

Figure 3.4.6. (a) Initial particle (egg) distribution for 12 March–3 June, as used in all model runs; (b) regional distribution of the total remaining virtual individuals within each model grid box at a length of 50 mm for 1998; (c) for 1999; and (d) for 2000.

3.5 Behaviour and settlement

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3.5.1 Introduction

Fish larvae are not passive particles, and it is becoming increasingly obvious that they have behavioural capabilities that may greatly influence dispersal outcomes and other biophysical processes (Leis, 2006). Thus, the simplifying assumption of passive behaviour, which has been the basis for many biophysical models in the past, can no longer be justified as the default assumption (Leis, 2007). Behaviour as a potentially important factor that can influence the outcomes of such models must be considered as a real alternative. This requires an understanding of the behaviour of the larvae, something that is frequently lacking. Recent research has demonstrated that fish larvae have behavioural capabilities in areas of swimming, orientation, and sensory abilities that were unknown and unexpected only ten years ago.

“Behaviour” refers to the actions or reactions of organisms, usually in relation to the environment. Larval behaviour can become overwhelmingly complex because individuals acquire behavioural capabilities as they develop. However, a “good” model should not try to be exhaustive, but only include observed behaviours that are sufficient to reproduce patterns and/or mechanisms relevant to the scope of the study. Sensitivity analyses, in which different behaviours are added to the model to assess their influence on outcomes, can aid in determining which behaviours to incorporate.

In this section, we consider vertical positioning, horizontal swimming, orientation, foraging, predator avoidance, schooling, and settlement. All these behaviours can influence the outcome of the larval phase and may need to be considered when de-

signing a model. The following sections provide clues on whether or not it is worth implementing each behaviour, depending on the *a priori* knowledge of the system and the other processes already included in the model. Each is organized in a similar fashion: (i) outlining how the behaviours can be important to the processes that the model seeks to address, (ii) proposing simple tests on how to determine whether or not it has any influence, (iii) giving insights on how to obtain relevant data and pointing to appropriate literature references, and (iv) suggesting implementations for this behaviour in a model.

We further encourage modellers to test the relative influence of separated physical conditions and behaviour for their particular model/species/area of interest. Sensitivity analysis of model output to behaviour-related parameters or functions should be done routinely after each behaviour is implemented, as well as comparison of predictions with empirical data. The following sections are intended to help the reader answer the question, what are the priorities for implementation of different behaviours?

3.5.2 General questions on behaviour-related traits

3.5.2.1 Mean vs. mean + variance vs. maximum

All behavioural traits are variable: swimming speeds and vertical position change among and between individuals; sensitivity to environmental cues for orientation can similarly vary, as can response to these cues, etc. Therefore, the description of behaviour has to be probabilistic to account for these variations. Behavioural studies, whether they are experimental or done in the field, allow an estimate of population traits. The question then is, which population descriptors are most relevant to a model of the early life history of fish?

In such models, we are mostly interested in the individuals that survive the larval phase and recruit successfully. If most larvae succeeded, their mean behavioural traits, and those of the whole population, would be similar. Hence, including mean population traits in models could suffice to predict recruitment correctly. However, very few larvae survive the larval phase (see Section 3.4 Mortality; Doherty, 1983), and the few that do probably succeed because their traits are different from the others and well suited to the circumstances they encountered within the heterogeneous pelagic environment (Fuiman and Cowan, 2003). For example, there is now evidence from several systems and species that the fastest growing individual larvae are most likely to survive, and the same may apply to behavioural performance. Therefore, using mean population performance in models will not be appropriate if the survivors constitute only a small portion of the performance distribution. Variance around the mean has to be derived from observations (e.g. Browman *et al.*, 2003) or estimated from published accounts and incorporated into the model to provide a realistic range of individual results. In addition, maximum values should also be considered because successful recruits may be the very few “best” individuals of each cohort. Comparison of model results based on both mean and best performance should be informative. Such a probabilistic approach can be accomplished through individual-based models (IBMs), where traits of individual particles can be assigned following a probability density function.

3.5.2.2 Ontogeny of behaviour

Like morphology, behaviour develops during the pelagic larval stage from essentially planktonic at its start to nektonic at its end. The passive portion of the pelagic larval stage is likely to be short, and models that make the simplifying assumption are

likely to be applicable to only a short portion of the larval stage. In addition to ontogenetic changes in behavioural ability, there are often ontogenetic changes in the use of those abilities (e.g. age-related changes in depth or in swimming direction). Methods for modelling behaviour need to be adjusted according to the state of knowledge of physical–biological interactions that result in larval growth. Indeed, most studies indicate that size (or stage of development) is a better predictor of behavioural ability than age (Fuiman and Higgs, 1997).

- When growth or development is explicitly included in the model (possibly via trophic interactions), behaviour can be formulated as a function of size or developmental stage. In addition, this relationship should consider not only the mean value for the population but also associated variation. In this case, as larvae are subjected to differential growth (e.g. in a model with heterogeneous spatially explicit resources), they will have differential performance of a given behaviour.
- When larval growth is not resolved in the model, or when not enough information is available to predict a continuous relationship between size and behavioural performance, milestones can be used to model behaviours in a simplified, stepwise manner. Morphological or ontogenetic stages can be expressed by a dimensionless metric, such as an ontogenetic index (Fuiman and Higgs, 1997) or developmental age (Job and Bellwood, 2000).

3.5.2.3 Taxonomic resolution of behaviour

Ideally, the behaviour of the larvae of the species to be modelled should be incorporated into the model. However, it is important to know the degree to which the behaviour of a particular species can be extrapolated to other taxa, because it is unlikely that we will ever have even partial information on the behaviour of all fish species. Currently, the amount of information available on any particular behaviour is limited to relatively few species and, for the vast majority of these, to only a portion of the larval stage (usually older larvae). When deciding whether or not behavioural information from species A can justifiably be used in a model for species B, two things must be considered at the outset: (i) the closeness of the relationships of the two species, and (ii) the similarity of the environment in which the species live.

The vast diversity of teleost fish species – approximately 27 000 species in 448 families divided among 40 orders (Nelson, 2006) – means that some species are very distantly related, with evolutionary histories that have been separate for tens of millions of years. Among orders in particular, there is no reason to assume that behaviours will be similar. Within mammals, for example, no one would assume that the behaviour of a tiger (Order Carnivora) would be similar to that of a dugong (Order Sirenia). Likewise, no one should assume that the behaviour of a plaice larva (Order Pleuronectiformes) would be similar to a herring larva (Order Clupeiformes). As a general rule of thumb, in the absence of other information, the closer the relationship between two species, the more justifiable it should be to assume they have equivalent behaviour. The use of well-corroborated phylogenies that encompass the species under consideration is essential in assessing the closeness of relationships, but such phylogenies do not exist for many fish taxa. Even this rule of thumb should be applied cautiously because there are many examples of larvae of confamilials with different behaviours. For example, in pomacentrids, the larvae of some species are found in midwater, whereas those of other species prefer the top few centimetres of the water column (Leis, 2004). Sibling species (e.g. Pacific herring and Atlantic herring) are more likely to have similar behaviour than randomly chosen confamilials.

At this point in our knowledge of the behaviour of fish larvae, it is difficult to make any defensible statement about how closely related two species must be before it is justified to assume that the behaviour of their larvae is similar. An analysis of the behaviour of fish larvae in the context of phylogeny, with a view to establishing whether relatedness provides a sound basis for inferring behaviour, would be most useful.

Even within a family, the larvae of a species that is pelagic as an adult is unlikely to behave similarly to the larvae of a species that lives on a coral reef or in an estuary. Therefore, if it is not possible to obtain behavioural data on the species of interest, the species supplying the behavioural data should at least live in the same habitat as the species of interest, in both the adult and larval stages. Echoing the comment above, an analysis of behaviour of fish larvae to determine the extent to which habitat similarity provides a sound basis for inferring behaviour would be very valuable. The use of behavioural data from a distantly related species that lives in a different habitat should be avoided.

