Australian Government

Department of the Environment and Water Resources

Marine and Tropical Sciences Research Facility (MTSRF) June 2007 Milestone Report

Project 4.8.1: Resilience and Connectivity

Project Leader: Professor Terry Hughes, ARC Centre of Excellence for Coral Reef Studies, James Cook University

Summary

Both Parts A and B of this project are on track and the main co-contributors (GBRMPA and CAPREEF) have been briefed on progress.

Part A.
Work on the dispersal model is underway with emphasis on conversion from two dimensions to three dimensions. Analysis of behavioural data on fish larvae is essentially complete, and the theoretical framework for the biophysical model is constructed. In next reporting period, we will continue the work of producing the species-specific behavioural modules and on the physical model itself.

Part B.
In this reporting period (2 Mar-10 Jun), laboratory studies for the full validation of the method for marking coral reef fish larvae using stable isotopes were completed according to the milestone schedule. This work has provided the necessary platform for the planned field experiment to be conducted in year 2 of the MTSRF project. In this future experiment, larvae of two commercially important reef fishes (coral trout – *Plectropomus maculatus*; and stripey sea perch – *Lutjanus carponotatus*) will be marked in selected Green Zones at the Keppel Islands, and the extent of supply to local Blue Zones will be evaluated. Validation and baseline studies by two PhD students (David Williamson and Richard Evans) and one MSc student (Thomas Mannering) have also been supported by MTSRF funding, and have successfully continued over the last three months. A postdoctoral research fellow (Glenn Almany), funded by the ARC Centre of Excellence, will join the project in year 2 for the field experiment.

The status of five sub-components of the validation work in Part B is as follows:

1. The laboratory experiments carried out in the James Cook University MARFU aquarium facility have shown that the stable isotope marking technique has no health risks for adult coral trout or human consumption (Williamson et al., submitted).
2. Laboratory experiments carried out at a larval rearing facility in Bali, Indonesia have established that stable isotope injections are effective in marking serranid larvae (Williamson et al., in preparation).
3. Laboratory trials carried out at Orpheus Island Research Station have provided at validation of the isotope marking technique for stripey sea perch (Evans et al., in preparation).
4. Development of genetic population markers for the two target species has been completed (Evans and van Herwerden, in preparation).

5. Baseline surveys have been carried out at the Keppel Islands and successfully determined the primary spawning aggregation sites and juvenile nursery sites for the two study species. In the next reporting period, we will begin a 1 population coral trout larval marking field experiment at the Keppel Islands.

For reference: Milestone extracted from Project Schedule

Description

- Milestone - Part A of project: Physical model components 50% complete; Complete theoretical framework, assembly of data from literature, and analysis of existing behavioural data. Behavioural data for 2 species prepared for model incorporation.
- Milestone – Part B of project: Complete validation of larval marking and genetic techniques. Analyse data from larval marking validation experiments and prepare publications.
- Milestone – Parts A and B: Presentation to end users and annual report.
- Milestone – Parts A and B: Industry, Sunfish, CapReef and other end user newsletter article.

Project Results

1. DESCRIPTION OF THE RESULTS ACHIEVED FOR THIS MILESTONE

Milestone – Part A of project:

1. Progress report: 3-D hydrodynamic model (50% complete).
2. Report on completed (50%) components of physical model; report describing complete theoretical framework: assembly of data from literature & analysis of existing behavioural data. Identification of 2 species and behavioural data prepared for model incorporation.

Results

Part A Physical model

We have decided to focus initially on the Lizard Island area and work out the details of the model and make sure it functions properly, and then scale up. The initial component of developing a 3D model for the Lizard Island area is the set-up of computational grids at desired resolutions. From previous work by Luciano and co-workers, a grid for the entire GBR already exists. This grid has a resolution of 1' (minute of arc) and when run in 2D mode was sufficiently refined to estimate broad scale inter-reef connectivity assuming passive larval behaviour during the pre-competent pelagic period. In the present project we are setting up a grid with 0.2' (370 m) resolution and perhaps a 0.04' (74 m) around Lizard Island to allow us to simulate and track the fine scale of dispersal of fish larvae.

