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Manual of recommended practices for modelling physical–biological interactions during fish early life

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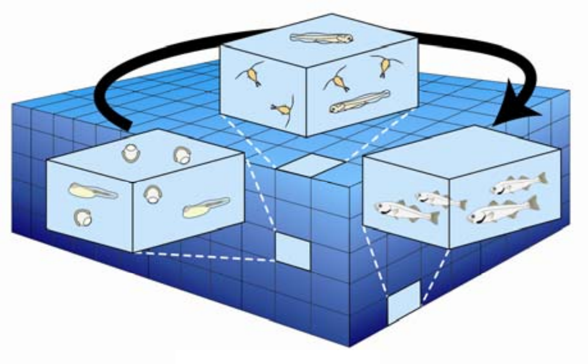
Foreword

This manual of recommended practices is a product of the "Workshop on Advancements in Modelling Physical–Biological Interactions in Fish Early Life History: Recommended Practices and Future Directions" (WKAMF; http://northweb.hpl.umces.edu/research/wkamf_intro.htm). The WKAMF was held 3–5 April 2006 in Nantes, France. The goal was to evaluate the current state and next steps in the developing field of modelling physical–biological interactions in the early life of fish. The workshop focused on recent advances in coupled biological–physical models that incorporate predictions from three-dimensional circulation models to determine the transit of fish eggs, larvae, and juveniles from spawning to nursery areas. These coupled biophysical models provide new insight into how planktonic dispersal, growth, and survival are mediated by physical and biological conditions, and how they have contributed to enhanced understanding of fish population variability and stock structure.


WKAMF logo.

The workshop was designed to survey major components of biophysical models of fish early life, address numerical techniques and validation issues, define recommended modelling practices, and identify future research needs. Several aspects of modelling fish early life history were addressed, including: initial conditions (egg production, spawning location/time), small-scale processes (turbulence, feeding success), mesoscale transport processes (physics and larval behaviour), and biological processes (development, growth, mortality, juvenile recruitment, metamorphosis, settlement). Workshop participants agreed on six major themes that represented important research needs in modelling physical–biological interactions and would result in advances in the field: validation and sensitivity methods, model complexity, mortality, behaviour and cues, energetics, and physics.

Papers based on some of the research presented at WKAMF appeared in a theme section in the *Marine Ecology Progress Series* entitled "Advances in modelling physical–biological interactions in fish early life history". These open-access publications can be found at http://www.int-res.com/abstracts/meps/v347/.

WKAMF was attended by 54 participants from 14 countries and was chaired by Alejandro Gallego (UK), Elizabeth North (USA), and Pierre Petitgas (France). WKAMF was held under the auspices of the ICES Working Group on Physical–Biological Interactions and the ICES Working Group on Recruitment Processes. It was hosted by the French Research Institute for Exploitation of the Sea (IFREMER) with support from IFREMER, US National Science Foundation (NSF), US National Marine Fisheries Service (NMFS), UK Fisheries Research Services (FRS), and the University of Maryland Center for Environmental Science (UMCES). It was endorsed by Global Ocean Ecosystems Dynamics (GLOBEC) and Eur-Oceans.

Executive summary

The objectives of this manual of recommended practices (MRP) are to summarize appropriate methods for modelling physical–biological interactions during the early life of fish, to recommend modelling techniques in the context of specific applications, and to identify gaps in knowledge. This manual is intended to provide a reference for early-career modellers who are interested in applying numerical models to fish early life and who would benefit from a summary of recommended practices for coupled biological–physical models that incorporate predictions from three-dimensional circulation models to determine the transit of fish eggs, larvae, and juveniles from spawning to nursery areas. For current practitioners of numerical modelling in fish early life, the manual provides updates on latest techniques and areas in need of further research. Although the manual focuses on finfish, many of the summarized modelling techniques and recommended practices apply to modelling planktonic organisms, including zooplankton and other meroplankton (e.g. molluscs and crustaceans).

It is important to recognize that "best" modelling practices depend upon the objective of the modelling exercise. In other words, no single model is appropriate to all applications. Instead, model formulations are situation-specific. Because methodologies depend upon the goal of the endeavour, this manual includes an overview of basic components of fish early life models and presents recommendations in the context of three specific applications: adaptive sampling, connectivity, and recruitment prediction.

The first three sections (Section 1–Hydrodynamic models, Section 2–Particle tracking, and Section 3–Biological processes) summarize methodologies that are important components of three-dimensional models of the early life of fish. The next three sections (Section 4–Application 1: adaptive sampling, Section 5–Application 2: connectivity, and Section 6–Application 3: recruitment prediction) discuss the application of selected methodologies to specific issues that are commonly addressed with these models. The final section summarizes the information gaps and research needs identified throughout the manual.

This MRP grew out of participant discussions at the "Workshop on Advancements in Modelling Physical–Biological Interactions in Fish Early Life History: Recommended Practices and Future Directions" (WKAMF) held on 3–5 April 2006 in Nantes, France. This manual does not contain an exhaustive review of all approaches to modelling the early life of fish. Instead, it is intended to be a general reference for fish early life modelling that includes citations that will direct readers to in-depth treatments of specific topics. In addition, it should be noted that this document does not represent the consensus recommendations of all authors. Each section was written separately. In some cases, differences in recommendations and perspectives exist. These apparent contradictions may stem from dissimilarity in the time or space scale of the models used by the authors or the ecosystem in which the authors are most experienced (e.g. temperate vs. tropical). The issues on which recommendations or perspective diverge are those that remain an active area of research. This manual is a "living" document: future revisions and updates are expected as our understanding and methods evolve.

1 Hydrodynamic models

Genevieve Lacroix, Paul McCloghrie, Martin Huret, and Elizabeth W. North

Three-dimensional hydrodynamic models form the basis for models of the early life history of fish. Predictions of current velocities and diffusivities are used to calculate movement of eggs and larvae. Salinity, temperature, and density predictions are used to estimate the buoyancy of fish eggs, as well as the development, growth, and mortality rates of eggs and larvae. An appropriate hydrodynamic model is critical. This section describes hydrodynamic model components and identifies the characteristics of an appropriate hydrodynamic model in the context of modelling fish early life. It is meant to provide information about aspects of hydrodynamic models that could influence biological predictions.

1.1 Hydrodynamic model components

From the so-called "primitive equations", hydrodynamic models calculate velocities, turbulence, temperature, and salinity (and from these, density). These equations are discretized, that is, formulated so that they can be evaluated at discrete points in space and time. There are several techniques employed for discretization that create different types of hydrodynamic models. A short description of the discretization methods and types of hydrodynamic models used in fish early life models follows. For a more comprehensive list of hydrodynamic models, see more complete reviews (e.g. Jones, 2002). These first steps towards developing a hydrodynamic model are critical because they will influence which physical processes can be resolved and how.

1.1.1 Horizontal discretization

The domain over which the primitive equations are solved must be discretized on the horizontal dimension in a given coordinate system. Most existing models use the spherical coordinate system to fit the natural shape of the Earth, although a simple Cartesian system may be acceptable for some local applications. Two main types of grids, structured or unstructured, can be applied to these coordinate systems (Figure 1.1.1).

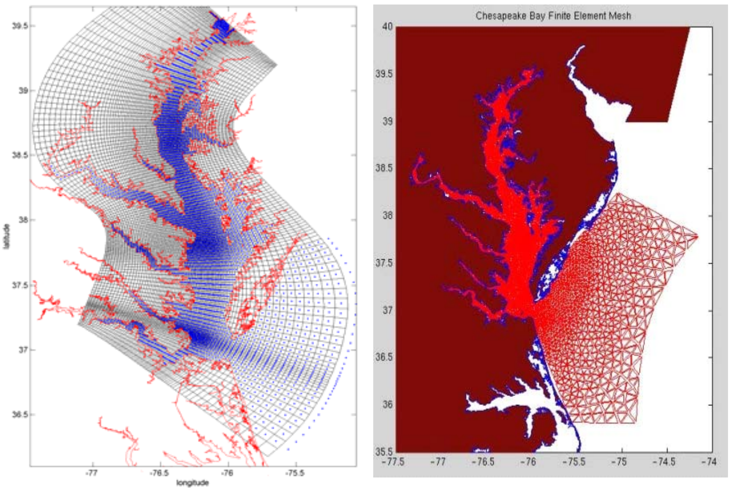


Figure 1.1.1. Left: example of structured curvilinear grid (courtesy of Ming Li (Li *et al.*, 2005)), and right: unstructured finite element grid (courtesy of Thomas Gross) for hydrodynamic models of Chesapeake Bay.

A structured grid uses quadrilateral grid cells. In most applications, these grids are approximately rectangular and regular, but possible transformations allow for local refinement in areas of interest (stretched or telescoping grids) and better coastline fitting (curvilinear grid; see Figure 1.1.1, left panel). With this type of grid, equations are solved with the simple and relatively fast finite-difference method of discretization (e.g. Blumberg and Mellor, 1987; Song and Haidvogel, 1994).

The most commonly used structured grids can be subdivided into a number of types (Arakawa, 1966), according to where in each cell the state variables are defined. The most common types are Arakawa-B and Arakawa-C grids, and it is important to know which grid type is being used to ensure that the correct interpolation locations are chosen when interpolating from the hydrodynamic output to the locations given by the early life-history model. An example of an Arakawa-C grid is given in Figure 1.1.2.

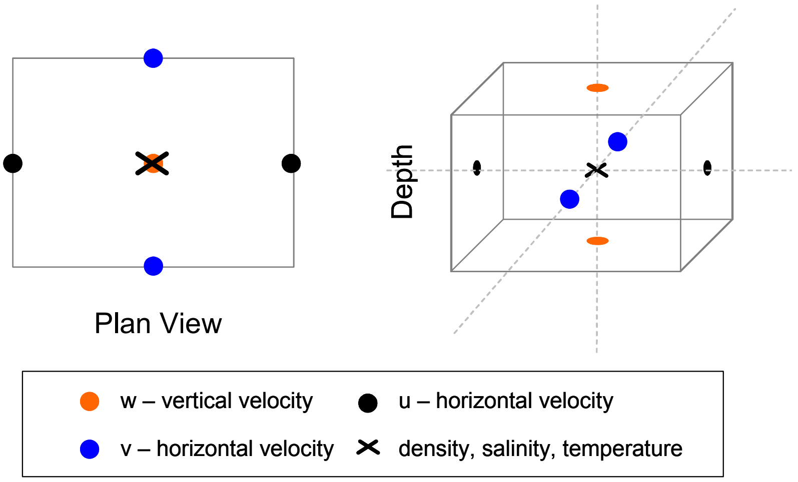


Figure 1.1.2. Schematic of Arakawa-C grid. Left: plan view, and right, depth view. Locations where water properties are estimated are indicated by coloured symbols. Dashed lines suggest perspective.

The unstructured grid type usually adopts triangular elements (Figure 1.1.1, right panel) and consequently requires other discretization methods to solve the equations, such as the element (variational approach, e.g. Lynch *et al.*, 1996) and finite-volume (integration approach, e.g. Chen *et al.*, 2006) methods. The flexibility of the unstructured grids helps resolve complex coastline and bathymetry, and associated processes, without dramatically increasing the computing time. The formulation of the finite-volume method ensures mass conservation, as may be the case for finite differences. Note that the finite-volume method is not restricted to the unstructured type of grid.

For all types of grids, nesting can be used to work with two different fixed resolutions, allowing refinement in the area of interest. The connection between the two grids is either “one-way”, where the inner model uses information from the outer model for boundary conditions, or “two-way”, where both models are dynamically linked.

1.1.2 Vertical discretization

In areas where the water column is consistently vertically well mixed, it may be advisable to use a two-dimensional model grid (no vertical dimension). However, for most early life-history models, vertical heterogeneity is important, and three-dimensional models are required.

There are also three common vertical grid set-ups. The first is the z-levels system, where each level represents a fixed depth. The second is the terrain-following coordinate system (or sigma-levels), which is also common in coastal applications. Here, each level is a fraction of the total local water-column depth, allowing for an improved representation of the bottom topography and time-evolving free surface. The third approach is to use isopycnal coordinates, where each level lies along a density surface, the preferential location of diffusion. This system is generally used for oceanic models.

Some vertical coordinate systems employ a hybrid of these methods, one of the goals of which is to avoid the generation of spurious circulation over steep bottom topography, which may be encountered when using sigma-coordinates. Double sigma-coordinates, where a fixed horizontal layer is specified with a set of sigma-coordinates above and below, will keep a sufficient refinement of sigma-layers at the surface when the domain covers both shallow and deep bathymetry. For the same purpose, s-coordinates, or generalized sigma-coordinates, use a function of the location (and hence bathymetry) to define the sigma-levels.

1.1.3 Time evolution

Hydrodynamic models predict their state at the next time-step from their current and prior states. The length of the time-step is restricted by the size of the grid cells and the speed of propagation of disturbances. This is known as the Courant–Friedrichs–Lewy (CFL) condition. In essence, the time-step used must be short enough to prevent a disturbance propagating across more than one grid cell in a time-step. Short time-steps are required at high spatial resolutions, which can lead to prohibitive computational costs. In order to alleviate this, some models use a technique called "mode splitting", where the fast (but computationally cheap) barotropic processes (such as the propagation of the tide) are calculated on a short time-step, whereas the slow baroclinic processes (computationally expensive because they must be calculated separately for each vertical level) are calculated on a longer time-step. The baroclinic (or internal) time-step can be as much as 40 times longer than the barotropic (or external) time-step.

1.1.4 Using hydrodynamic output for particle tracking

Particle-tracking models use the output of a hydrodynamic model to provide velocity fields. The gridded velocities are interpolated to the position of each particle, and the particles are moved to new locations based on the interpolated velocity and the time-step of the particle-tracking model. Particle-tracking models can be run either online or offline. Running online means that the particle-tracking calculations are made within the hydrodynamic model program; velocities are calculated, the particles are transported, and then, at the next time-step, velocities are calculated, particles are transported, and so on. Running offline means that the hydrodynamic model is run once and the velocity fields for the period required are saved. The particle-tracking model then reads the velocity fields, interpolates, and steps forward in time, then reads the next set of fields. Running online allows the particle-tracking model to use the velocity fields at the high native resolution (in both space and time) of the hydrodynamic model, but it means that each new particle-tracking experiment requires the hydrodynamic model to be rerun, which can be computationally prohibitive. Although running offline allows output from one hydrodynamic simulation to be used for multiple particle-tracking simulations, the saved velocity fields will usually be a lower resolution than the native hydrodynamic model output as a consequence of storage space and read–write speed constraints.

When interpolating gridded velocities to the particle locations, it is important to account for any horizontal offsets caused by the hydrodynamic grid type. The offsets are usually different for horizontal velocities (u, v), vertical velocities (w), and any scalar properties, such as temperature. This is equally true when interpolating in the vertical.

1.2 Characteristics of an appropriate hydrodynamic model

When assessing whether a hydrodynamic model is appropriate to particle tracking and early life-history modelling, there are a number of points to consider. Physical processes act on the transport/retention of larvae during their pelagic phase (e.g. wind-driven circulation, tides, freshwater buoyancy, fronts), on their settlement (e.g. bottom stress), and on conditions affecting larvae survival (e.g. temperature, light). Ensuring that the model (i) covers the domain of interest and (ii) simulates all the key physical processes for both circulation and larval fish (e.g. temperature) is of primary importance. Physical processes with temporal scales close to the time-scales of fish larvae (e.g. larval stage duration) should be considered. The choice of physical processes that are to be explicitly resolved should be made by considering the spawning frequency and the larval stage duration, and by taking into account possible links with larval behaviour (e.g. vertical and horizontal migration, feeding processes).

The following list includes some of the physical processes that can affect fish larvae during their pelagic phase and some possible links with larval behaviour. This list, far from being exhaustive, is given to help the modeller choose which physical processes to consider in the context of the spatio-temporal scales of the region of interest and the purpose of the study.

- **Ocean currents**. General circulation, coastal currents, meanders, jets, eddies, shelf-edge fronts. The main variability is “marine weather” (depression regimes, storms).
- **Tides**. Tidal currents (can be important in shallow waters and reefs, depending on the topography), residual circulation, tidal fronts, vertical gradients of horizontal currents. The main variability is (semi-)diurnal, lunar cycle (spring/neap tides), seasonal cycle (equinoxes, solstices). Possible relationships with “larval behaviour” (synchronization of vertical migration of larvae with ebb– flood tidal cycle), spawning timing (synchronization with spring–neap tidal cycle), and spawning location (spawning depth).
- **Freshwater input**. Presence of hydrological fronts in the proximity of river mouths, freshwater buoyancy circulation, water stratification density (may act as a barrier to vertical movements), periodic low-salinity water intrusions (may affect depth of larvae). The main variability is (semi-)diurnal (link with tides), seasonal, and interannual. Relationship with spawning timing (synchronization with high/low river discharges).
- **Wind**. Wind-driven circulation, internal waves, Langmuir cells, upwellings/downwellings (and associated fronts and convergences). The main variability is “marine weather" (duration, depression regimes, storms), seasonal (monsoons), and interannual.
- **Fronts**. Fronts (whatever their origin) can act as a barrier that limits larval transport, but they are also the seat of circulations leading to conver-

gence/divergence zones. Instabilities (e.g. eddies) can transport "isolated" water masses over long distances.

The size of the model domain and the grid size must be chosen in accordance with the physical processes to be included, the purpose of the study, and the biology of the fish. Processes smaller than the grid size must be parameterized (see Section 1.2.4 Small-scale physics), and processes acting at scales larger than the model domain should be considered by appropriate boundary conditions (e.g. harmonic tides) or by nesting. The limits of the domain should be chosen sufficiently far from the spawning location(s) and the assumed settlement region(s) to avoid problems related to boundary effects (loss of particles, uncertainties of boundary reflection scheme). For some particular studies, it may be necessary to consider a refined grid (e.g. shallow coastal waters, local retention, heterogeneity of sediment, needs of a fine vertical resolution). Sensitivity studies are recommended to determine the optimal grid resolution (vertical and horizontal). If a refined grid is needed, and if the model domain must encompass a whole region, it is appropriate to consider model nesting.

1.2.1 Boundaries and initial conditions

Close to their open (wet) boundaries, the predictions from hydrodynamic models are strongly influenced by the conditions imposed on the model at the boundaries. For example, baroclinic velocities depend on the density structure of the water, that is, both temperature and salinity. Surface temperatures will usually decrease close to dynamic equilibrium within days as a result of rapid heat exchange with the atmosphere, whereas bottom temperatures in stratified water may take much longer. Salinities in non-coastal areas can remain dominated by boundary effects throughout the model domain. Fortunately, when considering large areas, salinity gradients can often be accurately reproduced, although the absolute values may be incorrect. Barotropic velocities, driven by tidal boundary conditions, usually propagate through the entire model domain.

When choosing the extent of the model domain, it is important to exceed the area of interest for the tracking model because of the influence of boundary conditions on the model predictions. Boundary condition data are usually given at lower resolution and may be derived from a climatology rather than for the specific dates being simulated. These boundary values then propagate their influence into the model domain for a distance that is a factor of the local flow rates and the rate at which the values are modified to fit with the internal dynamics. The key to accurate representation is, therefore, using high-quality data on the boundaries and undertaking a careful validation process.

The same considerations need to be applied to the initial conditions for the hydrodynamic model. The period during which initialization effects are significant is a factor of the rate of change of the variables. To avoid initialization effects, a hydrodynamic model is usually "spun up" for a period of time before the outputs are used. For barotropic velocities, this may only require a couple of weeks; however, for baroclinic velocities, it will usually take months. Because of the slow rate of adjustment of temperature and salinity in stratified bottom waters and seasonally stratified areas, hydrodynamic models are usually spun up during winter.

1.2.2 Resolution

The choice of model resolution is usually strongly influenced by the available computer resources. Higher horizontal resolution allows models to resolve more of the physical processes. However, a doubling of horizontal resolution implies an eightfold increase in computational expense. (The factor of eight comes from a doubling in the x, y, and time dimensions. The requirement for shorter time-steps at higher resolution comes from the CFL condition). When an improvement in the resolution is not necessary over the whole domain, curvilinear and unstructured grids allow the resolution to be location-dependent (which does not remove the constraint on the time-step, but does reduce the number of cells over which the calculations are made).

The ability to resolve the mesoscale is a significant improvement gained from higher resolution. The size of mesoscale features (eddies, etc.) is determined by the local Rossby radius (L), which can be calculated from

$$L=\sqrt{gH}/f,$$

where H is the water depth, f is the Coriolis parameter, i.e. $2 \times 7.29 \times 10^{-5} \times \sin$ (latitude), and g is the reduced gravity at the pycnocline. A typical shelf-sea mesoscale eddy at 55°N will have a diameter of roughly 20 km. To resolve this eddy, a hydrodynamic model will need to have six to ten grid points across the eddy and therefore a resolution of at least 3 km.

1.2.3 Model validation

Only thoroughly validated hydrodynamic models, including all key physical processes, should be used for particle-tracking studies. The modeller should at least verify that current velocity (horizontal and vertical) and/or trajectory paths are correctly simulated. After that, depending on the situation or the purpose of the study, particular attention should be paid to the accuracy of additional parameters, such as salinity (regions of freshwater influence), light attenuation (predator-avoidance behaviour), temperature (if temperature-dependent processes are considered), and bottom stress (settlement). Model error quantification techniques include cost functions (Delhez *et al.*, 2004; Radach and Moll, 2006), root-mean-square error of modelled vs. observed values, model skill scores (Warner *et al.*, 2005), and Taylor diagrams (Taylor, 2001).

Sensitivity studies (combined with validation) should allow the modeller to determine the degree of importance of the physical processes and help when choosing the key processes to include, according to the purpose of the study and the larval behaviour considered (e.g. Hill, 1994; Lefebvre *et al.*, 2003; Ellien *et al.*, 2004; Sentchev and Korotenko, 2004).

1.2.4 Small-scale physics

In hydrodynamic modelling, processes that occur at scales too small for the model resolution to simulate accurately are parameterized to allow for their diffusive effect on the large-scale structure. (Note that models require a resolution in excess of five times the scale of a feature in order to be able to resolve the feature.) The parameter used is known as the "eddy diffusivity" and accounts for unresolved advective processes, such as frontal instabilities, steering by unresolved topographic features, and sea breezes. Omission of physical processes generally requires an increase in the specified eddy diffusivity. This parameter also depends largely on the method used to solve the advection equations. Low-order methods are inherently more diffusive than higher order approximations. In many cases, this numerical diffusion is enough to account for small-scale processes; however, additional diffusion is often added to improve model stability.

2 Particle tracking

David Brickman, Bjørn Ådlandsvik, Uffe H. Thygesen, Carolina Parada, Kenneth Rose, Albert J. Hermann, and Karen Edwards

Particle-tracking models form the backbone of three-dimensional models of fish early life. These models use predictions of current velocities and diffusivities from hydrodynamic models to calculate the movement of individual particles in space and time. The goal of this section is to provide a set of recommendations for particle tracking in estuary and ocean modelling. Because the motivation comes principally from its application to biophysical modelling, the case of biologically active particles is specifically considered. The first part of this section presents, in a concise form, the essential aspects of best practices for particle tracking. Extra material is contained in Annexes 1–5. The second part presents a number of cases designed to test the performance of a particle-tracking routine.

2.1 Best practices for particle tracking

What makes particle tracking in an oceanographic (biophysical modelling) context different from tracking in an atmospheric context? The simple answer is that, historically, development of particle-tracking theory and techniques in the atmosphere was concerned principally with the atmospheric boundary layer, with an emphasis on correctly describing the statistics of dispersion for time-scales shorter than the Lagrangian time-scale (T_L), the time-scale at which velocity fluctuations are correlated. Generally, the computations were done for short periods (minutes to hours) and in one or two dimensions (for which analytic models exist; see Wilson *et al.*, 1981; Legg and Raupach, 1982; Thomson, 1987). These Lagrangian stochastic models (LSMs), or "random flight models", are mathematically complicated, but are valid at all time scales (except below the Kolmogorov microscale, where viscosity becomes relevant; Thomson, 1987; Rodean, 1996). In addition, a critical problem of buoyant particles, "the trajectory crossing problem", has only approximate solutions for LSMs (Sawford and Guest, 1991; Olia, 2002).