There are indications that some behaviours, particularly swimming speed, can be predicted from the morphology of the larvae (Fisher and Hogan, 2007). Therefore, the use of swimming data from species with similar larval morphology might be appropriate. In addition, even larvae of the same species can exhibit significant differences in overall activity and swimming in different geographic locations (Skiftesvik, 1992; Puvanendran and Brown, 1998; Leis and Carson-Ewart, 2000; Leis, 2004). Therefore, any generalization should only be made with great caution.

3.5.3 Vertical position

3.5.3.1 Why incorporate this behaviour in a model?

Any vertical heterogeneity in the current field will interact with the vertical distribution of larvae and indirectly influence their dispersal, as demonstrated by modelling (Armsworth *et al.*, 2001) and empirical (Paris and Cowen, 2004) studies. Of course, many things in addition to current velocity vary vertically in the ocean (e.g. temperature, light, food concentration) and may influence growth, survival, or dispersal of fish larvae. Of all behaviours, vertical distribution is the most widely recognized as being influential, and it is the behaviour most often incorporated into biophysical models. Particles located at different depths will be subjected to different current vectors, and therefore their Lagrangian trajectories will be different. Temperature influences pelagic phase duration (Houde, 1989), development rates (Otterlei *et al.*, 1999), and swimming speed (Leis, 2006). Food resources are often greater near the thermocline, and fish larvae may accumulate in these depths (Boehlert *et al.*, 1992; Gray, 1996; Rissik and Suthers, 2000). Conversely, they may use diel vertical migration to avoid predation near the surface (Gray and Kingsford, 2003). Larvae may use sensory cues for orientation, such as sun angle or sound, so that the absolute depth or vertical position of a larva relative to the thermocline may influence its ability to detect such cues and orientate using them. The vertical position of larvae can, therefore, influence their feeding success, predation risk, growth, swimming ability, and ability to detect sensory cues, all of which can influence their trajectories (Fiksen *et al.*, 2007).

In coastal waters, larvae may occupy the epibenthic boundary layer, where current velocity can differ substantially from that in the water column. Unfortunately, information on the occurrence of fish larvae in the epibenthic boundary layer is limited, especially in deeper water and over a very irregular or hard bottom. Occupancy of the boundary layer not only places the larvae in a different current regime but may

also expose them to increased risk of predation from benthic predators and to increased turbidity, and may place them in a different food regime. Similarly, some marine structures, such as kelp beds and reefs or other high-relief bottom topography, provide areas of flow that differ substantially from those in the far-field water column; these should be taken into account if larvae occur near them.

3.5.3.2 How to determine whether or not this behaviour influences dispersal outcome

Current velocity, hydrography (e.g. salinity, temperature), and fluorometry profiles (or their modelled equivalents) over the estimated spatial scales and depth range of interest (i.e. observed larval fish depth range) are required to evaluate the degree of vertical shear in the current, temperature gradient, and depth of chlorophyll maximum. Larvae may use sensory cues for orientation, such as sun angle or sound emanating from a settlement habitat, so the absolute depth or vertical position of a larva relative to the thermocline may influence their ability to detect such cues and orientate using them. Clearly, if heterogeneity in the velocity field is detected, vertical distribution of larvae must be included in a model. If some model parameters or functions (such as survival, growth rate) explicitly depend on food availability or temperature, and if these are not homogeneous on the depth range of interest, vertical position must be included. Finally, sensory cues must be included if they are known to be used by larvae for orientation and are also affected by the vertical structure of the water column. Some models integrate water movement over the surface Ekman Layer, but water velocity over this layer is known to differ with depth. This means that larvae at different depths within the Ekman Layer will be subject to different current speeds and directions, and this should be reflected in the model.

3.5.3.3 Simple tests

When a three-dimensional oceanographic model is available, the influence of vertical migration can be assessed by comparing the fate of particles constrained to the top and bottom layers within the species' depth range. When three-dimensional oceanographic models are computationally infeasible, then two-dimensional models are often employed. If the model simulates horizontal (e.g. cross-shelf) and vertical (e.g. depth) dimensions, then the influence of vertical position can be tested in a manner similar to that used for three-dimensional models. If the model dimensions do not include the vertical, then there is no simple test for the potential influence of vertical migration in the model. If a strong vertical current shear is observed in the field and larvae are observed to migrate through it, then the use of a three-dimensional model is recommended.

3.5.3.4 How to obtain the relevant data

Vertical distribution is probably the behaviour about which we have the most information. It has been explored primarily with towed nets, performing stratified sampling of the water column. This requires multisampling nets, preferably the Multi Opening and Closing Net and Environmental Sensing System (MOCNESS), or repeated single-net (e.g. bongo net) sampling of the same area at different depths. To resolve diel vertical migration, a few stations should be sampled over several 24 h cycles. Similar information can be obtained from pump samples, but pumps suffer from significant avoidance, particularly when sampling larger larval stages. Nets also suffer from avoidance, and care must be taken when analysing ontogenetic vertical distribution data (e.g. gear selectivity can be calculated from the net opening, mesh size, and length–frequency distribution of the larvae caught).

Acoustic methods can also provide useful information on vertical distribution, but suffer from difficulties in identifying the species whose vertical distribution they portray. Finally, *in situ* observations of larvae by divers (Leis, 2004) can provide detailed information on vertical distribution and changes therein from the individual larvae that are caught, typically with light traps, and subsequently released. This approach is limited by diver-safety considerations to relatively shallow depths and can only be used in the daytime and for larvae > ca. 5 mm.

This kind of sampling provides information about the concentration of larvae caught within specific depth intervals. Sampling can be carried out repeatedly along a single transect, generating two-dimensional data, or over a spatial domain to obtain a three-dimensional description of larval patches (e.g. Paris and Cowen, 2004). In order to describe the vertical distribution of the larval population, two-dimensional sampling is adequate, and the resulting information needs to be summarized using statistical descriptors. Interesting descriptors are the depth centre of mass of the larval patch, its variance, the total depth range in which larvae are caught, and depth–frequency distribution. Each observation (i.e. depth interval) must be reduced to its mean depth. Raw larval counts should be converted to concentrations, using the volume sampled, and standardized using the depth range of the interval. Finally, mean depths should be weighted by these standardized concentrations to compute descriptive statistics of the vertical distribution of larvae: weighted mean depth (i.e. depth centre of mass), standard deviation, quantiles, etc. An alternative to a depth centre of mass portrayal of vertical distribution is a depth–frequency distribution. Depth bins, usually determined by the vertical resolution of the sampling design, are established, and the mean percentage (and associated variance) of the larval population in the sampled water column is calculated for each bin. This offers some advantages over the centre mass in terms of detail, but is less robust in respect to deviation from the sampling plan (e.g. different depth intervals between stations) and more difficult to transfer to a model.

In addition, these descriptive statistics should be discussed dynamically in time and ontogeny. For example, the differences between day and night conditions, or between several ontogenetic stages, should be investigated and described, if present.

Furthermore, the movement of individuals, and not only the distribution of the population mean, is important. A simple example highlights this fact taken from Leis (2006).

Imagine a stratified system with a flow of x in an upper layer equal, but opposite, to that in a lower layer, and with the larvae equally distributed vertically between the two layers. If there is no movement by individual larvae between layers, at the end of time t the larvae in the upper layer will be advected a horizontal distance of $2zt$ relative to those in the lower layer. If movement of larvae between layers is constant and individuals spend an equal amount of time in each layer, then the larvae in the two layers will not become horizontally separated at all. Depending on the proportion of time an individual spends in each layer, any other result intermediate between these extremes is possible.

This information can be obtained by *in situ* observations of larvae over time to determine their individual vertical movements (e.g. Leis, 2004) or by the use of specialized sampling equipment that can determine the upward and downward movement of individuals rather than vertical shifts of population means (e.g. Pearre, 1979).

3.5.3.5 How to incorporate data into the model

Vertical distribution can be introduced in a three-dimensional model (i) as a parameter referring to a user-controlled function, or (ii) as an emergent property of the model resulting from other processes being modelled explicitly.

