GBR-Larvo: A biophysical larval-fish dispersal model for the Great Barrier Reef based on empirical larval and adult behaviour data

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Summary
Larval-fish dispersal models increasingly include larval behaviour rather than assume passive larvae. But, few models include a full range of dispersal-relevant behaviours. Adult behaviours such as the where and when (seasonal, lunar and diel) of spawning are often over-generalized. When empirically-based behaviour is included, variation in behaviour among individuals is seldom included: rather, mean behaviour is used, resulting in unrealistically constrained dispersal outcomes. GBR-Larvo for coral-reef fishes of the Great Barrier Reef uses empirical measures of vertical distribution, swimming performance and orientation of larvae, and the variation in and ontogeny of these behaviours. The model allows to settle only the larvae entering a ‘detection zone’ around settlement habitat with sufficient swimming ability to overcome currents. Empirical spawning data are used to release the propagules at appropriate times and places. Fish-egg buoyancy is included because it can strongly influence modelled dispersal outcomes. Inclusion of behaviour strongly influences modelled dispersal outcomes. Preliminary tests of modelled dispersal predictions using genetic parentage of settled juveniles reveals good agreement.

Introduction
Most demersal marine animal species have a dispersive larval stage that is the principal means of both demographic and genetic connectivity. Understanding the scale over which connectivity takes place, and how this varies with changing conditions are important issues in marine ecology, fishery biology and marine spatial management. Dispersal of larval fishes is now recognized as a biophysical process involving both movement of water and behaviour of spawning adults and larvae (Leis 2006, 2007). An important approach to understanding larval dispersal is by individual-based coupled physical biological models (North et al. 2009). In spite of recent calls for behaviour to be fully integrated into dispersal modelling that were accompanied with detailed guidance on how to achieve this (North et al. 2009, Staaterman & Paris 2013), the extent to which behaviour of larvae is fully and realistically used differs widely (eg, compare Christie et al. 2010 with Paris et al. 2013). Until recently, the lack of integration of larval behaviour could be justified by scarce empirical behavioural data on species of interest, but such data are increasingly available, and methods to acquire them are available (Leis 2007, North et al. 2009).

The most important larval behaviour data for dispersal modelling are vertical distribution, horizontal swimming performance, and orientation abilities (North et al. 2009, Staaterman & Paris 2013). Larvae develop and grow while in the pelagic water column, and so do their behaviours which must be studied in an ontogenetic context. Many behaviours differ on a diel basis, so diel influences must be included. The exact location and time of propagule injection into the water must be included.

Variation in behaviour among individuals will strongly influence where and when larvae ultimately settle, and their condition and survival at settlement. Variation in behaviour among individual fish larvae is frequently large (Leis 2006, North et al. 2009): such variation must be included in dispersal models (North et al. 2009, Staaterman & Paris 2013). GBR-Larvo does all these things.

Materials and Methods
The Great Barrier Reef consists of over 2000 reefs on the continental shelf of eastern Queensland. The positions and shapes of the reefs were obtained from Great Barrier Reef Marine Park (GBRMP) Authority digital shape files, and converted into polygons. Three cross-shelf bioregions (inner, mid-shelf, and outer) were allocated for spawning and settlement. The hydrodynamic model has been developed from the 2D
models of James et al. (2002) and Luick et al. (2007). It is 3D with 6 vertical layers and nested grids of three resolutions of 1’ (1.853 km) to 0.04’ (74 m). It is forced by Australian Bureau of Meteorology wind data, tides and the East Australian Current. The Lagrangian larval tracking model predicts where a larva with a particular set of behavioural characteristics would move if exposed to the simulated current field. Propagules were input at reef edges, only at spawning seasons, during appropriate lunar and daily spawning times. The model includes buoyancy and incubation times of pelagic eggs. Behaviour varies with ontogeny, so the pelagic larval duration (PLD) is divided into ontogenetic intervals. All behaviour is based on empirical data, and a probability-density function (pdf) is constructed for each behaviour in each interval: the pdf is randomly sampled to assign behaviour to each particle. Vertical distribution of larvae changes on diel and ontogenetic basis and is adjusted for water column depth. A pdf of age-specific nett velocities (speed and direction pairs) was derived from field measurements. Once larvae are competent to settle, orientation is toward reefs if within detection zone defined by species ability. The reef closest to each model grid is identified, and larvae respond appropriately depending on their location. A competent larva reaching a reef settles. Mortality can be applied via post-processing. Behavioural data were available for larvae of a pomacentrid damselfish, 4 serranid groupers and a lutjanid snapper.

Results and Discussion
The Dispersal Curve (=frequency distribution of dispersal distance for all settlers, regardless of origin) shape differed among species. The damselfish has a trimodal curve, and the highest mode, mean, and median dispersal distance, with only 0.9% self-recruitment (within 5 km of origin). This is not expected a priori for a species with demersal eggs, but its vertical distribution in the rapidly moving upper water column may explain this result. Species with pelagic eggs had Dispersal Curves with a single mode at 25-30 km, and percent of self-recruitment varied from 1.9 to 4.1%. Median and mean serranids dispersal distances were 40-55 & 65-80 km, respectively. The lutjanid had higher median and mean (65-70 & 91 km), possibly due to a longer PLD and less orientated larval swimming. Annual variation in dispersal distances was minimal. All Connectivity Matrices have a self-recruitment ‘hotspot’ in the Lizard Island-Princess Charlotte Bay region, and another area of high self recruitment south of Townsville. Between 16 and 18°S, larvae are more widely dispersed. No-Take Zones export 60-70% of their propagules to fished GBRMP zones, and provide settlers to No-Take Zones. Cross-shelf dispersal is species-dependent, and depends on spawning location and larvae vertical distribution.

The model estimated dispersal for 2 serranid grouper species from spawning aggregations in 3 southern GBR island groups. Three model runs were: passive larval behaviour; full behaviour; and full behaviour, but with hypothetical SE swimming orientation (ie, into prevailing current). In collaboration with G Jones and D Williamson (James Cook University), juveniles were sampled at spawning season end and genetic parentage was used to match juveniles (n=1200) to adults (n=1500): 86 matches were detected. Both local retention and dispersal over 200km were found. Preliminary analysis indicates the full behaviour model prediction was the best match for observed dispersal distance and direction.

References