For biophysical modelling in the aquatic realm, we tend to be interested in time-scales longer than T_L and in three-dimensional drift for periods as long as several months. Another crucial difference is that many biophysical particles (representing planktonic larvae) have directed swimming motions that must be incorporated into the particle-tracking algorithm. This necessitates the use of random displacement models (RDMs, also known as random walk models). These models are valid for time-scales $>> T_L$ (T_L vertical = 3–10 min; T_L horizontal = 1–8 d (near surface; greater at depth)). That the time-scales of interest in the ocean are not always $>> T_L$ (especially on the horizontal plane) means that the use of RDMs in oceanographic particle tracking can be considered a "best-we-can-do" approach.

2.1.1 Choice of model

For the reasons outlined above, an RDM is recommended for oceanographic application. If we assume that the turbulence at each point is isotropic in the horizontal (i.e. its local statistics are invariant to rotations around a vertical axis), then turbulence is characterized by the horizontal diffusivity $K_{11} = K_{22}$ and the vertical diffusivity K_{33}. The three-dimensional RDM then becomes (Rodean, 1996):

$$dx_i = \left[U_i(\bar{x},t) + \frac{\partial K_{ii}(\bar{x},t)}{\partial x_i} \right] dt + (2K_{ii}(\bar{x},t)\,dt)^{1/2}\, Q_i, \tag{1}$$

where dx_i is the displacement in the ith direction ($i = 1, 2, 3 = x, y, z$), U_i is the velocity, $\bar{x}$ denotes three-dimensional position, t is time, K_{ii} is the eddy diffusivity, dt is the time-step, and Q is a Gaussian random variable with zero mean and unit variance. The term for the spatial derivative of the diffusivity $\partial K_{ii}(\bar{x},t)/\partial x_i$ is a drift correction term required to remove erroneous aggregations, or evacuations, of particles (see Hunter *et al.* (1993); Visser (1997) for other formulations of the RDM). This term is required in order to maintain a well-mixed condition (WMC), that is, the requirement that an initial uniform concentration of particles remains uniform for all time (Brickman and Smith, 2002). For most applications, the algorithm based on Equation (1) will use circulation model output to provide the velocity and diffusivity fields. These fields exist on discrete grids, which may be problematic (see below).

2.1.2 Time discretization

The RDM is a stochastic differential equation, which in practice is solved using a discretization technique. The two commonly used are the Euler and Runge–Kutta routines. The former is a simple, first-order forward discretization routine, which generally executes quickly but is subject to truncation errors and (possible) instabilities. The latter is a higher order routine that is numerically more accurate. In the absence of turbulence, a higher order differencing scheme is recommended.

In the presence of turbulence, the choice of discretization technique is less obvious, because the precision gained by a high-order routine could be lost as a result of the "noise" of the turbulence. To examine this possibility, experiments were performed comparing the Euler and the Runge–Kutta routines for two different analytic flowfields plus a turbulent component (see Annex 1). Histograms were created of the difference between endpoint positions for the two routines for 5000 different particle releases. These histograms resembled zero-mean Gaussian distributions, indicating that the difference between the two routines was random, not systematic. This suggests that the error introduced by use of an Euler stepping routine, in the presence of turbulence, itself looks "turbulent" and may reduce concerns about the relative accuracy of this scheme. Although the Euler scheme may be adequate for some situations, the effect of different discretization techniques on biological predictions has not been investigated and should be assessed in the context of specific modelling objectives.

2.1.3 Choice of time-step

In an RDM, as in any numeric algorithm for discretizing a continuous-time phenomenon, the time-step should be smaller than time constants of the system. This leads to upper bounds on the time-step (Thomson, 1987; Wilson and Flesch, 1993). The exception to this general rule is the Lagrangian time-scale characterizing the decorrelation of turbulent velocity fluctuations. RDMs are accurate descriptions of turbulent dispersal only on time-scales larger than the Lagrangian time-scale, so there is no reason to force the time-step below the Lagrangian time-scale.

For pure stationary diffusion in one dimension with diffusivity $D(z)$ ($\mathrm{m^2\,s^{-1}}$), the time constants $D/(\partial D/\partial z)^2$ and $1/|\partial^2 D/\partial z^2|$ describe when the expected change in diffusivity is larger than the diffusivity itself and, therefore, provide upper bounds on the time-steps. The time-scale of vertical mixing will, in most applications, be significantly larger; for Couette flow (the flow between two planes moving relative to each other), the half-time of the slowest mode of vertical mixing is $H^2(\log 2)/(8\max_z$

($D(z)$)), where H is the water depth. This time-scale can be used as a rough measure of vertical mixing in other flows as well, or more accurate time-scales can be obtained analytically or numerically for the specific flow.

Additional time-scales may characterize horizontal motion or other (e.g. biophysical) processes. The chosen time-step must ensure that all processes are accurately resolved. For an example of the effects of different choices of time-step see Annex 2.

2.1.4 Number of particles

A single-particle trajectory in a turbulent flowfield can be considered one trial of a statistical ensemble of which we are interested in the ensemble-averaged behaviour. If too few particles are released in a particle-tracking experiment, it is possible that the trajectories are polluted by statistical outliers and do not satisfactorily represent the desired ensemble average. There is a risk that this can lead to erroneous conclusions. Although there is no generic answer to this problem, we recommend that at least some tests be done to check whether or not sufficient particles are being used; for example, an experiment to measure the concentration of particles in some downstream grid cell at a given time after release (where concentration = # particles in grid cell/total number released) and repeating this experiment for an increasing total number of particles. This concentration, as a function of the total number of particles, will stop fluctuating when a sufficient number of particles are being used. For more details on such techniques, see Brickman and Smith (2002). In general, the oceanographic literature contains numerous instances of poorly performed particle-tracking experiments. The basic premise of performing a particle-tracking experiment should be the ability to do it correctly. There is no excuse for using too few particles.

2.1.5 Choice of random number generator

The random number generator should perform well enough to ensure that the results are not artefacts of the particular algorithm. Some fairly common random number generators have been demonstrated to be flawed; these generators have typically been included in general-purpose development environments, as opposed to environments designed specifically for scientific computing. The typical problems with poor generators are short periods and correlation in the random numbers. Short periods mean that the sequence of random numbers repeats itself too soon. Correlation in the random numbers may result in incorrect dispersion: either too weak or too strong, depending on the correlation pattern. Both flaws seriously undermine the credibility of the study.

There is no reason to use a random number generator with insufficient performance. It may be easier to obtain and install a state-of-the-art generator than to determine the properties of the built-in generator. Currently, the "Mersenne Twister" seems to be the strongest algorithm; this is, for example, the default generator in R and is also available in Matlab. C source code, made by the original designers of the algorithm, is available at http://www.math.sci.hiroshima-u.ac.jp/~m-mat/MT/emt.html. Source code in other languages and a list of libraries that include the algorithm can be found at http://www.Wikipedia.org under Mersenne Twister.

A general introduction to random number generators can be found in Ross (2001) and similar textbooks on stochastic simulation. The standard tool for verifying built-in random number generators is Marsaglia's Diehard battery of tests (see http://www.stat.fsu.edu/pub/diehard/).

2.1.6 Boundary conditions

The boundary conditions for an RDM are similar to those for an ocean circulation model, that is, a condition of no flux through the boundaries. For an RDM, this means that no particle should cross a boundary or, equivalently, that particle numbers should be conserved. This is important because the calculation of particle concentrations, or probability density functions (PDFs), can be incorrect if particles are lost from the domain. This boundary condition is enacted as a reflection scheme. However, the requirements of this scheme can be non-trivial, as certain properties have to be maintained upon reflection, especially the WMC. An incorrect reflection scheme can lead to spurious particle concentrations near boundaries. For an LSM, these requirements have been determined (Wilson and Flesch, 1993), but for the RDM, they are less clear. In practice, many of the theoretical requirements for a boundary reflection scheme are not met, but this does not seem to have any great effect on the result (Legg and Raupach, 1982).

Owing to the various uncertainties in the theory and practice of boundary reflection schemes, no simple best practice can be recommended, except to state that such a routine is required for a valid particle-tracking model. Experience indicates that these schemes can be complicated to code and should be tested carefully before proceeding.

2.1.7 Additional considerations

2.1.7.1 The use of discrete circulation model fields

Most particle-tracking models rely on space- and time-discretized fields from an ocean circulation model. A number of problems can arise because of this, including interpolation within grid cells near model boundaries and the use of discretized turbulence quantities.

- **Interpolation within grid cells near model boundaries**. Circulation models typically have no slip and no flux boundary conditions on velocity, so that flow runs parallel with closed boundaries. The determination of the velocity within such boundary cells can be complicated, especially where flows are "turning corners" following a coastline. This can result in particles erroneously crossing a boundary as a result of the combination of velocity and time-step, or drifting in an incorrect direction (see test case, Section 2.2.2 Flow around an obstacle). The addition of turbulence to this process is a further complication resulting in the expenditure of significant coding and execution time handling particle tracking near boundaries. The best practice recommendation in this case is to be aware of this problem and to check carefully that the algorithm is performing correctly.
- **The use of discretized turbulence quantities**. Circulation models can produce discontinuous turbulence fields, particularly in the vertical dimension. The particle-tracking model (Equation 1) requires values and derivatives of these quantities, which can lead to problems in the correct prediction of particle positions if these fields are sufficiently non-smooth (Brickman and Smith, 2002; Thygesen and Ådlandsvik, 2007). A solution can be to smooth these fields before use (Brickman and Smith, 2002; North *et al.*, 2006), but it is difficult to determine the degree to which this is necessary or successful in a complicated model setting. The best advice in this case is to be aware of this problem, proceed carefully, and check that the algorithm is performing correctly whenever possible.

2.1.7.2 Backwards particle tracking

In problems of egg/larval drift, we often have an estimate of the distribution of eggs or larvae, provided by survey data, but incomplete knowledge of the release area of the propagules. In other words, we often have more data at the endpoint than at the starting point. One benefit of the particle-tracking technique is the ability to reverse time and perform backward particle tracking in order to find the most likely origin for observed propagules. For example, we consider the case of truly planktonic particles in a flowfield u that is divergence-free and does not cross boundaries. In this case, it is reasonable to use the simple one-dimensional, time-reversed, Euler scheme:

$$x_{t-dt} = x_t - u(x_t)\,dt + \nabla K(x_t)\,dt + \sqrt{2K(x_t)\,dt}\,Q\,, \tag{2}$$

where Q has the same meaning as in Equation (1). Starting from the final position and time (x_f, t_f) when the simulation reaches the starting time t_0, the density of larvae at any position x_0 will be proportional to the likelihood function of the initial condition x_0, viewed as an unknown parameter. (For more details on this example, see Thygesen, in prep.). Other papers on biophysical backward particle tracking include Batchelder (2006) and Christensen *et al.* (2007). A paper to be recommended from the atmospheric literature is Flesch *et al.* (1995).

2.1.7.3 Coupling particle tracking with continuous fields from NPZ models

There are several issues to consider when coupling particle-tracking models to the continuous fields generated by nutrient-phytoplankton-zooplankton (NPZ) models. The continuous fields are the spatially explicit, physics-related outputs (e.g. velocities used for advection-diffusion movement of the particles) and biologically related outputs (e.g. zooplankton densities as prey for the particles) generated by the NPZ model. Some of these issues relate to the quality of these continuous fields, whereas other issues relate to the mechanics of how the particles are coupled to the fields.

The first issue is the quality of the outputted fields from the NPZ, including the overall stability of the NPZ model, the realism of the NPZ-related parameter values, the formulation of the predation-closure terms used to impose mortality on the zooplankton, and the information on model performance provided by data assimilation and validation efforts (see Annex 3).

The second issue also influences the quality of the fields and involves the way in which the NPZ submodel is coupled to the physics model. Issues such as whether the NPZ is run online or offline with the physics, and the compatibility of the spatial and temporal resolutions between the NPZ and physics models, affect the realism and quality of the outputted NPZ fields (see Annex 4).

The third issue relates to how the particles are coupled to the NPZ fields (see Annex 5), for example, whether or not a sufficient number of particles (e.g. larval fish) are followed in order to properly represent their interactions with prey patchiness, the fact that one-way coupling prevents trophic feedback from the particles to their prey and from prey exhibiting avoidance behaviours or other responses, and the degree to which movement of particles (e.g. larval fish) is purely physics-driven or involves active behaviour (e.g. vertical migration, swimming). Addressing the patchiness, trophic feedback, and prey-response issues requires the NPZ and particle-tracking models to be solved simultaneously using a large number of particles. How to meld advective and behaviour modes of movement remains an open question. Both the active behaviour of the particles and the reactions of the prey can change the trajectories of the particles (individuals in the model) and the predicted densities of the prey.

2.2 Test cases

In this section, we present a number of test cases designed to test the performance of a particle-tracking routine and illustrate problems that can arise when interpolating near boundaries.

2.2.1 Vertical distribution of buoyant particles

2.2.1.1 Purpose

The purpose is to test how well the particle-tracking code handles buoyant particles, especially in relationship to the surface and bottom boundary conditions.

2.2.1.2 Background

The need to handle non-neutral particles arises in many applications, including phytoplankton, sediments, or, in this test case, fish eggs. The stationary case was treated by Sundby (1983). The general problem is easily handled in the Eulerian (concentration-based) setting. A Matlab toolbox was developed by Ådlandsvik (2000). This point of view has been adopted for the sampling of anchovy and sardine eggs using the Continuous Underwater Fish Egg Sampler (CUFES; Boyra *et al.*, 2003). For particle tracking, the binned random walk part of this test case was given by Thygesen and Ådlandsvik (2007).

2.2.1.3 Analytical solution

This test case considers a one-dimensional water column with non-neutral particles with a buoyant velocity w and eddy diffusivity K. The vertical coordinate z points upwards, with $z = 0$ at bottom and $z = H$ at the surface. The concentration ϕ of particles is governed by the Eulerian conservation law,

$$\frac{\partial \phi}{\partial t} + \frac{\partial}{\partial z}(w\phi) = \frac{\partial}{\partial z}\left(K\frac{\partial \phi}{\partial z}\right). \tag{3}$$

The boundary conditions are zero flux through the surface:

$$w\phi = K\frac{\partial \phi}{\partial z}, \qquad z = 0, H. \tag{4}$$

The solution evolves towards a stationary solution where the flux is zero in the whole water column. With constant coefficients, this ordinary differential equation gives a truncated exponential distribution. With $m = w/K$ and a vertical integrated concentration Φ, this can be written

$$\phi = \Phi\frac{m}{e^{mH} - 1}e^{mz}. \tag{5}$$

This has mean height above bottom

$$\mu = H - \frac{1}{m} + \frac{H}{e^{mH} - 1}, \tag{6}$$

and variance

$$\sigma^2 = \frac{2e^{mH} - m^2H^2 - 2mH - 2}{m^2(e^{mH} - 1)} - \mu^2. \tag{7}$$

Further details are given in Sundby (1983) and Ådlandsvik (2000).

2.2.1.4 Specification

The specific values used for this test case are given in Table 2.2.1. These values give a stationary mean depth (from surface) of 9.25 m and a standard deviation of 8.34 m. The particles are released 12.5 m above bottom, and the simulation time is 48 h.

Table 2.2.1. Variable settings for the buoyant test case.

VARIABLE	VALUE	UNIT
H	40	m
w	0.001	m s^{-1}
K	0.01	m s^{-2}

2.2.1.5 Continuous random walk model

The continuous random walk model (i.e. RDM) for this problem with constant coefficients is implemented in a Euler–Forward fashion by,

$$Z^{n+1} = Z^{n} + w\Delta t + \sqrt{2K\Delta t}\,Q\,, \tag{8}$$

where Z is displacement and Q is a random variable with zero mean and unit variance. The boundary conditions are more difficult; the usual reflective boundary scheme at the surface,

$$Z^{n+1} \leftarrow 2H - Z^{n+1}\ 1, \text{ if } Z^{n+1} > H, \tag{9}$$

corresponds to

$$\frac{\partial \phi}{\partial z} = 0\,, \tag{10}$$

which differs from the correct boundary condition in Equation (4). In fact, the analytical stationary solution has the maximum of the derivative at the surface.

The number of particles in this test case is 40 000. Two different time-steps, 5 and 30 min, are considered, and a Gaussian distribution is used for the random walk. The 5 min case has also been run with a uniform (top-hat) distribution for the random component. The reflective boundary condition is applied. For the plot, the particles have been counted in 1 m bins.

The result demonstrates that the RDM solutions are good (Figure 2.2.1) except when they are close to the surface, where they underestimate the concentration. The height of the boundary zone depends on when the particle movement is influenced by the boundary, that is, the length scales $w\Delta t$ and $\sqrt{2K\Delta t}$. In this case, the shape of the random walk distribution influences the result, where the Gaussian shape is superior to the top-hat. This is probably caused by the top-hat distribution giving higher probabilities further from the mean, making the random walk "feel" the boundary at longer distance.

2.2.1.6 Binned random walk

The binned random walk does not have boundary problems because it is constructed by finite volume methods for the advection-diffusion equation (see Thygesen and Ådlandsvik, 2007). The water column was discretized into eight uneven bins, with depths of 10, 5, 5, 5, 5, 5, 3, and 2 m, counted from the bottom. The time-step used was 5 min, and both the first-order upstream and a second-order scheme were considered. The results are given in Figure 2.2.2. This figure also shows the analytical solution, averaged into the same bins. The upstream solution shows too much mixing: underestimating the concentration near the surface and overestimating it near the bottom. The second-order method follows the analytical solution well but overshoots near the surface.

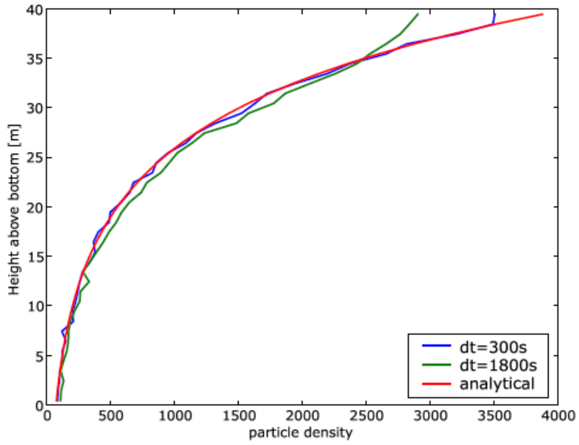


Figure 2.2.1. Results for the continuous random walk model.

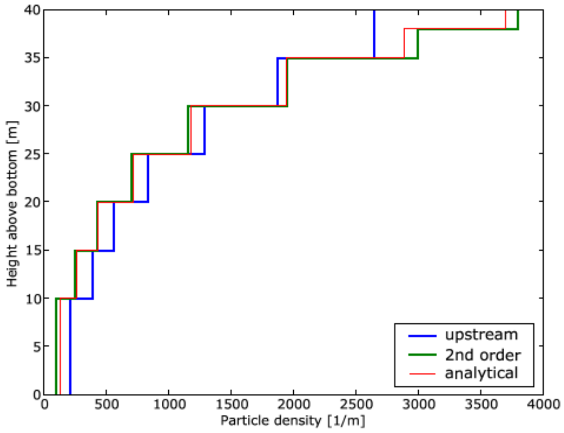


Figure 2.2.2. Results for the binned random walk model.

2.2.2 Flow around an obstacle

2.2.2.1 Purpose

The purpose is to test how different horizontal advection implementations handle a curved flowfield and a land obstacle.

2.2.2.2 Background

Non-rotational flow around a cylinder is one of the classical examples considered in almost all hydrodynamics textbooks. Of particular interest is the book by Bennett (2006), which takes a Lagrangian point of view.

2.2.2.3 Analytical considerations

The example is considered in a coastal oceanographic setting; the cylinder becomes a circular island. As the example is symmetric, only the upper half is considered. That is, we consider a straight coast at $y = 0$ with ocean in the upper half plane ($y > 0$) and with a half-circular peninsula with centre ($x_{0}, 0$) and radius R.

The steady non-rotational flow is given by a stream function

$$\psi = \frac{u_0 R^2 y}{(x - x_0)^2 + y^2} - u_0 y, \tag{11}$$

where u_0 is the along-coast velocity far from the obstacle. The stream function is normalized so that the land boundary is given by the contour $\psi = 0$. The flow follows the streamlines, that is, isolines of ψ with higher values to the right, more precisely

$$u = -\frac{\partial \psi}{\partial y} = u_0 - u_0 R^2 \frac{(x - x_0)^2 - y^2}{((x - x_0)^2 + y^2)^2} \tag{12}$$

and

$$v = \frac{\partial \psi}{\partial x} = -2u_0 R^2 \frac{(x - x_0) y}{((x - x_0)^2 + y^2)^2}. \tag{13}$$

According to Bennett (2006), it is unlikely that analytical expressions will be found for the time-dependent particle movement in this example. Bennet does, however, provide an analytical description of stream lines. The "exact" solution shown below is obtained by using converged Runge–Kutta with a small time-step (36 s), using the analytical expression above for the velocities without interpolation. The dashed stream lines are simply obtained by contouring the discretized version of the stream function.

2.2.2.4 Specification

A domain of length L along the coast and width W is considered. The peninsula centre is at $x = 0.5\ L$ and the radius $R = 0.32\ W$. The numerical values are specified in Table 2.2.2.

Table 2.2.2. Variable settings for the peninsula test case.

Variable	Value	Unit
L	100	km
W	50	km
u_0	1	m s^{-1}

The domain is discretized by $\Delta x = \Delta y = 1$ km. The grid coordinates are chosen so that grid cell (i, j) has its centre at $(x, y) = (i\Delta x, j\Delta x)$ for $i = 0, \ldots, 99$ and $j = 0, \ldots, 49$. The velocities are sampled in an A-grid, that is, in the grid centres. Denoting the velocity arrays U and V, we have

$$U(i, j) = u(i\Delta x, j\Delta x), \qquad V(i, j) = v(i\Delta x, j\Delta x), \tag{14}$$

where u and v are given by the analytical formulas above. The velocities are set to zero at land, that is, where $\psi \leq 0$, in particular $U(i, 0) = V(i, 0) = 0$. The initial particle distribution is 1000 particles on a line perpendicular to the coast:

$$X_k = 3, \qquad Y_k = 0.45 + 0.045k \qquad \text{for} \qquad k = 1, \ldots, 1000. \tag{15}$$

The simulation time is 24 h, for which the particles would be transported 86.4 km with the reference velocity u_0.

2.2.2.5 Simulations

The first-order Euler forward and the Runge–Kutta fourth-order method are considered. Both methods are used here with bilinear interpolation to interpolate from the grid-cell centres to the particle positions. The treatment of boundaries is simple, with the zero land velocity interpolated to the particle position and no reflection scheme implemented. This procedure may leave particles on land, but in the absence of turbulence, this was not considered to be important. A time-step of 1 h was used for both methods. The results from this test are presented in Figure 2.2.3. Far from the peninsula, both methods recapture the exact solution (green, red, and black symbols overlap). Close to the peninsula, the Euler method fails, leaving a trail of particles clearly separated from the peninsula. The Runge–Kutta method performs better, leaving a tiny tail of particles very close to the peninsula that do not overlap those produced by the exact solution.

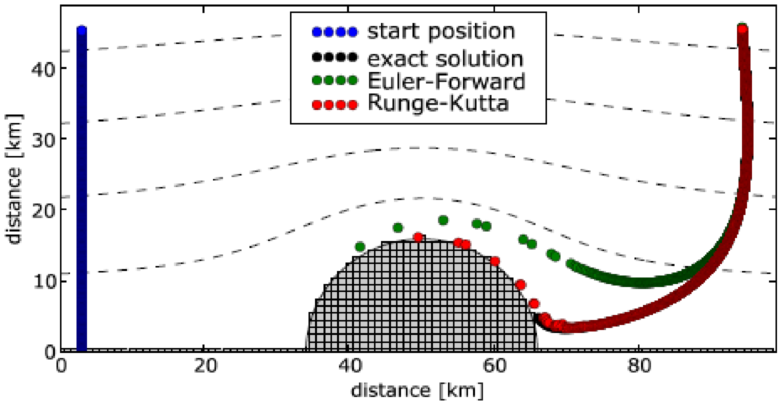


Figure 2.2.3. Peninsula test case.