A straightforward implementation of (i) is either to initialize the model with different numbers of particles in each depth stratum or to weight the results of dispersal in each depth layer using numbers or weights, which respect the observed vertical distribution of larvae (represented, e.g. by a probability density function). This is valid only if the structure of larval patches is constant throughout the larval phase. If not, at each time-step, particles can be moved between depths using a random process that represents the probability density function appropriate to the age or size of the larva as observed in the field (Paris *et al.*, 2007).

If vertical distribution is to be obtained as an emergent property of the system, the processes evoked above must be explicitly modelled. For heterogeneity of the current field to be exploited, vertical swimming with some sort of criteria to choose depth should be modelled (Vikebø *et al.*, 2007; Fiksen *et al.*, 2007). For food or temperature heterogeneity to be exploited, growth and/or survival should be modelled explicitly (see appropriate sections in this manual). If swimming speed depends on condition, food and temperature heterogeneities can have an indirect impact on dispersal trajectories by modifying larval condition, and hence swimming speed (although we currently know very little about such relationships). This is probably unimportant for vertical motion, in which even small swimming speeds can have a dramatic impact, but it is worth considering in the case of horizontal swimming.

3.5.4 Horizontal swimming

3.5.4.1 Why incorporate this behaviour in a model?

Horizontal swimming of larvae affects dispersal trajectories by partly disconnecting them from the current field (Brickman *et al.*, 2007); therefore, it has a direct influence on dispersal outcomes. Trajectories, including horizontal swimming, can diverge significantly from purely passive Lagrangian trajectories and can result in significantly different dispersal outcomes, especially if swimming is orientated. Unorientated swimming can increase the amount of search area covered by a larva, and hence improve survival or settlement probability by chance alone. Unorientated horizontal swimming can also increase variance in a manner similar to increasing diffusion, and hence increase the dispersal kernel (i.e. the probability distribution of distances in successful dispersal events).

In addition to resulting in different dispersal outcomes in terms of settlement position, these differences in trajectories could also influence growth, condition, and survival, for example, by passing into or out of food and/or predator-rich areas.

3.5.4.2 How to determine whether or not this behaviour influences dispersal outcome

This can be reformulated as, how great must swimming performance be before it can significantly influence trajectories? Numerical models of circulation indicate that modest speeds (0.3–10 cm s⁻¹) can have large effects on dispersal. Similarly, heuristic models inform us that speeds of 1–5 cm s⁻¹ can strongly influence dispersal outcomes (Codling *et al.*, 2004). The following are some examples from Leis (2006).

A vertical swimming speed of >5 cm s⁻¹ was considered necessary “to overcome vertical mixing” in a tidal channel (Smith and Stoner, 1993). Near Georges Bank, on-bank swimming by larvae of 0.3–1.0 cm s⁻¹ “would sub-

stantially enhance shoalward displacement” and result in modelled distributions consistent with field observations (Werner *et al.*, 1993). On the Newfoundland shelf, directed horizontal swimming of 1–3 cm s⁻¹ by cod larvae was considered able to “greatly increase their retention on the shelf (and on banks, too”; Pepin and Helbig, 1997). In a numerical model of the Florida coast, simulated larvae that swam at only 1 cm s⁻¹ had settlement 36 to 300% greater than passive larvae, whereas larvae that swam at 10 cm s⁻¹ had settlement rates “many times” greater (Porch, 1998). In a numerical model of an Australian coral reef, a swimming speed of 10 cm s⁻¹ by simulated settlement-stage larvae resulted in a duplication of measured distributions of larvae that was impossible to achieve with passively drifting model larvae (Wolanski and Sarenski, 1997).

Nevertheless, most of these examples assume orientated swimming, which underlines the fact that orientation is a very important factor.

3.5.4.3 Simple tests

Testing for the importance of unorientated swimming can be achieved by augmenting the variance of the random flight in the Lagrangian tracking scheme (see Annex 2 for a description of the random flight model). This is especially efficient for swimming speeds that are low relative to ambient current velocities (e.g. one or more orders of magnitude lower). If orientation behaviour is unknown, testing extreme orientated swimming scenarios can give insights on the extent to which swimming can influence trajectories. Such scenarios can include, for example, adding a movement at full speed, perpendicular to, or parallel with current direction at each time-step; and testing full-speed movement relative to whatever cues may exist (e.g. the presence of an island). If these tests lead to the conclusion that orientated swimming could make a large difference (which it will in most cases), then information on orientation is needed (see Section 3.5.5 Orientation).

3.5.4.4 How to obtain the relevant data

Information on horizontal swimming is becoming more widely available, but most of it concerns tropical species. In addition, several methods have been used to estimate larval fish swimming speeds (see Leis, 2006 for a review). These are (from high to low): burst speed, which measures the speed at which larvae flee in response to a stimulus; critical speed (U_{crit}), which measures the speed of flow against which larvae can maintain their position in swimming channels (Stobutzki and Bellwood, 1994); maximum sustainable swimming speed, which measures the speed that can be maintained in a swimming channel over 24 h (Fisher and Wilson, 2004); *in situ* speed in which scuba divers follow larvae in the sea and measure their speed (Leis *et al.*, 1996); and routine speed, which measures swimming speeds of undisturbed larvae in laboratory containers, which may be large or small (Fisher and Bellwood, 2003). These techniques do not measure the same thing, and the speed estimates that they provide differ. Therefore, they are not equally suitable for use in dispersal models, and care must be taken to ensure that the type of swimming-speed measurement is suitable for the purpose.

Routine speed has the advantage of being a measure of swimming speed undisturbed by divers or any overt forcing by the investigator, but carries the disadvantage of being measured in artificial laboratory conditions. *In situ* speed has the clear advantage of being measured in the sea, but with the unknown influence of the observing divers. U_{crit} is most relevant to comparisons of relative performance, but is not a per-

formance measure that can be included directly in dispersal models and is almost certainly faster than larvae actually swim in the sea. The least appropriate measure is burst speed (the highest speed of which a fish is capable), as this is measured and can be maintained only for very short periods and is considered to be fuelled anaerobically (Plaut, 2001). Because burst speeds can only be maintained over very short periods of time (typically <20 s; Plaut, 2001), they are inappropriate to considerations of dispersal, although they have been used for this purpose (e.g. Bradbury *et al.*, 2003). It would, however, be appropriate to use burst speed when examining predator escape or avoidance of plankton nets.

If actual swimming speeds are to be included “as is” in a model of the early life history of fish, *in situ* speed is the best existing measure of how fast larvae actually swim in the sea and, therefore, the most relevant to this purpose. On the other hand, if potential, rather than actual, swimming speeds are needed, the maximum sustainable swimming speed of Fisher and Wilson (2004) is a well-suited measure. It has to be noted that, for the nine species for which it was measured, maximum sustainable swimming speed was equal to about one half of U_{crit} and similar to values of *in situ* speed of settlement-stage larvae of the same or related species.

In addition, using a constant mean or maximum swimming speed is justifiable only if the larvae are considered never to be fatigued (food supplied *ad lib.*, no muscular fatigue, etc.). In most cases, mean swimming speed, variance in swimming speed, and swimming endurance should be estimated. This necessitates determining the relationship between swimming speed and endurance, which is theoretically cubic (Fisher and Bellwood, 2002; Fisher and Wilson, 2004). Furthermore, it is known that feeding greatly enhances endurance. Endurance of fed larvae may be virtually open-ended for some species, but significant swimming endurance may not develop until relatively late in ontogeny (Leis, 2006). Even so, comparison between fed and unfed larvae in swimming channels can provide valuable information, especially if some sort of energy budget is included in the model. Finally, swimming speed and endurance are highly variable throughout the larval phase and should be estimated for several ontogenetic stages (Leis, 2006).

If no information about swimming speed is available, some theoretical mechanistic rules should be represented when parameterizing maximum swimming speed (using relative speeds, as in Bellwood and Fisher, 2001), swimming endurance (Fisher and Bellwood, 2002), or development of swimming abilities (Fisher *et al.*, 2000). Note that these rules were all examined in a tropical context and, given that temperature has a great influence on swimming speed and energetics, it may be misleading to assume that they will apply in cold water.

