

# Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean

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## ABSTRACT

Pelagic organisms' movement and motion of buoyant particles are driven by processes operating across multiple, spatial and temporal scales. We developed a probabilistic, multi-scale model, the Connectivity Modeling System (CMS), to gain a mechanistic understanding of dispersion and migration processes in the ocean. The model couples offline a new nested-grid technique to a stochastic Lagrangian framework where individual variability is introduced by drawing particles' attributes at random from specified probability distributions of traits. This allows 1) to track seamlessly a large number of both actively swimming and inertial particles over multiple, independent ocean model domains and 2) to generate ensemble forecasts or hindcasts of the particles' three dimensional trajectories, dispersal kernels, and transition probability matrices used for connectivity estimates. In addition, CMS provides Lagrangian descriptions of oceanic phenomena (advection, dispersion, retention) and can be used in a broad range of oceanographic applications, from the fate of pollutants to the pathways of water masses in the global ocean. Here we describe the CMS modular system where particle behavior can be augmented with specific features, and a parallel module implementation simplifies data management and CPU intensive computations associated with solving for the tracking of millions of active particles. Some novel features include on-the-fly data access of operational hydrodynamic models, individual particle variability and inertial motion, and multi-nesting capabilities to optimize resolution. We demonstrate the performance of the interpolation algorithm by testing accuracy in tracing the flow stream lines in both time and space and the efficacy of probabilistic modeling in evaluating the bio-physical coupling against empirical data. Finally, following recommended practices for the development of community models, we provide an open source code with a series of coupled standalone, optional modules detailed in a user's guide.

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## Software availability

Name of software: Connectivity Modeling System

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Contact details: [cparis@rsmas.miami.edu](mailto:cparis@rsmas.miami.edu)

Year first available: 2012

Hardware required: Linux system

Software required: Fortran 90 compiler, C-compiler, and NetCDF libraries

Program language: Fortran 90

Program size: 1.6 MB

Availability and cost: Free Open Source Software (OSS) declared under GNU Lesser General Public License

Availability: download from <http://code.google.com/p/connectivity-modeling-system>

## 1. Introduction

Lagrangian numerical modeling is an increasingly popular approach among physical and biological oceanographers seeking to better understand the influence of transport processes on marine ecosystems. The variability of major currents and of recruitment, population connectivity, the spread of invasive species and of marine diseases, the transport and fate of atmospheric dust and pollutants, all are examples of phenomena that can be investigated using a particle-tracking framework. Models are indeed the best tools available to learn how dynamic marine ecosystems operate by testing hypotheses and teasing apart the role of often non-linear factors.

Individual movement is the result of interactions with external factors, and as such is of central importance to almost any

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ecological and evolutionary process (Nathan, 2008). To get a mechanistic understanding of these processes, it becomes thus important to develop probabilistic, Individual-Based Models (IBMs) that can solve for individual attributes (Grimm et al., 2006). For most marine organisms with sessile, benthic or relatively sedentary adult phases, movement is often limited to their larval phase and often referred to as “dispersal”. However, these early life history stages are never entirely passive (Leis, 2006) and represent a unique opportunity for individuals to “migrate” between geographically separated populations using the currents. In regions of complex ocean circulation patterns, transport may differ widely at the individual level as a result of changing environmental conditions during the spawning season. These changing factors may result in variable probability of survival and dispersal to different distances often portrayed in terms of the “dispersal kernel” (Nathan, 2006), ultimately leading to multiple adaptive routes and difference in stock structure.

During the last decade, numerical models of the early life stages of marine organisms have emerged as a powerful tool for investigating the linkages between mixing of sedentary populations and the spatial history of successful migrants. These models are generally referred to as coupled bio-physical models. In such approaches, the early life of target species and their interaction with the environment is simulated by combining a stochastic biological model with ocean circulation models. These models typically use a Lagrangian particle-tracking framework to deal with explicit individuals, and use information on currents and environmental conditions from ocean circulation models to track the movement of a large number of individuals through space and time (Paris et al., 2007).