The velocities from the formulas above are also defined for $\psi > 0$, giving a circulation within the "peninsula". Using these velocities in the interpolation and intermediate Runge–Kutta steps gives a reference solution with ideal land treatment. This land treatment makes the Runge–Kutta indistinguishable from the exact solution and also improves the results from the Euler method. These results are shown in Figure 2.2.4 in which symbols for the Runge–Kutta method overlap those of the exact solution.

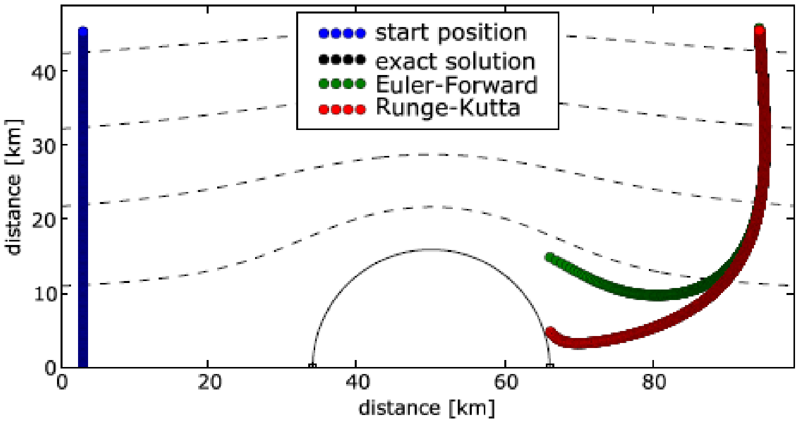


Figure 2.2.4. Peninsula test case with circulation within the "peninsula".

2.2.2.6 Comment

This test was designed to demonstrate the difference between the Euler method and higher order methods, such as Runge–Kutta, and to point out problems associated with interpolation near boundaries. No random walk diffusion has been applied, which could reduce the advantage of higher order methods (see Annex 1). Also, shorter time-steps improve the performance of both models and may decrease the difference between them.

3 Biological processes

3.1 Initial conditions: spawning locations

Alejandro Gallego and Elizabeth W. North

The starting position of particles in a heterogeneous flowfield fundamentally controls the direction and distance of particle transport. Therefore, the space and time structures of spawning patterns (where, when, and what magnitude) are the initial conditions for individually based models of fish early life that begin with egg stages. Initial conditions differ in degree of complexity, depending on the objective of the modelling effort. For example, interannual differences in the magnitude of egg production are needed for predicting recruitment variability but may not be necessary for understanding transport pathways between spawning and settlement areas.

Ideally, fine-scale information on spatial and temporal patterns in spawning is needed to initialize models (e.g. frequent surveys of egg distribution and abundance throughout a spawning area over multiple years). However, this information is often limited or non-existent. Therefore, an estimate of initial conditions is needed. In the most basic formulation, randomly distributed particles could be released within the spawning area throughout the duration of the spawning time window. This may provide information about all possible trajectories through space and time, but not the actual trajectories of the simulated populations in each year because spawning times, locations, and magnitudes vary from year to year. For simulating the magnitude and timing of spawning events, egg-production models are often required (see Section 3.1.1 Egg-production models).

When incorporating initial conditions into models, the following questions should be asked (C. Mullon, pers. comm.): what are the spawning patterns that: (i) emerge from observations, (ii) can be modelled with simple assumptions on individual behaviour, and (iii) could be related to different regimes of population dynamics? Several factors should be considered (C. Mullon, pers. comm.).

- **Spatial structure of spawning**. Spawning locations/features can affect the population structure in a way that can be modelled. With information on different spawning features, the model can predict the spatial distribution of recruits and allow identification of the ways in which behavioural processes may be mediated by environmental conditions, parental condition, and gregarious behaviour.
- **Time structure of spawning**. Spawning features can be related to environmental conditions. With observations of spawning events (space, time) and observed concomitant environmental parameters, modelling results can be used to determine if individual spawners use environmental cues to optimize their reproductive success (fitness).
- **Evolutionary processes**. Spawning behaviour is the result of an evolutionary process. With different sets of constraints that affect fitness and taking account of the spawning choices of individuals, predicted spawning patterns can be analysed to understand how evolutionary processes influence opportunism, natal homing, and bet-hedging strategies.

See Mullon *et al.* (2002), Grimm and Railsback (2005), and Jørgensen *et al.* (2008) for additional information.

3.1.1 Egg-production models

Egg-production models use information about adult spawners to calculate the magnitude and timing of egg production in a given spawning season. A detailed mechanistic fish egg-production model was published by Scott *et al.* (2006) for a batch-spawning species (Icelandic Atlantic cod, *Gadus morhua*). The fundamentals of the model can be applied to other batch-spawning species by using species-specific parameters and other input data. The model requires length, weight, and expected weight-at-length data for individual adult fish or age/size classes. The model is composed of four modules (Figure 3.1.1). The first module uses equations that are functions of the state (length and weight) of individual fish and calculates condition, prespawning atresia, maximum potential fecundity, maximum egg size, number of batches, proportion of sexually mature individuals, and proportion of first-time spawners. The second module calculates the variables that change during an individual's spawning period (egg size, number of eggs per batch, seasonal atresia, and period between batches). The third module calculates the timing of the start of spawning for a fraction of the population. The final module summarizes the output of the previous three modules and calculates the reproductive potential of the population. On any given day throughout the spawning season, fish in different states may be spawning, resulting in temporal patterns that are a function of fish state (such as length) and number of individuals in a given state. If the available input data are spatially disaggregated, this model can output the spatial and temporal distributions of egg production.

The model presented by Scott *et al.* (2006) requires a comprehensive knowledge of a number of relationships (see their Appendix A), which are most probably species-specific and perhaps even stock-specific. This information may not be available for a large number of species/stocks, so such a detailed mechanistic modelling approach may not be possible. If detailed information is available, then sensitivity analysis can be used to determine if a less parameter-rich approach could produce a similar outcome.

Other, simpler methods for estimating egg production exist. Heath and Gallego (1998) published an egg-production model based on field data for North Sea haddock. Haddock are also batch-spawners, with a spawning period spanning several weeks. Although the authors recognized that batch size, number of batches, and spawning duration of individuals may vary with age, size, or condition, and that a proportion of the potential annual fecundity may be resorbed (atresia), their model did not attempt to incorporate comprehensively all factors affecting population egg production. It did, however, attempt to reflect the main features of the spatial and temporal distribution of spawning, which is neither synchronized in the population as a whole nor at a given spawning location. The model required an estimate of the age composition of the stock and was achieved by using trawl-survey data (providing the relative age-class distribution) to disaggregate stock-assessment data, which estimated the relative abundance of these age classes. The model was temporally resolved by assuming that a normal distribution can be used to represent the spawning fraction of female fish of a given age class (parameterized from survey data). The level of daily egg production by each age class was estimated from the annual relative fecundity, mean weight-at-age (from stock-assessment data), and an estimate of the spawning duration for individual fish. The model assumed that all of the potential annual fecundity is realized, that a constant fraction of the annual fecundity is spawned per day during the spawning period of individual fish, and that the proportion of spawning females of a given age class in the population can be described by a normal distribution centred on the date of peak spawning.

In cases where the information (data, parameters, and functional relationships) required for the modelling approaches described above is not available, information about the peak and variability of spawning at a given location may be sufficient to give approximate daily egg production. For example, a normal distribution with the mean equal to the peak spawning date could be used, along with a spawning season that would correspond to two standard deviations, as long as there is an estimate of total spawning (directly from stock assessment or from estimates of spawning-stock biomass and a weight–fecundity relationship).

Some of the modelling approaches (e.g. those described above) may result in distributions of spawning with unrealistically long "tails", which would imply that some spawning takes place well outside the observed spawning season. A practical solution is to establish a cut-off threshold (e.g. based on field observations), outside of which egg production is considered negligible and ignored. For accuracy, the egg production that would have taken place at the tails should be redistributed within the accepted distribution of spawning.

In the absence of sufficient data/information to model egg production or the distribution of spawning, it may be possible to use data on the observed distribution of larvae to identify the timing and location of spawning. Of course, this approach is only valid if the sampling covers the full geographical domain occupied by the larvae of the species of interest, and if estimates of the age and mortality of the eggs and larvae are available. Knowledge of the duration of the egg stage is necessary to identify the spawning location of pelagic eggs. Information on the mortality level experienced by the eggs and larvae is needed if quantitative estimates of spawning are required. Unless we are dealing with very young larvae of demersal-spawning species (or with a very short egg-stage duration), where we may choose to disregard transport from the spawning grounds, we need to account for transport processes from spawning to sampling. To do so, the biophysical model can be run backwards (see Section 2.1.7 Additional considerations; Batchelder, 2006; Christensen *et al.*, 2007), or a forward-running model may be used, covering at least all possible spawning sites over at least the full duration of spawning.

When using an egg-production model to provide initial conditions for a particle-tracking model, the spatial and temporal resolution of the hydrodynamic and particle-tracking models should be kept in mind. Egg-production models often provide continuous predictions (e.g. a continuous function in time), although data used to force the model are of coarse resolution (e.g. length–weight frequency distribution of adults, stock-assessment abundance data, etc.). Even so, releases of particles within a hydrodynamic model occur at discrete times and locations. Predictions from the egg-production model need to be converted into numbers of particles (or super-individuals) per unit time/space (e.g. daily releases covering the spawning area with particles distributed some distance apart). When choosing the number of particles to employ, consideration should be given to the time-step of the particle-tracking model and the spatial resolution of the physical model, in addition to the biology of the species. Finally, buoyancy may influence the vertical position of eggs in the water column and affect their transport. Observations or models (e.g. Boyra *et al.*, 2003; Petitgas *et al.*, 2006) may be used to parameterize the initial vertical distribution of eggs.

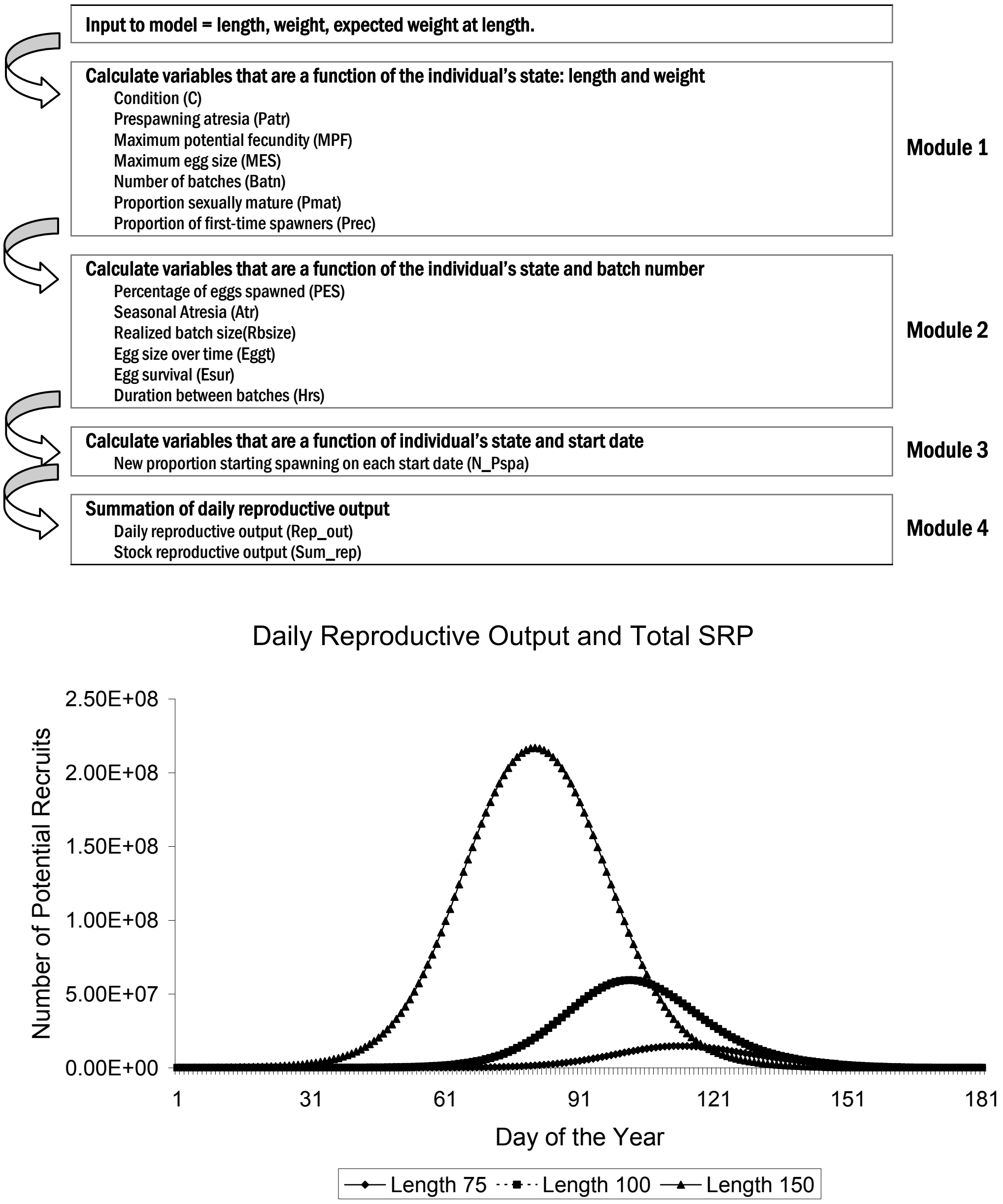


Figure 3.1.1. Flow diagram of the calculations in an egg-production model (upper panel), with example model predictions (lower panel) of reproductive output for three different age/size classes of fish (derived from Scott *et al.*, 2006).

3.2 Pelagic larval duration

Claire B. Paris, Jeffrey M. Leis, and Jean-Olivier Irisson

Pelagic larval duration (PLD) is an important feature of early life-history models and can be defined within a morphological or ecological framework.

The morphological concept of the PLD represents an important key transition from the larval to the juvenile phase and is defined as the time from spawning to metamorphosis into the juvenile stage (frequently defined as when squamation is completed). The PLD corresponds to the entire pelagic phase in most demersal species. For pelagic species, PLD is defined as the time from spawning to the transition to the schooling juvenile phase or when larvae enter the nursery grounds. There may be good reasons for using morphological criteria to determine the limits of the model run. For example, we may wish to run the model only until the larva reaches a particular size, or morphological stage, such as full squamation. This would be equally applicable to demersal or pelagic species. Terms such as "metamorphosis" should not be used unless clearly defined for the species of interest.

For demersal species, the ecological concept of the PLD may be applied. This is the period from entry of the egg or hatched larva into the pelagic environment to exit from the pelagic environment (i.e. settlement) by the young fish. This ecological concept cannot be applied to pelagic species because they never leave the pelagic environment. Rather, the modeller may wish to model the dispersal of a pelagic species from spawning until the larvae reach a nursery area or achieve some other ecological milestone, either spatial or otherwise (e.g. achievement of schooling or a given swimming ability).

The PLD can then be subdivided into various stages, determining either a morphological change (e.g. Kendall *et al.*, 1984) or the onset of ontogenic behaviours (see Section 3.5.2.2 Ontogeny of behaviour). Pelagic larval durations are highly variable among species, ranging from a few days to a few months. Within some species, PLDs are relatively constant, with a small variance around the mean, and they are usually treated as fixed parameters in connectivity models. However, as with behaviour, individual PLDs need to be adjusted according to the state of knowledge of physical–biological interactions (PBIs) that result in larval growth. A faster-growing larva typically has a better condition, which is associated with shorter PLD (Searcy and Sponaugle, 2001). Conversely, some species have a more variable PLD, allowing them to extend the larval duration if conditions are not met for the metamorphosis (Victor, 1986; Sponaugle and Cowen, 1994). If PLD plasticity is modelled, it is imperative to include a mortality function or parameter in order to account for the differential survival because larvae with extended PLDs sustain daily mortality rates for a longer period. For plastic PLDs, rather than having a single parameter to model PLD, two fixed parameters are needed.

1) **Precompetency period**, before which larvae may not undergo metamorphosis (for pelagic species) or settle (for benthic species).
2) **Maximum competency period**, after which the larval stage ends, corresponding to the endpoint of the individual trajectory. For benthic species, if the larva has not found a suitable settlement habitat by this time, the particle is removed from the modelling system.

Ultimately, the timing of the competency period and/or PLD depends on the growth of the larvae. A faster growing larva will more quickly achieve the competency/recruitment or transition size. The advantage of an individual-based model is that individual particles can be assigned a Gaussian distribution of PLDs, with a mean value and standard deviation. Again, because larvae with longer PLDs sustain daily mortality rates for a longer period, mortality rates need to be applied to account for differences in individual survival. The only instance for which mortality can be treated as a post-process is when all particles have the same PLD and mortality is non-spatially explicit. Finally, it is important to note that PLD is temperature dependent and, within limits, will decrease with increasing temperature (O'Connor *et al.*, 2007). This has obvious implications for climate-change scenarios.

3.3 Growth

Thomas Miller, Øyvind Fiksen, and Alejandro Gallego

Decisions regarding the representation of feeding and growth in coupled physical–biological models of fish early life history are intimately linked. The bioenergetics of individual fish represent an energy balance in which any excess energy resulting from the feeding process, once metabolic costs have been paid, can be invested in growth. The specific form of the functional relationship between feeding conditions (or a proxy of those) and growth may vary from a detailed bioenergetic description to a simple, empirical statistical relationship. Modelling the feeding process may not be necessary if the sole objective is to model growth itself, provided that there is no density-dependent impact of cohort abundance on food availability. A number of approaches of varying degrees of complexity (from highly complex, mechanistic models to simple phenomenological models) have been implemented successfully in coupled physical–biological models. These include mechanistic bioenergetics models, empirical food –growth models, and empirical temperature, age–growth models. Here, we examine each approach, identifying its strengths and weaknesses, and providing recommendations for each category of growth model.

There are numerous examples of the application of mechanistic feeding models to forecast growth in coupled physical–biological models (Werner *et al.*, 1994, 1995, 1996, 2001; Hermann *et al.*, 1996; Hinckley *et al.*, 1996, 2001; Fiksen *et al.*, 1998; Fiksen and Folkvord, 1999; Leising and Franks, 1999; Megrey and Hinckley, 2001; Fiksen and MacKenzie, 2002; Lough *et al.*, 2005; Maes *et al.*, 2005; Kristiansen *et al.*, 2007).

Many of these examples have a heritage that can be traced to individual-based models (IBMs) in the ecological arena that considered feeding, bioenergetics, and growth of larval fish in a simple, well-mixed compartment (Cowan *et al.*, 1993; Rose and Cowan, 1993; Letcher *et al.*, 1996; Rose *et al.*, 1996, 1999). At their heart, these models used a simple, stochastic scheme for determining encounters with food and whether or not consumption per given encounter occurred. The estimates of consumption were then used in a simple, bioenergetic model to forecast surplus energy and, hence, growth. When applied in a model of a simple, well-mixed compartment, the approach assumes random encounters described by a Poisson process. It is conceptually straightforward to include the impacts of environmental factors, such as light (Aksnes and Giske, 1993), temperature (Kitchell *et al.*, 1977), and small-scale turbulence (MacKenzie *et al.*, 1994), provided that the distributions of these parameters are known. Parameter estimates used in the models should be specific to both the species and the ontogenetic stage being modelled, and population-specific when evidence suggests it is necessary. Modellers can choose: (i) to make parameter values a characteristic of the individual, by drawing parameter estimates from appropriate statistical distributions; or (ii) to update parameter estimates dynamically to reflect the different histories and trajectories of each individual (Rice *et al.*, 1993). However, the accuracy and precision with which the distribution of these environmental covariates can be defined does introduce uncertainty into predictions of foraging rates (e.g. Sundby, 1997; Visser and MacKenzie, 1998).

There are numerous challenges when applying mechanistic feeding and growth models. The highly detailed nature of these approaches requires a large number of parameter estimates and functional relationships. For example, in their model of the effects of small-scale turbulence on feeding and growth of walleye pollock, Megrey and Hinckley (2001) required estimates for 119 parameters. Therefore, the application of this approach to any species and ontogenetic stages that have not been studied comprehensively requires either a substantial amount of prior experimental work (with the associated problems of ensuring realistic conditions applicable to field situations, etc.) or the "borrowing" of parameter estimates from taxonomically related species (a potentially risky approach, given the degree of specialization often observed when related species are investigated in depth). Even where this is not a concern, encounter processes between planktonic predators and prey are generally not well quantified. This area is a focus of considerable research (Visser and Kiørboe, 2006) and, although it is beginning to be better understood, empirical work remains a critical need. Inferential approaches can be used to select from alternative parameterizations (Megrey and Hinckley, 2001; Fiksen and MacKenzie, 2002; Lough *et al.*, 2005), and sensitivity analysis should be carried out to inform the modeller about the level of effort worth putting into the detailed parameterization of individual processes.

Thus, the application of process-specific, biophysical models may help inform our understanding of the importance of individual steps in the feeding cycle or of growth bioenergetics on recruitment. Within coupled physical–biological models, the application of mechanistic growth models presents special challenges. Models require forecasts of the prey community and physical environment at perhaps two to four orders of magnitude smaller than the minimum horizontal resolution of the hydrographic model. Importantly, many hydrographic properties used in mechanistic feeding models are unlikely to be well represented across the multiple spatial scales. The issue of subgrid processes in biological variables is even more challenging than for the physical variables. For example, vertical environmental gradients are typically strong, and this imposes a particular challenge in modelling the vertical positioning of predators, larval fish, and their prey.

Other approaches used to model growth rely on empirical relationships. The independent variables in these phenomenological models differ, but often include fish age and temperature (Heath and Gallego, 1997, 1998; Brickman and Frank, 2000; Brickman *et al.*, 2001; Mullon *et al.*, 2003; Suda and Kishida, 2003). This approach is motivated by concerns over the accuracy of the representation of subgrid scale processes in the hydrographic model, as well as other physical and biological variables, not necessarily predicted by it, such as light, turbidity, and prey fields. The conservative nature of temperature means that it is less sensitive to subgrid scale concerns, except in the vertical in stratified regions, and is therefore likely to be a reliable foundation for spatially explicit predictions of growth. Additionally, this approach has the advantage that there is no need to model prey populations, because it is assumed that temperature, in addition to its direct (physiological) effect, acts as a proxy for the environmental changes that tend to correlate with the seasonal temperature cycle (e.g. food availability, daylight length, light intensity).

However, there are also potential pitfalls to this approach if the underlying temperature-dependent growth model is incorrectly parameterized or applied to a population for which it was not developed (Folkvord, 2005). The parameterization of a temperature-dependent growth model may not be as straightforward as it seems. In particular, matching the spatial scale of the larvae with that of the temperature field can be difficult. For example, earlier approaches (e.g. Campana and Hurley, 1989) used daily temperature estimates for the area of interest (Browns and Georges Banks), common to all larvae in the area, whereas Gallego *et al.* (1999) used a particle-tracking model that projected individual larval trajectories over a spatially and temporally resolved temperature field to estimate the daily temperature history of individual larvae. Additionally, the phenomenological models are often based on the observed growth of survivors, which may be different from the average growth observed in the cohort from which they were derived (Meekan and Fortier, 1996). However, Folkvord (2005) has demonstrated that field growth rates are often maximal, although Beaugrand *et al.* (2003) found that prey abundance influenced recruitment success of North Sea cod. When food is not included in the phenomenological model, the approach also implicitly assumes that there is no food-dependent growth variation, or that such variation is negligible, beyond what may be captured by temperature as a proxy variable. To address this concern, several authors (Leising and Franks, 1999; Bartsch and Coombs, 2004; Bartsch *et al.*, 2004) have included food dependence in the phenomenological model. This offers the attraction of coupling food to growth, but it reintroduces the difficulties over subgrid scale predictions of prey distribution already discussed, even if these are generated externally to the model (Bartsch *et al.*, 2004).