3.5.4.5 How to incorporate data into the model

Lagrangian stochastic models (LSMs) can be used to incorporate horizontal swimming. The baseline random walk model (i.e. RDM) is first-order Markovian for the particle position (x) and velocity field (u), and is the most commonly used stochastic transport model, for which the governing equations are (for each axis)

$$dx = [\langle u(x) \rangle + u'] dt + du' dt \quad (33)$$

$$du' = [-u'/T_L + a(x, u')] dt + b(x) dW(t), \quad (34)$$

where the first and second terms in Equation (33) are the mean velocity and the turbulent velocity, respectively, dt is the time-step, x is the vector of coordinates. The first term in Equation (34) represents a fading memory for velocity fluctuations, and

a , the drift correction term, is zero when turbulence is stationary and homogeneous (Veneziani *et al.*, 2004). The second term in Equation (34) represents random forcing, where dW is a random increment from a Wiener process (i.e. continuous-time Gaussian stochastic process) with zero mean and variance dt ; b , the tensor amplitude, multiplies the random increment (*sensu* Berloff and McWilliams, 2002). Thus, b can describe larval swimming with random or oriented motion (Codling *et al.*, 2004).

However, caution is advised for situations where the decorrelation time-scales in the Lagrangian equation, dictated by the velocity field, do not correspond to that of the active larva. Choosing the swimming direction and speed should be based on behavioural rules, which depend on the environment of the larvae. This is discussed in Section 3.5.5 below. An alternative is to include non-explicit swimming behaviour during the end of the larval pelagic phase by assuming that a larva can actively recruit once it is found at a determined distance from the nursery habitat (Cowen *et al.*, 2003).

3.5.5 Orientation

3.5.5.1 Why incorporate this behaviour in a model?

As mentioned in Section 3.5.4, random horizontal swimming can change the outcome of the larval phase. The impact of swimming can be even greater if, for example, the larvae are able to orient towards areas of greater food supply or towards settlement sites. Such orientation abilities exist even if the associated environmental cues are not always known. Current knowledge related to each potential cue (which mainly concerns coral reef fish) is summarized in Table 3.5.1.

Table 3.5.1. Potential orientation cues for coral reef fish.

CUE	COMMENT	REFERENCES
Vision	Can improve the choice of settlement site; visual acuity in surface layers (where light is abundant) is 12 – 30 m for late larvae; can mediate schooling.	Lara, 2001; Kingsford <i>et al.</i> , 2002.
Hearing	Detection of coastal areas using reef-associated choruses, or breaking waves at distances of kms, but probably not tens of kms.	Kingsford <i>et al.</i> , 2002; Leis and Lockett, 2005; Montgomery <i>et al.</i> , 2006; K. J. Wright, pers. comm.
Olfaction	Land-associated chemicals could guide larvae towards the coast. At a smaller spatial scale, settling individuals can detect conspecifics or habitats using chemical signals.	Sweatman, 1988; Kingsford <i>et al.</i> , 2002; Atema <i>et al.</i> , 2002.
Magnetic sense	Could be used for navigation; sensitivity to electromagnetic fields has been demonstrated in hammerhead sharks, salmon, tuna, and eel, but not in larval stages of marine fish.	Klimley <i>et al.</i> , 1992; Nishi <i>et al.</i> , 2004; Kingsford <i>et al.</i> , 2002.
Lateral line	Associated with behavioural responses, e.g. prey detection, obstacle or predator avoidance, and schooling, but only over short distances.	Alexandre and Ghysen, 1999; Fuiman and Magurran, 1994.
Solar compass	Sun angle could be used as a compass; implied but not demonstrated in larval fish.	Leis and Carson-Ewart, 2003.
Polarized light	Could be used for navigation; never demonstrated in the larval stage.	Hawryshyn, 2000.

Evidence that orientation occurs, or at least can occur, is needed before it is incorporated into the model. For other larvae, orientation can be demonstrated in laboratory experiments that test the preference of larvae for a given environmental signal (e.g. coastal vs. oceanic water, reef sounds vs. random sound). However, field observations are necessary to demonstrate that orientation truly occurs. These observations

can be performed without any hypothesis about the cues involved. Such laboratory and field experiments have revealed that coral-reef fish larvae can swim directionally at sustained speeds for long periods (hours to days; for a review, see Leis, 2006) before settlement. However, the onset of this behaviour is not certain, nor do we know the distance from which a larva, or schooling larvae, can “sense” the reef.

3.5.5.2 Simple tests

Orientation can be added gradually, starting with a very simple set of behavioural rules, then testing the impact of each step of the implementation.

3.5.5.3 How to obtain the relevant data

Information on the orientation of fish larvae is limited to relatively few studies (see review by Leis, 2006). Orientation data can be provided by field studies involving the release of wild or reared larvae at sea and tracking by divers (Elliott *et al.*, 1995; Leis *et al.*, 1996; Trnski, 2002; Hindell *et al.*, 2003). *In situ* orientation chambers can also provide similar information on the orientation of fish larvae (Stobutzki and Bellwood, 1998; Paris *et al.*, unpublished data). Testing the ability of larvae to detect a cue is a second step (Sweatman, 1988; Arvedlund *et al.*, 1999; Atema *et al.*, 2002; Tolimieri *et al.*, 2002, 2004; Leis and Lockett, 2005; Wright *et al.*, 2005), and the last step would be to describe thresholds for detection. The first step is testing for the ability to detect a cue in the laboratory or in field experiments (Sweatman, 1988; Arvedlund *et al.*, 1999; Atema *et al.*, 2002; Tolimieri *et al.*, 2002; Wright *et al.*, 2005), but this can only reveal whether the cue can be detected and at what level. It will not reveal whether or not the cue is actually used for orientation or over what scales, although it can describe the ontogeny of this sensory ability. Understanding the spatial scale over which cues can be detected and used for orientation is difficult, but this is essential information for incorporation into the model.

Nevertheless, knowing the cue used for orientation is not mandatory for incorporating orientation data in a model. If orientation behaviour is observed repeatedly in a specific location, it can be incorporated “as is” in a model of this location. Alternatively, it may be possible to establish that the given orientation is not site-specific, in which case the orientation can be incorporated throughout the model. Thus, orientation data can be thought of as cue-specific (e.g. swimming towards a sound source), location-specific (e.g. swimming away from a reef during the day), or general (e.g. swimming west). This can help to determine how to incorporate such orientation into the model.

3.5.5.4 How to incorporate data into the model

Incorporating orientation into a model is closely associated with the incorporation of swimming (both horizontal and vertical); orientation is simply a choice among the set of possible swimming vectors. Once again, two approaches can be taken: (i) behavioural rules in response to the environment can be defined *a priori*, based on observations and experimental work; and (ii) these behavioural rules can emerge from the model by defining the set of possible swimming vectors, a “goal” for the larva (e.g. settlement), and letting an algorithm choose the suite of best decisions to achieve this goal (see Irisson *et al.*, 2004 for an example of the use of an optimization algorithm).

In both cases, orientation is a function that associates a behavioural decision to a state of the larva, such as

$$f: (\text{state}) \times (\text{time}) \times (\text{environment}) \rightarrow (\text{swimming speed}) \times (\text{swimming direction}).$$

The amount of detail of the orientation behaviour is determined by what is incorporated in each of the left-hand variables. In the simplest model in which orientation is observed but the cues are unknown, orientation depends only on the position (state) of the larva and time. Where responses to sensory cues are involved, the environment may include temperature, food, predators, current fields, land-associated chemical concentrations, sun orientation, etc. If some kind of energy budget is present, the state of the larvae also encompasses energy reserves. This formalization is very scalable.

3.5.6 Foraging

3.5.6.1 Why incorporate this behaviour in a model?

Behaviours associated with prey search and foraging are unlikely to have a strong and direct influence on the trajectories of dispersing larvae. Indeed, for most of the larval period, these behaviours will occur on a relatively small spatial scale. Nonetheless, if these behaviours motivate the larva to undertake vertical and/or horizontal movements in search of food, such repositioning could indirectly influence pelagic trajectories in conjunction with the behaviours discussed above. The likelihood of this will increase rapidly as the larva's activity and swimming ability increase.

