fig. 3C. When the effects of turbulence on P(feed) are included, ingestion rate exhibits a domed response. To demonstrate the sensitivity of the model to the parameters used we present the predicted ingestion rates when both R and t are varied by approximately 50% in Fig. 4. As we express encounter relative to the non-turbulent condition, changing R will not alter the predicted encounter relationship. Thus changes in the predicted ingestion relationship resulting from changes in R and t arise solely due to their effect on P(sp).
Figure 3. The influence of turbulence on (A) relative encounter, (B) the probability of successful pursuit and (C) relative ingestion in larval cod subject to a turbulent velocity. All components are plotted with respect to the turbulent velocity, and equivalent surface wind, calculated for the scale of the reactive distance. Model inputs were: larval swimming speed, $u = 2.0 \text{ mm s}^{-1}$; prey swimming speed, $v = 0.2 \text{ mm s}^{-1}$; prey density = 5 prey $\text{l}^{-1}$ -- Sundby and Fossum (1990). We assumed reactive distance, $R = 6 \text{ mm}$, and pursuit time = 1.7 $s$ -- H. I. Browman (pers. comm.).
It is noteworthy that in all cases at high turbulent velocities the predicted ingestion rate falls below the nonturbulent ingestion rate. The effects of increases in parameter values on the zone in which turbulence increases predicted ingestion rates are opposite. Greater reactive distances increase the beneficial effects of turbulence (Fig. 4A), whereas longer minimum pursuit times lead to a reduction in the benefits of turbulence (Fig. 4B). Furthermore, the results of varying the parameter values indicate that the predicted ingestion function is most sensitive to variability in minimum pursuit time.

The position and height of the peak ingestion rate, \( I_{\text{max}} \), is a function of \( R \), the reactive distance and \( t \), the minimum pursuit time. The overlap of encounter and excursion spheres is greatest when \( R = \gamma t \). Furthermore as the slope of the encounter function is less than the slope of the successful pursuit function at this point, the maximum ingestion will occur when

When \( \gamma = R/t \), \( P(sp) \) is a constant. Thus \( I_{\text{max}} \) can be described by

\[
I_{\text{max}} = \frac{Z^*_{\gamma}}{41/64} @ Z^*_{\gamma = 0}
\]

(12)

where \( Z^*_\gamma \) and \( Z^*_{\gamma = 0} \) are the rates of encounter under turbulent and non-turbulent conditions. To demonstrate the behavior of \( I_{\text{max}} \), we show the variation of \( I_{\text{max}} \) as a function of a restricted range of \( R \) and \( t \) in Fig. 5 using parameter estimates from the base simulation.
Figure 4. Sensitivity of relative ingestion to variations in parameter estimates. All components are plotted with respect to the turbulent velocity, and equivalent surface wind, calculated for the scale of the reactive distance. A. Predicted ingestion for three levels of reactive distance, R (chained line, R=4 mm; solid line, R=6mm, and dotted line, R=8 mm). B. Predicted ingestion for three levels of minimum pursuit time, t (chained line: pursuit time = 0.9 s; solid line: pursuit time = 1.7 s; dotted line: pursuit time = 2.6 s).
Figure 5. The behaviour of $I_{\text{max}}$ as a function of $R$, the reactive distance, and $t$, the minimum pursuit time for parameter estimates given in Fig. 3.

We also used the model to explore how ingestion in larval cod might vary with depth during wind-induced turbulent mixing. MacKenzie and Leggett (1991) showed that encounter, and possibly feeding, rates would be higher near the surface where wind-induced turbulent velocities would be higher than at depths (Fig. 6A). However, these calculations excluded the effects of turbulence on post-encounter processes. Incorporation of these effects changes the prediction markedly (Fig. 6B). At low winds speeds, and hence low turbulence, the predictions of the two models are identical. However, as wind speeds and turbulence increase, the higher turbulent velocities eventually lead to declines in predicted ingestion rates in surface waters when post-encounter processes are incorporated. Under these conditions, $I_{\text{max}}$ occurs at depth (Fig 6B). We predict that if larvae regulate their depth distribution to maximize their ingestion rate, the centre of mass of depth of actively feeding larvae should increase as wind and turbulence increase,
and that this relationship would be intensified if the influence of reduced illumination in deeper water were also included in our simulations.