Growth and mortality are intimately coupled through a range of mechanisms, such as size-dependent predation patterns, starvation, and growth-dependent larval stage duration. These mechanisms have received well-deserved attention from modellers for some time. However, growth and mortality are also intimately coupled through larval behaviour, because behaviour-promoting growth typically also increases the risk of predation (Lima and Dill, 1990; Walters and Juanes, 1993). Such processes have received less attention in fishery oceanography, both empirically and in models, although they have been incorporated in ecosystem-based approaches (Pauly *et al.*, 2000). One example is the trade-off between being spotted by visually searching predators and the need to find food through visual detection of prey, which is the main forcing of diel vertical migration. Another example is the risk of encountering tactile or ambush predators through increased swimming activity, which also increases the encounter rate with potential prey items. There are also good reasons to argue that such behaviours are state- and size-dependent, and that they interact with larval dispersal and drift trajectories. Approaches adopted from behavioural and evolutionary ecology are required to increase understanding of these processes.

Another issue is the need to separate growth and development (ontogeny) in determining sensory and biomechanical abilities of larvae. All models of larval fish early life history that include larval sensory or other abilities couple such traits to body size, with direct feedback on feeding history. In reality, ontogeny can proceed (for some time) without food supplies, improving larval abilities to find and capture prey, and currently we are ignoring this in our models. However, although some experimental work has already been carried out on the subject (e.g. Skajaa *et al.*, 2004), a greater quantitative understanding of the relative importance of ontogeny vs. growth for predation vulnerability and foraging ability, for example, is still required for most species and ontogenetic stages.

3.4 Mortality

Edward Houde and Joachim Bartsch

3.4.1 Introduction

Only in the most studied species (e.g. cod, herring, walleye pollock, some sardines, and anchovies) are estimates of early life-stage mortality available. Even in these species, stage-specific mortalities or relationships between early-life mortality and environmental factors generally are lacking. Parameterizing and calibrating coupled biophysical models in order to obtain an accurate projection of survival is obviously important, but it is not a simple task.

Fish have high fecundities and experience high and variable mortality rates during early life. In many stocks, the numbers of eggs spawned annually, or numbers of newly hatched larvae, are 1×10^{12} or higher. Reductions in abundance during egg and larval stages clearly must be precipitous and, if only moderately variable, will generate order-of-magnitude differences in abundance of recruits. Natural mortality rates are highest in the smallest and youngest early life stages and decline during ontogeny and growth before becoming relatively stable after fish recruitment (Figure 3.4.1; Table 3.4.1).

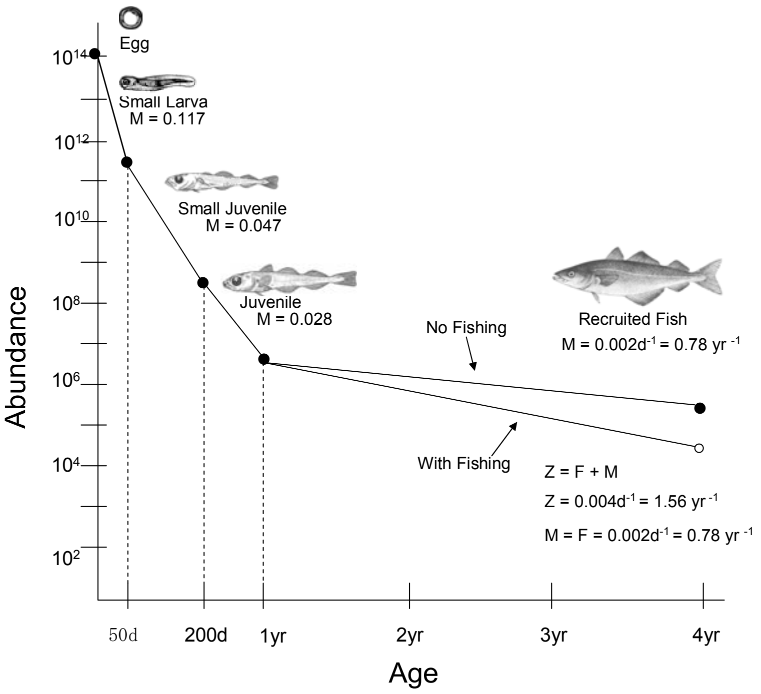


Figure 3.4.1. Survivorship curve for a typical marine fish. Three early life stages are represented. Also represented is the age 1–4 recruited stage, with and without fishing mortality (from Houde, 2002).

Table 3.4.1. Daily mortality rates (*M*), cumulative mortalities (M_T), and per cent mortalities within each life stage during development and growth of a typical marine fish. Rates resemble those of walleye pollock (based on Houde, 2002).

STAGE (AGE)	*M*	M_T	PER CENT MORTALITY
Egg/larva (0 – 50 days)	0.117	5.850	99.71
Early juvenile (50 – 200 days)	0.047	7.050	99.91
Late juvenile (200 – 365 days)	0.028	4.620	99.01
Recruited stage (1 – 4 years)	0.002	2.190	88.81

Early life stages die from many causes, but predation is usually the principal factor. Other factors are poor nutrition, disease, and unfavourable environmental conditions. Dispersal losses can be a major determinant of survival potential. Partitioning component losses into death attributable to biotic causes (e.g. starvation, predation, disease) and abiotic causes (e.g. dispersive losses, hydrographic variability) is only rarely accomplished in field experiments, but is critical in coupled biophysical models. In many cases, dispersive losses equate to mortality, but unless a nursery ground is sampled exhaustively, both spatially and temporally, the survival rate and abundance of dispersed individuals will be unknown.

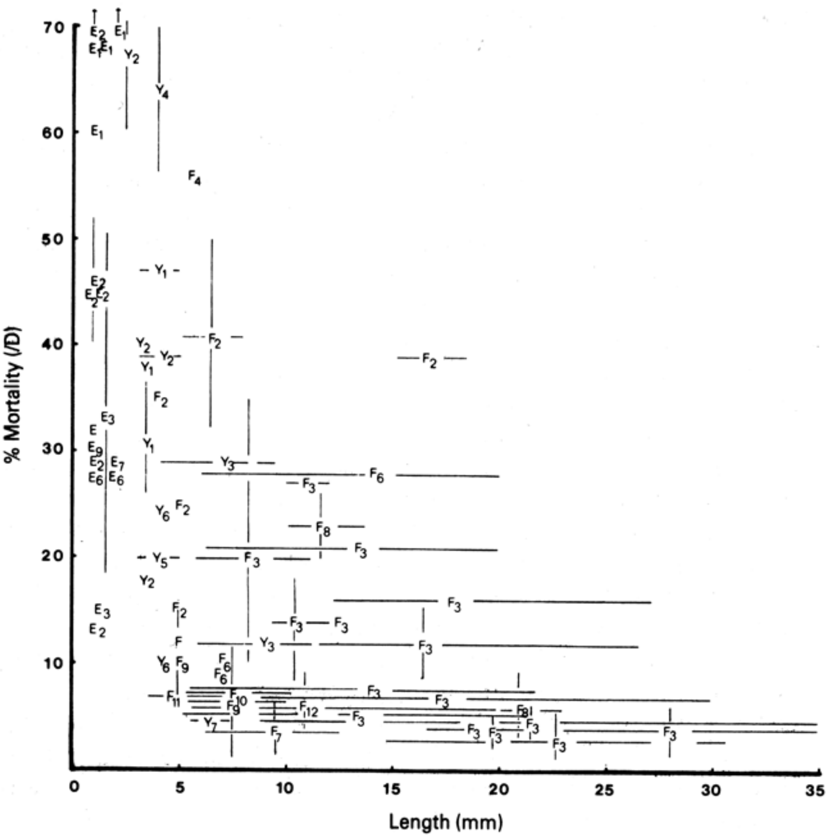


Figure 3.4.2. Summary of mortality rates for eggs (E), yolk-sac larvae (Y), and feeding-stage larvae (F) of marine fish in relation to length (from Bailey and Houde, 1989).

In general, mortality rates of early life stages are inversely related to size, in accordance with expectations from size-spectrum theory (Figure 3.4.2). Natural mortality rates of marine organisms, ranging from the smallest invertebrate larvae to whales, are strongly size-dependent and decline approximately as $M = 0.0053\ W^{-0.25}$ (Peterson and Wroblewski, 1984; McGurk, 1986), where W is individual weight. The power relationship expressed here is believed to represent the outcome of predation in size-structured aquatic ecosystems. Natural mortality rates of juvenile and adult fish fit this picture reasonably well. However, for eggs and larvae, the exponent tends to be more negative than −0.25, indicating higher-than-expected mortality rates during these stages, followed by rapid declines in M with growth (McGurk, 1986; Bailey and Houde, 1989; Houde, 1997). Mortality rates and their decline with respect to size in early life are not only high, but vary among cohorts (or year classes; Table 3.4.2). In modelling mortality rates in early life, it may be sufficient in some circumstances to estimate average levels of mortality for defined life stages. However, it may be more important to model patterns of mortality and include variability in stage-specific mortality in order to obtain accurate projections of survivorship.

Table 3.4.2. Relationships between M and W for five species of fish during the larval stage. M = daily mortality rate. W = dry weight (μg; from Houde, 1997).

Species	Year	Relationship	Averaged relationship
American shad	1979	$M = 4.477\ W^{-0.564}$	
	1980	$M = 0.973\ W^{-0.319}$	
	1981	$M = 1.126\ W^{-0.339}$	
	1982	$M = 1.917\ W^{-0.381}$	$M = 1.724\ W^{-0.392}$
	1983	$M = 0.782\ W^{-0.292}$	
	1984	$M = 33.294\ W^{-0.889}$	
Northern anchovy	–	–	$M = 1.073\ W^{-0.353}$
Bay anchovy	–	–	$M = 2.284\ W^{-0.318}$
Walleye pollock	1985	$M = 1.724\ W^{-0.522}$	
	1986	$M = 1.697\ W^{-0.457}$	
	1987	$M = 2.430\ W^{-0.515}$	
	1988	$M = 68.590\ W^{-1.207}$	$M = 3.874\ W^{-0.622}$
	1989	$M = 4.379\ W^{-0.661}$	
	1990	$M = 1.311\ W^{-0.456}$	
	1991	$M = 13.515\ W^{-0.820}$	
Striped bass	1987	$M = 0.371\ W^{-0.082}$	
	1988	$M = 41.857\ W^{-0.766}$	
	1989	$M = 22.671\ W^{-0.747}$	$M = 4.875\ W^{-0.424}$
	1992	$M = 10.823\ W^{-0.490}$	
	1993	$M = 0.284\ W^{-0.009}$	

3.4.2 Larval mortality: concepts and relationships

3.4.2.1 Survivorship curves

A plot of $\log_e$ numbers of survivors with respect to age generates a survivorship curve, or "catch curve". Its slope represents the age-specific (or instantaneous) mortality rate. Even small shifts in the slope, when numbers are high, will generate order-of-magnitude differences in abundance by the end of the larval stage (Figure 3.4.3). Simple simulations convincingly demonstrate that even modest variability in loss rates early in life, from whatever cause, has the potential to coarsely control the fate of a cohort's abundance at recruitment.

Survival in a population, at least over relatively small size ranges, is often described reasonably well by a simple exponential model

$$-dN = M \cdot N_t\, dt, \tag{16}$$

where N is the number of individuals, M is the mortality rate, and t is age, solving

$$-M\, dt = 1/N_t \cdot dN \text{ and } N_t = N_0\, e^{-M \cdot t}. \tag{17}$$

Mortality rates can be partitioned into component causes. For exploitable sizes, natural mortality M and fishing mortality F are the two categories contributing to total mortality $Z = F + M$. In unfished early life stages, $Z = M$. In theory (and rarely in practice), M can be partitioned into its component causes ($M_1, M_2, \ldots, M_k$, e.g. predation, starvation, dispersal losses). In biophysical coupled models, it may be a goal to partition the mortality and losses into constituent causes.

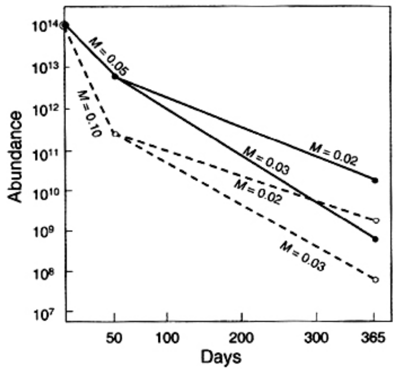


Figure 3.4.3. Survivorship curve, showing effects of different mortality rates during early life stages (from Houde, 2002).

Mortality rates decline with size and age during early life. Initially, rates may be very high, exceeding 50% d^{-1} in some species and commonly exceeding 10% d^{-1} (Figure 3.4.1). In a review of estimates, the mean mortality rate (temperature-adjusted) for larval stages of marine fish was $M = 0.24$, that is, 21.3% d^{-1} loss (Houde and Zastrow, 1993). The mean M for freshwater fish larvae is somewhat lower, on average $M = 0.16$, that is, 14.8% d^{-1}. The greater mortality rate for marine larvae is probably a consequence of their much smaller average size (Houde, 1994) and higher vulnerability to a more diverse community of predators. The average rates for the larval stage do not represent the pattern of decline in M that generally occurs as larvae grow. For marine species dying at the mean rate >99.95%, mortality occurs during the mean larval stage duration ($D = 36$ d). For "average" freshwater fish larvae, cumulative mortality is lower, but 96.4% are expected to die in the $D = 20.7$ d mean larval-stage duration.

3.4.2.2 Temperature effects

In broad, cross-taxa analyses, mortality rates of early life stages scale directly with temperature. Species developing in low latitudes, or at seasonally high temperatures, suffer high mortality rates, whereas species from cold environments suffer lower mortality rates. Houde (1989) and Pepin (1991) quantified the relationships for larval stages. Mortality rates (at the ecosystem level, across taxa) increase at approximately 0.01 per degree C. For 26 marine species, Houde and Zastrow (1993) derived the relationship

$$M = 0.0149 + 0.0129T \qquad s_b = 0.0029 \qquad r^2 = 0.46, \qquad (18)$$

where T represents temperature and s_b represents the standard error of the regression coefficient. This relationship may be useful in exploratory modelling if estimates of M for a species are unavailable.

Across taxa, mortality and growth rates of marine fish larvae are strongly coupled during early life. Species suffering high mortality rates also have high growth rates, and both rates are strongly and positively correlated with temperature (Figure 3.4.4). Species from temperate and high latitudes die and grow at slower rates than species spawning in tropical habitats or under seasonally warm conditions. For weight-specific growth of marine fish larvae (across ecosystems and taxa), the relationship with temperature is (Houde and Zastrow, 1993)

$$G = 0.0230 + 0.0106T \qquad s_b = 0.0016 \qquad r^2 = 0.35. \qquad (19)$$

Lacking other knowledge, a first-cut (and coarse) estimate of mortality could be derived from the respective M and G ecosystem-level estimators with respect to temperature. Furthermore, estimates of growth rates are more often available than mortality rates for larval fish. If an estimate of G is available at known temperatures, then a crude, first-cut estimate of larval-stage M is

$$M = 1.2170G - 0.0131. \tag{20}$$

Despite differences in stage durations and daily rates of mortality and growth for species from warm or cold environments, their cumulative or stage-specific mortalities are similar because of the strong concordance between mortality and growth rates. That knowledge can be used to crudely parameterize models and derive estimates of M. For example, species such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), which spawn at temperatures <10°C, spend approximately 100 d in the larval stage, whereas tropical species, such as the damselfish (Pomacentridae), spawn at temperatures >25°C and spend only 25 d in the larval stage. Yet, average survival at the end of their respective larval stages is similar because M and G are strongly correlated and increase at approximately the same rate with respect to temperature (Figure 3.4.4).

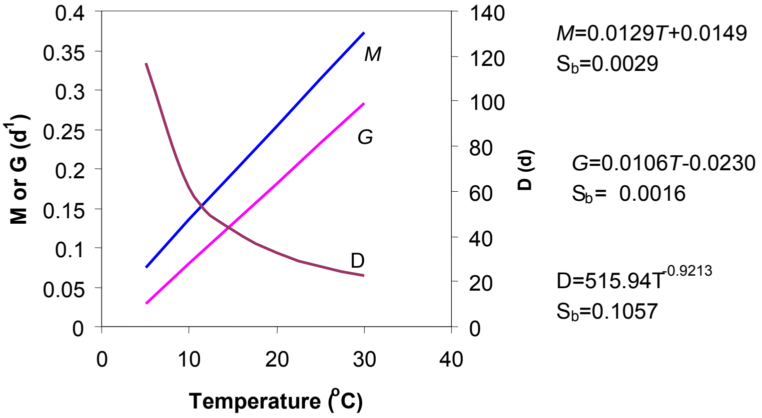


Figure 3.4.4. Effects of temperature on weight-specific growth (*G*), mortality (*M*), and larval stage duration (*D*) for marine fish larvae. Averaged results for a combined taxa analysis (based on data from Houde and Zastrow, 1993).

3.4.2.3 Size effects

Although mortality rates decline as development and growth of larvae occur, the rate of decline with respect to body size or age varies among species and among cohorts (or year classes). For five species, the average relationships describing declines in M with respect to weight (W) during the larval stage (Table 3.4.2) ranged from $W^{-0.318}$ to $W^{-0.622}$. Relationships for clupeoid species (e.g. American shad, *Alosa sapidissima*, $W^{-0.392}$; northern anchovy, *Engraulis mordax*, $W^{-0.353}$; bay anchovy *Anchoa mitchilli*, $W^{-0.318}$) had less negative exponents than perciform (striped bass, *Morone saxatilis*, $W^{-0.424}$) or gadid (walleye pollock, *Theragra chalcogramma*, $W^{-0.622}$) larvae. In all cases analysed (Houde, 1997), declines in M were more rapid than the $W^{-0.25}$ predicted from allometric-scaling and size-spectrum theory. As an example of declines in mortality with respect to size, the averaged, estimated declines in M for walleye pollock (*T. chalcogramma*) for seven years were: 5 days old (5.8 mm, 95 µg dry wt), $M = 0.23$; 15 days old (8.5 mm, 400 µg dry wt), $M = 0.09$; 26 days old (12.2 mm, 1600 µg dry wt), $M = 0.04$. The mortality rates and patterns of declines in M during the larval stage can differ among cohorts and interannually in response to variable oceanographic conditions and predation that larvae encounter. Because even relatively small changes in stage-specific mortality rates can generate major variability in abundance of survivors, only coarse estimates of survival can be obtained by parameterizing models with averaged relationships and rates. These may still serve a useful purpose to initialize modelling and gauge sensitivity in model output to variability in stage-specific mortality rates.

3.4.2.4 Stage-specific mortality and estimates of abundance

When mortality is size- or stage-specific, it may be desirable to estimate stage-specific mortality and survival rates for early life stages. These rates can be derived from estimates of M and G and weights (W) at stages. The ratio M/G, sometimes referred to as the "physiological mortality rate" (Beyer, 1989; Houde, 1997), can be applied to define mortality within a stage(s)

$$M_s = (M/G)\cdot \log_e[W_s / W_{s-1}], \tag{21}$$

and survival rate is

$$S_s = N_s / N_{s-1} = e^{-M_s} = [W_s / W_{s-1}]^{-M/G}. \tag{22}$$

When abundance-at-stages (or sizes) is determined and growth rates can be estimated, M can be derived from this relationship. Estimates of M_s range widely, differing among species and interannually in response to particular life history and ontogenic patterns, and to environmental effects (e.g. temperature; Houde, 1997).

The M/G index is useful for interpretation of cohort dynamics: when its value is >1, cohort biomass (B) is declining; when its value is <1, B is increasing. M/G tends to be >1 for most marine fish in the earliest larval stages. Relative, stage-specific cohort biomass (B_s) and its trends during the growth of larvae can be derived as

$$B_s / B_{s-1} = [W_s / W_{s-1}]^{(1-[M/G])}. \tag{23}$$

The among-cohort or year-class variability in size and age at which early life stages transition from M/G >1 to <1 describes variability in size-specific survival patterns and may be of use in distinguishing successful from unsuccessful cohorts (successful cohorts making the transition at small size and young age).

3.4.2.5 Size-selective and growth-rate-selective mortality

Compensation and density dependence. A significant fraction of mortality in early life may be density-dependent and can be modelled based on assumptions (or observations) of effects of prey limitation on growth (e.g. see Shepherd and Cushing, 1980). Small density-dependent regulations of either G or M can generate substantial variability in survivor abundance and act to regulate recruitment levels. In practice, few estimates of the density-dependent component of mortality in early life are available.

To estimate density-dependent mortality, pairwise plots of $\log_{10}$ abundance estimates for cohorts sampled at two or more early life stages can be plotted (e.g. $\log_{10} N_{t+1}$ plotted on $\log_{10} N_t$) and the slope of the resulting relationship estimated; if <1.0, there is evidence of density-dependent mortality, and its magnitude can be estimated from the regression statistics (Myers and Cadigan, 1993). Alternatively, the presence and magnitude of density-dependent mortality can be estimated from the regression relationship between estimates of cumulative mortality in early life (M_A) and initial abundance (A) of cohorts or year classes of eggs or larvae. A significant regression slope in this relationship indicates that density-dependent mortality occurs. The y-intercept of the regression (M_0) is an estimate of the average density-independent component of cumulative mortality (Savoy and Crecco, 1988). Estimates of the degree of density-dependence for any initial level of abundance for cohorts or year classes can be derived from the regression ($M_A - M_0$). These approaches may be useful in parameterizing models for early life stages of species where annual or cohort-specific estimates of abundance-at-stage or estimates of M are available.

Estimating larval mortality. Successful estimation of mortality depends on accurate determination of abundance and dependable assignment of individuals to age classes or stages. The general pattern of survivorship curves in early life is known (Figures 3.4.1 and 3.4.5). The difficulty and cost of estimating mortality of eggs and larvae are greatest in large ecosystems, which essentially may be unbounded and subject to significant losses through dispersal and translocation, in addition to mortality losses. The possibility of success increases in embayments, estuaries, and freshwater habitats that are bounded and where dispersal losses are minor or are of little consequence if the entire system is sampled.

Age-specific losses are often estimated from a "catch curve", in which abundance-at-age of survivors is plotted on age (Figure 3.4.5). A log-linear regression equation of $\log_e$ abundance on age (stage) estimates the instantaneous mortality rate:

$$\log_e N_t = \log_e N_0 - M \cdot t, \tag{24}$$

where N_t is abundance at age t (usually days for early life stages), N_0 is estimated abundance at the beginning of the stage, and the regression coefficient M estimates the instantaneous mortality rate. Cumulative mortality is $M \cdot t$ and the survival rate is $S = e^{-M \cdot t}$. In practice, catch curves are best fitted to stages with relatively short durations (age intervals) to minimize errors in M associated with its decline during growth.

A hypothetical survivorship curve (Figure 3.4.1) and tabulated summary (Table 3.4.1) illustrate a survivorship analysis based on catch curves for three prerecruit stages and a post-recruit stage of a typical marine fish (parameter estimates resemble those of walleye pollock, *T. chalcogramma*). At youngest ages and smallest sizes, mortality rates are highest, often >10% d^{-1}. They generally decline during growth and ontogeny. Cumulative mortalities ($M \cdot t$) are high during the egg-larval (high M, short duration) and juvenile stages (low M, long duration) when >99.5% of individuals may perish.