The usual sources of high resolution digital bathymetric data for the region, such as previously digitised charts or LADS, excluded Lizard Island. Fortunately, Lizard Island was surveyed for the GBRMPA in 1982 and is available in hard copy format. This survey comes on 10 large format sheets which have been scanned and are in the process of manual digitisation. Once this process is complete the fine resolutions grids of Lizard Island will be produced.

MMUTRACK is the lagrangian tracking model previously used to compute inter-reef connectivity by tracking the movement of neutrally buoyant and passive particles.

MMUTRACK was limited to tracking particles within a stored 2D current fields produced by a single hydrodynamic model grid. In previous projects the movement of fish larvae within the Great Barrier Reef World Heritage Area was studied by storing 2D currents from one grid that encompassed the entire GBR region. However in the present project, the objective is to use multiple nested grids that accurately resolve horizontal and vertical distribution of currents at a finer scale, initially near Lizard Island.

Using this multiple grid system will result in sets of current data with varying orientations, timesteps and horizontal and vertical resolutions. To accommodate this new system, a new version of the particle tracking model has been written that allows particles to be seamlessly tracked through the multiple current fields. At present the new tracking model is only set-up for 2D currents but will soon be able to accommodate 3D current fields. This will be followed by the addition of behavioural algorithms in the form of species-specific behavioural modules.

Part A Theoretical framework for a biophysical dispersal model – Only certain types of behaviours are relevant to predicting dispersal of fish larvae (eg, swimming behaviour is relevant, but feeding behaviour is not), and because behaviour, like morphology, develops and changes during the larval phase, information on behaviour at different stages in larval development is required. Thus, behavioural capabilities are dependent on the stage of development: larval size, rather than age, is the best proxy for this. However, dispersal operates over a given period of time (ie, the duration of the pelagic larval stage, or PLD) so we must be able to link time (typically measured in days since hatching) to size. Thus, it is necessary to include larval growth rates in the model. Independent of size (or age), larva behaviour may vary with spatial or temporal factors (eg, proximity to a reef, or time of day), and these factors must be included in the model. In addition, choice rules have to be developed. For example, for a spatially-determined behaviour, to which of several reefs in an area will the larva respond (the closest? the largest? the one with optimal settlement habitat?)? Finally, temperature must be taken into account, as some biological items (eg, PLD, swimming speed) are temperature-dependent. This has implications for both seasonal and climate change inputs. The theoretical framework developed for the dispersal model takes these factors into account, and combines them with the appropriate behaviour for the size (age) of the larva, and the correct spatial, temporal and biological inputs. As the model is developed further, and the biological inputs integrated with the physical ones, the theoretical framework will be further modified and refined.

The behavioural data are derived from two principal sources: published information, much of it by Leis and co-workers, and unpublished data from Leis' previous ARC-funded research (much of which required additional processing and analysis for it to be suitable for the model). The data are assembled into a standard format for each species to facilitate incorporation into the model.

The biophysical dispersal model will be configured to incorporate species-specific behavioural modules (a background document that details the types of information to be incorporated is attached), as behaviour differs among species, as does the duration of the pelagic larval stage (which then determines the time period over which the model is to be run). The species for which behavioural modules are developed are those for which the best behavioural information is available. In the first instance, these include the following reef-fish species that cover a wide taxonomic and life history range: *Pomacentridae*, *Amblyglyphidodon curacao* (Staghorn Damsel); *Lutjanidae*, *Lutjanus malabaricus* (Saddletail Snapper); *Serranidae*, *Epinephelus coioides* (Goldspotted Rockcod), *Epinephelus fuscoguttatus* (Flowery Rockcod). Eventually, we hope to be able to include a behavioural module for coral trout (*Plectropomus leopardus*) if we can obtain information on behaviour of younger larvae, but this is dependent on identifying a reliable source of reared larvae. In addition, if time permits or end users would prefer, species-specific behavioural models can also be developed for the several species for which we have data on behaviour over a range

of development stages: *Ephippididae*, *Platax teira* (Roundface Batfish); *Carangidae*, *Caranx ignobilis* (Giant Trevally); *Leiognathidae*, *Leiognathus equulus* (Common Ponyfish); and *Polynemidae*, *Eleutheronema tetradactylum* (Blue Threadfin). Finally, Leis has extensive behavioural information on the settlement-stage larvae of a wide variety of reef-fish species, and it will be possible to include these species if assumptions are made about their behaviour earlier in development (eg, if the behaviour of the younger larvae of related species can be used).

