‘Sticky water’ enables the retention of larvae in a reef mosaic

Fernando Andutta^{1,2,*}, Michael Kingsford³, Eric Wolanski³

¹ School of Engineering and Physical sciences, James Cook University, Townsville QLD 4811, Australia.

² ACTFR, James Cook University, Townsville, QLD, 4811, and Australian Institute of Marine Science, Townsville, Australia

³ School of Marine and Tropical Biology, James Cook University, Townsville, QLD, 4811, Australia

* Corresponding author. Email: fernando.andutta@jcu.edu.au

ABSTRACT

To study retention of waterborn larvae in a reef matrix we used a finite element unstructured numerical model with a minimum horizontal resolution of 150 m that can capture variability of currents on a spatial scale relevant to coral reefs in the Great Barrier Reef (GBR). Areas of high reef density (i.e. closely aggregated reefs) are poorly flushed because the prevailing currents are steered around and away from these regions, which is an oceanographic process called the ‘sticky water’ effect. The model showed that the sticky water effect leads to decreased flushing and a high exposure time in high reef density areas in the southern and central regions of the GBR matrix. In turn this generated hotspots of high self-seeding, and these hotspots existed under both calm weather conditions and wind conditions typical of those during the coral spawning season. Away from these areas, self-seeding was less likely to occur and larval replenishment would result mainly from connectivity between reefs located kilometers to tens of kilometers apart.

The location of sticky water areas varied spatially within the reef matrix according to tidal and mean currents, local bathymetry and reef density (defined as the degree of aggregation by reefs). A simple analytical formula is presented that explains about ~70% of the variation in larval retention in both calm weather and windy conditions. Complex reef mosaics and the related sticky water effect may have significant implications on the fate of larvae, and thus on connectivity for coral reefs worldwide.

Keywords: exposure time; patchiness; tidal currents; residual currents; larval dispersion; self-seeding.

1. Introduction

The circulation of water around islands and reefs is a key driver of ecological factors such as connectivity, dispersal and species assemblages (Wolanski et al., 1997; Jones et al., 1999 and 2005; Swearer et al., 1999; Carleton et al., 2001; Almanay et al., 2007; Paris et al., 2007; Burgess et al., 2007; Munday et al., 2009; Christie et al., 2010a,b, Hamann et al., 2011). Most of these studies have focused on relatively isolated reefs. Coral eggs and fish larvae spawned in isolated reefs may be potentially easily expatriated. Retention of these eggs and larvae near their natal reefs has commonly been attributed to eddies (Graber and Limouzy-Paris, 1997; Crawford et al., 1990). Indeed, large-scale eddies in the ocean outside a reef can return larvae to their natal reefs after weeks to months (Lobel and Robinson, 1986; Lee et al., 2002). For some reef fishes and corals the lower rates of flow commonly at neap tides may improve retention of fish larvae and coral eggs near natal reef (e.g. Babcock et al., 1986; Gladstone and Westoby, 1988; Robertson et al., 1990; Reyns and Sponaugle, 1999; Sponaugle et al., 2002). Levels of natal recruitment are known to be high at some reefs (e.g. 30 – 60%; e.g. , Jones et al., 2005; Almanay et al., 2007), this level of self-recruitment is likely to vary by bathymetric and oceanographic context (i.e. tidal and residual currents) as well as the role of larval behavior (Kingsford et al., 2002). Large-scale oceanic eddies do not exist in a reef matrix (Wolanski, 1994) and reef-induced, reef-size eddies are short-lived (e.g. tidal phase eddies, Black and Gay 1987; Wolanski et al., 2003; Burgess et al., 2007). Retention in semi-permanent eddies from strong current flow on the wake of shallow individual reef, therefore, lasts only hours to a few days at most (Spagnol et al., 2002). However fish and coral larvae commonly remain at sea for days to weeks before they settle, i.e. when recruitment occurs (Hutchings et al., 2008). Accordingly, it is unlikely that reef-induced phase-eddies can generate a high degree of reef self-seeding. Recruitment to many reefs is likely to be highly subsidized by connectivity with reefs that are km to tens of km apart, and occasionally hundreds of km apart (e.g. Cowen et al., 2006 for Caribbean reefs, and Ayre and Hughes 2000; Bode et al., 2006; and van Oppen et al., 2008 for the Great Barrier Reef).