**Figure 6.** A comparison of the influence of turbulence on ingestion at depth predicted by (A) an encounter rate only model (Rothschild and Osborn 1988) and (B) a complete model of ingestion for different levels wind stress. Turbulence at depth during wind speeds was approximated from boundary layer theory (MacKenzie and Leggett 1993; see also text). In these simulations prey were uniformly distributed with depth at a concentration of 5 prey liter$^{-1}$.

**Discussion**
We have developed a model of the influence of small-scale turbulence on post-encounter processes in larval fish. In combination with an existing model of turbulent-dependent encounter, we used our model to assess the overall influence of small-scale turbulence on ingestion. We conclude that turbulence can have either an overall beneficial or detrimental effect on larval fish ingestion rate, depending on its magnitude and on larval behaviour. Our main conclusion, which deviates fundamentally from previous points of view, is that larval fish ingestion rates are likely to be maximal at intermediate, rather than high, levels of turbulence. This dome-shaped response occurs because, while encounter rates increase with turbulence, the probability of successful pursuit, once an encounter has occurred, decreases as turbulence increases. The reduction in pursuit success that occurs in highly turbulent environments eventually negates the increase in ingestion rate caused by the increase in encounter rate due to turbulence.

Some immediate conclusions of the effect of turbulence on ingestion rate can be drawn. Although high levels of turbulence are likely to be detrimental, these negative effects may be partly offset by changes in larval behaviors (e.g. faster pursuit times, or increased reactive fields) within and among individuals (Miller 1990; Wanzenböck 1992). For example, our model indicates that the maximum ingestion rate for a given combination of prey density and predator-prey swimming speeds is inversely proportional to the minimum pursuit time. This finding leads us to hypothesize that larval diet selectivity should shift in turbulent regimes towards more vulnerable prey, for which minimum pursuit times are shorter. Alternatively, larvae could shift to larger prey, for which R is greater. The possibility that planktonic organisms inhabiting highly turbulent environments have evolved such behavioral responses to increase their feeding success has not been explored.
Our configuration of the effect of turbulence on larval fish ingestion rates assumes that pursuit is the predatory behaviour most likely to be detrimentally affected by turbulence. However, in turbulent environments, prey behaviour may also reduce pursuit success independently of the advective effect of turbulent water motion. For example, activity levels of at least one copepod species (Acartia clausii) are higher in turbulent water than in calm water (Saiz and Alcaraz 1992). If higher prey activity translates into reduced residence time within the larval visual field, then changes in prey behaviour in turbulent environments may have the consequence of increasing larval pursuit times. Such reductions in the time available to larvae to pursue their prey lead to reductions in ingestion rate (e.g. Fig. 3). However, these aspects of larval fish-prey interactions need further study, and we note that no descriptions of larval pursuit behaviour or estimates of capture success in water having quantified levels of turbulence have been published.

The negative influence of turbulence in our simulations begins to be expressed at turbulent velocities induced by wind speeds comparable to those commonly observed in nature. We note that our use of Eq. 11 provides only an average estimate of turbulent velocity which, because of the intermittent and patchy nature of turbulent dissipation (Oakey 1985), will differ from the instantaneous turbulent velocity perceived by a larval fish. As a consequence, the success of individual pursuit events across time or space may differ from that expected using a constant turbulent velocity. In the case of a fluctuating turbulent velocity, the distribution of success probability is more likely to be lognormal, because of the lognormal distribution of surface layer turbulent dissipation rates (Oakey 1985).