We now have this level of information on *Lutjanus carponotatus* (Stripey) analysed and available for model incorporation based on work performed by Ms Gäelle Quéré, an intern from the University of Paris in Leis' lab. This fits in with the work on this species planned in part B (see below).

The two species for which behavioural information is currently prepared are: *Amblyglyphidodon curacao* and *Lutjanus malabaricus*.

Milestone

Part B of project:

Complete validation of larval marking and genetic techniques. Analyse data from larval marking validation experiments and prepare publications.

Results

All research activities planned for part B of this project have progressed according to the milestone schedule. This work represents a team effort involving G. Jones (JCU), G. Russ (JCU), S. Thorrold (Woods Hole), L. van Herwerden (JCU) and three graduate students partially supported by MTSRF funding (D. Williamson, R. Evans, T Mannering). The foundation for this project was provided by the paper fully describing a new technique for marking larval fishes using a low dosage of enriched stable isotopes of barium chloride (BaCl2) injected into females prior to spawning (published in the first reporting period of the MTSRF project, Thorrold et al., 2006, Can. J. Fish. Aquat. Sci.). It showed that a Barium marker is transmitted to developing eggs and is subsequently detectable in larvae and juveniles. During the current reporting period, co-workers associated with the MTSRF project have published a paper establishing that this technique can successfully be applied in the field and can establish local scales of larval dispersal in small reef fishes (see Almany et al., 2007, Science).

The validation procedures and baseline surveys necessary prior to conducting a mass-marking experiment in the field (Part B) have been divided into 5 sub-projects:

1. Effects of BaCl2 injections on adult coral trout (P. maculatus) and health risks. In an experiment conducted at the JCU MARFU aquarium facility, we have now demonstrated that injections of BaCl2 solution at dosages up to 4mg Ba2+/kg of fish body weight produce no detectable effects on the physiology or condition of injected fish and present no risk to humans who may consume injected fish. This work was submitted for publication in May 2007 (see Williamson et al., in review).
2. Validation of BaCl2 injections for marking grouper larvae (Pisces: Serranidae). In an experiment conducted at the Research Institute for Mariculture in Bali, Indonesia, we have established that injections of enriched isotope BaCl2 injections produce effective markers in the otoliths of fishes closely allied to coral trout (family Serranidae). This experiment has shown that application of the isotope produces no negative effects on the growth, survival or development of larvae (see Williamson et al., in prep).

3. Effects of BaCl2 injections on adult stripey sea perch (Lutjanus carponotatus) and health risks. In an experiment conducted at Orpheus Island Research Station, we have shown that injections of BaCl2 at doses sufficient to mark larvae provide no negative effects on the adult survival or body condition (data currently being analysed).
4. Identifying microsatellite markers to examine population connectivity in coral trout and stripey sea perch. Development of both mtDNA and microsatellite markers has been completed. Genetic samples collected in the Keppel, Whitsunday and Palm Island groups are set to provide insight into the broad-scale population connectivity of the two stud species between inshore reefs of GBRMP (Evans et al. in prep).
5. Baseline surveys of adult spawning aggregation sites and juvenile nursery sites for both coral trout and stripey sea perch at the Keppel Islands. The Keppel Group has been selected as the location for the first field experiment which aims to track dispersal of larval coral trout and stripey sea perch from natal marine reserve reefs to surrounding fished reefs (year 2). We have completed underwater visual censuses (UVC) of fish and benthic communities on fringing reefs of the Keppel Island group. Underwater surveys of P. maculatus and L. carponotatus have identified the locations of spawning aggregation sites, the timing of spawning and identified areas of high larval recruitment. Accurate estimates of mean adult and recruit abundances have also been calculated from UVC data. Samples collected during 2006 are providing information on recruitment dynamics and first year growth rates of the target species (Williamson et al. in prep).