Modelling mortality when rates are declining during early life may be best accomplished with a model other than the log-linear catch curve. For example, the Pareto model assumes that mortality is a power function of age (or size):

$$\log_e N_t = \log_e N_0 + \beta \cdot t^{\alpha}, \tag{25}$$

where the coefficient β estimates the overall rate of decline and α is the shape parameter. This model may be particularly effective in estimating mortality when the decrease in mortality is particularly steep between the earliest life stages (e.g. eggs or yolk-sac larvae) and later stages (Figure 3.4.5).

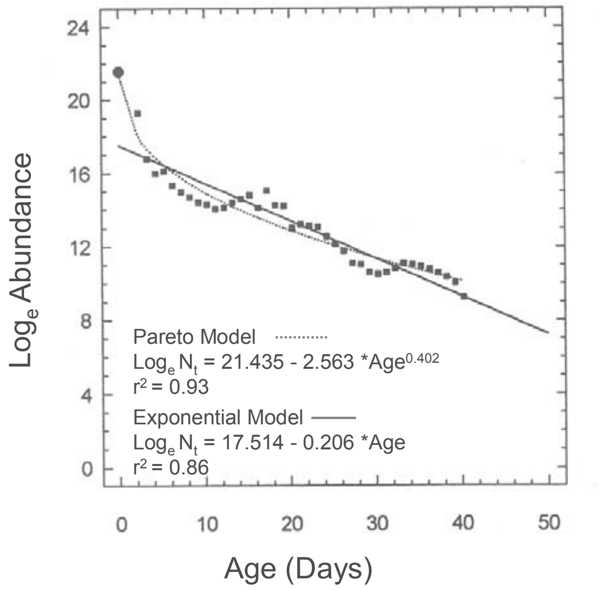


Figure 3.4.5. Survivorship curve (catch curve) for early life stages of striped bass, *Morone saxatilis*. Results of two model fits are included: exponential model ($r^2 = 0.86$) and Pareto model ($r^2 = 0.93$). Data point at day 0 represents egg abundance; remainder of data are for larvae (from Houde and Secor, 1996; unpublished report).

3.4.3 Causes of early-life mortality

3.4.3.1 Starvation and nutritional deficiencies (and critical periods)

Larval fish may die from starvation or other nutrition-related causes. Estimating or modelling this component of mortality may be important. Direct estimates are difficult to obtain because poorly nourished larvae weaken, become increasingly vulnerable to predation, and therefore occur less frequently than expected in ichthyoplankton collections. Selective predation on slower growing but healthy individuals may also occur, a mortality process potentially independent of larval nutritional condition, but still nutrition related. Back-calculation procedures, based on otolith microstructure analysis of early life stages sampled in two or more periods, can document and quantify relative losses to mortality of slow- and fast-growing larvae in a population, allowing estimates of growth-related mortality to be made.

Critical periods (*sensu* Hjort) are observed infrequently in the sea. High mortalities of larvae at the time of first feeding, resulting in order-of-magnitude losses to the population and concentrated in period of a few days, signify a critical period. Critical periods certainly can be evaluated in field research and simulated/parameterized in models.

3.4.3.2 Predation

Predators are probably the biggest single cause of mortality to early life stages of fish. Explicitly estimating the component of mortality attributable to predation is difficult. Predation losses may be linked to nutritional deficiencies that increase vulnerability of young fish to predators. Predation on fish eggs is size-specific, and predation on larvae may be both size-specific and growth-rate-dependent. As larvae grow and develop, becoming less vulnerable to predators, mortality rates attributable to predation decline. Despite a wealth of laboratory research evaluating predation on fish eggs and larvae, and a proliferation of models on the predation process, predation remains difficult to detect or evaluate in the sea. Eggs and especially larvae are soft-bodied and are destroyed upon consumption or are digested quickly. As a consequence, eggs and larvae may go undetected or be underrepresented as prey in predator guts.

Important predators of fish eggs and larvae include juvenile and adult fish, jellyfish (ctenophores and medusae), chaetognaths, and euphausiids. There is a general lack of information on the community of predators consuming fish eggs and larvae, especially in quantifying mortality attributable to specific predators, making it difficult to evaluate predator taxa and the taxon-specific mortality imposed on eggs and larvae. Research to date, including modelling approaches, has rarely succeeded in convincingly partitioning mortality of young stages of fish among the array of predator taxa and sizes present in the sea.

Vulnerability of larval fish to types of predators can be modelled and illustrated principally by dome-shaped curves in relation to larval size (see Figure 9 in Bailey and Houde, 1989). The susceptibility of larvae to attack and capture by a particular type and size of predator generally declines as larvae grow, being a function of increases in swimming speeds, improved ability to detect predators, and better avoidance and escape capability. Vulnerability, representing the net effect of ontogenetic changes in encounter probability and susceptibility, may increase for intermediate-sized larvae, at least for a particular predator of specific size and capability. With continued growth, fish larvae become increasingly adept at avoiding predation, thus reducing their vulnerability, despite the increased probability of encounter. Through growth, larvae also eventually reach sizes that reduce their vulnerability to gape-limited predators.

Laboratory experiments have demonstrated the size-specific nature of predation. Predators, independent of taxon, tend to consume larval fish prey that, on average, are about 10% of the predator's body size (Paradis *et al.*, 1996); this is a useful value for exploratory modelling applications. Perhaps surprisingly, Paradis *et al.* (1996) found that the 10% value applied to both invertebrate and vertebrate predators.

Mortality from cannibalism on pelagic eggs is common in some clupeoid fish, either by incidental filter-feeding or by selective consumption. A significant fraction of egg and yolk-sac larval mortality (e.g. 20%) in sardines (*Sardinops* spp.) and anchovies (*Engraulis* spp.) in upwelling ecosystems can be accounted for by egg cannibalism. Cannibalism may also occur when metamorphosing larvae settle onto substrate already occupied by older and larger conspecifics. Sibling cannibalism, in which larvae prey upon siblings, is reported in many taxa, including freshwater characids and marine scombrids.

3.4.3.3 Physics: transport, retention, and dispersal

Losses of early life stages to dispersal must be accounted for in coupled biophysical models. If eggs and larvae were passive particles, estimation of dispersal losses would be fairly straightforward. Behaviour of larvae, especially vertical migratory behaviour, in a stratified ocean adds complexity to estimating the loss term from dispersal. Dispersal losses may be a component of mortality if eggs or larvae cannot survive in environments where they are dispersed or cannot return to juvenile nurseries. Fine-scale variability in water-column properties, especially stratification and its relationship with vertical distributions of fish eggs and larvae, their predators, and prey, plays a critical role in controlling conditions that determine retention or dispersal of early life stages and their potential for survival.

Dispersal losses are generally higher in smaller (or partly sampled) ecosystems than in larger ecosystems. Helbig and Pepin (1998b) defined methods useful for providing coarse estimates of advective losses as a function of ecosystem size. Their approach and results may be useful in parameterizing models that explicitly attempt to estimate mortality and advective losses (see Figure 1 in Helbig and Pepin, 1998b). Helbig and Pepin (1998b) defined relationships for apparent mortality rate (M_t) and advective losses (M_d) with respect to size of the sampled ecosystem based on several studies, from which they then derived estimates of actual mortality (M):

$$M = M_t - M_d. \tag{26}$$

Although it is clear that physics at meso- and broader scales (from one to hundreds of kilometres) plays a role in controlling levels of mortality of larval stages, physics at finer scales (e.g. on millimetre to metre scales) can also be important. It is these spatial scales that determine contact rates between young fish, their prey, and predators. Rates of contact, controlled by micro-scale turbulence, for example, can directly influence the nutritional status of larvae and indirectly affect their vulnerability to predation. Modelling research, laboratory experiments, and some field observations on the role of micro-turbulence in promoting larval feeding success, growth, and survival have helped to explain how high survival of fish larvae in the sea is possible under conditions where average prey levels apparently are lower than required for larval survival. For Atlantic cod larvae (and by inference, other species), it is apparent that survival is maximized under moderate wind conditions, which generate micro-turbulence sufficient to enhance encounter rates between larvae and prey, but not so turbulent that larvae are unable to capture prey (MacKenzie and Kiørboe, 2000).

3.4.3.4 Water quality and habitats

Contaminants and toxic materials, acting either chronically or episodically, can be lethal to eggs and larvae of fish, or may prevent successful spawning by adults. This is probably most important in small ecosystems, such as bays and estuaries, and for populations quasi-restricted to these areas. Other water-quality factors may act indirectly or interactively. For example, increased loadings of nutrient, such as nitrogen and phosphorus, can lead to eutrophication of many fresh waters, estuaries, and coastal ecosystems, which can deplete dissolved oxygen, leading to hypoxia or anoxia that is lethal to fish eggs and larvae. In another example, effects of contaminants or poor water quality may alter behaviour of larvae, so impeding feeding and reducing growth rates, or making larvae more vulnerable to predation.

3.4.3.5 Diseases and parasites

Except in aquaculture, we seldom consider or estimate mortality of fish eggs and larvae from diseases or parasites, although these sources of mortality may be important. Parasites of eggs and larvae, including dinoflagellates, protozoans, helminths, and copepods, have been reported regularly, although mortality rates and population-level consequences are unevaluated. In the sea, diseased, parasitized, and poorly conditioned larvae and eggs disappear rapidly from populations either through selective predation or through decomposition and settlement of dead bodies.

3.4.3.6 Interacting factors

In many circumstances, it is a simplification to assign conditional probabilities to sources of mortality without understanding potential interactions. For example, the fraction of young stages dying from starvation or predation cannot be easily partitioned because the two sources of mortality interact. Poorly fed, slow-growing larvae are more vulnerable to predators. In laboratory experiments and model simulations, such larvae are selectively predated and have a relatively low probability of survival.

In the sea, it remains problematic to quantify the fractional mortalities on larval fish from either starvation or predation. Low prey levels reduce growth rates, leading to longer stage durations during early life and a greater probability of being predated. Modelling experiments (IBMs) have demonstrated how growth rate and its variability can modify effects of predation on survival of larval fish (Rice *et al.*, 1993; Cowan *et al.*, 1996; Letcher *et al.*, 1996). High growth rates, and also variable growth rates, lower the overall expectation of mortality in a larval population vulnerable to size-selective predation.

Parameterizing models to depict accurate mortality requires consideration of the interactions among the physical and biological processes affecting survival. In many cases, failed retention, unfavourable transport, or poor environmental conditions (e.g. temperature, pH, hypoxia) act directly to kill some fraction of eggs and larvae, but these same conditions will also affect the predators and prey of early life stages, creating a complex web of interactions affecting early life survival. Cascading effects can increase the mortality risk to eggs and larvae in stressed ecosystems. For example, an excess of nutrients can promote eutrophication, leading to low dissolved oxygen, harmful algal blooms, losses of aquatic vegetation, and probable increases in some larval predators (e.g. jellyfish), as the trophic state of an ecosystem shifts. Evaluating the effects of such multiple, complex sources on early-life mortality is difficult and seldom achieved, except in modelling, where simulations may provide valuable insight into these interacting processes.

3.4.4 Case study: mortality and the super-individual concept

A major problem in an individual-based model, once mortality is included, is that extraordinarily large numbers of individuals are needed at the start of a simulation if they are to be continually eliminated by a mortality function during the course of the simulation. Obviously, this procedure results in prohibitive computational times and may cause storage problems. Additionally, this common solution, that is, the continual reduction of the number of individuals in the model, can lead to loss of variation, irregular dynamics, and a large sensitivity to the value of the random generator seeds introduced at the start (Scheffer *et al.*, 1995). The super-individual concept developed by Scheffer *et al.* (1995) is ideally suited to eliminate, or rather circumvent, these problems. The solution is to add an extra variable to each model individual, namely the number of individuals it actually represents. In essence, each particle is considered as a super-individual representing a specific number of eggs at the outset of the simulation, with this number declining according to the mortality function applied during the course of the simulation. Thus, the resulting super-individuals are, in fact, classes of individuals (Scheffer *et al.*, 1995).

To elucidate the incorporation of mortality in individual-based models (IBMs) using the super-individual concept, an example of a mackerel IBM is presented below, which has been successfully used to predict the survival of mackerel post-larval stages in the Northeast Atlantic (Bartsch and Coombs, 2004; Bartsch *et al.*, 2004; Bartsch, 2005). This IBM is composed of a number of physical and biological modules to simulate transport, growth, and mortality. It is an *i*-space configuration model (DeAngelis and Rose, 1992) in which large numbers of individuals are followed as discrete entities. As the parameterization of mortality in this IBM is based on daily absolute growth rates, a brief description of the growth module is given for the sake of both clarity and completeness.

3.4.4.1 Growth module

In the growth module, the growth rates of larvae and post-larvae are calculated daily as a function of temperature, length, and ambient food concentration. In the absence of sufficient detailed information on the changing spatial and seasonal vertical distribution of food particles, the food-concentration data are specified as being vertically homogeneous within the entire depth range of the larvae and post-larvae (the upper 60 m of the water column). The data were computed as weekly fields for the model area for the period from mid-January to mid-September for each of the years 1998, 1999, and 2000.

Food concentrations were modelled from egg-production rates of representative large (*Calanus*) and small (*Acartia*) copepods, these constituting 39–58 % of the diet of larval and post-larval mackerel (Hillgruber *et al.*, 1997; Conway *et al.*, 1999; Hillgruber and Kloppmann, 2001; SEAMAR, 2002). Based on the formulations given in Prestidge *et al.* (1995), the egg-production rates were calculated based on the input variables of satellite-derived sea surface temperature (SST) and chlorophyll *a* concentration, providing monthly fields interpolated to weekly averages for each year. Egg-production rates per female were raised to population-production rates using Continuous Plankton Recorder data (Sir Alistair Hardy Foundation for Ocean Science, Plymouth, UK) and SEAMAR field sampling data on sex ratio and relative abundance of copepodite stages. Finally, production was converted to biomass using published copepod demographics and raised proportionately to total biomass based on the observed fraction of plankton dry weight represented by *Calanus* and *Acartia*. A full description of the food availability model is given in SEAMAR (2002).

A first analysis of growth from field data sampled on cruises during 1999 demonstrated that a logistic curve was an appropriate approximation of mackerel larval and early post-larval growth (SEAMAR, 2002), using a variable exponential parameter *r* (Bartsch, 2002):

$$L = \mathrm{L}_{\infty}(1 + \exp(-rt + \mathrm{c}))^{-1}, \tag{27}$$

where L is the length in mm at time t, L_{∞} is a constant representing the maximum length attainable in the initial larval and early post-larval growth stanza (set at 80 mm), r is a function of temperature and food concentration (see below), c is the constant of integration, and L = 3 mm at time $t = 0$, that is, at hatch.

The absolute growth rate is a function of length and the exponential parameter *r*:

$$dL/dt = G = rL(1 - (L / \mathrm{L}_{\infty})). \tag{28}$$

Temperature and food mediation of the parameter *r* is carried out as follows:

$$r = (\mathrm{r}_{\mathrm{opt}} - \mathrm{d}(\mathrm{T}_{\mathrm{opt}} - T)^2)F_i \tag{29}$$

where $\mathrm{r}_{\mathrm{opt}}$ is the maximum specific growth rate ($\mathrm{r}_{\mathrm{opt}} = 0.125$), d is a constant (d = 0.00085), $\mathrm{T}_{\mathrm{opt}}$ is the optimum temperature for growth (19°C), T is the temperature encountered, and F_i is a model food index (MFI: see below).

The range of appropriate values for r_{opt} and d depends mainly on the seasonal temperature range and growth rates. Using the available field data, values for the parameters r_{opt} and d were determined in order to provide realistic values of r, that is, r must remain positive and should tend to some minimum value r_{min} (Bartsch, 2002) that corresponds to the lowest growth rates observed in the field when substituted into Equation (28). The temperature optimum for growth ($T_{\mathrm{opt}} = 19$°C) was selected on the basis of the field temperatures likely to be encountered by larval and post-larval mackerel (maximum of ca. 20°C) and the general energetic consideration that, within the normal ecological range of a species, higher temperatures lead to increased growth rates (see e.g. Otterlei *et al.* (1999) for optimum growth temperature for larval cod, *Gadus morhua*).

The first stage in setting the MFI in Equation (29) is calculation of the ratio of available food to the required daily ration for a particular sized larva or post-larva. This is based on a simple energetics model (SEAMAR, 2002) of weight-based daily growth rate, body length, food concentration, light level, and food capture efficiency. The numerical value of the ratio varies between 0.00001 and >>1. Values >1 are set to unity, because these values denote maximum growth in optimum food concentrations (i.e. food concentrations above which no further food assimilation can be achieved). For use in Equation (29), the range of ratio values was linearly rescaled to give an MFI with a range of 0.4–1.0. The lower boundary for the MFI was determined from sensitivity tests, such that growth rates from Equation (28), using r from Equation (29) and substituting MFI = 0.4, were not lower than observed in the field during SEAMAR. A full description of the parameterization of the food and growth relationship is given in SEAMAR (2002).

For each super-individual in each grid box, the calculated MFI is modified by a random ΔMFI to mimic subgrid variations in food concentration, which are not resolved by the model grid. These random ΔMFI are drawn from a top-hat distribution of width 0.2, which results in a maximum deviation of ± 0.1 from the calculated MFI for a super-individual d^{-1}. Values calculated at < 0.4 were set to 0.4. The choice of the numerical value for ΔMFI was based on the requirement to allow subgrid variation without modifying MFI significantly.

3.4.4.2 Mortality module

The daily mortality rates of the super-individuals are calculated as a function of length and absolute growth rates. This determines the daily decrease in numbers of the original 10^6 individuals represented by each super-individual in the mackerel IBM. Conceptually, each super-individual can be considered a subset of a cohort. On any day D, $N_{D,i}$ is the number of eggs or larvae represented by each super-individual and is termed the number of "virtual individuals". In essence, $N_{D,i}$ is different for each particle, because egg-development time is temperature-dependent, growth is temperature- and food-dependent, and mortality depends on absolute growth rates and length, and so implicitly dependent on temperature and food concentration.

The mathematical relationships between growth and mortality have been examined in a number of papers, those of most significance to the present formulation being Anderson (1988), Miller *et al.* (1988), Beyer (1989), Morse (1989), Houde (1989, 1997), and Pepin (1991, 1993). The conclusion is that growth can be used to represent relative survival, because length-specific growth rates and mortality interact to determine survival of a cohort during the prerecruit period. Mortality considered here is caused by both starvation and predation. Based on this, mortality was formulated such that:

- Absolute growth rates and mortality rates are positively correlated;
- Mortality rates are inversely correlated with larval length, that is, mortality decreases as length increases;
- Cumulative mortality within a specific length range decreases with increasing length.

The mathematical relationship linking mortality with growth rates and length in the mackerel IBM was based on an empirical relationship given by Pepin (1991):

$$M = 5.17G^{0.74}L^{-1.17}, \tag{30}$$

where G is the absolute growth rate in mm d^{-1} and L is length in mm. The empirical formulation given above is principally similar to an equation of the form

$$M = cG^{1-x}/L^{1+x}, \tag{31}$$

where c is a constant.

Using daily data over a length range of 3–80 mm from the logistic curve for G and L (Equations (27) and (28)), a range of sensitivity tests were carried out to find an appropriate value for x in Equation (32) below that would satisfy the above three criteria. These results demonstrated that x should be ≥0.3. A numerical value of $x = 0.3$ was selected, because this provided exponential values for G and L that were sufficient for meeting the criteria and closest to their exponential values in Equation (30). Thus, the final formulation for the daily mortality rate in the mackerel IBM was

$$M = 5.0G^{0.7}/L^{1.3}. \tag{32}$$

The super-individual concept used in the deterministic mackerel IBM described above has the following advantages over IBMs that do not use this concept.

- There is no need for extraordinarily large numbers of particles at the beginning of the simulation.
- Computational time is drastically reduced.
- There is no need to remove specific particles from the simulation, that is, the problem of reseeding does not arise.

The mathematical formulation described here to parameterize larval mackerel mortality yields higher growth rates at higher temperatures and, hence, higher daily mortality rates, but the stage-specific mortality rates are lower for fast-growing individuals, that is, they move faster through (not only) vulnerable stages.

Generally, larval mackerel mortality rates in the IBM usually start off at about 30–40% d^{-1} and drop below 10% d^{-1} after about 35–45 d. However, it should be noted that these values vary widely between separate individuals because mortality depends on temperature and food concentration, which are both spatially and temporally variable. This results in a wide range of surviving virtual individuals per super-individual and, hence, a marked inhomogeneous distribution of model survivors over the whole model area (Bartsch *et al.*, 2004). This is demonstrated in Figure 3.4.6.

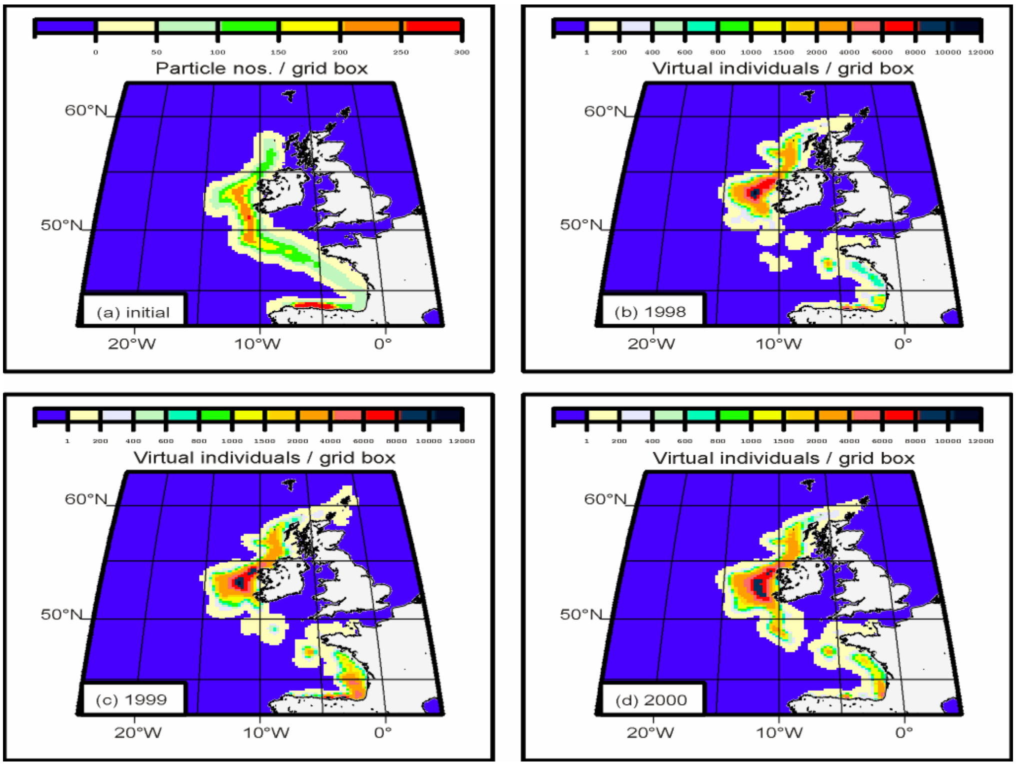


Figure 3.4.6. (a) Initial particle (egg) distribution for 12 March–3 June, as used in all model runs; (b) regional distribution of the total remaining virtual individuals within each model grid box at a length of 50 mm for 1998; (c) for 1999; and (d) for 2000.

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 designing 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 timestep; 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 performance 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)

$$dx = [<u\ (x)> + u']\ dt + du'dt \tag{33}$$

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

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 *et al.*, 2002.
Hearing	Detection of coastal areas using reef-associated choruses, or breaking waves at distances of kms, but probably not tens of kms.	Kingsford *et al.*, 2002; Leis and Lockett, 2005; Montgomery *et al.*, 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 *et al.*, 2002; Atema *et al.*, 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 *et al.*, 1992; Nishi *et al.*, 2004; Kingsford *et al.*, 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

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

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 developed 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.