Food is typically limiting for fish larvae, at least in respect of it being less than they would require to achieve maximal growth rates. Growth rate, in turn, influences swimming speed, survival probability, and pelagic larval duration, which are all key processes in the early life-history models of fish. For most larvae, the efficiency of foraging probably has little influence early on (except in terms of conserving energy and delaying the "point of no return"), but perhaps has more as they approach the juvenile stage.

3.5.6.2 How to obtain the relevant data and incorporate it into a model

The temporal and spatial scales over which fish larvae can perceive their prey are orders of magnitude smaller than the scales over which their prey fields are surveyed (Pepin, 2004). Therefore, when modelling the encounter rates between fish larvae and their prey, there is a discontinuity between the data available to characterize the prey fields that are available to fish larvae vs. the operational prey field (from the perspective of what the larva can actually perceive). Two things are required to bridge this gap: (i) sampling of prey fields at temporal and spatial intervals that are more closely aligned with the perceptual abilities of the larvae; and (ii) empirical characterization of the perceptual fields of fish larvae for different prey under different conditions (e.g. light, turbulence) and at different sizes (developmental stages).

3.5.6.3 Turbulence and predator-prey interactions in the plankton

Substantial effort has been applied to demonstrate that microscale turbulence can significantly increase the feeding rate of planktonic predators (reviewed in Dower *et al.*, 1997). This effort has been driven by the theoretically derived conclusion that microscale turbulence increases the encounter rate between planktonic predators and their prey. The original theory assumed that the geometry of the water volume perceived (i.e. searched for prey) by a predator is spherical (Rothschild and Osborn, 1988). More recent theoretical formulations assume a forwards-projecting hemispherical perceptual volume (reviewed in Dower *et al.*, 1997; Galbraith *et al.*, 2004). However, for all planktonic taxa for which such information exists, the geometry of the perceptual field is neither a sphere nor a hemisphere (Lewis, 2003; Galbraith *et al.*, 2004).

The manner in which a non-symmetrical perceptual field might affect the conclusions of turbulence-encounter theory was recently examined by Lewis (2003) for cruise-searching copepods. He concludes that, under turbulent conditions, the optimal swimming strategy (associated with prey search) for predators with non-symmetrical perceptual fields differs radically from what is otherwise predicted. Analogous work on larvae of Atlantic cod (*Gadus morhua*) produced a similar result: the advantage of turbulence is greatly reduced when the perceptual space is parameterized with more realistic geometry (Galbraith *et al.*, 2004). Because virtually all models of predator–prey interactions in plankton have, at their heart, a parameter for the distance at which prey can be located, this demonstrates how empirical knowledge of the perceptual abilities of marine organisms is essential. Without such information, we risk making large errors in prediction, which can lead to misleading and/or incorrect conclusions.

3.5.6.4 “Operational” prey abundance and the myth of prey choice/prey selectivity by small zooplanktivores

Although the abundance of prey that could be consumed by small zooplanktivores is highly variable, both temporally and spatially, it is reasonable to state that it most often ranges between 0 and 100 l⁻¹. The volume of water contained in the visual perceptual field (VPF) of a 6–10 mm fish larva is approximately 0.8–1.0 ml (Browman and Skiftesvik, 1996; Galbraith *et al.*, 2004). Thus, at an absolute prey abundance (AA) of 100 l⁻¹, only 0.08–0.1 prey items would be within the VPF at any given instant. The number of prey per VPF is the visual abundance (VA) and, from the perceptual perspective of the predator, VA, not AA, is the operational measure of prey availability. Thus, for this predator, AA would have to be >2000 l⁻¹ in order for VA to be >1 (prey aggregations at thin boundary layers may be this dense; Gallager *et al.*, 2004). These VA numbers illustrate that small zooplanktivores (e.g. carnivorous copepods or fish larvae) will only rarely have an opportunity to choose actively from among several simultaneously available prey items. It is possible that these predators make choices from among prey encountered sequentially, but under anything but the highest of prey abundance, they must eat whatever and whenever they can or risk starvation. Discussions of prey choice and/or active prey selectivity in these taxa must be undertaken within this context.

Conceptual and/or numerical models that attempt to define feeding rate, prey choice, or prey selectivity in small zooplanktivores all use AA as an input variable. Because VA is three orders of magnitude less than AA, this represents another example of the need for accurate characterization of the perceptual abilities of these organisms to parameterize such models realistically. Failure to do so raises the risk of making interpretive and predictive errors about predator–prey dynamics in marine foodwebs.

If it is necessary to introduce a condition factor for the larva into the model, there is probably no need for a detailed subcomponent on foraging. For a model that is designed to predict larval trajectories (and not growth or recruitment), there is no need to incorporate prey search and foraging unless there is evidence that these are the primary motivators for relatively local changes in vertical and/or horizontal position that might move the larvae into different water masses. There is very little evidence to support this in the literature.

3.5.7 Predator avoidance

3.5.7.1 Why incorporate this behaviour in a model?

Traditional aquatic foodwebs place plankton at the base of the food chain, often with fish as the top predator. However, during ontogeny, fish go through a phase as important (albeit transient) members of the plankton. At this small size, fish larvae are subject to predation by other plankters: carnivorous copepods (such as *Paraeuchaeta norvegica*), chaetognaths, gelatinous zooplankton, and other ichthyoplankton.

As early larvae, fish have only a limited capability to perceive and escape from predators. In contrast, many adult invertebrates and/or older larval or juvenile fish are formidable predators, against which early-stage fish larvae would have virtually no chance. There are almost no empirical observations of such interactions (Yen and Okubo, 2002; Browman *et al.*, in prep.). For larvae of greater swimming capability, the probability of escape depends strongly on the type of predator. For example, an aggregation of gelatinous zooplankton sweeping through a population of larvae could result in high mortality.

As with foraging, predator avoidance occurs on a relatively small spatial scale for most of the larval period and is therefore unlikely to exert a strong influence on dispersal trajectories. If predator-avoidance behaviour motivates the larva to undertake vertical and/or horizontal movements in an attempt to distance itself from predators (unlikely early in the larval period), such repositioning could indirectly influence dispersal (in conjunction with the behaviours discussed above).

3.5.7.2 How to incorporate data into the model

For a model that is designed to predict larval trajectories (and not mortality or recruitment), it is not necessary to incorporate predator avoidance unless there is evidence that this is the primary motivator for relatively local changes in vertical and/or horizontal position, which might move the larvae into different water masses.

3.5.8 Schooling

3.5.8.1 Why incorporate this behaviour in a model?

Schooling behaviour typically occurs prior to the transition period from the larval to the juvenile phase in some pelagic and benthic species (Leis, 1986; Breitburg, 1989; Gallego and Heath, 1994; Masuda *et al.*, 2003). Potter and Chitre (2006) used simple numerical experiments to demonstrate that schooling is capable of generating emerging larval behaviours that enhance the location of reefs by sounds, ultimately affecting the choice of settlement and changing the endpoint of individual trajectories (see also Simons, 2004). As schooling is also a strategy to avoid predation, it may ultimately affect survival and simulated levels of recruitment. Therefore, implementation of schooling in models of the early life history of fish can become important when modelling recruitment to specific nursery areas or settlement to benthic habitats, as well as for testing hypotheses on the orientation and sensory capabilities of larvae. Schooling will also alter the patchiness of pelagic larvae distributions, which has implications for sampling, predation, feeding, and patterns of settlement.

Field observations, net sampling, and acoustic traces indicate that some fish larvae undergo a near-bottom schooling phase prior to recruitment (Breitburg, 1989; Nelson *et al.*, 2006). The size of these larvae may be intermediate between the sizes of larvae collected in plankton tows and metamorphosed juveniles collected from benthos (e.g. Breitburg, 1989). Rearing experiments also demonstrated that this behaviour is de-

veloped early during ontogeny among pelagic species (Masuda *et al.*, 2003). Although schooling is mediated primarily by visual cues triggering aggregation, formation of the lateral-line canals appears to improve coordination of school members for parallel orientation (Fuiman and Magurran, 1994).