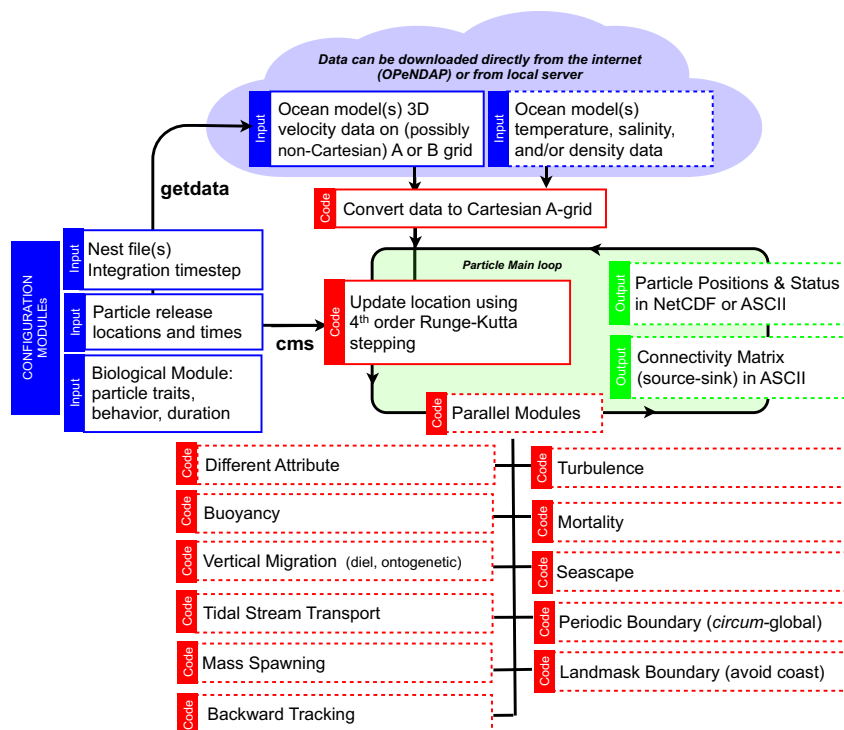
In many applications, several hundred millions of abiotic or biotic particles need to be simulated by coupling their varying traits with an ocean circulation model. In addition, many particles (or larvae) might have to be advected with the currents along a very long distance (Fiksen et al., 2007). Tracking particles for longer time

periods, from shallow coastal areas to the deep ocean and back, is typically solved with a tradeoff between domain extent and spatial resolution. It thus becomes critical to use simultaneously several distinct circulation models to evaluate coastal and ocean scale conditions in order to improve the accuracy of Lagrangian predictions. These requirements are often computationally complex and very demanding, with large data management efforts that can limit the scope of the applications.

Here, we present the Connectivity Modeling System (CMS) version 1.0. The CMS is a multi-scale bio-physical modeling system, based on an Individual-Based Model (IBM) and Lagrangian framework. It has been developed originally to study complex larval migrations (Paris et al., 2005a, 2005b) and give probability estimates of population connectivity (Cowen et al., 2006). The CMS can also provide a Lagrangian description of oceanic phenomena of advection, dispersion, and retention with great precision (van Sebille et al., 2012a, 2012b), and can thus be used for the dispersion of abiotic particles such as pollutants (Paris et al., 2012). We describe the standalone sub-models (modules) that have been developed for this open-source first version 1.0 in Section 2 (Model Description) to facilitate community contribution. These modules are optional and can be turned on and off in the IBM to describe particle behavior and environmental attributes. We then assess the skill of the non-biological part of the CMS and the capabilities of the modeling system to represent biological processes by performing with a number of test cases in Section 3 (Model Evaluation).

## 2. Model description

Speed and efficiency are of the utmost importance in the applications that the CMS is designed for, therefore the CMS is written in Fortran and should be installed on Linux systems with Fortran and NetCDF libraries installed. A flow chart of the model code, input, and output of the CMS is shown in Fig. 1. The CMS operates



**Fig. 1.** Flow chart for the CMS, with code in red, input in blue, and output in green. Optional modules and input/output is shown as dashed boxes. In this version 1.0 of the CMS, ten different modules are available that can be turned on and off at run-time. The optional modules are referenced from the model description section.

offline, so it uses archived ocean velocity data. The CMS can access on-the-fly ocean circulation data via OPeNDAP (Open-source Project for a Network Data Access Protocol) or access local files of archived blocks of data. The CMS is model-independent and can be coupled to ocean circulation model data on Arakawa grids (A-grids or B-grids), in (possibly tilted) Cartesian coordinates.

The CMS is multi-scale, particles can be tracked seamlessly over a series of multiple nested-grid ocean model domains. The nesting is independent from the ocean modeling system (e.g., nest 1 can be HYCOM data, while nest 2 is ROMS).

The CMS is a parallel implementation of a stochastic particle-tracking model and provides the computational efficiency of evaluating a full range of transport and fate variability. Moreover, the attributes of individual particles are drawn at random from a set distribution with specified boundary conditions. It can run in parallel (i.e., using message passing interface, MPI) ensemble simulations of millions of passive and/or active particles over large time scales. Its main core is a fourth order Runge–Kutta stepping scheme that is applied both in space and time. In addition, the interpolation of the water properties to the position of the particle is adaptive. The CMS performs a tricubic interpolation ( $4 \times 4 \times 4 = 64$  points) over the three dimensions by fitting a third-degree polynomial to the values on the four points along the dimension. If one or more of each 64 points is found on land, the CMS tries a trilinear interpolation ( $2 \times 2 \times 2$ ) whereby only 8 neighboring points are needed for this interpolation.