4 Application 1: adaptive sampling

Pierre Pepin, Cisco Werner, and Johan van der Molen

Adaptive sampling often refers to survey strategies that are modified based on the presence and absence of organisms along a planned course or grid of stations. Within the context of the workshop, adaptive sampling primarily involves the use of circulation models or prior knowledge of the physical features of a region of interest (ROI) to guide the field operations. In some instances, adaptive sampling strategies may be developed using coupled biological and physical models if the population(s) under study are expected to undergo significant changes in state (e.g. individual size or condition, population numbers) that could affect their interaction with the physical environment. Adaptive sampling strategies are aimed at repeated sampling of a unit, whether this is an entire population or a patch, in response to observed or expected changes in the currents in the ROI. In contrast to fixed-grid strategies, whether these are based on systematic or random sampling designs, adaptive sampling schemes are intended to direct field activities towards ensuring that the unit of interest is sampled in the most effective manner to meet programme objectives.

4.1 Key considerations and processes

Adaptive sampling strategies in oceanographic research are needed because the frame of reference for population studies is changing continuously as a result of stochastic variations in environmental forcing. Transport is one of the most important factors influencing the distribution of plankton, and short-term variations in circulation can move a significant portion of a population out of or into an ROI during the course of a sampling programme. Flux across the boundary of a ROI can represent a substantial element in a population’s vital rates (Taggart and Leggett, 1987; Helbig and Pepin, 1998a), which can alter the interpretation of estimates of growth or mortality if not taken into consideration.

Real-time studies of biophysical interactions have dominated the development of adaptive sampling strategies (e.g. Bowen *et al.*, 1995; Cummings, 2005; Wilkin *et al.*, 2005) owing to their need to forecast the movement of the population or patch of interest to ensure that sequential observations are based on locating the same unit. Projects of this nature generally involve short-term forecasting of current fields based on assimilation of data from wind measurements, current meters, drifter buoys, and vertical profiles of temperature and salinity. However, adaptive sampling strategies can also be used in the development of scenarios to ensure that large-scale surveys are designed to provide sufficient coverage and accuracy of the entire population(s) being monitored. Under such schemes, regional circulation models, forced by long-term series of wind observations, can be used to assess the range of probable drift and dispersal patterns, which can then be used to identify an optimal survey design to meet the programme’s objectives.

Results from numerous regional studies of the drift and dispersal of fish eggs and larvae, as well as zooplankton, clearly indicate that the minimal requirements for the use of Lagrangian particle-tracking models in the development of adaptive sampling strategies involve mesoscale, vertically resolved models that capture key physical oceanographic processes within the ROI. The role of eddies and fronts in the dispersal and retention of plankton makes it imperative that models are able to permit the occurrence of these key features as well as forecasting their dynamics. Vertical resolution, to allow for regional variations in shear, also requires some basic biological knowledge of the species of interest, which may involve short-term (e.g. diurnal) behaviour or longer term ontogenetic changes in behaviour, depending on the application. For large-scale and long-term projections, models may require the incorporation of growth, if the latter may affect the vulnerability of the species of interest to variations in physical forcing.

A sound knowledge of the initial conditions is a critical element in using coupled models in the development of adaptive sampling strategies. For real-time programmes, data collection at the outset of the field programme plays a key role in balancing the logistical requirements and effectiveness of the project. Survey precision and accuracy become increasingly important as the degree of spatial and temporal variability of the circulation in the ROI increases, because the uncertainty in model projections will affect the interpretation of the resulting sampling programme. Most biological variables can only be sampled to a limited degree because of the need for physical observations collected from ships. In contrast, some physical variables can be updated continuously through remote sensing or communication systems, thus allowing more effective updating of projections than is possible for some biological variables. Such updates may allow scientists to modify field activities so that they can better achieve the programme objectives. For scenario building, the resolution of initial conditions may rely more on historical observations that allow projections based on the general accuracy of the observational base rather than on the precision of individual realizations.

4.2 Best practices

Adaptive sampling will only be as effective as the circulation model on which it is based. This is not a "motherhood" statement. Uncertainty plays an important role in the ability of a scientific team to interpret their findings and determine with confidence that the sequential collections of data represent a consistent unit (e.g. population or patch). Consequently, adaptive sampling should

- Be based on validated state-of-the-art circulation models suited to handling data assimilation and variable forcing;
- Include key physical processes in the region of interest;
- Provide the capacity for scenario building and sensitivity analysis that can be used to assess alternative approaches to sampling the region of interest – such schemes will clearly depend on the programme objectives;
- Include input and output capacity (e.g. bandwidth, communication, power) to allow maximum adaptability of the sampling process;
- Include backup capacity to ensure that breakdown in one element of the programme does not restrict the team's ability to fulfil programme objectives;
- Evaluate forecasting accuracy based on the sequence of data availability as a post-programme hindcasting exercise in order to provide background information that will help in the interpretation of the cruise observations.

Best practices represent a compromise between available capacity (i.e. skills and knowledge) and resources. When ideal circumstances cannot be achieved, recognition of the uncertainty in projections becomes imperative in order to ensure credibility in the interpretation of observations.

4.3 Research needs

Development of data-assimilation methodology represents a critical issue in the implementation of adaptive sampling strategies in oceanographic research. To date, there has been greater progress in the application of data-assimilation methods to circulation models than to biological models. This dichotomy partly reflects the differences in the knowledge of the fundamental principles that govern the processes represented in each type of model. However, the paucity of biological data, which has limited our ability to effectively implement data-assimilation schemes in real time, is also an important factor.

It follows that the development of sampling devices or approaches that allow increased resolution in space or time represents a key area of research if we are to move towards more effective real-time coupling of biological and physical oceanographic models. Earth observation arrays and autonomous profilers currently represent cutting-edge elements aimed at increasing data availability for real-time forecasting of the ocean environment. However, there is limited capacity in terms of the array of biological variables that can be collected with current technology. There is a growing need for reliable *in situ* sensors that can measure particle characteristics (i.e. not only size, but also shape, fluorescence, colour) for a wide range of organisms. Similarly, the development of rapid biochemical assays that can be performed reliably under field settings would provide observations of rate processes (e.g. production, growth, and uptake) that can now only be supplied to observation programmes in a *post hoc* manner.

Scientists involved in multidisciplinary programmes also face the difficulty of coping with large quantities of complex output. As a result, development of data-visualization tools, query capacity, and connectivity are important elements needed to allow operational adaptability. Increased capacity to interpret the output of coupled models will allow research to identify areas of dynamic change or response to environmental forcing and thus permit more effective sampling of the ROI.

Finally, there is a need for focused research on the development of capacity for Observing System Simulation Experiments (OSSEs), particularly for coupled physical–biological processes that may be operating at different scales. The use of climatologic time-series could serve to guide adaptive sampling strategies that would assist in the development of field-observation programmes, even before the proposal stage. Ease of access to simulation tools for a range of regions could lead to improved cost-effectiveness and sampling efficiency in the design and implementation of field programmes in order to better address the needs of multidisciplinary research teams.

4.4 Final recommendations

Ocean observatories and observing systems represent essential elements if marine scientists are to move towards a more accurate understanding of the dynamic processes that affect fish eggs and larvae, and zooplankton. The Global Ocean Observing System (GOOS) and national funding agencies should be informed of the need to provide a more widespread observation system designed to meet the needs of biophysical studies and models.

5 Application 2: connectivity

Claire B. Paris, Jean-Olivier Irisson, Geneviève Lacroix, Øyvind Fiksen, Jeffrey M. Leis, and Christian Mullon

5.1 Definition of connectivity and scope of connectivity models

Connectivity represents the dynamic interactions between geographically separated populations via the movement of individuals. This terminology comes from the metapopulation theory, which states that spatially structured populations, with distinct units separated by space or barriers, are connected by dispersal (Levins, 1969). In the marine environment, pelagic fish are often very mobile, and populations can be kept demographically open on very large spatial scales by movement of the adults. For coastal and benthic species, most interactions between breeding populations take place through natal dispersal (*sensu* Sugden and Pennisi, 2006) during the pelagic larval phase; for some species, they also occur through spawning migrations. Thus, population connectivity depends on both seascape (i.e. currents and habitat patches) and fish life history.

Connectivity studies provide a continuum between the time- and space-scales of ecology and evolution. Evolutionary studies explore long-term processes, such as biodiversity, biogeography, historical events, and population persistence (Hanski, 1989). Low dispersal rates are sufficient to shift the metapopulation distribution pattern over time by the turnover of populations becoming locally extinct and re-established elsewhere (Levins, 1969). In ecology, the focus is on the larval fluxes required to sustain a population (e.g. the design of marine protected areas (MPAs) to protect a fished stock, or explaining recent or current genetic population structures). Such demographic connectivity usually implies that a substantial number of individuals are exchanged at each generation. Therefore, the scales of dispersal relevant to ecology are reduced to areas of strong exchange and can be approximated to the mode of a dispersal kernel (DK; i.e. probability of successful dispersal). Alternatively, from the evolutionary point of view, a small number of exchanged individuals is enough to maintain genetic homogeneity between discrete populations. Therefore, larval exchange relevant to evolution occurs typically at larger spatial scales (i.e. the tail of the DK) and on longer temporal scales. Because of the differences between the temporal scales necessary for studies of connectivity, it is critical to formulate the questions and related hypotheses before setting up the model.

Connectivity models are aimed at predicting the rate of exchange of individuals (i.e. larval fluxes) between the populations forming a metapopulation. Therefore, spatially explicit individual-based models (IBMs) have become the most efficient tools in connectivity studies (Werner *et al.*, 2001). The typical output for n populations is an $n \times n$ matrix in which element (i,j) is the probability for an individual to transit from i to j during the time $t+k$, where t and k represent the generation time and the pelagic larval duration (PLD), respectively. These square matrices are called connectivity matrices, or transition probability matrices (TPMs), each of whose rows (i) contains numbers summing to 1. In order to describe a system at ecological scales, the proportion of successful recruits must reflect the recruitment rates (i.e. number of recruits per generation) required to replenish the local population to a minimum of zero growth (Cowen *et al.*, 2006). Such recruitment rates can be estimated *a posteriori* to match adult mortality rates using simple population growth models (e.g. $N_t = N_{t-1}\,e^{-rt}$). Similarly, demographic connectivity models can be *a posteriori* scaled by production (e.g. relative spawning biomass per unit population, or proportion of adult habitat in each population). Because connectivity models are by their nature spatially explicit, it is recommended to couple the Lagrangian tracking algorithm with a geographic information system (GIS). The GIS serves to delineate the source populations, as well as the recruitment habitat, along the path of an individual particle. It is also important to incorporate uncertainties into the connectivity model (e.g. Lagrangian stochastic model (LSM), stochastic mortality); otherwise, the analytical value of the transition matrices is limited.

5.2 Decide which questions the model should answer

Connectivity models can be used efficiently in several contexts, such as predictive (H_0 in terms of expected results), explanatory (explain observed patterns), inferential to deduct mechanisms (H_0 in terms of processes), or as a tool testing hypothesis (experimental modelling). Some typical examples are:

- **Siting of MPAs**. In a metapopulation, some populations act as sources and other as sinks, so the siting of an MPA has a great influence on their success. Metapopulation models can be used to predict which MPA setting can be the most efficient (Crowder *et al.*, 2000).
- **Spread of invasive species**. Connectivity models can be used to estimate the tails of the DKs or the likelihood of long-distance dispersal, as well as the most probable direction of spread.
- **Explanation of present-day genetic patterns and biogeographic breaks**. Genetic patterns are the result of gene exchange over multiple generations or of isolation between populations. Therefore, connectivity studies are key in determining the mechanism responsible for these patterns (Baums *et al.*, 2006). Connectivity matrices computed using one typical year of climatology can be used as input for genetic models to estimate gene flow across multiple generations.
- **Selective advantage of life histories**. Experimental modelling mode can be used to estimate relative measures of self-recruitment, subsidies, and survival with various reproductive strategies.

5.3 Identify the scale of the connectivity model

5.3.1 Spatial scales

A fundamental difference between recruitment and connectivity models is the focus on temporal and spatial scales. In recruitment studies, emphases are on the temporal patterns (i.e. when?) and the quantitative aspects (i.e. how much?) of the successful dispersal. It is, therefore, important to identify the physical–biological interactions that drive high recruitment vs. low recruitment; i. e. growth and mortality are key processes. Behaviours related to feeding are also important. Alternatively, in connectivity studies, the emphasis is on spatial patterns related to population linkages (i.e. where?). Such models need to be spatially explicit and resolve the scales of source and sink populations. Initial conditions and accuracy of the trajectory thus become important issues in which larval behaviour (i.e. swimming and orientation) plays a large role (see Section 5.8 Larval traits: larval behaviour).

The realism of ocean generalized circulation models (OGCMs) has provided the base of an effective tool for the investigation of population connectivity. The OGCM grid resolution should be at less than half the scale of the initial conditions (e.g. spawning population) and the arrival locations (e.g. suitable settlement/recruitment habitat, nursery grounds), which represent the starting and endpoints of the trajectories. Alternatively, the population source size (grid or polygon size) should not be smaller than the resolution of the OGCM. This grid-size requirement allows the particles to be released at each source population and recruited within a particular location at each time-step without missing any unit population. In most cases, these locations are within the coastal realm in relatively shallow waters. OGCMs should cover larger areas than are significant for connectivity networks, but models that cover large areas usually do not adequately resolve the complexity of coastal dynamics, nor the resolution of the unit populations. Therefore, nested models are recommended, with higher resolution both on spawning and recruitment areas. Note that, at the scales of local retention, DKs could be limited by the spatial resolution of the model (e.g. smaller than the model's mesh size).

5.3.2 Temporal scales

Ecological time-scales are relevant to the demographic structure whereby a substantial number of individuals are necessary to sustain (i.e. minimum of zero growth) a population. In this case, it is necessary to estimate the spatial probability of larval exchange or probability density functions (PDFs) over multiple years of daily forcing. Resulting transition matrices need to be scaled by species-specific demographic parameters (e.g. birth, longevity, mortality). Geologic time-scales are relevant to the evolutionary structure, whereby a few individuals exchanged per generation suffice to maintain genetic connectivity between populations. In this case, providing paths and relative percentage of larval exchange using one typical year of climatology with monthly forcing is appropriate.

Finally, connectivity models must explicitly span the relevant spatial and temporal scales of the target organisms (e.g. decadal variability of taxa with basin-scale distributions).

5.4 Gain knowledge of processes relevant to modelling connectivity

5.4.1 Initial conditions: spawning time and locations

Spawning locations should be mapped into GISs, serving both as initialization of the particle-tracking system and as "source" locations in the connectivity model. A distance matrix D*ij* is built (where *i* = source location and *j* = arrival location) and is used to generate DKs (Figure 5.4.1). For more information on this topic, see Section 3.1 Initial conditions: spawning locations.

5.4.2 Suitable settlement locations

The endpoint or targets for the model need to be determined. For demersal species, this is usually the location and habitat where the pelagic early life-history stage makes the transition to the demersal (bottom-associated) stage. For pelagic species, this may be a nursery area, even if it is broad and diffuse (e.g. shallow coastal waters). The key point, however, is that particular habitat requirements for many species must be met at a particular stage in the life history. For some species, these requirements are well understood, but for many others, particularly in tropical areas, such requirements are not well known. The term "nursery area" has taken on a somewhat more precise definition recently (Beck *et al.*, 2001; Dahlgren *et al.*, 2006), and with application of this definition, some reassessment of what were traditionally thought of as nurseries may be in order. Furthermore, settlement and nursery locations may not coincide for some species. Therefore, the modeller needs to consider carefully what the model is trying to achieve. For example, if the goal is to predict the distribution and numbers of a demersal species at settlement, the modeller has a different task than if the goal is to predict the numbers of individuals entering a fishery, or the numbers of individuals vulnerable to entrainment through the cooling system of an electricity-generating station.

For connectivity models, the main goal is to map networks of larval linkages between populations, and although spawning and recruitment areas may be different, each paired set (spawning–recruitment locations) must represent a unit population. The modeller must obtain information on the settlement requirements of the species of interest, and then the spatial distribution of the appropriate habitat must be determined. This information may be available in the literature, but if not, appropriate surveys must be undertaken. An additional factor to consider is that, even if a particular location is understood to be suitable settlement habitat for species A, this can change with time by virtue of year-to-year fluctuations, anthropogenic influences (e.g. pollution or other habitat alteration), or by long-term climate or other environmental change (e.g. coral bleaching or cyclones can kill corals into which fish normally settle). It is therefore necessary to ensure that such occurrences have not altered the nature or distribution of the required habitat, because the initial studies of the habitat, if there are seasonal factors at play, incorporate a seasonal assessment of settlement habitat quality or distribution. Suitable settlement locations should then be mapped into GIS layers that are fully integrated into the particle-tracking modelling system, serving as "receiving" locations in the connectivity model.

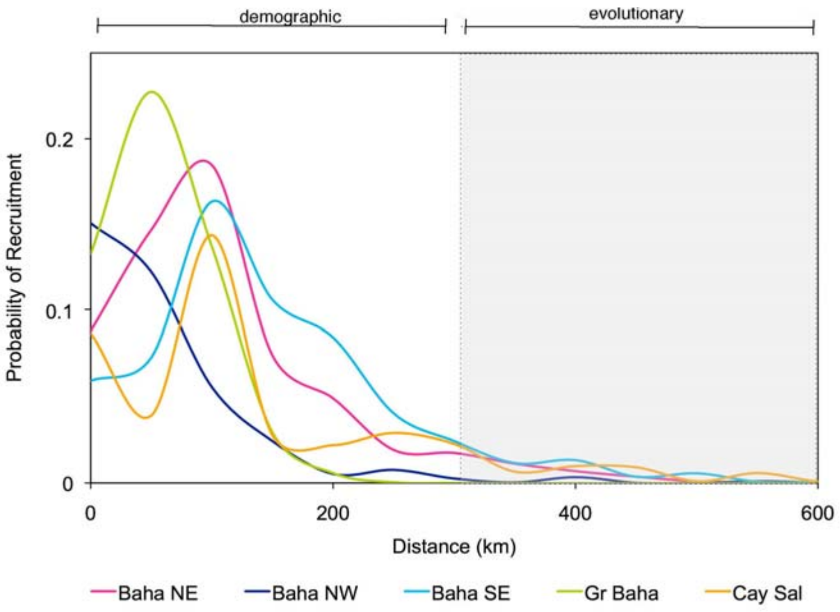

Figure 5.4.1. Dispersal kernels or probability of dispersal to a suitable nursery habitat, showing the spatial scales associated with a 30-day dispersal of fish larvae for various regions in the Caribbean. The transition to the shaded area indicates the range of distances over which dispersal (and perhaps also survival) becomes irrelevant to demographic time-scales. Mean dispersal distances are reflected in the modes that vary with locations, whereas self-recruitment is the value at the origin.

5.4.3 Small-scale physics: turbulence

Physical processes occurring on scales smaller than the grid scale used in the model are often parameterized using a turbulent "diffusion" parameter, often called "eddy diffusivity". This parameter should also include a factor to account for physical processes not included in the circulation model, and it does not represent the true advective processes that may be taking place.

5.4.4 Large-scale physics: grid size and domain

The physical processes discussed in this section refer only to large-scale physical processes (i.e. larger than the grid resolution of the model).

Physical processes act on the transport/retention of larvae during their pelagic phase (e.g. wind-driven circulation, tides, freshwater buoyancy, fronts), on settlement (e.g. bottom stress, sediment type), and on conditions affecting larvae survival (e.g. temperature, short-term event enhancing local increase of food). The combination of transport/retention, good conditions for settlement, and larvae survival can lead to sustainability or extinction of subpopulations, to exchanges between subpopulations, and to new subpopulations (colonization of new habitats).

The choice of which physical processes to explicitly resolve requires careful consideration because it may not be necessary to include every process that might influence the transport path of larvae and the possibility of retention and settlement, taking into account the larval phase (pelagic) duration. According to the situation (e.g. coral reefs, shallow continental shelf, proximity of river mouth), not all of the physical processes, such as ocean currents, tides, wind, or freshwater inputs, will have the same importance. We recommend conducting sensitivity studies in order to determine the degree of importance of each physical process before choosing those that are key to the purpose of the study and the larval behaviour under consideration.

The physical processes to consider depend strongly on the region of interest (ROI) and also on the species under investigation. There is a strong link between physical processes, spawning frequency/duration, and larval behaviour (e.g. vertical migration). Spawning time/location, larval traits, and larval behaviour are the subject of other sections, and only some examples of situations where they should be taken into account are given in the list of physical processes below. This list, far from being exhaustive, is intended to help the modeller choose which physical processes to consider as a function of the ROI. The "typical" spatio-temporal scales of these physical processes are given in Section 1 Hydrodynamic models.

- **Ocean currents**. General circulation, coastal currents, meanders, jets, eddies, shelf-edge fronts.
- **Tides**. Tidal currents (can be important in shallow waters, reefs, etc., depending on the topography), residual circulation, tidal fronts, vertical gradients of horizontal currents, relationship with "larval behaviour" (synchronization of vertical migration of larvae with ebb–flood tidal cycle), spawning timing (synchronization with spring neap tidal cycle), and spawning location ("choice" of spawning depth).
- **Freshwater input**. Presence of hydrological fronts in the proximity of river mouths, freshwater buoyancy circulation, water stratification density (may act as a barrier to vertical movements), periodic low-salinity water intrusions (may affect depth of larvae), relationship with spawning timing (synchronization with high/low river discharges).
- **Wind**. Wind-driven circulation, internal waves, Langmuir cells, upwellings/downwellings (and associated fronts and convergences).
- **Fronts**. Fronts (whatever their origin), which can act as a barrier that limits the larvae transport but are also the seat of circulations leading to conver-

gence/divergence zones; instabilities (e.g. eddies), can transport "isolated" water masses over long distances.

In addition to the "typical" distribution pattern resulting from averaged physical processes, the variability of these processes (e.g. extreme events, perturbations, instabilities) can have a strong impact on larval transport or retention. Colonization of new habitats, for instance, could result from a particular event, and the spatial–temporal variability (e.g. interannual) of physical processes should be considered.

Model domain size and grid size must be chosen in accordance with the physical processes to be included. Processes smaller than the grid size must be parameterized, and processes acting at scales larger than the model domain should be considered according to appropriate boundary conditions (e.g. harmonic tides) or nesting. For the purpose of connectivity studies, grid size should be significantly smaller than the "assumed" distances between subpopulations and significantly smaller than a subpopulation. The model domain should at least encompass the whole region of possible exchanges between subpopulations and should include possible new habitats. For connectivity studies, it may be necessary to consider a whole region in order to encompass all existing subpopulations and possible new habitats, and also to consider a refined grid at the subpopulation level (e.g. shallow coastal waters, local retention, heterogeneity of sediment, needs of a fine vertical resolution). For this particular case, it could be interesting to consider model nesting.

Only thoroughly validated hydrodynamic models should be used for connectivity studies. The modeller should at least verify that current velocity (horizontal and vertical) and/or trajectory path are correctly simulated. For more details, see Section 5.11 Model validation.

5.5 Lagrangian parameterization and online–offline methods

5.5.1 Parameterization of the Lagrangian statistics

In larval dispersal applications, the uncertainties in particle trajectories are usually parameterized, adding a stochastic component to the model-predicted trajectories,

$$dx/dt = u_m + u', \qquad (35)$$

where x is the particle position, u_m is the model velocity, and u' is a stochastic velocity, which is typically described by a simple LSM (e.g. Griffa, 1996) and parameterized by the horizontal grid-scale diffusion according to Okubo (1971). However, the true eddy kinetic energy occurring at the subgrid scale can vary both spatially and temporally. Comparison between the kinetic energy content of the Eulerian velocity field for various grid sizes of the OGCM provides us with the energy cascade from the large-scale to the submesoscale processes absent from the coarse-grid simulation. Therefore, different regions with different processes (e.g. tide, shelf waves, eddies, currents, topography steering) are characterized by an energy-spectrum structure from which can be extracted, in terms of percentage of total variance, the contribution of the submesoscale processes to the coarse-grid flow. Spatial probability distributions of Eulerian decorrelation time-scales and variances can be used to estimate the corresponding Lagrangian scales (Paris *et al.*, 2007).