There are few field studies with which we can compare our model predictions. Sundby and Fossum (1990), in the only field estimates of the influence of small-scale turbulence on larval fish
ingestion rate, predicted that winds greater than 6 m s$^{-1}$ would generate the optimal level of turbulence for feeding by larval cod. More recent field data (Sundby et al. 1993) indicate that the wind speed which yields highest feeding rates exceeds 10 m s$^{-1}$. Our model predicts an I$_{\text{max}}$ at a wind speed of 15.3 m s$^{-1}$ based on a minimum pursuit time $= 1.7$ s, a reactive distance of 6 mm and swimming speeds and prey densities reported by Sundby and Fossum. The consistency of our prediction with the field results is encouraging, given the variable nature of larval behaviour (e.g. Munk and Kiørboe 1985; Wanzenböck 1992; Browman and O'Brien 1992), prey distributions (Haury et al. 1990) and in situ measures of water column turbulence (Oakey 1985; MacKenzie and Leggett 1993). Our interpretation of the influence of turbulence on larval fish ingestion rate appears to represent most of the major characteristics of larval fish feeding behavior in turbulent environments.

The model we developed follows Holling's (1959) characterization of the predation sequence as the product of encounter, pursuit and capture processes. Our representation is likely indicative of a class of models that could generate a nonlinear feeding rate response. For example, Jenkinson and Wyatt (1992) have shown that laminar shear at scales smaller than the Kolmogorov scale affects predation and grazing rates in a dome-shaped manner, and that an extension of their model to supra-Kolmogorov scales also gives a dome-shaped relationship. In our model, we assumed that encounter rates between larval fish and their prey are adequately described by Rothschild and Osborn's (1988) extension of Gerritsen and Strickler's (1977) encounter model. This assumption includes the implication that larval fish are cruise predators (e.g. Munk and Kiørboe 1985). Some larval fish are known to be pause-travel predators (Browman and O'Brien 1992). However, theoretical studies suggest that, under non-turbulent
conditions, rates of encounter of pause-travel and cruise predators do not differ substantially (Getty and Pulliam 1991), and both search strategies would experience lower pursuit success in a turbulent environment. Thus, when the probabilities of encounter and pursuit are combined a nonlinear ingestion function will result for both strategies. Therefore, we conclude that our model is not likely to be sensitive to violations of this assumption.

We also assumed that larvae have a spherical pursuit volume. Recent empirical evidence suggests that for many larvae the reactive field may be a forward-directed conical section (e.g. Browman and O'Brien 1992). Our failure to incorporate the reduced encounter volume associated with a conical shape may lead us to overestimate the effects of encounter on ingestion because there would be less overlap between prey excursion and encounter volumes. However, this bias does not affect the important and general conclusion that turbulence reduces pursuit success thereby generating nonlinearities in the relationship between ingestion and turbulent velocity. For example, we note that three zooplankton species have been shown to feed at lower rates in highly turbulent water than in calmer water (Saiz et al. 1992).

Our results provide several insights into the ecology and abundance of fish larvae. At the coarsest scale our results suggest an additional mechanism to explain several recent observations on the link between wind speed and recruitment in marine fish (see details in Cury et al, in press). They demonstrated, that maximum recruitment success occurs at intermediate wind stresses for several clupeid populations in upwelling areas. The general relationship between environmental turbulence and ingestion rates we document here is consistent with their observations. At low wind stresses, larval ingestion rates would be increased over those occurring under calm conditions leading to higher rates of growth and survival. However, as wind stress increases, we
hypothesize that the benefits of increased encounter rate would be cancelled by the reduced rate of successful pursuit such that the overall ingestion rate, and hence growth and survival, might decline. Furthermore, increased wind stress would lead to the dispersion of prey patches (Peterman and Bradford 1987; Haury et al. 1990), reducing local encounter rates and feeding success further. Ware and Thomson (1991) analyzed long-term recruitment data for the sardine, *Sardinops sagax*, in the northeast Pacific Ocean and report optimal recruitment occurred at intermediate winds speeds of 7-8 m s\(^{-1}\). We suggest that feeding success, and perhaps growth and recruitment, of fish populations living in areas characterized by wind-induced mixing and upwelling can be expected to be maximal during years of moderate turbulence (e.g. Ware and Thompson 1991; Cury et al. in press).

In conclusion, our results show that to understand fully the effects of turbulence on larval fish feeding success, one must consider its influence on the entire sequence of predatory events (encounter, pursuit, capture). Turbulence will impact individual components of predator-prey interactions in potentially complex ways, but these effects have only recently begun to be investigated fully. Nevertheless feeding success in some turbulent environments will almost certainly be lower than in calmer areas.
References


