Needless to say, to date we have touched upon only the tip of an iceberg Much more research of this nature will be needed if we want to make our models more realistic, albeit more complex.

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# Effects of turbulence on the predation cycle of fish larvae: comments on some of the issues

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Turbulence-induced changes in ichthyoplankton-zooplankton (I-Z) contact rate (as a function of absolute prey abundance) have been proposed as an important factor in determining prey ingestion rate and, therefore, growth and mortality rates in fish larvae (reviewed by Dower et al. in press). The role of turbulence in the feeding ecology of fish larvae has been evaluated through various combinations of laboratory, field and analytical exercises (e.g. Kiørboe & MacKenzie 1995, MacKenzie & Kiørboe 1995, Sundby 1995). As outlined in the introduction to this Comments Section, each of these approaches is associated with a series of inter-related assumptions which have only rarely been subjected to rigorous scrutiny (although see MacKenzie et al. 1994, MacKenzie & Kiørboe 1995, Dower et al. in press).

Here, we comment upon some of the issues surrounding turbulence-induced effects on the predation cycle of fish larvae.

(1) All of the components of the predation cycle—search, location, pursuit or abort (i.e. the choice not to pursue a located prey), attack and capture, ingestion and retention—might be affected by turbulence. However, most of the attention has focussed on the rate of prey encounter (or contact) which, from the behavioural perspective, is operationally equivalent to prey location. Little effort, particularly in the form of empirical observations, has yet been devoted to evaluations of the effects of turbulence on any other component of the predation cycle. In addition, and as noted in the Comment by Sundby, clear differentiation amongst the possible effects of turbulence on each component of the predation cycle has been lacking in many studies.

(2) For small planktivores, which scan the water near to them for discrete and sparsely distributed prey items, search is the most time consuming component of the predation cycle (O'Brien et al. 1990). To illustrate: the volume of water contained in the visual perceptual field (VPF) of a 6 to 10 mm fish larva is approximately 0.8 to 1.0 ml. At an absolute prey abundance of 50 $l^{-1}$, there would be only 0.04 to 0.05 prey items within the VPF at any given moment (the number of prey per VPF is the visual abundance, VA. Note that the VA is, in this

case, 3 orders of magnitude less than the absolute abundance). Clearly, fish larvae must scan a significant amount of water in order to locate a prey item, and that takes a great deal of time.

Turbulence may reduce search time by bringing more prey items into the larva's VPF than would have been present in static water; that is, by increasing the VA. However, for the reasons outlined below, an increase in the VA does not necessarily equate to an increase in the rate of prey location, nor ingestion.

(3) The geometry of a fish larva's VPF determines its volume and, therefore, the number of prey that are contained within it. As a result, VPF geometry is central to analytical and/or numerical evaluations of the effects of turbulence on I-Z interactions.

The VPF geometry most often employed in analytical models is a sphere or a hemisphere (e.g. MacKenzie et al. 1994, Muelbert et al. 1994, Jenkinson 1995, MacKenzie & Kiørboe 1995). Several authors have recognized that this characterization of the VPF is inaccurate (e.g. MacKenzie et al. 1994, Dower et al. in press), yet there has been little discussion of alternate VPF geometries nor of the effect that they might have on model predictions. Although VPF geometries have been reported for only a very small number of species, none are spherical or hemispherical. Rather, VPFs most often resemble a piece of pie with maximum lateral angles approximating 80 to 120° to each side of the fish's midline (Arnold & Holford 1989, Browman & O'Brien 1992a, b, Coughlin 1993). In the vertical dimension, the VPF is shallow at the triangular pie slice's point (at the fish's eyes), thickens towards its outer edge (the pie's crust), and usually includes more of the volume of water above the larva's midline than below (see Browman et al. 1990, Fig. 1 therein). Several important points follow from this.