5.5.2 Online–offline methods

In connectivity modelling, thousands of particles are typically released simultaneously and repeatedly from hundreds of locations. Although computational speed has recently increased with the technique of parallel computing, offline modelling brings a considerable computational advantage. Indeed, it is important to seek economies of central processing unit (CPU) resources to allow multidecadal studies over large domains while still resolving mesoscale motion. In addition, the "active" tracking scheme (e.g. with larval behaviour) is modulated by species-specific suitable habitats that are also stage-specific (e.g. the larval habitat is different from that of juvenile and adult fish). Although the GIS-based habitats are fully coupled to the Lagrangian scheme in the offline model, these habitats are not an integrated part of the OGCMs, which represents a serious limitation in the use of online tracking models.

The offline method uses time-averaged flowfields (e.g. hourly to daily), diffusion coefficients (e.g. decorrelation time-scales, variance, spin), and any other fields of interest (e.g. temperature, salinity, nutrients–phytoplankton–zooplankton–detritus (NPZD)) that are stored during prior online runs and reused, leaving only the Lagrangian equation to be integrated. To reproduce online trajectories with no significant departure, the flowfields used to drive the offline calculation must be averaged on time-scales close to or below the inertial period. Consequently, the offline time-step is no longer limited by dynamical constraints and can be increased by almost an order of magnitude relative to the online value, whereas calculation time is significantly decreased (Hill *et al.*, 2004). Other important considerations between online–offline methods are trade-offs between computational efficiency, model integrity, and storage requirement when using an offline tracking approach at high resolution, where there is strong spatio-temporal variability in the flowfield. The fidelity of the trajectories can be assessed with spatial correlations of the control "online" matrix with the "offline" probability transition matrices generated at different time-steps ($D_{\text{t-off}}$) and time-averaging frequencies (T_{avg}). The CPU cost (M_t) can be calculated as a function of the change in online ($D_{\text{t-on}}$) to offline particle time-step and time-averaging frequency:

$$\mathrm{M_t} = \log\,[(D_{\text{t-off}}\,/D_{\text{t-on}})\mathrm{T_{avg}}]. \tag{36}$$

The offline method is very useful for performing multiple integrations for various life-history strategies using the same flowfield. Another advantage of the offline method is that daily mortality rates can be implemented without having to model super-individuals.

5.6 Larval stage duration

This parameter, often referred to as pelagic larval duration (PLD), is one of the more basic life-history traits to input into the connectivity model because it is used to establish the transition time k in the connectivity matrix. For more information on this topic, see Section 3.2 Pelagic larval duration.

5.7 Larval traits: growth and mortality

Growth and mortality are intimately coupled through a range of mechanisms, such as size-dependent predation patterns, starvation, and growth-dependent, larval-stage duration. These mechanisms have received well-deserved attention from modellers for quite some time. For more information, see Sections 3.3 Growth and 3.4 Mortality.)

Growth and mortality are also intimately coupled through larval behaviour, because behaviour-promoting growth may also increase the risk of predation. Such processes have received less attention in fishery oceanography, both empirically and in models. One example is the trade-off between being spotted by visually searching predators and the need to find food through visual detection of prey. Another example is the risk of encountering tactile or ambush predators through increased swimming activity, which may be necessary to increase the encounter rate with potential prey items. There are also good reasons to argue that such behaviours are state- and size-dependent, and that they interact with larval dispersal and drift trajectories. There is a need to adopt approaches from behavioural and evolutionary ecology to improve understanding of these processes.

Growth is often modelled in great detail, with much attention to processes and environmental forcing. However, mortality is typically either not modelled at all or taken from statistical size-dependent relationships with low mechanistic content and justification. However, the predation efficiency of invertebrates and fish typically varies predictably with a number of environmental factors, such as light, turbulence, and bottom depth, as well as larval behaviour (diel vertical migration, activity, and internal body condition). More efforts are required to include such processes in biophysical models.

5.8 Larval traits: larval behaviour

Fish larvae are not passive particles, and they have the potential to influence their dispersal (see review by Leis, 2006; Leis, 2007). Heterogeneous vertical positioning can result in divergent dispersal trajectories as well as differential survival (Paris and Cowen, 2004). Horizontal swimming can have a large influence on dispersal trajectories and on the success of settlement, particularly when larvae are able to orientate and in ecosystems, such as coral reefs, in which most fish larvae are very strong swimmers by the time they settle. Orientation can be further enhanced by schooling, because a school of larvae can act like a larger organism, with more precise sensory organs (Potter and Chitre, 2006). Schooling also influences feeding and predation rate, and hence has consequences for both growth and survival. Feeding behaviour and predator avoidance also contribute to differing survival rates. Finally, available suitable habitat and, at finer scales, habitat preferences during recruitment, can affect dispersal outcomes. Because larval behaviour influences both the endpoint of individual trajectories and survival, it is particularly important to include behaviour in population connectivity models where these factors are vital. For more information, see Section 3.5 Behaviour and settlement.

5.9 Steps towards the state-of-the-art model

Exhaustive, perfect ground-truth models are usually not produced on the first attempt. We suggest here the order in which components should be implemented in a connectivity model, given its objectives. The minimum model should have relevant starting and ending locations and represent the main exchanges between them. Subsequent steps should simulate active larval trajectories and, hence, produce more accurate connectivity probabilities.

5.9.1 Step 1: minimum model

Start and end are defined by

- Locations and time of spawning (*a priori* breeding populations);
- Location of potential settlement (e.g. GIS-based habitat map, divided spatially into localities);
- Integration time (e.g. PLD).

Trajectories should be computed using the Lagrangian approach, with a well-parameterized, particle-tracking model embedded in an OGCM (online), or operating offline (see Section 5.5 Lagrangian parameterization and online–offline methods). Initial dispersal is critical for the trajectories; therefore, the resolution of the model should be fine enough to capture features of the initial dispersal. However, connectivity models usually represent large areas, and a fine-resolution model over very large scales is not currently feasible. This calls for nested hydrological models; see Section 5.3 Identify the scale of the connectivity model.

5.9.2 Step 2: biological features

These include:

- **Vertical distribution behaviour**. If the biophysical conditions (i.e. currents, temperature, food) are not homogeneous vertically.
- **Mortality**. This must be included if the mortality probability cannot be considered homogeneous in space, or if the target species has a plastic larval duration (see Sections 3.3 Growth, 3.4 Mortality, and 5.6 Larval stage duration). However, very few estimates of survival rates are available for larval fish, most of which are from temperate coastal species (Houde, 1989; Santos *et al.*, 2005). Currently, there is only one published account for tropical reef fish species, and in this case, mortality rates and advective losses varied through ontogeny as a result of vertical migration (see Paris-Limouzy, 2001).

In addition, the representation of biological traits should be probabilistic (i.e. represent variance and not just the mean), because the traits of surviving individuals are usually not in the mode of the population distribution.

5.9.3 Step 3: small-scale features

Previous components of the model were aimed at correctly representing the shape of trajectories from where they start to where they end. Along these trajectories, small-scale features can induce some variability.

- Horizontal swimming and associated orientation obviously affect the trajectories. In systems where fish larvae have strong swimming abilities, horizontal swimming should be incorporated at step 2.
- Feeding, small-scale turbulence, and growth are worth including when food appears to be a limiting factor for the survival of fish larvae. In addition to possible starvation, limited growth or poor body condition can influence swimming abilities.
- Schooling has an effect on the functional response of predators (Cosner *et al.*, 1999) and therefore mortality rates, and on the path of individual larvae (Flierl *et al.*, 1999). It is therefore important to include this behaviour for both pelagic coastal fish and benthic species if presettlement schooling is known.

5.10 Result analysis and model validation

Population connectivity modelling results can be visualized and analysed in two basic forms: (i) PDFs and (ii) connectivity networks.

5.10.1 Dispersal kernel

A dispersal kernel (DK) is a two-dimensional PDF that describes the probability of successful dispersal to different distances (Nathan, 2006). In connectivity studies, it is used to scale dispersal. The mode of the DK is relevant to ecological studies, whereas the tails (i.e. the frequency and spatial extent of long distance dispersal events) are relevant to biogeographical studies (e.g. multiple colonizations, disjunctions). Dispersal kernels can be represented for single locations or as "total" DKs, which incorporate the contribution of multiple dispersal vectors.

5.10.2 Transition probability matrix

A transition probability matrix (TPM) is a three-dimensional PDF representing the probabilities of larvae moving from one state (e.g. gametes, early larvae) to another (e.g. recruitment-stage larvae) in a dynamic system (Figure 5.10.1). The likelihood of larval exchange from one population to another, each associated with a given area, is represented in a TPM where columns are source locations (population *i*) and rows are destination locations (population *j*). The content of a given matrix element describes the probability of an individual larva making the transition from its source population to the recruitment stage in the destination population. Elements along the diagonal of the matrix represent self-recruitment within a local population. These matrices are usually sparse where zeros represent regions of no connectivity. The TPMs are of considerable value for metapopulation studies as well as for spatial management because they are three-dimensional. TPMs also provide an ideal means of conducting sensitivity analyses using spatial autocorrelations.

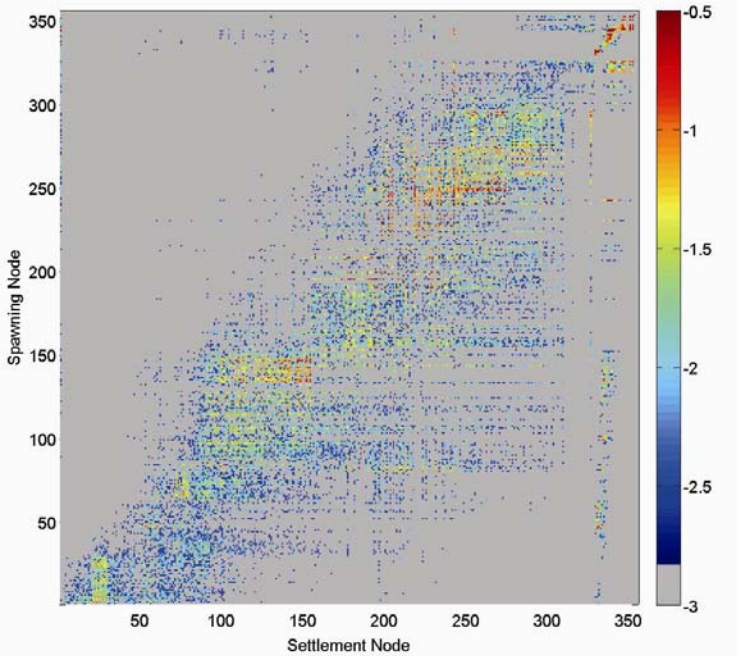

Figure 5.10.1. Transition probability matrix. The contents of a given matrix element describe the probability of individual larvae making the transition from its source population (*y*-axis) to the destination population (*x*-axis), computed over several generations. Elements along the diagonal represent self-recruitment within a population. The matrix is sparse where the grey area represents regions of no connectivity; the colour code indicates levels of connectivity from high (red) to low (blue). Higher connectivity on one side of the matrix corresponds to a drift in the direction of main currents.

Graph theory represents an effective means of visualizing population connectivity networks (e.g. Figure 5.10.2; see also Cowen *et al.*, 2006). The relationships between populations are described by an adjacency matrix, derived from the probability transition matrix output by the connectivity model. The adjacency matrix (or edge) is a binary matrix in which each element is defined as A*ij* = 1, if populations *i* and *j* are connected by edges, or A*ij* = 0 if they are not connected. This matrix is mostly used to analyse connectivity networks (Urban and Keitt, 2001) and is extremely powerful for conservation issues such as strategic placement of MPAs and identification of source and sink populations, as well as key corridors (e.g. populations that are key to maintain the network).

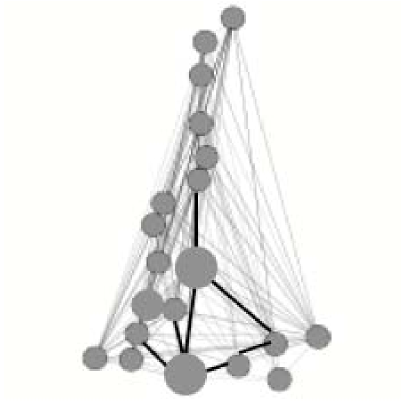

Figure 5.10.2. Population Connectivity Network. Habitat patches are represented by nodes, for which size represents population density. When larvae from a given patch reach a downstream site, a dispersal connection is made. The thickness of the edge reflects the strength of the connection. This theoretical graph approach is useful to identify the spatial structure of the population sources, sinks, and corridors. The network is built directly for the transition probability matrix.

5.11 Model validation

There are two types of validation.

- **Validation of trajectory path**, using a combination of acoustic and hydrological (e.g. acoustic Doppler current profiler (ADCP) and conductivity, temperature, depth (CTD)), Lagrangian (e.g. satellite tracked floats, fluorescent wax particles), tagging or mass marking (e.g. otolith), and plankton (e.g. trawls, optical sampling) sampling tools. Trajectory validations are expensive and labour intensive. These direct methods of measuring connectivity provide snapshots in time, but reveal mechanisms or physical–biological interactions that can be modelled.
- **Validation of population connectivity results**, using genetic tools that provide the genetic structure of populations (demographic time-scales) or metapopulation (evolutionary time-scales) depending on the gene used (review by Planes, 2002). Measurements of post-larval supply at multiple sites can also produce a very consistent validation of the connectivity results (e.g. relative levels of recruitment into spatially explicit population units, Figure 5.11.1), without providing explicit knowledge of the source locations (i.e. TPM).

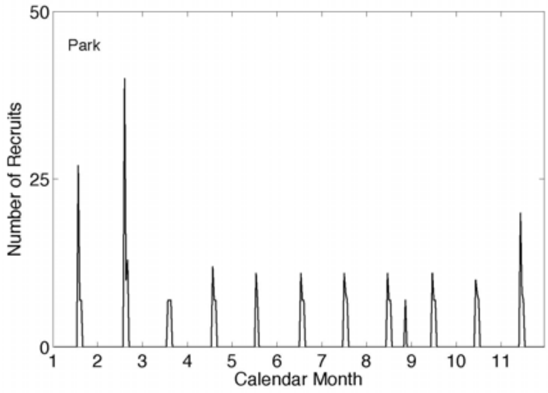

Figure 5.11.1. Daily predicted larval supply of *Sparisoma viride* for the months February–December 2004 south of Sea Park in the Bahamas in ca. 50 km^2 coral reef habitat. Note that the *y*-axis represents simulated larvae and cannot be interpreted as an absolute measure of larval supply.

5.11.1 Trajectory path

Trajectory paths need to be validated (i) for their passive component and (ii) for their active component, which includes a series of larval behaviours. Validation should proceed as larval behaviours are introduced stepwise into the tracking scheme. See Section 5.8 Larval traits: larval behaviour.

Passive component of the trajectories:

- Ocean-observing systems are always very useful. For example, time-series of ADCPs moored in strategic locations can be used to improve the coupled OGCM with data assimilation.
- To validate the small-scale physical and biological processes operating at the starting (initial dispersal) or ending points (settlement processes) of the trajectories, gliders can be used, affording very high-resolution, three-dimensional hydrological data at specific spawning and recruitment sites.
- A series of floats deployed at various time frequencies and depths from distinct locations corresponding to an onshore–offshore gradient and different oceanographic regimes can be used to check the consistency of the trajectory predictions with the passive particle-tracking code. Float data are also useful to compute diffusion parameterizations for the LSM.

Active component of the trajectories:

- Initial gamete dispersion can be assessed by conducting intensive Lagrangian field experiments with synoptic three-dimensional hydrodynamic observations. The use of fluorescent wax particles calibrated with the egg density/size of the target species is recommended for the Lagrangian experiment.
- To verify the accuracy of simulated trajectories of active larvae (e.g. ontogenic vertical migration), repeated stratified samples of larval fish are necessary. This sampling can be achieved using trawlnets, such as the Multi Opening and Closing Net and Environmental Sensing System (MOCNESS), or with well-calibrated optical instruments, which take very high-resolution shadow images.
- Proper validation of trajectory endpoints requires data on larval supply at multiple sites.

- Other behaviours can be added stepwise to the model to perform sensitivity analyses, and the model outputs can then be compared with otolith microchemistry and genetic patterns or settled individuals.

5.11.2 Population connectivity results

Genetic validations can provide non-directional (gene flow over several generations) and directional (DNA paternity analyses) connectivity networks, but do not reveal the mechanisms or physical–biological interactions that lead to connectivity. Genetic data based on fast-evolving genes (such as microsatellite DNA) are extremely powerful in validating models of demographic connectivity. Paternity analyses or fingerprinting can provide detailed information on the parent–offspring relationships (Jones *et al.*, 2005) and validate the direction and strength of connections. These innovative genetic techniques are the best possible validations for connectivity models operating at the demographic scales. They provide a directional linkage between populations. To address questions at evolutionary time-scales, mitochondrial DNA or slower-evolving genes are useful to verify the spatial extent of the metapopulation (or species biogeography). However, caution is required for non-directional types of validation. The TPM (or a powered TPM) assumes that migration is the main contributing factor. Thus, the connectivity model assesses gene flow for neutral evolution (i.e. drift and recombination). Other processes, such as homoplasy and selection, even operating over relatively short time-scales, can change genetic patterns. In addition, if genetic data do not resemble the connectivity model, it may not be the result of the connectivity model being flawed. Rather, it may be that demographic and post-settlement processes (e.g. density, predation, latitudinal gradient, depth of settlement) also contribute to the population structure.

5.12 Research needs

One of the limitations when modelling connectivity is the unavailability of nested OGCMs (highest resolution in the order of hundreds of metres resolving small-scale processes at the spawning and recruitment areas) that operate at long time-scales (resolving interannual variability over decadal time-scales). Two-way nested models are needed, with higher resolution both on spawning and recruitment areas. Information on species-specific larval behaviour and mortality rates (including how both change with development) is also needed for more realistic biological connectivity models (Werner *et al.*, 2007).

5.12.1 Initial dispersal

Lagrangian *in situ* measurements are needed to measure the dispersal statistics at spawning sites, which are not usually resolved by an OGCM. In particular, very little is known about diffusion in areas of steep slopes (e.g. promontories and capes), near the shelf break, and in shallow coral reef environments. To resolve initial dispersal, measurement of egg buoyancy is similarly important. Some fish species form transient spawning aggregations during a very narrow window in time, which usually coincides with a lunar phase and changes in water temperature and current intensity. For connectivity studies, there is a need to understand the cues utilized for spawning and to measure the associated physical features and dispersion parameters.

5.12.2 Settlement

More research is also needed (i) into the swimming and orientation of larval fish and their related cues (see Section 5.8 Larval traits: larval behaviour); and (ii) on the rates of larval mortality (see Section 3.4 Mortality) through ontogeny. Connectivity results are very sensitive to these parameters (Paris *et al.*, unpublished data).

6 Application 3: recruitment prediction

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6.1 Definition

What do we mean by recruitment prediction? The first thing to consider in defining this term is the time horizon of the prediction. Short-term predictions mean the use of individual-based, coupled physical–biological models (ICPBMs) of fish early life history to predict annual recruitment, most usually to aid managers of fish stocks. These predictions may be made via indices or other measures of prerecruitment or recruitment, derived from ICPBM output, that correlate well with other independent, reasonable predictors of recruitment (derived from stock-assessment models, reasonable independent juvenile or prerecruit surveys conducted with acoustic or trawl, or other net-based survey methods). These may be used alone or in conjunction with other predictors, such as spawning-stock biomass. Actual numerical estimates (of the correct magnitude) derived from ICPBMs may be possible, but only if certain conditions are met (e.g. the super-individual method, proportionality indices, or other methods of relating model indices to real population numbers are used, and spawning-biomass or egg-production estimates as initial conditions are included). A benefit of these indices is that they could serve as a replacement for expensive juvenile surveys.

Under this definition, the forecast window for recruitment predictions would be limited to the number of years from spawning to recruitment for each species of interest. This is because of the fundamental lack of predictability of regional and small-scale ocean physics. These prediction windows will be different for each species owing to differences in the unique aspects of a species' life history.

Longer-term recruitment predictions that are likely under different future scenarios (e.g. of climate, fishing, or ocean variability) may also be derived from ICPBMs through the use of the models to gain a mechanistic understanding of the important biophysical processes underlying recruitment variability. This knowledge may, for example, help us to understand simple correlations between biophysical factors and recruitment, and when such correlations may or may not hold up.

The development of recruitment predictors from ICPBMs requires careful consideration of what we mean by recruitment. There are many ways of defining recruitment. The operational definition depends on the purpose or goal of the prediction. Are we predicting recruitment for management purposes? If so, then recruitment is often defined as the number of fish entering the exploited segment of the population, where the meaning of "exploited segment" depends on the distinctive attributes of each fishery (i.e. gear type, time and space scales). If examining life-history characteristics or gaining ecological understanding is the goal, recruitment could be defined as the number of fish reaching a juvenile nursery area, the number reaching maturity, or the number reaching a particular age, size, or stage.

6.2 Objectives of recruitment prediction

There can be several different objectives for recruitment prediction, and these will affect not only how we select a predictive index from the model, but how the ICPBM itself is constructed and its relevant physical and biological details. Recruitment prediction may be undertaken to test our understanding of the processes that affect recruitment. ICPBMs may be developed to clarify mechanistic processes underlying correlations between physical or biological factors and recruitment. Recruitment prediction may be applied or pragmatic, for example, to aid in the reduction of the number of recruitment scenarios that must be performed in the stock-assessment modelling process.

Who are the clients/consumers of the forecasts? To maximize the usefulness of recruitment forecasts, they need to be tailored to the user. The needs of scientific researchers, resource managers, and commercial fishery concerns may be different. For example, a forecast prepared for a scientist might be used as a null hypothesis to demonstrate whether or not the forecast embodies a sufficient understanding of the processes and mechanisms that cause good and bad year classes. In contrast, decision-makers in commercial fisheries may require a forecast only as a basis for future buying decisions regarding capital expenditures for equipment or ship improvements. In this case, the emphasis is not so much on perfect understanding. For example, if a forecast tells them to expect several years of good recruitment, they may decide to purchase automatic fish-filleting equipment optimized for smaller fish. If recruitment is expected to be poor, they may conclude that they will be exploiting older individuals from the population and should purchase filleting machines optimized for larger fish. In both cases, their goal is to maximize product recovery, and having the right equipment for the circumstances plays a large role in attaining their goal.

6.3 Indices of recruitment from ICPBMs

When using ICPBMs to aid in the prediction of recruitment, an index that appears to correlate well with recruitment can be used. Often, these indices relate to some underlying theory about recruitment success. Some examples of recruitment or prerecruitment indices that have been, or could be, derived from ICPBMs are (i) the number of larvae or juveniles that reach a specified nursery area, weighted by their residence time there (Parada *et al.*, in review); (ii) the number that reach a nursery area by a particular date, size, or age (Bartsch *et al.*, 2004; Baumann *et al.*, 2006); (iii) indices of larval drift or retention, such as the number going in a predefined direction (Wespestad *et al.*, 2000; Wilderbuer *et al.*, 2002; Stockhausen, pers. comm.) that experience different levels of bottom depth anomalies (Baumann *et al.*, 2006), or a survival rate after a certain number of days of drift (Allain *et al.*, 2007); (iv) indices of overlap of larvae with their prey (Hinrichsen *et al.*, 2005); or (v) indices of juvenile particle density at the end of a simulation to look for density-dependent processes related to recruitment (Baumann *et al.*, 2006).

Indices may be compared with data, for example, surveys of prerecruits or recruits. Indices may also be compared with stock-assessment model estimates of recruitment. In this case, caution is needed. The same data may be used in the ICPBM and the stock-assessment model (e.g. spawning-stock biomass); therefore, the indices produced by the two models may not be independent.

The proper choice of recruitment indices will depend on the objectives of the work, the life history of the species, and theories (conceptual models) of what processes are critical to recruitment variability. The development of a conceptual model (see Section 6.4) can aid in the choice of indices.