Publication outcomes for first year:

Thorrold, S.R., G.P. Jones, S. Planes and J.A. Hare (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Canadian Journal of Fisheries and Aquatic Science 63:1193-1197.

Williamson, D.H., G.P. Jones, S.R. Thorrold and A.J. Frisch. Toxicological responses and physiological effects of low dosage barium chloride injection for trans-generational marking of coral reef fish larvae. Canadian Journal of Fisheries and Aquatic Science, in review.

Williamson, D.H., S.R. Thorrold and G.P. Jones. Experimental evaluation of transgenerational marking of grouper larvae. Manuscript in preparation.

Related publications (not directly funded by MTSRF):

Almany, G.R., M.L. Berumen, S.R. Thorrold, S. Planes and G.P. Jones (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316:742-744.
Jones, G.P., M. Srinivasan and G.R. Almany. Population connectivity and conservation of marine biodiversity. Oceanography, in press

Milestone - Parts A and B of project:

Presentation to end users and annual report.

Refer to section on communications, major activities and events section below. GBRMPA was provided with a comprehensive report in March 2007 (attached to previous milestone report). As the June 10 milestone report is only 3 months after the previous one, the next report and presentation to GBRMPA has been postponed to coincide with an international workshop on marine connectivity that will take place in Townsville in October 2007.All chief investigators and students involved with the MTSRF project will give presentations at this workshop.

Milestone

Parts A and B of project: Objective (a) and (b) Industry, Sunfish, CapReef & other end user newsletter article.

The program 8 newsletter article originally scheduled for the previous milestone reporting period has been written and will appear in the next edition of the Program 8 newsletter (currently in preparation by the communications project 4.8.8).

David Williamson met with Sunfish and CapRef representatives in early June 2007, both to brief them about the larval marking experiment planned for the end of 2007 and to seek experienced fishers to assist with this experiment.

A number of ex-commercial and recreational fishers have pledged their support, including use of their boats and fishing expertise.

Explanation of Activity changes

Problems and opportunities

Project Part A:

Problems: we have focused on the Lizard Island area for the initial working out of details of the model. Unexpectedly, we found that the detailed bathymetry immediately around Lizard Island that is required for the 3D model was available only in hard copy and this has resulted in considerable effort on our part to get this information digitized.

We had anticipated that we would be able to study the behaviour of larval coral trout under co-investment from GBRMPA, but it appears that the reliability of rearing larvae of coral trout is not as advanced as we had expected at either the Bali aquaculture facility or in Taiwan, the leading centre for culture of tropical, marine fishes. We will remain in contact with our associates in both localities, and when rearing reliability reaches the level at which a field trip to work on reared larvae is justified, we will approach GBRMPA for support. If this does not occur, we will use the larval behaviour of a closely related rock cod species (Epinephelus fuscoguttatus or E. coioides) in the model.

Leis' technical officer on this project will be leaving her position at the end of June 2007, but a replacement has been appointed with a short overlap to ensure continuity.

Opportunities:

Leis has secured funding from the Hermon Slade Foundation to extend his larval-fish behaviour research at Lizard Island in summer 07/08 and 08/09. The work will be in collaboration with Dr Claire Paris of the University of Miami. This will enable the gathering of more relevant information on larval-fish behaviour that can be incorporated into the Biophysical Dispersal Model.

Project Part B:

Problems:

Nil

Opportunities:

Additional funding to augment Part B of the project is being sought as a component of a set of larval marking experiments in Australia and Papua New Guinea. The proposal went to the Packard Foundation (U.S.) in April and we expect notification of the outcome in late June. If successful, this will allow the expansion the larval project to the full experimental design outlined under funding model 1 in the original MTSRF proposal. The proposal was written and sponsored by Dr Simon Thorrold at the Woods Hole Oceanographic Institute. Dr Thorrold is a key collaborator on this MTSRF project.

Other issues

Parts A&B:

Nil

Communications, major activities or events

During milestone reporting period

Parts A and B:
Communication material on the background and progress of project 4.8.1 was prepared and supplied to Colin Simpfendorfer in April 2007. Colin presented this at the MTSRF synthesis conference.