(a) The volume of water contained in a shallow pie-wedge (and scanned for prey) is approximately 4.5 times less than that in a hemisphere of equivalent radius. Thus, at any given absolute prey abundance, the VA for a pie-wedge VPF is 4.5 times less than the VA for a hemispherical VPF

(b) The probability of a prey item being flushed into a pie-wedge VPF by turbulent water motion is significantly less than that for a hemispherical VPF This is based mainly upon the difference in geometry and is relatively independent of volume.

(c) The probability of a prey item entering a hemispherical VPF is the same for any incident vector. For a pie-wedge VPF, this probability will vary with the angle at which the prey is being flushed through the VPF's volume. To visualize the significance of this it may help to imagine a prey item moving through a pie-wedge along the vertical vs the horizontal axes and to compare the length of its trajectory within the VPF to

that for a hemispherical VPF; for most angles of incidence, the trajectories are much shorter for a pie-wedge.

(d) For asymmetrical VPFs, quantifying the probabilities just defined will not be trivial.

(e) Since scanning the VPF takes time, a prey item which is entrained in a turbulent eddy may move through the larva's VPF in less time than it takes to scan the entire volume. Thus, just because a prey item is within the VPF at any given instant does not mean that it will be located (i.e. contacted, or encountered). Restated, although turbulence affects the probability of a prey item entering the VPF, it also affects the probability of it remaining there long enough to be located. Further, even if the prey does remain within the VPF long enough to be located, the larva needs still more time to pursue, attack and ingest it.

Unfortunately, scan time is a variable that has not been measured for fish larvae, although it may be related to the duration of stationary periods, at least in some species (O'Brien et al. 1990, Browman & O'Brien 1992a, b, MacKenzie & Kiørboe 1995).

(f) A critical issue in assessing the effects of turbulence on I-Z interactions is the choice of d, the distance between 2 points for which the velocity difference due to fluid motion (w) is to be calculated. Some authors (e.g. Kiørboe & MacKenzie 1995) argue that d should be the maximum distance at which the predator can perceive prey, the reaction distance (RD). The rationale for this proposal is based upon the assertion that the turbulence-generated prey location rate is equal to the rate at which particles arrive at the surface of the larva's VPF (Kiørboe & MacKenzie 1995). However, for any asymmetrical VPF geometry (including a hemisphere), the use of RD in this context is not tenable since the surface of the larva's VPF and, therefore, d, will be a variable distance away (and often much less than the maximum RD value) and dependent upon the prey's angle of incidence.

(g) Clearly, the results of any analytical or numerical evaluation of the effects of turbulence on I-Z interactions will be strongly affected by the choice of VPF geometry. Based upon volumes and geometries alone, the outcomes could be different by at least 1 order of magnitude.

(4) VPF geometries and volumes are estimated from maximum prey location distances (Browman et al. 1990). For non-hemispherical VPFs, these maximum distances vary significantly with the relative angle at which the prey was located and are typically greatest straight in front of the larva and on the same vertical plane (Browman et al. 1990, Browman & O'Brien 1992a, b). However, at any given angle, prey location events within a larva's VPF are distributed from very close to the fish out to the maximum location distance

(i.e. the RD). As an aside: although not yet widely known, this appears to be true for both pause-travel and cruise searchers (Arnold & Holford 1989, authors' unpubl. obs.).

It follows from these observations that using the RD to calculate the VPF's volume will yield an overestimate, even if the geometry is correct. Using the frequency distribution of prey location distances, or the median location distance, and not the RD, would be more accurate.

Since both the geometry and the volume of the VPF are at the heart of the encounter rate calculation [e.g. see Eq. (4) in Kiørboe & MacKenzie 1995 or Eqs. (1a) & (1b) in MacKenzie & Kiørboe 1995], and since RD enters these equations as a squared term, clarifying the manner in which this variable is applied, and using accurate values, is essential.