The output of the CMS is designed to facilitate easy and quick post-processing of both oceanographic and connectivity applications by providing two types of output formats 1) the Connectivity Matrix Output (source/sink), and 2) the Trajectory Output (location/status), with the latter in two type of output format (NETCDF or ASCII). In addition, the CMS has the option to either generate a single file of the ensemble simulations (e.g., oceanographic application) or multiple files corresponding to different initial conditions (e.g., connectivity application).

The CMS can be run using many different types of vertical movement by simulating various behavior and transport processes in the velocity of individual particles (i.e., buoyancy and sinking, ontogenetic and diel vertical migration, tidal stream transport, upwelling and subduction, and any combinations of these types of vertical movements).

The CMS is designed as a modular system, where particle behavior can be augmented with specific features by adding different modules. Each of these modules can be turned on or off within the configuration files, without need for recompilation of the code. In this version 1.0, the following modules are available. The first five modules describe vertical (1–4) and stochastic (5) movements. The next three modules deal with larval traits (6–7) and spawning grounds (8), and the final two modules (9–10) describe the interplay of the particles with the benthic and coastal boundaries. The CMS is particularly good at moving particles along complex and steep topography.

#### 1. Buoyancy module:

Lagrangian particles are neutrally buoyant and follow the flow, but the eggs of most marine fish and invertebrates are positively buoyant at the time of release. Their initial transport may be one of the major factors impacting the recruitment success (Mullon et al., 2002). How millions of eggs are initially transported and where they end up before hatching (e.g., fish) or settling (e.g., coral) depends on the interplay between their density and the flow stratification and turbulence. In this module we use the Stoke's equation to move particles through inertial motion, parameterized by a specified density and size. The terminal velocity ( $V_T$ ) of individual

particles varies in time and space, driven by the temperature and salinity output by the ocean circulation model.

$$V_T = w + \left( 9.81 d^2 * \Delta\rho \right) / (18 * \mu) \quad (1)$$

where  $w$  (m/s) is the local vertical velocity in the circulation model,  $d$  (m) the particle diameter,  $\Delta\rho$  the density difference between the particle and the fluid, and  $\mu$  (kg/s m) the viscosity of the fluid computed as follows:

$$\mu = 1.88 \cdot 10^{-3} - (T * 4 \cdot 10^{-5}) \quad (2)$$

where  $T$  (°C) is the temperature of the water. Note that for this module to work, the water temperature has to be available in the oceanographic data.

#### 2. Vertical migration module:

Most marine larvae undergo ontogenetic vertical migration whereby they swim or adjust their buoyancy to move downward from the upper part of the water column to deeper layers or conversely, upward into the neuston as they age. As a result, vertical distribution patterns can be observed via plankton surveys and can be statistically described as stage-specific probability density distributions with depth. Ontogenetic behaviors are typically species-specific and the center of mass and vertical spread of a particular organism can be constrained by varying environmental conditions. This module takes into account the observations by forcing individual particles to move vertically as specified by a matrix ( $m \times n$ ) of probability density distribution in the water column ( $m$ ) through time ( $n$ ). Similarly, this module can be used to describe diel vertical migration, whereby the larvae move toward the surface at night and dive to a specified depth during the day, or vice versa.

#### 3. Tidal transport module:

Many estuarine fish and invertebrate species undergo vertical migrations that are coordinated with phases of the tide in order to achieve horizontal movement. This general mechanism is known as Selective Tidal Stream Transport (Criales et al., 2011), and more than one behavior has been associated with it. A flood-tide transport occurs when organisms use the flood phase for shoreward transport and immigration to estuaries, while an ebb-tide transport or ebb-phased migration is used for seaward transport and out-migration from estuaries. The CMS can use sea surface height fields from the ocean circulation model to take this tidal movement into account.

#### 4. Mass spawning module:

Many organisms gather in large aggregations for synchronized mass spawning. These gatherings produce enormous numbers of gametes concentrated in space and time, that initially disperse as a cloud of buoyant particles, become less buoyant after fertilization, and increase in specific gravity prior to hatching into swimming larvae. The CMS can directly resolve the transition from the egg to the larval stages with this mass spawning module, which is a combination of the Buoyancy and Vertical Migration modules.

#### 5. Turbulence module:

A random component can be added to the motion of the particles to represent three-dimensional turbulent diffusion. This random displacement module (RDM) assumes that turbulence is isotropic in

the horizontal direction recommended for oceanographic applications (Brickman et al., 2009; Brickman and Taylor, 2007).

$$X^{n+1} = X^n + u\Delta t + (2K_x/\Delta t)^{1/2} Q \quad (3)$$

where  $X$  is displacement in the  $x$  direction,  $K_x$  the turbulent diffusion coefficient and  $Q$  is a random variable with zero mean and unit variance. This module has the potential to be modified to a biased random walk (Codling et al., 2004) to simulate directed horizontal swimming of larvae in realistic currents and complex habitat patches (Staaterman et al., 2012).