3.5.8.2 Simple tests

As this behaviour may change spatial patterns of settlement, the rule of thumb is to verify that the model grid-scale can resolve those spatial differences. The extent of the spatial differences (with and without schooling) can be estimated as the distance travelled by larvae at the mean velocity of the flowfield near the settlement area from the onset of schooling to settlement.

In addition, schooling may enhance the sensibility and precision in orientation. Therefore, in a model with orientation implemented as a response to environmental cues, the sensory sensitivity of larvae can be artificially increased and checked to see if it has an influence on both survival rates (ability to find suitable recruitment habitat before the end of the pelagic phase) and spatial patterns of settlement.

3.5.8.3 How to obtain the relevant data

Unfortunately, there is little published information on schooling behaviour during the transition from the larval to the juvenile phase in fish. Data can be obtained through rearing experiments (Masuda *et al.*, 2003), direct *in situ* observations (Leis, 1986; Breitburg, 1989), and also through acoustic measurements combined with net tows (Nelson *et al.*, 2006). Development of optical and acoustic technologies will provide new information on larval behaviour. Observations should aim at giving crucial information on the timing of the onset of schooling behaviour because this behaviour can occur in the oceanic realm, far from settlement habitat (Leis and Carson-Ewart, 1998; P. Fanning, pers. comm.), or in the coastal environment just prior to recruitment or settlement.

3.5.8.4 How to incorporate data into the model

Implementation of schooling behaviour is similar to that of orientation in that it entails following a set of rules for individual particles. Schooling may be related to a taxis-type behaviour whereby swimming direction and speed depend on the intensity of a cue source (sound, chemicals). As the cue decreases in intensity, each swimming particle takes a random step. Alternatively, swimming may be non-directional in response to a gradient (i.e. kinesis), whereby particles increase or decrease their random acceleration. An additional rule for schooling is that the swimming direction of each particle is slightly biased towards the centre of its surrounding neighbours (e.g. the averaging method; see Potter and Chitre, 2006). However, schooling can also be based on the influence of a single neighbour at any one time by a decision algorithm (Huth and Wissel, 1992). Because schooling is a poorly understood social behaviour, Lagrangian models can end up containing assumptions (e.g. modulation of response to neighbours by separation distance, relative orientation, and limits) that may have large effects on the characteristic aggregation length scales and therefore on the dynamics of the aggregation (i.e. when fragmentation and coalescence occur). For examples on modelling various fish aggregation behaviours in a Lagrangian context, see Flierl *et al.* (1999).

3.5.9 Choice of settlement

3.5.9.1 Why incorporate this behaviour in a model?

At the end of the pelagic larval stage of demersal teleost fish, there is a major ecological (and often morphological) transition that turns a pelagic animal into a benthic one. This transitional process is called settlement; without it, the life cycle of demersal fish species cannot be completed, nor can the individual fish recruit to a fishery. In most species of demersal fish, settlement-stage (i.e. competent) larvae have particular habitat requirements and will not settle just anywhere. Similarly, some species will settle only, or primarily, at certain times, for example, at night or on a lunar cycle. Hence, settlement behaviour can influence both the endpoints and the length of dispersal trajectories, so it is important to obtain such information for the species of interest.

Larvae may decline to settle on the first seemingly “appropriate” habitat that they encounter after becoming competent to settle (Leis and Carson-Ewart, 1999, 2002). Sometimes, this is for apparently obvious reasons (e.g. the presence of predators), but in other situations (up to 30% of the time), there is no obvious explanation for the rejection of appropriate habitat.

The question of whether larvae become decreasingly selective about where they settle the longer they are competent to settle (the “desperate larvae hypothesis”; Botello and Krug, 2006) remains unanswered, although circumstantial evidence indicates that this may be a real phenomenon. For example, tropical fish larvae advected into temperate areas in poleward currents sometimes settle into habitats in which they are never found in the tropics (e.g. butterflyfish in New Jersey estuaries; McBride and Able, 1998). If decreasing selectivity with time can be documented or reasonably inferred, then it should be incorporated into the model.

Mesoscale selectivity of settlement location has been demonstrated in a variety of species. For example, larvae of some reef fish will not settle on either leeward or windward portions of a coral reef, but only within lagoons (Leis and McCormick, 2002), whereas other species settle only into sheltered seagrass beds, often in estuaries. At smaller scales, larvae may select particular microhabitats upon which to settle; for example, among pomacentrids, anemone fish (*Amphiprion* spp.) only settle into particular species of anemones (Elliott *et al.*, 1995; Arvedlund *et al.*, 1999), and *Dischistodus* spp. only settle into sand patches on coral reefs (Leis and Carson-Ewart, 2002). The extent to which these behaviours may be important for any model depends upon the model’s grid size; such processes will be subgrid in many models.

Interaction with benthic resident fish, both predators (real and potential) and less directly deadly residents, can strongly influence the distribution of settlement. Obviously, predation by benthic residents will prevent settlement. Schools of planktivorous fish hovering off a reef edge and aggressive approaches by other resident fish (even herbivores) can both cause a larva to swim back out to sea rather than settle (Leis and Carson-Ewart, 2002). At least, this will influence the distribution of settlement but it may also influence its magnitude if the larvae driven back to sea are subsequently unable to locate suitable settlement habitat.

Several interacting sensory cues are probably involved in the selection of settlement sites (Kingsford *et al.*, 2002). Unlike some invertebrates, no “settlement stimulating compound” has been identified for marine demersal fish (Hadfield, 1998), but different studies have identified vision, olfaction (including detection of salinity), and audition as important factors (Leis, 2006; Montgomery *et al.*, 2006). There is probably

a continuum of cues involved in moving from open water to settlement sites, and the point where pelagic orientation ends and settlement behaviour begins is not clear. Therefore, these are not treated here (but see Section 3.5.5 Orientation).

3.5.9.2 How to determine whether or not this behaviour influences dispersal outcome

The degree to which settlement behaviour is relevant to a given model depends on the spatial scale over which the behaviour operates and on the grid size of the model. If the behaviours are subscale, they may have implications for the numbers of larvae that survive settlement, but they will not influence the spatial pattern of settlement at the scale of the model. The non-random spatial and temporal patterns of abundance of recently settled fish might be the result of random settlement followed by selective mortality. However, careful studies of settlement reveal that there is strong selectivity, either shortly before or at the time of settlement, which results in non-random settlement patterns.

3.5.9.3 How to obtain the relevant data

Unfortunately, there is no broad review of settlement behaviour in marine demersal fish, although there is substantial literature on the subject. Aspects of settlement behaviour have been studied in laboratory experiments, but these results should be verified by field experiments. Some field studies make inferences about settlement behaviour based on the spatial and temporal distribution of recruits, often weeks or even months following settlement. Although the shorter the interval between settlement and study the better, such studies should be treated cautiously for several reasons.

First, mortality rates of settling and newly settled larvae are extremely high (Doherty *et al.*, 2004) and, in many cases, have been demonstrated to be density dependent (Schmitt and Holbrook, 1999). Therefore, the distribution of recruits can differ markedly from that of settlers. Second, a number of species settle in one place or habitat and then move to another over a period of days to months (McCormick and Mackey, 1997; Nagelkerken and van der Velde, 2003), so the distribution of recruits, even seemingly recently settled ones, may differ substantially from that of settling fish. Therefore, unless it can be established that such alterations do not take place between settlement and whenever the study took place, inferences about settlement behaviour based on distribution of recruits should be treated with great caution. Well-designed field observations and experiments involving settlement behaviour provide the most reliable information. These include measuring what settles onto artificial habitat (Leis and McCormick, 2002), use of video (Holbrook and Schmitt, 1999) or other remote sensing equipment to watch natural settlement onto unaltered habitat, complex multifactorial designs (Almany, 2003), and divers directly observing larvae that they have released into different habitats (Leis and Carson-Ewart, 2002). Published examples of all of these can be found, although the range of species covered is narrow. It may often be possible to conduct similar experiments or observations on the species of interest, and examination of published work in this area is recommended to assist in their design. It might be tempting to use recently settled individuals for these experiments or observations, but given the extent and rapidity with which metamorphosis and alterations in behaviour take place upon settlement, there is little assurance that recently settled juveniles will behave with any similarity to settling larvae (e.g. Stobutzki and Bellwood, 1994).