Part A:
An article on Leis' research on larval-fish behaviour and its relevance to marine parks appeared in the June issue of Explore (published by the Australian Museum). The research described was done under ARC support, but the issues involved are identical to those being dealt with under MTSRF support. A copy of this article (in pdf format) was sent to Ann Penny on 14 May 2007. Leis presented seminars on his larval-behaviour work and its relevance to marine parks at the NSW AMSA meeting of 30 March 2007, and at the Sydney Harbour Institute of Marine Science Open Day on 4 March 2007.

Part B: Jones made a presentation to selected representatives from GBRMPA at a Centre of Excellence in Coral Reef Studies, Program 3 Connectivity workshop in early May 2007.

The first paper to demonstrate the success of the isotope marking technique was published in May 2007 [Almany, G.R., M.L. Berumen, S.R. Thorrold, S. Planes and G.P. Jones (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316:742-744]. Although based on work carried out prior to the MTSRF project, this publication has resulted in substantial media interest in Australia and overseas, and has provided a platform to present the planned coral trout marking experiment to the media.

During next milestone reporting period

Parts A and B:

All investigators on this MTSRF project will participate in a major international workshop on marine connectivity in October 2007. The workshop "Connectivity and population resilience -- sustaining coral reefs during the coming century" will be held at Townsville 13-16 October, 2007. This workshop is to be an equal partnership between the Australian Research Council Centre of Excellence for Coral Reef Studies at James Cook University, and the Connectivity Working Group of the Global Environment Fund Targeted Research and Capacity Building Project. The aim will be to explore recent advances in our understanding of larval

connectivity and retention on coral reefs, the implications for understanding the resilience of coral reef systems, and how to sustain biodiversity during a predicted period of dramatic change. Professors G. Jones and G. Russ will co-host this workshop.

Part A:

Leis will be presenting a Plenary Talk titled “Ontogeny of Behaviour in Fish Larvae” at the Annual Larval Fish Conference as part of a symposium on larval dispersal and connectivity to be held in Newfoundland in July 2007. Although, the bulk of this talk is about research done under ARC support, he will be talking about his MTSRF project, and how this meshes with his previous research (nb – no MTSRF funds are being used to support Leis’ travel to or participation in this conference). Leis will be based in Tasmania in Aug/Sept 07 which will enable him to work more closely with Mason (based at the Australian Maritime College, Launceston) on the biophysical model. Leis will be participating in the "Connectivity and population resilience -- sustaining coral reefs during the coming century" workshop being organized by the ARC Centre of Excellence for Coral Reef Studies in Townsville in October. The Biophysical Model we are developing will be of direct relevance to this workshop. In addition, Leis will stay on in Townsville the following week to interact with end-users and other stakeholders.

Forecast variations to planned milestones

Parts: A & B: Nil

APPENDIX 1
Note: This is a working document produced for the in-house use of members of Leis' MTSRF team.

BACKGROUND INFORMATION

Behavioural information for dispersal modelling (indicate source – literature, our data, where are data – spreadsheet, etc):
Include variation and temperature where known.

May be necessary to include information from related species to fill gaps.

All sizes in mm SL, preserved, or noted if otherwise

Species (include Family):

Spawning Location and Timing:

This provides the starting point for the modelling. Does spawning take place throughout the adult habitat of the species, or only in subsections (eg, only on mid-shelf reefs, or on forereef edges)? Does the species form spawning aggregations in predictable locations? We want to distinguish in particular, whether there is a diffuse source of propagules (as is the case for pomacentrids, which spawn in their adult territories) or more discrete point sources (as in the case for coral trout, which spawn in particular sites to which the adults migrate over 100s of m to form aggregations). Similarly, timing of spawning may be diffuse (eg, labrids, which may spawn daily) or discrete (eg, with lunar periodicity, for example). May come from our data, but most from the literature.

PLD:
Range, mean, mode, if there is geographic or temporal variation, and method of determining age (is it validated?). Some species may have temporal behaviour in settlement that may partially decouple spawning periodicity from settlement periodicity, for example settlement may take place with lunar periodicity that may be lacking in spawning. May come from our data, but most from the literature.