Reefs in the Great Barrier Reef (GBR) are not distributed uniformly; most reefs are aggregated in a matrix of reefs. Where the density of the reef matrix is high (i.e. reefs closely aggregated), the self-seeding potential may increase because the reef matrix steers the mean circulation away from and around the reef matrix (Figure 1). This process was demonstrated

from field and model studies by Wolanski and Spagnol (2000) and Spagnol et al. (2001) and was coined the ‘sticky water effect’ by Wolanski (1994). The focus of their study was on the deflection of the mean circulation away from and around the reef matrix. These authors did not study variation in the reef matrix, namely that as the complexity of within reef and among reef architecture goes up, the sticky water effect should increasingly dominate, reducing expatriation and increase retention of waterborne larvae.

Preferred position for Figure 1

In this paper we used a high resolution oceanographic model to demonstrate that in areas of high reef density waterborne larvae may be retained for several weeks, a period long enough for the larvae to develop to a competent settlement size. The choice of the numerical model was crucial because the model must be able to cope with details of the complexity of the bathymetry. To model the GBR accurately one must cope with 2,800 reefs scattered over its 2,600 km length, with reefs ranging in area from ~ 0.1 to $\sim 100 \text{ km}^2$ and often separated by narrow passages (i.e. tens to a few hundred meters). Finite-difference, regular grid models would need millions of grid points to represent the whole GBR at small scales of about 150 m. This is prohibitive and as a result modelers generally use a coarse grid to cope with the whole GBR. For instance Dight et al. (1990) used a 9.26 km grid, King and Wolanski (1996) and Brinkman et al. (2001) used a 2 km grid, and Luick et al. (2007) used a 1.8 km grid. In contrast a non-structured grid model, such as the SLIM (Second-generation Louvain-la-Neuve Ice-ocean Model) model of Lambrechts et al. (2008) allows for fine-scale resolution ($\sim 150 \text{ m}$) near reefs and a coarser resolution far from reefs, where high resolution mesh is not needed (Legrand et al., 2006; Andutta et al., 2011), so that the numbers of grid points typically is less than 0.1 million. 2D vertically-integrated numerical models are useful tools to simulate the hydrodynamics in the GBR because Luick et al. (2007) found few differences between the results from a 3D model and a 2D vertical integrated model for the GBR; this is because with the exception of upwelling events at the shelf break (Andrews and Furnas, 1986), and short periods of stratification where large rivers discharge in the coastal zone (Wolanski and van Senden, 1983) there is negligible density stratification with depth.

We used the SLIM model to demonstrate that the sticky water occurs in patches throughout areas of high reef density in the southern GBR matrix. We show that these areas have a high self-seeding potential and that their location is determined by the interaction between the reef density and the oceanography of surrounding waters. We suggest that the GBR, and by inference also reef archipelagos elsewhere, have hot spots of high self-seeding reefs imbedded within a network of reefs that are heavily subsidized by larvae from other

reefs. We argue that this self-seeding effect has important ecological and management implications for coral reefs.

2. Methods

We used the vertical integrated SLIM non-structured finite-element model of Lambrechts et al. (2008). This depth-averaged barotropic model computes the horizontal velocity and sea surface elevation. Unlike previous models of the GBR, the equations are discretized on a fully unstructured mesh. Thus, the resolution was very high (~ 150 m) near reefs where it is needed and coarse (~ 5 km) in open waters far from reefs (Figure 2).

TOPEX data was used to force sea level variation and currents at the open boundaries. The exposure time was calculated for simulations starting at 1st August 2006 and 8th August 2006 for conditions initially under neap and spring tides, respectively. For the Coral Sea inflow (Figure 2) we applied 4 Sv to the open boundary, between $\sim 16.3^\circ$ S and 17.4° S ($1 \text{ Sv} = 1 \times 10^6 \text{ m}^3 \text{ s}^{-1}$). This inflow was the North Caledonia Jet (NCJ) (Andrews and Clegg, 1989; Wolanski, 1994; Ganachaud et al., 2007; Lambrechts et al., 2008; Andutta et al., 2011). For the bottom friction we used high values of the Manning roughness coefficients over the reef zones ($2.5 \times 10^{-1} \text{ m}^{-1/3} \text{ s}$) to simulate high roughness and lower values ($2.5 \times 10^{-3} \text{ m}^{-1/3} \text{ s}$) elsewhere. The eddy viscosity parameterization of Smagorinsky (1963) was used. The coefficient for the horizontal diffusion of mass, K_h , is assumed to be a function of the mesh resolution, but constant in time. The detailed description of the physical and numerical parameters used in the simulations follows Andutta et al. (2011).