#### 6. Mortality module:

Larval mortality is an important parameter that can change the dispersal distance of an organism, influencing the structure of the metapopulation (Paris et al., 2007). Larval mortality rates are not constant throughout larval life and larvae acquire and lose competence at varying time/age. As a result, the pelagic larval duration is often very plastic. Similarly, abiotic particles may have important fate processes that need to be taken into account during dispersion (Houde, 1989). Here we introduce a simple half-life mortality function formulated as an exponential decay that can be further modified to match experimental or observational survivorship curves. For example, coral planulae mortality rate increase with age (Connolly and Baird, 2010), while mortality of fish larvae decrease with pelagic duration (Paris, 2009).

$$S_{t+1} = S_t * e^{-\lambda t} \quad (4)$$

where  $S_{t+1}$  is the proportion of larvae surviving at time  $t+1$  and  $\lambda$  the mortality rate or decay constant computed as:

$$\lambda = \ln(2)/(PLD/2) \quad (5)$$

where PLD is the pelagic larval duration or the maximum competency period. This equation can be readily changed in the code to fit empirically-derived survivorship curves (Graham et al., 2008).

#### 7. Different particle attributes module:

Early life history traits such as egg size, density, and larval mortality rates are bounded by species-specific values. Yet, these traits are variable among individuals of a same species. This is reflected in this module, where the particles' attributes (or traits) are represented by a probability distribution function within a range of minimum and maximum values. Individual particle attributes are drawn at random within the specified distribution and boundary conditions. Similarly, the dispersion of abiotic particles can have varying characteristics and fate. The CMS can simultaneously advect particles with different attributes.

#### 8. Backtracking module:

The CMS can integrate the velocity field backward to backtrack the birthplace of larvae collected during plankton surveys or the origin of pollutants in the sea. This module should be coupled with the Turbulent and Vertical Migration modules. Indeed, both spatio-temporal resolution of the turbulent and hydrodynamics fields, and of the larval swimming behavior are essential to accurate predictions of spawning locations (Christensen et al., 2007).

#### 9. Seascape module:

Polygons are the representation of marine habitats, describing the location of both the spawning and the nursery areas. Within the

CMS, these polygons can be used to simulate two essential processes: release and settlement. Consequently, this module is essential in producing the Connectivity Matrix output.

#### 10. Landmask boundary module:

The CMS is particularly apt for moving particles along complex topography such as steep slopes and convoluted coastlines, avoiding the boundary with a variable spatial interpolation scheme of the velocity field around the particle. Alternatively, the CMS provides the option to stop integration of the particles at the boundary (i.e., make landfall).

#### 11. Parallel module:

The CMS is a parallel implementation of a Lagrangian stochastic particle model and provides the computational efficiency of evaluating a full range of transport and fate variability. It runs in parallel ensemble simulations of millions of passive and/or active particles over large time scales.

Detailed information on the model architecture and algorithms for the 3-D spatio-temporal interpolations of the input and the integration for the various optional modules can be found in the User's Guide provided with the open-source CMS package. The User's Guide also provides information for the setup and implementation of the CMS. The CMS is composed of two main executable programs that are run in sequence to eliminate dependencies and duplications across the oceanographic and biological input. The first program (getdata) accesses the ocean circulation data by reading the nest input files, and the second program (cms) moves and tracks the particles by reading the input parameter and configuration files (Fig. 1). The CMS package also provides some simple Matlab® code for output visualization and matrix-based post-processes.

### 3. Model evaluation

In order to assess the skill and capabilities of both the non-biological Runge–Kutta part of the CMS and the most important biological capabilities and modules, a number of test cases have been performed.

#### 3.1. CMS test in a time-mean idealized flow

In this first test case, modeled after the idealized flow test case suggested by Brickman et al. (2009) we test the ability of particles to trace out a steady flow around an obstacle. The benefit of this test case, where particles are advected around a cylinder, is that the flow field can be analytically solved and the particle trajectories can therefore be assessed against the 'truth'. Following Brickman et al. (2009), we consider the case of a half cylinder of radius  $R$  in the  $x$ – $y$  plane, with the center on the cylinder at  $x = x_0$  and  $y = 0$ . There is a meridionally uniform zonal flow  $u_0$  far from the cylinder. In that case, the steady non-rotational flow around a cylinder is given by the stream function:

$$\psi = \frac{u_0 R^2 y}{(x - x_0)^2 + y^2} - u_0 y \quad (6)$$

Using the identities

$$u = \frac{\partial \psi}{\partial y}, \quad v = \frac{\partial \psi}{\partial x} \quad (7)$$

the stream function can be converted into a flow field, and this flow field can then be used (in netcdf format) as input for CMS, which allows advection of particles around the cylinder.