Size at hatch:

Also note state of development (eg, large yolk sac? Eye pigmented and functional? Mouth open?). May come from our data, but most from the literature.

Size at settlement*:*

As per PLD. May come from our data, but most from the literature.

Settlement habitat:

Coral reef, estuary sea grass, low-relief hard bottom, etc. Needed to determine model end point. May come from our data, but most from the literature. This should also be at both large and meso-scale. For example, a species may settle on a coral reef, but only on the windward reefs (so a larva of this species arriving at the leeward side of the reef would either have to be able to make its way to the windward side of that reef, or keep going until it encountered a windward side of a reef). Micro-scale (eg, settle only to a particular coral species) is probably sub grid in any realistic model, so should be ignored, unless this micro selectivity results in a meso or larger pattern: if, eg, that particular coral lives only on offshore reefs, or only in reef lagoons.

Settlement behaviour:

Aside from habitat issues (see above), settlement behaviour that might be relevant includes, the propensity of larvae of a species to swim back to sea from a reef it encounters (this can exceed 30%), or if it settles only at particular times of the day.

Growth rate (to relate age and size): in most cases this will be = {[(size at settlement)-(size at hatch)]/PLD} to give mm/day – from the literature. Most behavioural data are size related, whereas the dispersal model is time related, so we must be able to relate size to age. Some actual larval growth data exist in the literature, but they are rare for coral-reef species.

Mortality rates: Need to determine what proportion of larvae are left by the time of settlement. This will only come from literature, and may be very generalized due to scarce data.

***In situ* swim speed** (relate to size, usually through regression equation):

For some sizes, it may be necessary to estimate *in situ* speed from U crit (ie, speed measured in lab raceways), or morphology considerations in Becky Fisher's papers (eg, Fisher et al. 2005; Fisher 2005. May come from our data or literature.

- **Relationship between U crit and i*n situ* speed**: in some spp this is a constant, whereas in others it is size-related. See Leis et al. 2006a; Leis et al. 2006b
- **Speed:** need range, mean and mode. For some analyses, it will be important to know the speed of the fastest individual at any given size.
- **Proportion of time swimming takes place (could be factored into speed)**: available from lab data on a few species (see Fisher & Bellwood 2003)
- **Day/night differences:** See Fisher & Bellwood (2003) on this: very little actual data

Endurance (relate to size and test speed):

This is primarily of use here to see if the larvae have any endurance at all. If endurance is very small, horizontal swimming will not be a factor. Actual endurance values are method-dependent.

- Unfed: basically a measure of condition, rather than a very meaningful ecological measure of how long/far larvae can swim.
- Fed: May be essentially open-ended if larvae are able to feed – see Fisher & Bellwood (2001); Leis & Clark (2005).

Orientation (relate both direction and precision to size):

Swimming without orientation will primarily increase diffusion, but may increase chance encounters with suitable settlement habitat. If individuals swam directionally, but overall, the population of individuals did not have an overall direction, some might be able to counteract advection, and remain in the vicinity of their natal reef, leading to a degree of self-recruitment that would not happen if the larvae drifted passively.

- **Does orientation change with size?:** eg see Leis et al. (2006b)
- **Day/night differences:** very little info on night time – see Stobutzki & Bellwood , 1998; Tolimieri et al. 2004
- **Other temporal factors:** eg, if solar compass implicated, the orientation may change through the day (Leis & Carson-Ewart 2003)
- **Spatial differences:** orientation may change with location (eg always toward or away from a reef) – see Leis & Carson-Ewart (2003); Leis et al. (2006a)
- **Scale of orientation:** for example, if hearing a reef is the cue used, then how far from the reef can it be heard?

Depth (relate to size):

For smaller individuals, must rely on studies with towed nets – for GBR waters, see Leis 1986; Leis 1991. For larger individuals, in situ observations will be useful (eg, Leis 2004). NB – most studies of vertical distribution examine this in respect to the population of larvae, whereas, in some cases, it might be more relevant to look at what individual larvae are doing (see Leis 2006, for examples).