To verify the model we used the data from tide gauges and moored current meters of Andrews (1983), Wolanski et al. (1989), Spagnol et al. (2001), Middleton and Cunningham (1984) and the salinity data from Andutta et al. (2011). The location of the current meter moorings is shown in Figure 2; the moorings were all deployed outside of the GBR reef matrix except for those of Spagnol et al. (2001). The residual currents were measured at 10 moored sites, and tidal currents at 10 sites.

Preferred position for Figure 2

While the open boundary conditions for the model, namely the tides and the inflow from the Coral Sea, are well known, the wind is an additional independent variable. On the GBR mass coral spawning usually occurs in November and December. We used two wind conditions typical of those months, namely (1) no wind conditions (Oliver et al., 1992), and

(2) a southeasterly wind at 6.67 m s^{-1} , which is the long-term wind speed and direction for the southern GBR during that period (Wolanski, 1994).

This model provided the current data needed to track waterborne larvae using the Lagrangian advection-diffusion model of Spagnol et al. (2002). One hundred thousand virtual non-swimming larvae were released in one batch at each of the 17 spawning sites (Figure 2B) for a 2 months simulation. Each such site was a $10 \times 10 \text{ km}$ square (i.e. 10^3 virtual lagrangian particles per km^2). It was not useful to use a smaller square because it needs to be larger than the maximum tidal excursion length ($\sim 6 \text{ km}$). It was not useful either to use a larger size (e.g. $100 \times 100 \text{ km}$) because that scale is much larger than that of which reef density varies ($\sim 10 \text{ km}$). A $10 \times 10 \text{ km}$ box was adequate because numerical experiments showed that particles released at small reefs within such a box quickly filled that box, while large reefs fill the box and thus spawning can be considered uniform within the box.

The spawning sites were chosen to encompass a range of reef architecture from isolated reefs to complex reef mosaics to lagoons. Coral eggs are buoyant and are not uniformly distributed vertically; this lasts less than a day at which time larvae emerge. Coral larvae are largely not buoyant (Black et al., 1990; Black, 1993), and thus vertically integrated models may be used to study their fate.

Our terminology for reef architecture (Figure 1b) was as follows. Firstly, an *archipelago* is a reef mosaic bigger than the $10 \times 10 \text{ km}$ site and the reef density A ($0 < A < 1$) is the fraction of the area covered by reefs; a reef is defined as an area of depth less than 5 m ; for instance $A = 1$ means that reefs cover the entire spawning $10 \times 10 \text{ km}$ spawning site. Secondly, a *lagoon* is an area of the shelf that is partially enclosed by reefs that are outside the $10 \times 10 \text{ km}$ site; reefs within the $10 \times 10 \text{ km}$ site may contain reefs at a density A ; the degree of closure of the lagoon perimeter is the ‘lagoon closure’ B ($0 < B < 1$); for instance, $B = 0$ if there is no lagoon enclosing the spawning site, and $B = 1$ if the lagoon fully encloses the spawning site (i.e. the lagoon is mainly flushed by flows over the reef flat). Thirdly, a *cluster* refers to an assemblage of reefs where some reefs are partially shielded by adjacent reefs (i.e. a lagoon closure $B < 0.5$). Fourthly, a *ribbon* refers to a series of linear reefs separated by a narrow passage. The characteristics of the reef architecture and the value of the parameters A and B for the 17 spawning sites are listed in Table 2.

The self-seeding potential was estimated as the mean exposure time, which is defined as the time needed for the number of larvae in the spawning site to finally decrease to $1/e \sim 0.37$ of its initial value (Deleersnijder et al., 2001; Delhez, 2006; Monsen et al., 2002; Lucas

et al., 2009; Valle-Levinson, 2010). Therefore, the exposure time is the time necessary for ~ 67% of the larvae to leave the spawning site and never return. The self-seeding potential was also calculated as the percentage of larvae remaining in the spawning site after 12 and 24 days.