6.4 The need for a conceptual model

Development of a conceptual model of the processes controlling recruitment for each species and area is key to the use of ICPBMs in recruitment prediction, and also to the choice of the proper indices derived from the models. Development of a conceptual model is a way of organizing what is important, the importance of the roles played by particular processes, and what life stages are affected. If this is neglected, important factors or processes may be missed in the ICBPM.

- Life stages and their duration
- Variation in mortality at each stage
- Biological and physical factors affecting each stage and the "intensity" of the effect
- Processes important within each stage

If different processes at different life stages are thought to be important, it may be necessary to develop different conceptual models for the same species in different areas. For example, the walleye pollock conceptual models for the Gulf of Alaska (http://www.pmel.noaa.gov/foci/forecast/mgt.html; Figure 6.4.1) and Bering Sea (http://www.pmel.noaa.gov/foci/sebscc/results/megrey/bs_concept.html; Figure 6.4.2) contain the same life stages and duration, but they differ with respect to which life stages experience the most variability in mortality and the factors that influence mortality and survival. Therefore, somewhat different ICPBMs have been developed, and different indices may be necessary to predict recruitment.

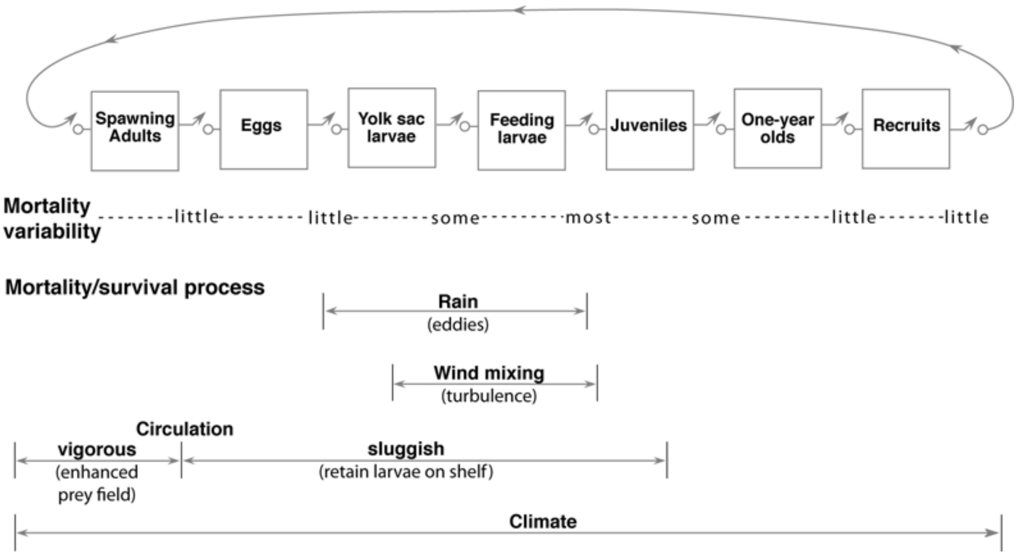

Figure 6.4.1. Gulf of Alaska walleye pollock conceptual model (from Megrey and Wespestad, 1997).

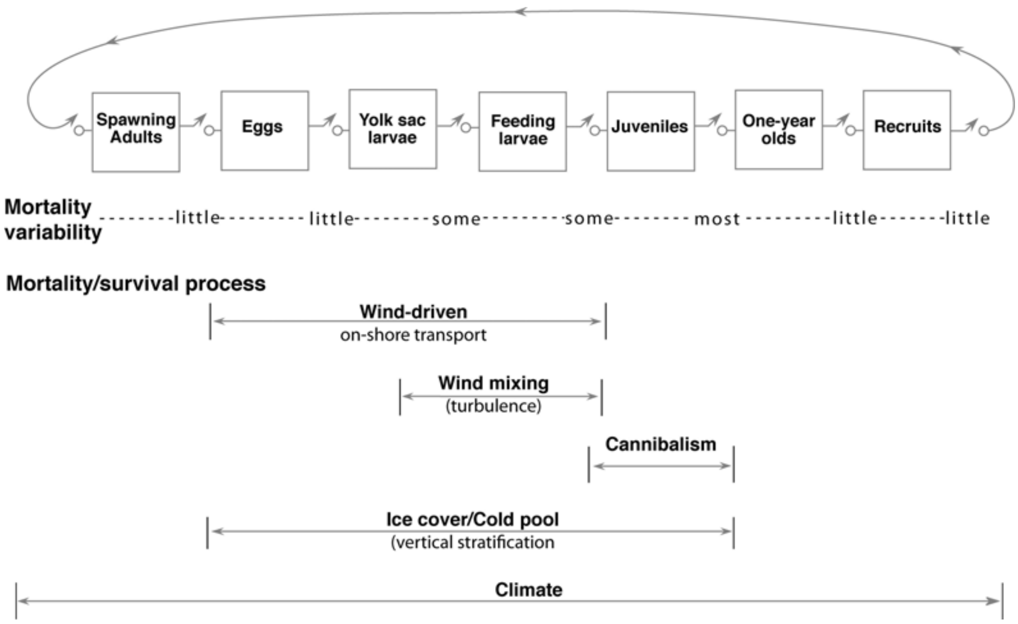

Figure 6.4.2. Southeast Bering Sea walleye pollock conceptual model (from Megrey *et al.*, 1996).

Conceptual models are not stagnant. They evolve as new information and understanding become available. For example, the original Gulf of Alaska pollock conceptual model (Figure 6.4.1) has recently been modified to include the effects of regime-scale climate impacts, as well as predation and competition effects (species-to-species interactions) known to be important at the ecosystem level (Bailey, 2000; Bailey *et al.*, 2005; Megrey and Macklin, unpublished report).

6.5 Forecasting accuracy

How accurate do recruitment forecasts have to be before they become useful? This is a difficult yet relevant question that needs immediate research attention. A recent paper by De Oliveira and Butterworth (2005) offers a concrete example of a possible approach. The premise in this paper was that environmental indices that provide short-term predictions of recruitment have the potential to improve the average yield from highly productive resources that sustain recruit fisheries without an associated increase in risk (of resource "collapse"). This paper's authors asked the question, how accurate does an environment-dependent, spawner–recruit relationship have to be before it affects management decisions? Specifically, what are the benefits of using environmental indices to set appropriate total allowable catches? Through a controlled simulation experiment, they concluded that an environmental index needs to explain roughly 50% or more of the total variation in recruitment ($r^2 \geq 0.5$) before the management procedure starts revealing benefits in terms of the summary performance statistics for risk and average catch. Having similar quantitative information on recruitment forecasts from ICPBM models would help frame the circumstances in which it could prove to be of benefit.

If an index derived from an ICPBM is to be used for recruitment forecasting, it is critical to assess its accuracy and to build trust in its ability to forecast.

6.6 Techniques for forecasting

Forecasts can take many different forms. They can take the form of quantitative annual estimates of absolute abundance (e.g. there will be 5.5 billion recruits next year). We do not believe these are very useful, and they are difficult to produce with any accuracy and precision. They can also be qualitative. For example, the forecast could be given in terms of recruitment being in a particular state — below average, average, and above average (low, medium, and high) — with appropriate methods used to define, in operational terms, states such as long-term averages or quantiles (33%, 50%, or 66%) based on observed recruitment trends. Rothschild and Mullen (1985) give a good example of how recruitment information (from data or models) can be usefully described by non-parametric classification based on Markov chains. Finally, a recruitment forecast could be the result of an ensemble estimate from numerous stochastic-forecast implementations. The forecast can be delivered as a probability statement; for example, the probability of achieving a given recruitment level or state based on x conditions and y assumptions is 10%. The most appropriate form depends on many factors including many that have been discussed above, such as for whom the forecast is being prepared, how it will be used, the required accuracy, and the required forecast horizon.

A caution should be offered regarding the use of recruitment estimates from stock-assessment models to calculate metrics as described above. Changes/updates in annual stock-assessment/cohort-analysis models and resulting recruitment estimates make the most recent estimates of "recruitment" somewhat of a moving target. Stock-assessment models estimate recruitment by summing all fish from a cohort (all individuals with the same birth year) that have died as a result of the fishery (i.e. the catches) and then including the fish that have died from natural causes (also estimated by assuming a particular rate of natural mortality). In other words, the recruitment estimate is the population that would have existed in order to generate the observed catches. The data point of most interest is usually the current year. If a cohort is still contributing to the catch, then in next year's assessment, an additional year of catches and losses from natural mortality will increase the recruitment estimate relative to the current year. The recruitment estimate will gradually increase over time and finally stabilize once the cohort is completely fished out (i.e. no more individuals of the cohort survive to add to the catches).

6.7 Philosophy of modelling

Approaches to understanding mechanisms that regulate recruitment in fish have increasingly taken an individual-based approach. This approach can be justified on two general grounds. First, field research into recruitment processes in fish has demonstrated that the individuals that survive early life often possess a unique suite of genotypic or phenotype traits that are not simply a random draw from the distribution present at spawning. For example, numerous studies involving otolith microstructure have demonstrated that survivors are selected from a narrow window of the original distribution of birthdates. Other research has revealed selection based on growth rate, size at settlement, spawning location, and maternal influence. Together, these studies have highlighted the fact that we would probably not understand mechanisms regulating recruitment by measuring mean rates; instead, we needed to characterize the sources, patterns, and consequences of variation among individuals in early life traits and understand why the unique subset of traits possessed by recruits conferred a survival advantage.

The second justification for individual-based approaches invokes the importance of spatial processes in regulating recruitment. Sinclair and Iles (1988) proposed a member-vagrant hypothesis in which population persistence relied upon the existence of closed trajectories that allowed surviving larvae to complete their life cycle. Those larvae that "followed" appropriate trajectories became members of the reproductive population; individuals that "followed" inappropriate trajectories were lost to the reproductive population. This hypothesis, built on the existing understanding of the importance of population structure within a species, emphasizes the importance of the spatial location of larvae at different points in development on their subsequent survival.

Coupled physical–biological models addressing questions involving fish early life histories have typically adopted an individual-based approach. The majority of such models have used a grid-based hydrodynamic model to predict currents at nodes on the grid, which are then used in a Lagrangian particle-tracking algorithm to move particles that represent the early life stages around the model domain. For example, in one of the earliest applications of such models, Bartsch and colleagues (Bartsch, 1988, 1993; Bartsch *et al.*, 1989) considered the trajectories of herring larvae in the North Sea. The model results indicated the importance of a retentive area off the east coast of Scotland. Subsequently, ICPBMs have become more sophisticated in both the representation of the current fields and the biological representation of individual fish. Such models have been used to quantify the contribution of different spawning locations to recruitment, the role of physical processes in regulating feeding, and the influence of mortality on spatial distributions.

However, it is vital to assess and separate the biological motivations for individual-based approaches to the study of fish populations from the computational motivation. Computationally, individual-based approaches are attractive because they elegantly combine the grid-based, spatially specific predictions of hydrodynamic models with biological processes. In so doing, such models portray individuals that differ with respect to their trajectories and thus their exposures to environmental forcing. To ease computational demands, population-level predictions are derived by expanding the predictions for a single particle by a multiplier to represent the contribution to the population. This approach implicitly assumes that all variability in early life history is spatially determined. Simply stated, this approach assumes that all variability is caused by differences among the trajectories followed by individuals, and not by inherent biological interindividual variability. The approach emphasizes the importance of member–vagrant-type ideas at the expense of phenotypic variability among individuals. Not all models make this assumption. A few do include and sample from distributions of traits. For example, in their detailed model of feeding, Fiksen and Mackenzie (2002) sampled from distributions of reactive distances to estimate feeding incidence. However, ICPBMs of the entire early life history that incorporate inherent interindividual variability have yet to be developed. Whether or not the development of such models is important depends entirely on how total phenotypic variability is partitioned between spatially derived sources and inherent interindividual differences. This partitioning is, as yet, unexplored and unquantified.

7 Looking to the future: recommendations and research needs

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The goal of this section is to summarize the major recommendations and research needs that were identified during the WKAMF workshop and in the process of developing this Manual of Recommended Practices. We address and elaborate on the six major themes necessary to advance the field of modelling physical–biological interactions in the early life stages of fish that were identified by WKAMF participants.

1) Validation and sensitivity methods
2) Model complexity
3) Physics
4) Energetics
5) Mortality
6) Behaviour and cues

High-quality data and improved and widely implemented methods for model validation are fundamental needs that limit the ultimate utility of fish early-life models and the advancement of the field. Consistency of model with observations is important, and data quality is paramount. Methods of model–data comparison need to be applied and developed. In addition, the validity of quantitative metrics should be addressed. Central to the issue of validation is the availability of good-quality data at the appropriate resolution. All too often, modelling is seen as a cheap(er) alternative to empirical work, particularly in the marine field, where data acquisition is challenging and expensive. Modellers are expected to work with data that are sometimes old or of questionable quality, and with coarse spatial and/or temporal resolution.

These problems affect not only model validation, but also initialization (boundary and initial conditions) and operation (forcing data). It is vital to communicate to the non-modelling community that the quality of the biophysical modelling output depends strongly on a basic knowledge of physical and biological processes, and on the quality of empirical data used for model initialization and validation. Fortunately, technical advances in field-, laboratory-, and data-processing tools are likely to result in considerable progress in the near future, although they may not completely replace the more traditional, labour-intensive and knowledge-rich methodologies. Another challenge is the development of data-assimilation methodology to incorporate observations of physical and biological parameters (especially those from automated data-acquisition systems) into biophysical models (see Section 4 Application 1: adaptive sampling). This is a critical requirement if we are to make biophysical models operational.

The model is a platform that coherently integrates multidisciplinary knowledge. Appropriate model complexity is a research need. Models should be as simple as possible but as complex as necessary. Additional layers of complexity should only be added after (i) assessment of need, based on the objectives of the modelling endeavour; and (ii) analysis of the sensitivity of the model to the process(es) under consideration. The GLOBEC "rhomboid approach" (with complexity greatest at the level of the target organism and decreasing towards higher and lower trophic levels; De Young *et al.*, 2004) was suggested as a conceptual framework for addressing model complexity. Although model complexity may be constrained by lack of knowledge of physical and/or biological processes and/or operational limitations (e.g. computing hardware or software), these limitations should be seen as a challenge to overcome, not as reasons for making do with the *status quo*. The modelling process should explicitly document knowledge gaps, thus providing the direction for advancing the field.

After choosing the appropriate complexity, the next step is to document model sensitivity. Sensitivity analysis of model outputs to variations in model complexity or parameter values should be considered thoroughly. Methods for sensitivity analysis of complex models have been developed in industry, including group screening, simulation designs, partial regressions, and benchmarking. Their applicability and usefulness for biophysical IBMs is a challenging research need. An introduction on the topic can be found in Kleijnen (2005).

Hydrodynamic model predictions critically influence biological predictions. Basic improvements in understanding of turbulence and in predicting mixing and circulation patterns will advance the field of larval fish modelling. Ensemble methods (combining a suite of simulations that have slightly different starting conditions or model assumptions; Gneiting and Raftery, 2005) and probabilistic approaches (e.g. Brickman *et al.*, 2007) offer promising techniques that should be implemented when possible. We need to (i) develop measurements of turbulence and any other relevant physical and biological parameters at scales that are appropriate to predator–prey interactions; and (ii) parameterize encounter, capture, and feeding processes at scales from 1 mm to 1 m (see below). It is important, therefore, to develop sampling devices or approaches that allow increased resolution in space or time, in addition to data processing and visualization tools, that allow researchers to interpret large volumes of complex multidimensional and multidisciplinary data.

The choices of Lagrangian model type and implementation techniques are not consistent, despite the fact that these models provide the basic structure for individual-based, coupled physical–biological models (ICPBMs). For Lagrangian particle tracking, a standard set of test cases should be established and published (see Section 2 Particle tracking), both in the literature and on a dedicated website, for advection and subgrid-scale turbulence models in the horizontal and vertical directions. The tests should be easy to implement, cover the practical issues, and become standard procedure. From a technical standpoint, theory development/elucidation is needed to determine whether or not numerical methods satisfy theoretical requirements (e.g. when subgrid-scale turbulence and directed swimming are combined in particle-tracking models). The need for a systematic assessment of Lagrangian model types and implementation techniques is elucidated by the differences in recommendations between sections of this manual. The authors of Section 2 recommend using a random displacement model (RDM), whereas those of Section 5 recommend the use of a Lagrangian stochastic model (LSM). These apparent contradictions may stem from dissimilarity in the time- and space-scale of the hydrodynamic models used by the authors. The choice of appropriate model remains an active area of research; clarification is needed if the field is to evolve.

Fundamental information is needed on the biological processes of mortality, behaviour, and energetics to advance models of the early life of fish. These stage-dependent, and often species-specific, processes pose challenges for investigation, but recent advances in field and laboratory techniques will most probably revolutionize the field of larval fish modelling. The need for improved understanding of basic processes is exemplified by the discrepancy in the assumption that fish larvae are food-limited (Section 3.5 Behaviour and settlement) or are not food-limited (Section

3.3 Growth). This and other differences in perception between sections could simply be based on the ecosystem in which the authors are most experienced (e.g. temperate vs. tropical) and point to the need to assess and unify our understanding of biological processes across taxa and ecosystems. Despite these differences, it is becoming broadly recognized that it may not be sufficient just to incorporate "means" into our models. Instead, the effect of individual variability (including "extreme" values) needs to be assessed, because the survivors may not just be the "lucky few", but may be drawn from the extremes of a given distribution (e.g. fastest growers). In many current biophysical models, individual variability is purely the result of spatial (environmental history) variability.

The following are some specific recommendations relevant to biological processes.

- Better information on the underlying mechanisms that drive spatial and temporal patterns in spawning, including adult characteristics (e.g. behaviour, maternal effects), is critical for defining appropriate initial conditions for biophysical modelling of early life stages of fish (e.g. the formulation and validation of egg-production models).
- We need to understand the mechanisms of internal (physiology) and external (environmental signals, prey, predators) drivers. The influence of the light environment, as affected by geography, seasonality, primary production, suspended sediment, and associated sources of freshwater, needs to be evaluated.
- There is a clear need for field/laboratory studies of behaviour, especially related to horizontal orientation/directed swimming and the physical/biological factors that cue larval behaviour. We should challenge established parameter values (e.g. swimming speeds) in experimental and more realistic settings, and compare them (at least for some species). In addition, some generally accepted assumptions should be assessed, such as the absence of directed swimming among temperate fish species or the parameterization of behaviour based on similarity in phylogeny (when data are lacking for the species of interest).
- Techniques for validation of larval transport predictions and connectivity patterns are needed. Although methods for validating hydrodynamic and particle-tracking models are either well established (for hydrodynamics) or in development (for particle tracking), a systematic set of methods is needed for validation of biological trajectories (i.e. ones that include behaviour). High-frequency sampling permitted by underway identification systems or genetic-based approaches may provide the means of accomplishing this.
- A variety of growth models have proven to be very sensitive to assimilation efficiency as well as to changes in size spectrum of prey; a better understanding of the causal mechanisms is required. Mechanistic (bioenergetic) modelling of growth is attracting considerable interest, probably as a result of the proliferation of ecosystem models that provide prey fields for the larvae. The sensitivity of these models to assumptions and uncertainties in parameter values/functional relationships should be carefully assessed.
- Predictions of predator feeding rates (i.e. mortality on larvae) from laboratory, field, and simple models differ significantly (by tenfold in some cases). Consequently, modelling predator feeding requires improved ob-

servations and greater effort to validate any model developments. Mortality is often not incorporated in biophysical models of fish early life stages or is modelled as a size-dependent function with low (or no) mechanistic content. The development of mechanistic models of predation is fraught with difficulties: predation efficiency of invertebrates and fish is typically influenced by a suite of environmental factors (light, turbulence, the prey environment, prey "behaviour" in general), and the dynamic representation of predator fields is a momentous task. However, it is clear that, for an adequate representation of mortality in the models, more effort is required to include such processes.

- The role of density-dependence in nature needs to be further investigated and, where appropriate, incorporated into models. This is also related to the requirement to increase our understanding of the ecology of the early juvenile stage. The arrival at (and survival within) suitable nursery areas has been identified as critical to year-class strength in numerous species, but our knowledge of the main ecological processes during that period is still largely inadequate.

The use of ICPBMs has increased our understanding of the interacting factors that influence fish early life. Although research needs are many, the field holds great promise for advancing our understanding of fish-population variability and the influence of changing climate on fish stocks and the humans who depend on them. Further advances in the field of larval fish modelling and prediction will probably arise from dynamic teams of scientists who can unite laboratory, field, and modelling expertise. Importantly, for the utility and impact of these models, the translation of results to managers, stakeholders, and the general public is desirable. Scientists should collaborate in the communication process to ensure correct interpretation and use of model results.

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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.

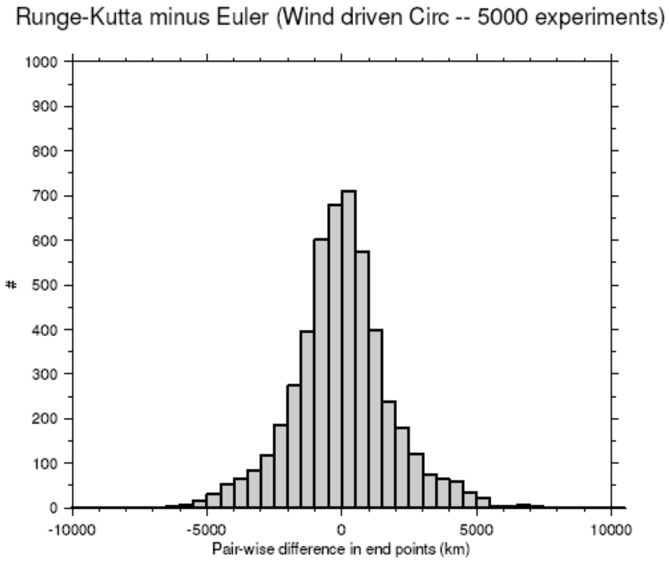

Figure A.1.1. Comparison of EU with RK time-stepping routines.

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:

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

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 ξ_1, ξ_2, ξ_3. . . . for $B_h - B_0$, $B_{2h} - B_h$, $B_{3h} - B_{2h}$ . . .. These ξ_i should all be Gaussian distributed with mean 0 and variance *h*. Next, double the time-step to obtain a recursion for $Z_t^{(2h)}$:

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

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 2*h*; 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 $H^2/4\overline{D}$, where $\overline{D}$ 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.

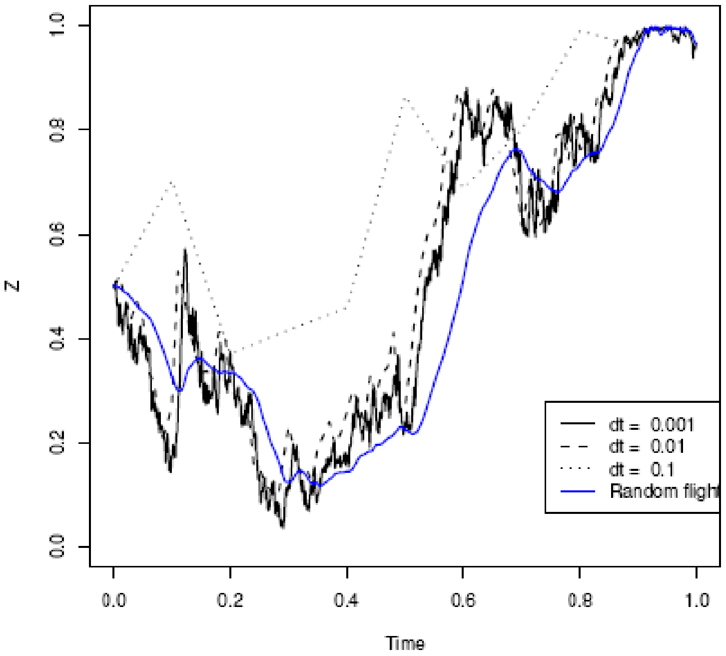

Figure A.2.1. The simulated vertical position of a particle, with three different time-steps and the same stochastic realization.

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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