- **Depth-frequency:** probably link to spreadsheet to show either 1) net-tow data on concentration (numbers per volume sampled) in different depth strata, or 2) *in situ* data that give % of observations in each depth stratum.
- **Median (or mean depth):** especially, does it vary with size?
- **Amplitude:** using *in situ* data, this will be the amplitudes (ie, max depth minus min depth) of the individual larvae observed. Then, one can talk about mean amplitude for a group of larvae.
- **Vertical movement of *individuals*:** using *in situ* data, this will involve the individual trajectories of each fish to show their individual vertical movements (as well as overall amplitude, the numbers of changes of vertical direction and their magnitude are relevant). In other words, do the individual larvae move over substantial vertical distances, and, if so, then over what time scales? See Leis , 2004. Leis & Carson-Ewart , 2001
- **Spatial differences:** depth may vary with location (eg, Leis & Carson-Ewart , 2001; Leis , 2004). This can be either differences in depth frequency, or perhaps differences in mean depth between location.
- **Influence of water-column depth:** (difficult to separate from location, but water depth may influence vertical distribution (see Leis & Carson-Ewart , 2001; Leis , 2004)
- **Day/night differences:** towed-net studies, also light-trap studies Fisher , 2004 vs day-time in situ studies (refs above).

Temperature effects on any of above:

Some things may change predictably with temperature (eg growth, pld, swimming speed), so the temperatures at which these things were measured is relevant wrt the temperature within the modelled area. Where available, the relationships (for example regressions) between temp and variable should be included.

Reference List

Fisher, R. 2004. Nocturnal vertical distribution of late-stage larval coral reef fishes off the leeward side of Lizard Island, Great Barrier Reef, Australia. *Bulletin of Marine Science* 75: 439-451.

Fisher, R. 2005. Swimming speeds of larval coral reef fishes: impacts on self-recruitment and dispersal. *Marine Ecology Progress Series* 285: 223-232.

Fisher, R. & D.R. Bellwood , 2001. Effects of feeding on the sustained swimming abilities of late-stage larval *Amphiprion melanopus*. *Coral Reefs* 20: 151-154.

Fisher, R. & Bellwood, D. R. 2003.Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. Marine Ecology Progress Series 263, 177-188.

Fisher, R., J.M. Leis, D.L. Clark & S.K. Wilson , 2005. Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Marine Biology* 147: 1201-1212.

Leis, J. M. 1986.Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Marine Biology 90, 505-516.

Leis, J.M. 1991. Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. *Marine Biology* 109: 157-166.

Leis, J.M. 2004. Vertical distribution behaviour and its spatial variation in late-stage larvae of coral-reef fishes during the day. *Marine and Freshwater Behaviour and Physiology* 37: 65-88.
Leis, J.M. 2006. Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* 51: 59-141.

Leis, J. M. & Carson-Ewart, B. M. 2001.Behavioural differences in pelagic larvae of four species of coral-reef fishes between two environments: ocean and atoll lagoon. Coral Reefs 19, 247-257.

Leis, J.M. & B.M. Carson-Ewart , 2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. *Marine Ecology Progress Series* 252: 239-253.

Leis, J.M. & D.L. Clark , 2005. Feeding greatly enhances endurance swimming of settlement-stage reef-fish larvae (Pomacentridae). *Ichthyological Research* 52: 185-188.

Leis, J.M., A.C. Hay, D.A. Clark, I.-S. Chen & K.-T. Shao , 2006a. Behavioral ontogeny in larvae and early juveniles of the giant trevally, *Caranx ignobilis* (Pisces: Carangidae). *US Fishery Bulletin* 104: 401-414.

Leis, J.M., A.C. Hay & T. Trnski , 2006b. *In situ* behavioural ontogeny in larvae of three temperate, marine fishes. *Marine Biology* 148: 655-669.

Stobutzki, I. C. & Bellwood, D. R. 1998.Nocturnal orientation to reefs by late pelagic stage coral reef fishes. Coral Reefs 17, 103-110.

Tolimieri, N., Haine, O., Jeffs, A., McCauley, R. & Montgomery, J. 2004. Directional orientation of pomacentrid larvae to ambient reef sound. Coral Reefs 23, 184-194.