3.5.9.4 How to incorporate data into the model

Where there is evidence of temporal factors in settlement, a decision will be needed as to whether the model larvae can remain near the settlement habitat if they arrive at the “wrong” time. For example, consider a larva arriving off a reef during daytime when it only settles at night, or a larva arriving off an estuary on an outgoing tide when it only enters an estuary to settle on an incoming tide. Would these larvae simply continue past the suitable habitat, using whatever combination of currents and behaviour they had used so far, or would they somehow sense the presence of the habitat and behave in a way that keeps them in the vicinity until the time is “right” (e.g. until nightfall or until the tide turns)? There is little direct information on this sort of behaviour, although circumstantial evidence indicates that larvae do accumulate in the vicinity of settlement habitat to wait for the appropriate time (e.g. Doherty and McIlwain, 1996). This circumstantial evidence does not, however, help to determine over what periods of time such accumulation might take place. Perhaps information on the swimming, orientation, or sensory abilities of the larvae can be used to determine whether or not such accumulation is possible; this might, at least, allow us to eliminate from consideration accumulation that is beyond the capabilities of the larvae.

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Annex 1: Particle tracking: Euler vs. Runge–Kutta stepping schemes

Experiments were performed to compare the performance of the Euler (EU) and Runge–Kutta (RK) time-stepping routines in the presence of turbulence. For each stepping routine, particles were released repeatedly at the same location in a steady-state, analytic flowfield with a spatially uniform, random drift component. Two flowfields were used, characterized by closed streamlines: (i) a simple circular vortex ($\vec{V} = Cr$, r = radius), and (ii) the Stommel solution to wind-driven ocean circulation. In both cases, circulation and turbulent parameters were chosen to yield realistic oceanographic flows.

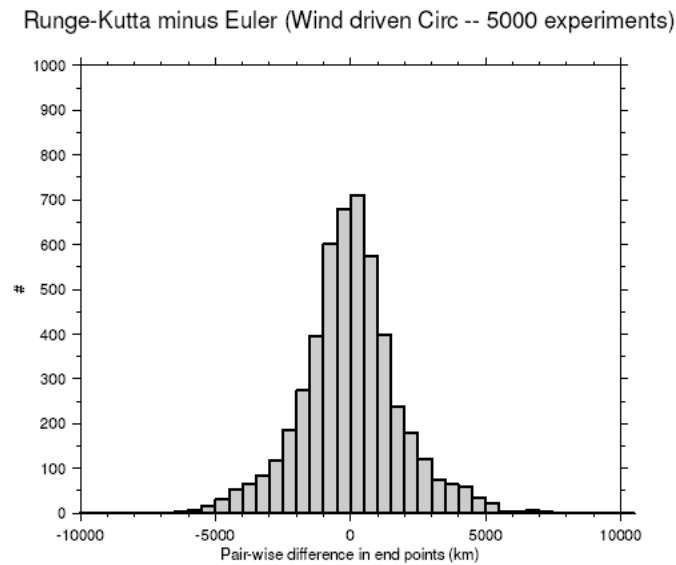


Figure A.1.1. Comparison of EU with RK time-stepping routines.

Particles were tracked for about 1.5 circuits of the flowfield. The time-step was chosen to yield noticeable errors in the closed streamlines for the EU routine, in the absence of turbulence, relative to the RK routine. The same time-step was used for each of the stepping routines. For each of the flowfields, 5000 particles were tracked, and a histogram was created of the pairwise difference in distance of the endpoint positions from a common origin (RK minus EU). That is, a histogram of $RK_i - EU_i$ was computed, where $RK_i = |(x_i - x_0, y_i - y_0)_{RK}|$ is the distance of the i th RK endpoint from the origin (x_0, y_0) . For the wind-driven circulation, we find (Figure A.1.1) that the distribution resembles a zero mean Gaussian. In other words, the difference between the two routines looks random. A similar result was found for the circular vortex experiment.

Annex 2: Particle tracking: the effect of time-steps

To examine the effect of time-steps, it is possible to make a run with a moderate number of particles, then repeat the same stochastic realization with larger time-steps. For example, consider the Euler scheme in one dimension:

$$Z_{t+h}^{(h)} = Z_t^{(h)} + D'(Z_t^{(h)})h + \sqrt{2D(Z_t^{(h)})} (B_{t+h} - B_t), \tag{A2.1}$$

which is the standard way of simulating vertical dispersal. Here, $Z_t^{(h)}$ denotes the numerical approximation, using the time-step h to the vertical position Z_t of a tracer at time t , D is diffusivity, and $D' = \partial D/\partial z$.

First, fix the time-step h and generate random numbers $\xi_1, \xi_2, \xi_3, \dots$ for $B_h - B_0, B_{2h} - B_h, B_{3h} - B_{2h}, \dots$. These ξ_i should all be Gaussian distributed with mean 0 and variance h . Next, double the time-step to obtain a recursion for $Z_t^{(2h)}$:

$$Z_{t+2h}^{(2h)} = Z_t^{(2h)} + D'(Z_t^{(2h)})2h + \sqrt{2D(Z_t^{(2h)})} (B_{t+2h} - B_t). \tag{A2.2}$$

Here, we re-use the same sequence of random numbers, so that $B_{2h} - B_0 = \xi_1 + \xi_2, B_{4h} - B_{2h} = \xi_3 + \xi_4$, etc. In this way, we can compare the individual trajectory obtained with a time-step of h with what would be obtained with a time-step of $2h$; that is, we compare $Z_t^{(h)}$ with $Z_t^{(2h)}$. This gives a much better resolution of the effect of the time-step than comparing the statistics of many runs obtained with new random numbers for each run. See Kloeden and Platen (1995) for background material and for systematic error analysis.

Example. We consider the one-dimensional case of Couette flow. We model the height of a particle over the seabed. We non-dimensionalize space with the depth H and time with the characteristic time $H^2/4\bar{D}$, where \bar{D} is the maximum eddy diffusivity, so that the height Z ranges between 0 and 1, and the diffusivity profile is $D(z) = z(1 - z)$.

For this case, the time-scale $1/D''(z)$ is constant over the water column and is equal to 0.5. The time-scale $D/(D')^2$ varies over the water column, vanishing at the boundaries and increasing towards the middle of the column. It exceeds 0.1 in 80% of the column. These time-scales are at least five times greater than the Lagrangian time-scale. Finally, the time-scale of vertical mixing, as defined above, is 0.35. This suggests that the time-step in the integration should be smaller than 0.1.

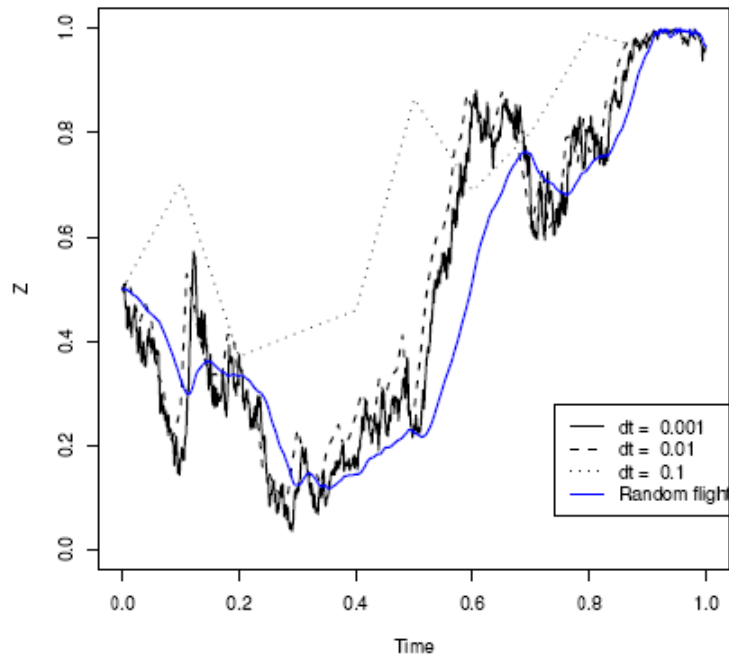


Figure A.2.1. The simulated vertical position of a particle, with three different time-steps and the same stochastic realization.