(5) Behavioural responses to turbulence have been observed in copepods (e.g. Marrasé et al. 1990, Hwang et al. 1994, Saiz 1994; see Comment by Strickler & Costello). In fish larvae, such behavioural responses might include turbulence-induced changes in various components of the predation cycle, for example, swimming speed, stop frequencies and durations, move distances, turn angles, the geometry and volume of the VPF, the time required to scan the VPF for prey, or the proportion of attacks initiated that are aborted. We are aware of only 1 study that has examined such effects in fish larvae (MacKenzie & Kiørboe 1995). These authors quantified larval attack posture rate at different prey abundances and under turbulent vs non-turbulent conditions. For any given prey abundance, the static water treatment was considered as the control/base-line against which the effect of turbulence was evaluated. However, since the possibility of an inherent behavioural response to turbulence cannot be excluded, a more appropriate control would be to measure the larva's response to turbulence in the *absence* of prey and to use *this* as a base-line against which to evaluate the responses at higher prey abundances. The choice of control in such experiments is critical.

(6) The rate at which fish larvae take up attack postures has been considered a reasonable proxy for prey location rate (MacKenzie & Kiørboe 1995). In this context, it is worth noting that fish larvae often take up attack postures without ever actually striking at a prey item. These 'aborted' attacks can comprise 50% or more of all the observed attack postures (Browman & O'Brien 1992b). Since turbulence will constantly be moving prey items into and out of the VPF, it seems reasonable to predict that the proportion of all prey attacks that are aborted will be related to the level of turbulence. If this is the case, determining the relationships between the rates of prey location, attack and ingestion under turbulent conditions will be difficult.

(7) Several recent analytical models use components of the larval prey search pattern (duration of stationary pauses and moves, move distances, stationary pause frequencies, etc.) as model inputs (MacKenzie & Kiørboe 1995, Kiørboe & MacKenzie 1995, reviewed by Dower et al. in press). Model output will be strongly affected by the values entered for these variables, although this has not been carefully assessed (however, see MacKenzie et al. 1994, Jenkinson 1995, MacKenzie & Kiørboe 1995). Values for these parameters are drawn from a very limited body of literature and, so, suffer from the same problems as defined above for RDs. Further, the great majority of data on these variables has been generated in static water conditions. Since they are all likely to vary significantly under turbulent conditions, use of these data in analytical models should be undertaken with some caution. We propose that it would be more appropriate to use median values or frequency distributions, and not means, in parameterizing these variables.

(8) Some attempt has been made to evaluate the different effect that turbulence might have on pause-travel (PT) vs 'cruise' searching fish larvae (Kiørboe & MacKenzie 1995, MacKenzie & Kiørboe 1995). These analytical exercises have modelled 'cruise' searchers as scanning while swimming and perceiving prey as they pass across the boundary of the VPF (the classical characterization of Rosenthal & Hempel 1970). However, there is no empirical evidence to support this characterization of 'cruise' searching and recent evidence indicates that it may be incorrect (Arnold & Holford 1989, authors' unpubl. obs.).

Search strategies have only been carefully evaluated for a very small number of fishes (O'Brien et al. 1990). Until more such characterizations are available, particularly for search patterns other than PT, the value of analytical exercises such as those referred to above will be limited.

(9) Turbulence may affect the contact rate between fish larvae and those planktonic organisms that feed on them: the role that turbulence plays in altering the predation rate on fish larvae requires more attention than it has received to date.

To summarize: empirical evidence to support the behavioural characterizations and assumptions made in many analytical evaluations of the effects of turbulence on the feeding ecology of fish larvae is sparse. Until the issues discussed above can be addressed, studies on the role of turbulence on I-Z interactions, or on fish larval growth or survivorship, should be interpreted cautiously. Laboratory experiments and/or field measurements that attempt to evaluate the effect of turbulence on growth rate or survivorship (e.g. Sundby et al. 1994, Landry et al. 1995). without regard to the mechanism, may be the most appropriate approach at

this time. Such observations may serve to tell us whether turbulence is, in fact, so important in I-Z interactions that it merits the significant effort that will be required to determine and model its mechanism of action.

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