Fig. 2 shows both the stream function (in colors) and the trajectories of particles released at the open dots, upstream of the cylinder. Here, we consider only those particles that start at  $y > 0$ , but the solution is symmetrical around  $y$ . The particles are advected for one day using a 30 s time step and with the turbulence module turned off. After this one day period, the particles end up at the closed black dots in Fig. 2. The paths taken by the particles almost perfectly follow the stream lines (the colors) and the results are also very similar to those obtained by Brickman et al. (2009), essentially validating the implementation of the fourth order Runge–Kutta scheme in CMS. Note also that, since the landmask boundary module was turned on during these computations, the particles are able to skim closely around the cylinder without making landfall.

### 3.2. CMS test in a simple time-varying flow

In order to test the ability of the CMS to cope with time varying velocity fields, a second test case is considered. In this test case, we use velocity data from an experiment with a freely evolving two-layer primitive equation model, as described in van Sebille and van Leeuwen (2007). The model velocity fields represent an idealized Agulhas ring (see e.g., Beal et al. (2011) for a review of Agulhas rings) propagating through the Southern Atlantic Ocean. Here, we use only the first year of the experiment data, and then specifically the zonal and meridional fields in the upper layer, which have been saved every 10 days.

Particles have been released within the Agulhas ring at the start of the experiment, and the trajectories of the four particles that start out closest to the ring center are shown in Fig. 3a. In a similar experiment using the same velocity data, particles have been released on a line across the ring, and their evolution is captured in a movie which is available as supplementary material (downloadable from <http://code.google.com/p/connectivity-modeling-system/downloads/list>). The time step for the Runge–Kutta method is 1 h in both the figure and the movie, which is relatively large.

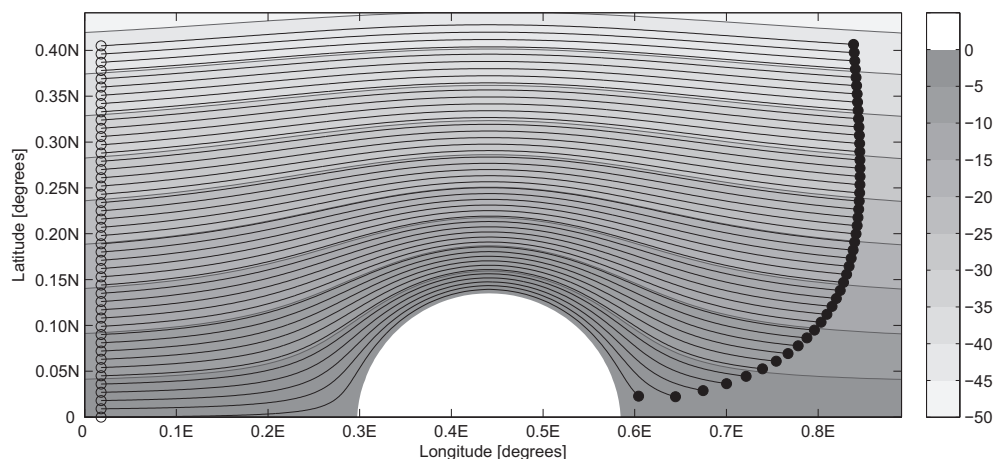
Both from this movie and from Fig. 3, it is clear that the particles that start out near the core of the ring will remain in the ring for the entire one-year period. In particular, the CMS particles in the Agulhas ring keep circulating on approximately the same stream lines (Fig. 3b–e). This is expected from ocean eddy dynamics,

where eddies and rings are capable of capturing and transporting water over large distances (e.g., Flierl, 1981). This result shows that even though the flow patterns is non-linear and the velocity fields were only available every 10 days in this test case, the temporal interpolation is sufficiently good to be able to keep the particles within the rings for extended periods in time.