We simulate the motion of a single particle using the Euler scheme Equation (A2.1) over the time-interval $[0,1]$ using time-steps of 0.001, 0.01, and 0.1, and the same stochastic realization. The result is given in Figure A.2.1. Notice that the trajectories for the two smaller time-steps are nearly indistinguishable at the scale of the plot, but that some differences are visible with the larger time-step. It is also possible to simulate a random *flight* model (i.e. Lagrangian stochastic model (LSM)) of the same trajectory, using the same stochastic realization (i.e. the same random numbers) and the technique in Thygesen and Visser (in prep.). The result is shown in the figure (smooth solid blue curve). Notice that the error between the random flight model and the high-resolution, random walk model (or RDM) is of similar magnitude as the error between the high-resolution and the low-resolution random walk model. In this sense, a time-step of 0.1 is at the limit of being acceptable.

Annex 3: NPZ parameters, functions, and data assimilation

Several functional forms describing zooplankton grazing and predation closure terms have been used in nutrient–phytoplankton–zooplankton (NPZ) models. The choice of which to use, and the specific values assigned to parameters, can strongly influence the dynamics of the NPZ model (Edwards and Brindley, 1996; Edwards and Yool, 2000; Edwards *et al.*, 2000). For example, the use of the quadratic term for predation mortality can increase the short-term oscillations of predicted zooplankton concentrations (Edwards and Yool, 2000; Gibson *et al.*, 2005). Even the selection of different parameter values, within the same formulation, can affect NPZ predictions.

Effective linkage of particles to the fields output by the NPZ model is predicated on the assumption that the output fields are realistic. It is necessary to check that the inputs to the NPZ (e.g. grazing and closure terms, and parameter values) are reasonable, and to confirm that the NPZ model has been satisfactorily evaluated against field data by examining goodness-of-fit and diagnostics from data assimilation and validation analyses.

Data-assimilation techniques have been proposed as a way of systematically using data to constrain mathematical models, thereby ensuring more accurate model predictions (Hofmann and Friedrichs, 2002). In situations of limited data, some effort should be devoted to examining NPZ output and behaviour in order to ensure an adequate degree of realism before the fields are coupled to a particle-tracking model.

Annex 4: Coupling NPZ to physical models: types of coupling, scaling, and resolution

The quality of nutrient–phytoplankton–zooplankton (NPZ) generated fields also depends on how the NPZ submodel is coupled to the physics model. NPZ models may be coupled online or offline with physical models. Online coupling involves the simultaneous execution of the physical and NPZ models. Offline coupling involves the use of prestored fields of velocities, temperature, and salinity from the physical model, which are then used as inputs to the NPZ model. In general, with online coupling, the NPZ and the physics models usually use the same spatial grid and numerical time-steps so that interpolation of the physics is not needed. However, although the characteristic time-scales of the NPZ dynamics strongly correspond to the scales important in the physics, they are not identical (Hermann *et al.*, 2001). Ideally, the spatial and temporal scales should be resolved to the finest level needed to include all relevant scales to the physics and biology, but this is not possible, owing to high computing costs and our lack of knowledge.

We do know that much of the plankton dynamics in the NPZ is very sensitive to the dynamics of the mixed layer, and that the ideal vertical resolution for the biology is often finer than that represented in physical models (Hermann *et al.*, 2001). In an offline situation, filtering can be used to obtain information on a higher vertical resolution grid for the NPZ than that represented in the physical model (e.g. 100 layers vs. 9 layers; Hermann *et al.*, 2001; Hinckley *et al.*, in press). Some caution is needed because subsampling of the physical model output in time without filtering could lead to aliasing errors, especially when considerable high-frequency energy (e.g. near-inertial waves or tides) is present. Lowpass filtering can solve this aliasing problem, but can result in the loss of information on tide-related effects on advection.

Annex 5: Coupling NPZ and particle-tracking models: patchiness, trophic feedback, and behavioural responses

Issues related to coupling of Eulerian prey (nutrient–phytoplankton–zooplankton (NPZ)) and Lagrangian particle-tracking models include (i) the representation of particle interactions with prey patchiness, (ii) limitations imposed by one-way coupling, and (iii) the degree to which movement of particles is purely physics-driven or involves active behaviour. A large number of particles (individual larval fish) may be required in order to obtain an accurate representation of the encounters of individuals with zooplankton, especially when the zooplankton is patchily distributed in time and space. If too few particles are followed, growth rates of the particles can be underestimated and, therefore, mortality overestimated. Two possible solutions are to increase the number of particles followed or, if biological considerations permit, to broaden the sampling radius with which the particles experience the prey field.

Particle tracking is most often done in the offline mode, which imposes constraints on the feedback between the particles and their prey. Offline use of the NPZ fields prevents any trophic feedback between the particles (e.g. larval fish) and their zooplankton prey. Runge *et al.* (2005) discuss how this lack of feedback can be important when the species represented by the particles exerts significant mortality on its prey. Lack of feedback prevents density-dependent growth responses of the particles. From a fish-population perspective, this feedback is fundamental to using larval fish particle-tracking predictions to infer longer term population responses. Including this feedback is difficult in most situations because of the computational complexity and expense of solving the NPZ and particle-tracking models simultaneously, and because of the complexity of properly imposing consumption from Lagrangian particles with prey dynamics in Eulerian space. For example, if an insufficient number of particles is followed, and only the prey immediately surrounding these individuals is consumed, a “Swiss cheese” topology can be generated in the continuous prey fields. Offline use of NPZ fields also prevents including prey responses to predation pressure. Continuous prey fields do not allow avoidance behaviour *per se*, but the effects of avoidance can be mimicked when the NPZ and particle-tracking models are solved together by the addition of terms to the zooplankton equations that account for changes in density as a result of the presence of predators.

Organisms such as fish larvae are affected by advective processes, but can also exhibit active swimming behaviour in response to environmental and prey conditions (Runge *et al.*, 2005). Small contributions from active behaviour can alter the trajectories of particles, especially when the environmental and prey cues demonstrate gradients and patchiness that are superimposed on strongly sheared circulation fields. Some progress has been made in simulating active behaviour (e.g. Humston *et al.*, 2004), but it remains an open-ended question, and it is unclear how optimally to combine the physics-related and behaviour-related components of movement (Tyler and Rose, 1994).

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Acronyms and abbreviations

AA	absolute prey abundance
ADCP	acoustic Doppler current profiler
CFL condition	Courant–Friedrichs–Lewy condition
CPU	central processing unit
CTD	conductivity, temperature, depth
DK	dispersal kernel
GIS	geographic information system
GOOS	Global Ocean Observing System
IBM	individual-based model
ICPBM	individual-based, coupled physical–biological model
LSM	Lagrangian stochastic model (also called random flight model)
MFI	model food index
MOCNESS	Multi Opening and Closing Net and Environmental Sensing System
MPA	marine protected area
MRP	manual of recommended practices
NPZ model	nutrient–phytoplankton–zooplankton model
NPZD model	nutrient–phytoplankton–zooplankton–detritus model
OGCM	ocean generalized circulation model
OSSE	Observing System Simulation Experiment
PBI	physical–biological interaction
PDF	probability density function
PLD	pelagic larval duration
RDM	random displacement model (also called random walk model)
ROI	region of interest
SST	sea surface temperature
TAC	total allowable catch
TPM	transition probability matrix
VA	visual abundance
VPF	visual perceptual field
WKAMF	Workshop on Advancements in Modelling Physical–Biological Interactions in Fish Early Life History: Recommended Practices and Future Directions
WMC	well-mixed condition

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