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.
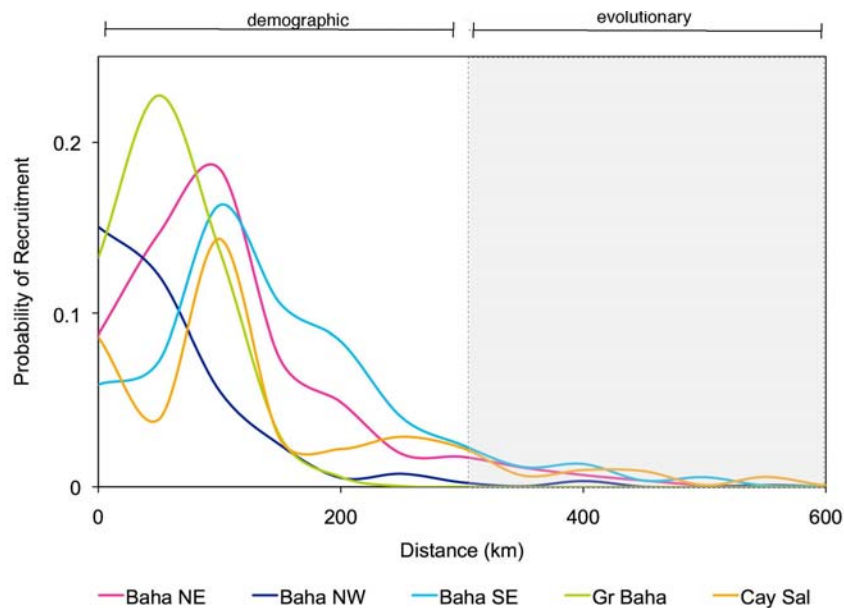

Figure 5.4.1. Dispersal kernels or probability of dispersal to a suitable nursery habitat, showing the spatial scales associated with a 30-day dispersal of fish larvae for various regions in the Caribbean. The transition to the shaded area indicates the range of distances over which dispersal (and perhaps 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 proc-

esses 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,

$$dx/dt = u_m + u', \tag{35}$$

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 ($D_{t\text{-off}}$) and time-averaging frequencies (T_{avg}). The CPU cost (M_t) can be calculated as a function of the change in online ($D_{t\text{-on}}$) to offline particle time-step and time-averaging frequency:

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

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.
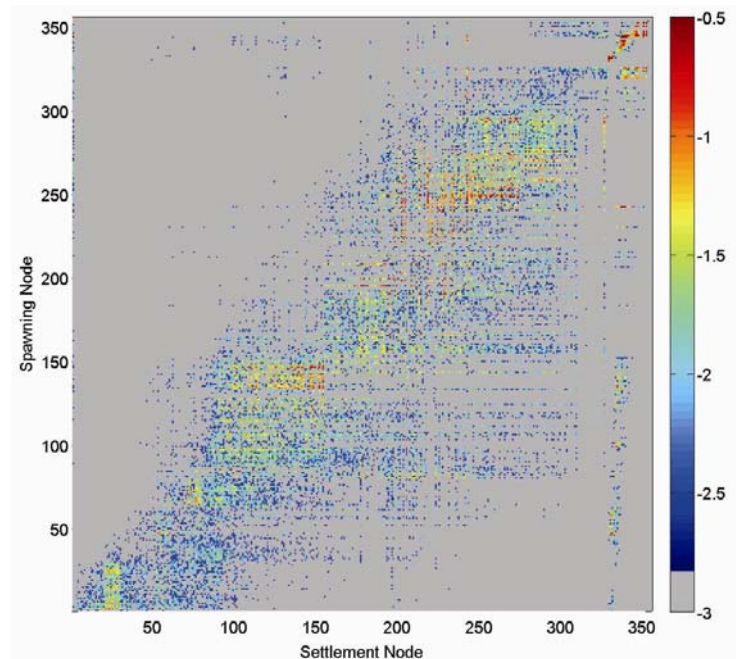

Figure 5.10.1. Transition probability matrix. The contents of a given matrix element describe the probability of individual larvae making the transition from its source population (*y*-axis) to the destination population (*x*-axis), computed over several generations. Elements along the diagonal represent 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 Aij = 1, if populations i and j are connected by edges, or Aij = 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).
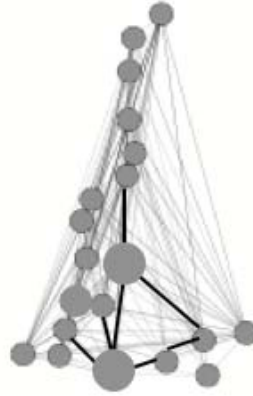

Figure 5.10.2. Population Connectivity Network. Habitat patches are represented by nodes, for which size represents population density. When larvae from a given patch reach a downstream site, a dispersal connection is made. The thickness of the edge reflects the strength of the connection. This theoretical 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).
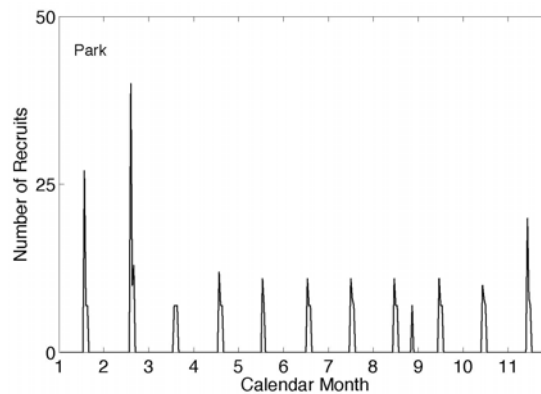
Figure 5.11.1. Daily predicted larval supply of *Sparisoma viride* for the months February–December 2004 south of Sea Park in the Bahamas in ca. 50 km² coral reef habitat. Note that the *y*-axis represents simulated larvae and cannot be interpreted as an absolute measure of larval supply.

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).

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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