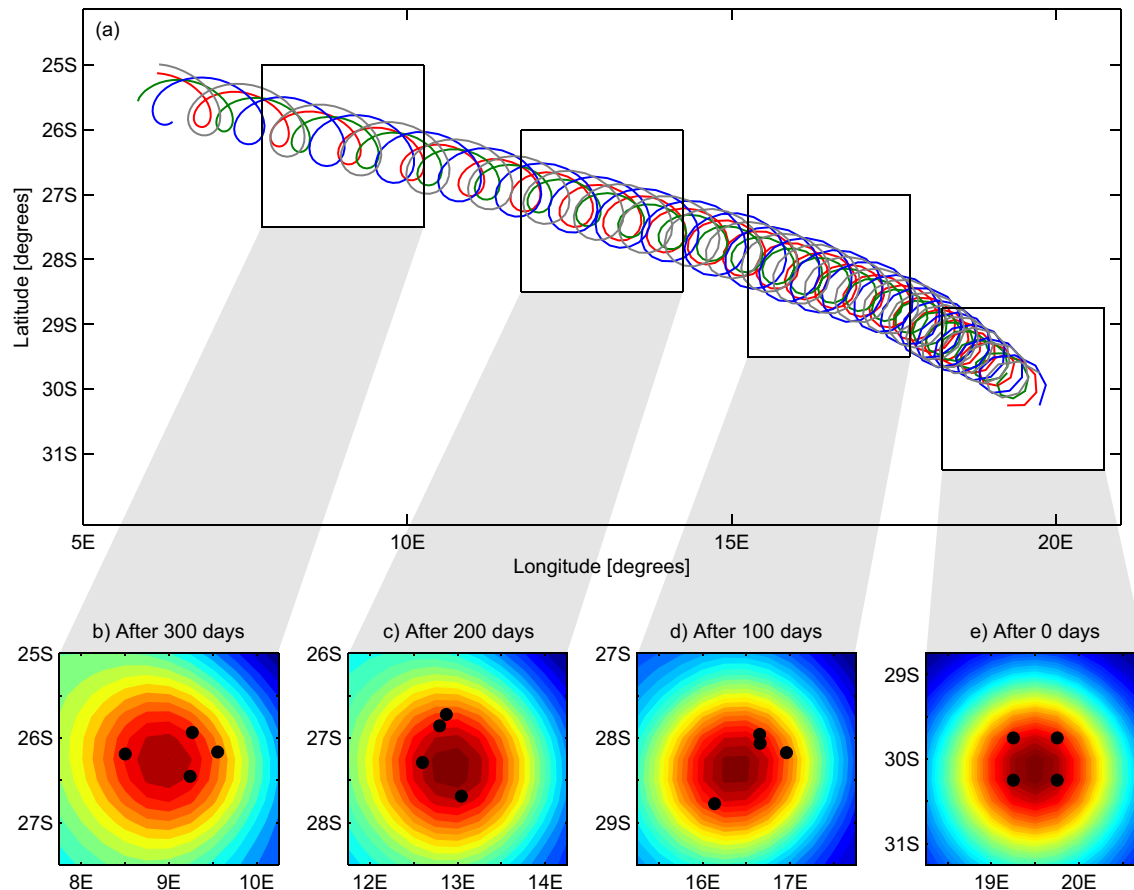
### 3.3. CMS test for “Lagrangian nesting” or multi-scale connectivity

As discussed above, the CMS has a unique multi-scale capability to grab data through OPeNDAP from a hierarchy of nested ocean circulation models and thus optimize resolution of the currents during the larval tracking. The importance of the multi-nested approach is demonstrated in investigating the population connectivity of a common reef fish, the bicolor damselfish, *Stegastes partitus* in the Florida Keys. This small coral dwelling species deposits demersal eggs on a smooth coral reef surface. Thus, the larvae hatch in a few meters of water where they are entrained by the coastal current and settle onto the reef after spending about a month in the plankton. While survival of the larval stages is constrained by the nearshore habitat, they have the potential of dispersing offshore. In addition, the pelagic larva is not passive and migrates in the vertical down to ca. 80 m during development (Paris and Cowen, 2004). Quantification of larval fluxes between source (spawning) and sink (settlement) locations requires the simulation of complex larval behaviors as well as the use of high-resolution models that can capture the complex sub-mesoscale coastal dynamics together with mesoscale oceanographic models (Werner et al., 2007). The latter are typically used for boundary conditions for the higher-resolution simulation models, yet ran separately (i.e., one-way nesting) and have different archived output frequency. So far, larval tracking models are unable to move particles across a series of overlapping OGCMs without re-initializing the particles at the boundaries.

We used a hierarchy of three hydrodynamic models nested one-way within each other (input: 3 Nests, Ocean model 3D velocity, Fig. 1), all based on the community code of the Hybrid Coordinate Ocean Model (HYCOM; <http://hycom.org>, Chassignet et al., 2003): the very high resolution Florida Keys and Florida Straits model (FKeys-HYCOM 1/100°, ca. 900 m; Kourafalou et al., 2009) is nested within the data assimilative regional Gulf of Mexico model (GoM-HYCOM 1/25°, ca. 3.7 km), and the data assimilative Global-HYCOM



**Fig. 2.** Flow around a peninsula, the white obstacle halfway into the model domain where velocities are not defined. The black lines are the trajectories of the particles, with the open circles indicating the starting positions and the black circles the ending positions. The colors denote the values of the stream function used to compute the velocity fields, and the thick white line is the boundary of the region where  $\Psi = 0$  (the ‘peninsula’). At all distances from the peninsula, the CMS method performs well, leaving no particles on the peninsula and capturing the exact solution by following perfectly the stream lines. The Runge–Kutta 4th-order method is used with tricubic (i.e.,  $4 \times 4 \times 4 = 64$  points) interpolation from the grid cell centers to the particle positions and a time step of 30 s was used. The avoid-coastline module is turned on, the turbulence module is turned off.

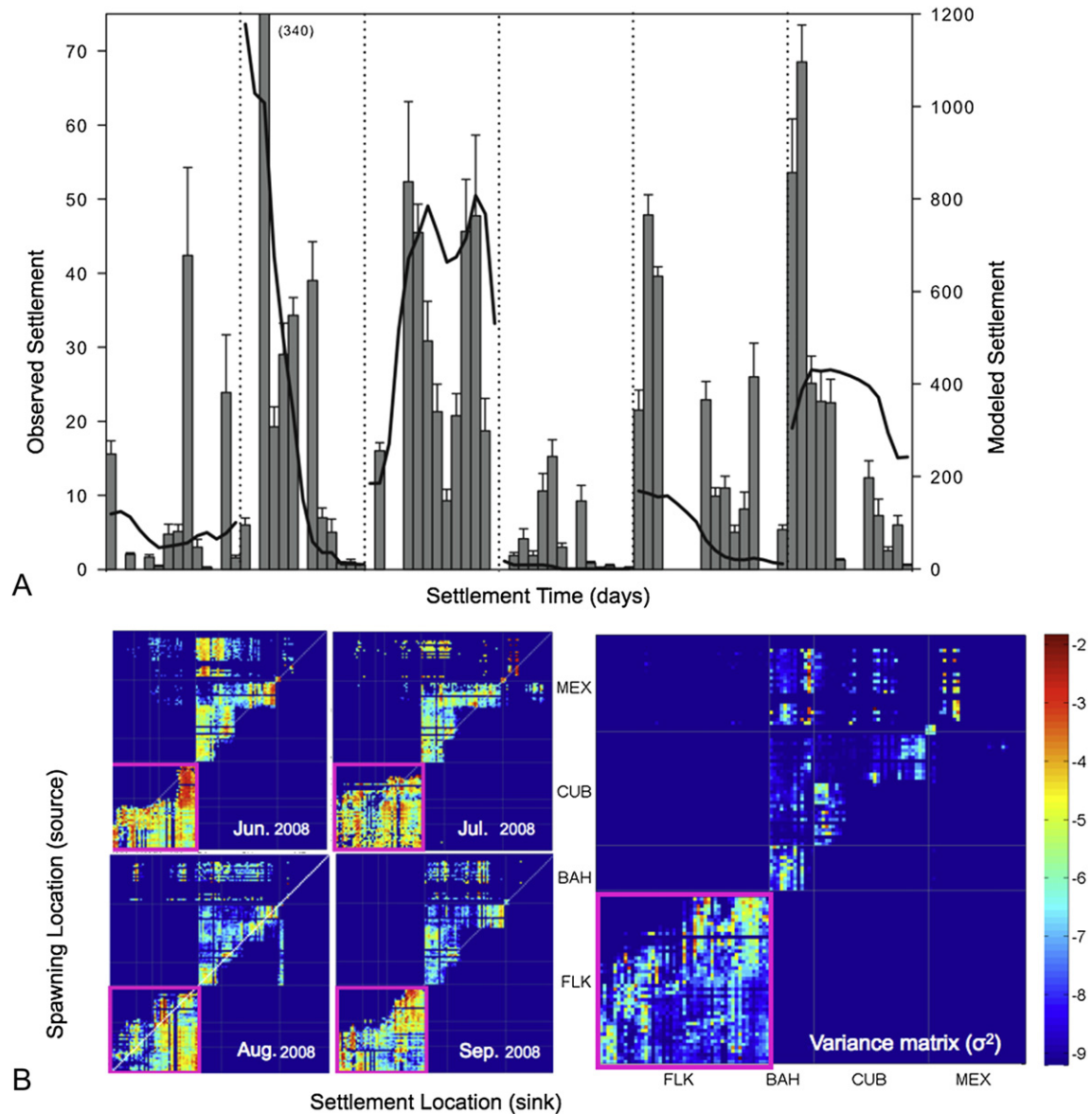


**Fig. 3.** Particle trajectories within a freely evolving idealized Agulhas ring. The velocity fields for this release are obtained from the experiment described in van Sebille and van Leeuwen (2007). Four particle trajectories are shown here (panel a), all seeded in the core of the Agulhas ring. As the ring moves northwestward, the particles keep circulating around the ring center, as can be seen in panels b–e which show snapshots of both the ring profile (colors) and the positions of the particles (black dots) every 100 days. The advection of the particles within the ring is expected behavior, because strong ocean eddies such as this Agulhas ring are capable of transporting water over large distances. A movie of a similar experiment using the same velocity data but more particles is available as supplementary material (downloadable from <http://code.google.com/p/connectivity-modeling-system/downloads/list>).

( $1/12^\circ$ , ca. 7 km) (Cummings, 2005). Daily GoM-HYCOM and Global-HYCOM and 6-hourly FKeys-HYCOM archives for 2007 and 2008 were used for the coupled simulations. The Seascape module (Fig. 1) was created in ArcMap® by overlaying the Coral Reef Millennium Mapping dataset (Andréfouët, 2008) of the model domain with a 2.5-km buffer (sensory zone) and segmented using a 10-km tension, generating 50 unit polygons of ca.  $5 \text{ km} \times 10 \text{ km}$  along the Florida Keys. Additional polygons in potential upstream locations were created and used to determine the spatial resolution of the connectivity matrix for both spawning production and larval supply patterns. The Biological Module (Fig. 1) was parametrized with early life history traits' distributions, rather than single values, bounded by observed ranges from Paris and Cowen (2004) and the number of particles released was scaled by the lunar cyclic hatching. In addition to realistically representing biological traits variations, a very high-release frequency of particles ( $\leq$  archive frequency of the lower resolution model) was paramount to assimilate all possible current variability and reproduce settlement events; otherwise, large settlement pulses seen in Fig. 4A were missed. Therefore, a massive number of  $1.2 \times 10^6$  particles were released monthly, for which efficient tracking was only possible with the Parallel Module (Fig. 1). Particles experienced a mortality rate of  $0.02 \text{ d}^{-1}$ , were competent to settle at 22 days and “died” if they did not encountered suitable habitat (i.e., Seascape Module, Fig. 1) after 32 days. Simulated settlement time series were

evaluated against larvae settling on the reef (Fig. 4A). The model could predict 70% of the observed settlement variations (Sponaugle et al., 2012), demonstrating the efficacy of the probabilistic modeling system in predicting biological variability.

Based on this good fit between expected and predicted settlement, the model can be used to compute the likelihood of larval exchange between spawning locations. The latter is a direct output of CMS (Output: Connectivity Matrix, Fig. 1), represented by a transition probability matrix  $M_{T,ij}$ , where columns are source locations (population  $i$ ) and rows are destination locations (population  $j$ ) (Fig. 4B). Elements along the diagonal of the matrix represent self-recruitment within a local population ( $i = j$ ). The use of two nests (Input Nest Files, Fig. 1) allowed to estimate the probability of larval supply to the Florida Keys from remote, upstream coral reefs. Contrary to previous findings using a single OGCM to investigate larval exchanges among coral reefs over large areas (Cowen et al., 2006; Trembl et al., 2008), this multi-scale Lagrangian approach reveals that local settlement can dominate even in an area influenced by strong boundary currents such as the Gulf Stream. Most of the variance in larval linkages is in fact contained locally for the Florida Keys and not from subsidies (Fig. 4B). Understanding of marine population connectivity networks and population resilience relies heavily on resolving the oceanic and coastal dispersions. The unique multi-nesting capability of CMS proves a critical practice to resolve source-sink dynamics (Paris et al., 2009).



**Fig. 4.** Model evaluation for biotic particles: A) comparison of larval bicolor damselfish observed settlement (gray bars) and 10-days moving average simulated settlement to the Florida Keys (solid line). B) Connectivity Matrices: monthly probability of migration of larvae between the Florida Keys (FLK), Mexico (ME), Cuba (CU), and the Bahamas (BA) from June to September of 2008 and variance matrix. Connectivity below and above diagonal indicates downstream and upstream settlement, respectively. Magenta squares delineate the FKeys-HYCOM 1/100° (nest 2) domain from GoM-HYCOM 1/25° (nest 1). Values (logarithm scale) indicate the probability that particles released from sites along the y-axis settle to sites along the x-axis; values along the diagonal represents self-recruitment, i.e., release and settlement sites are equal. Modified from Sponaugle et al. (2012).

#### 4. Conclusions

The Connectivity Modeling System (CMS version 1.0) is an open and free software tool to track the paths of biotic and abiotic particles in the ocean. Although software packages are already available that can perform a similar task (i.e., ICHTHYOPS, Lett et al., 2008; LTRANS, Schlag et al., 2008; North et al., 2008), the CMS differentiates itself as a probabilistic model treating specifically biological variability as continuous distributions of variable attribute input. Similarly, the dispersion of abiotic particles can have varying characteristics and fate. In addition, the focus in the design of the CMS has been on ease-of-use, particularly with the ability to download ocean velocity data in-the-fly from the internet and multi-scale nesting capabilities of independent, overlapping data to maximize resolution. The CMS is also very efficient in evaluating the causes and consequences of natural variability in marine

systems by manipulation of the multiples modules through numerical experiments.

Although the CMS has primarily been originally developed for use in the marine ecology community (Paris et al., 2005a, 2005b; Cowen et al., 2006; Sponaugle et al., 2012; Staaterman et al., 2012), it has already been used quite intensively by physical oceanographers (Weijer et al., 2012; van Sebille et al., 2012a, 2012b) and in the context of oil spill (DeGouw et al., 2011; Le Hénaff et al., 2012; Paris et al., 2012). The modular design of the CMS allows for easy selection of different components of particle behavior. When all biotic modules are turned off, the particles behave essentially as passive water parcels, and will follow accurately the flow. This can yield a Lagrangian description of the ocean circulation. Therefore, the CMS can be used in addition to and compared with the already available TRACMASS (Döös, 1995) and ARIANE (Blanke and Raynaud, 1997) packages. The repository of the connectivity-

modeling-system serves to facilitate community contributions to the CMS suite of modules.

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