3. Results

The whole GBR model was successfully verified against observations of residual currents at ten sites of tidal currents (Table 1; Fig. 2B), of tidal currents at the same ten sites (not shown), and of tides at another ten sites (not shown). The root-mean square error (RMSE) for the residual currents was only 0.03 m s^{-1} . While most data are for open waters far from reefs, the model within the GBR matrix was also verified (Table 1) for the high reef density area shown in Figure 2C using the oceanographic data of Wolanski and Spagnol (2000) to demonstrate that the currents upstream of a high reef density area are steered away from the area to flow around it instead of through it – i.e. the ‘sticky water effect’ of Wolanski and Spagnol (2000).

Preferred position for Table 1

Where the reef density was high the tidal currents were also the smallest except in small isolated reef passages (Fig. 3). There was a great variation in the residual currents and the peak tidal currents for the Swain reef area (Fig. 3). Three virtual spawning sites (a) – (c), each $10 \times 10 \text{ km}$, were within the Swain reef area and were within a relatively short distance from each other (Fig. 4A). The residual currents (Fig. 3) were found to be the smallest in site (a) of high reef density; they were the largest in the site (c) of small reef density, and intermediate in site (b) of moderate reef density.

Preferred position for Figure 3

In calm weather conditions, most (~ 62%) simulated larvae remained after 12 days in the spawning site (a) where reef density was high (95%, see Table 2), and about 30% of the larvae remained after 24 days. In contrast only few (~ 3%) larvae remained after 12 days and no larvae remained after 24 days at site (c) where reef density was small (3%). At site (b) where the reef density was 55%, about 16% and 4% of the larvae remained after 12 and 24 days respectively.

The rate of loss of larvae from spawning sites was the smallest at site (a) where reef density was the highest, it was the largest at site (c) where reef density was the lowest, and it was intermediate at site (b) where reef density was about half way between that at sites (a)

and (c) (Fig. 4B). This decrease in larvae number was modulated by the tides that resulted in rises and falls in number of larvae as the larval plume moved in and out of the spawning sites.

Preferred position for Figure 4

The trapping efficiency was parameterized by the exposure time. During calm weather conditions (see Table 2) it was 20.6 days for site (a), 7.5 days for site (b), and 2.5 days for site (c). During windy conditions the exposure time was 18.4, 8.7 and 4.8 days for sites (a), (b) and (c) respectively.

Seventeen sites with various reef architecture were selected (Fig. 2) for a sensitivity study. Exposure time results varies greatly from site to site (mean = 7.15 ± 6.6 days; maximum = 22.8 days; Table 2). Areas in a high-density archipelago (high value of A) or those in a highly restricted lagoon (high value of B) had the largest exposure times (14.8 to 22.8 days). Areas partially sheltered upstream by large reefs (i.e. in the lee of a large reef or sandwiched between two reefs) had a relatively high exposure time (4.7 – 6.6 days) but only if the tidal currents were small, otherwise the exposure time was much smaller (e.g. 1.8 days at site J). By contrast the flushing of larvae was very swift at isolated reefs at sites l and m in open offshore waters, with an exposure time of 1 day (Table 2, Fig. 4B). Open inshore waters similarly had an exposure time of 1.3 day (site m in Table 2). The Ribbon Reefs (site q, Table 2) had an exposure time of 1.1 day, similar to that in open waters site q.

Preferred position for Table 2

A MODIS satellite image (Fig. 5) is shown to gain confidence in the model skills of capturing the retention of larvae, and to provide a real demonstration of the existence of the sticky water effect within high reef density zones. The MODIS chlorophyll-a image of the central and southern GBR shows oceanic water intruding in the central GBR and flowing southward inshore between the high reef density area and the coast. Therefore, the oceanic inflow from the Coral Sea is mostly deflected away from the high reef density matrix. High chlorophyll-a concentration within closely aggregated reefs evidence the high exposure time, and thus the sticky water effect.

Preferred position for Figure 5

There was a high degree of spatial variability in the exposure time in the GBR (Table 2); and, therefore this implies a high spatial variability of the self-seeding potential of various reef areas in the GBR. This variability is partly predictable as a function of the oceanography and the reef architecture. No oceanography field data or models have so far been proposed to predict the self-seeding potential of a reef matrix. To provide such a predictive tool, two simple equations are proposed below to estimate the exposure time T of the 10 x 10 km

spawning sites and thus by inference the self-seeding potential. If oceanographic data are available, we propose the simple empirical formula

$$T = \alpha / (U_R U_T), \text{ where } U_R \neq 0 \text{ and } U_T \neq 0, \quad (1)$$

where T is in days and U_R and U_T (in m s^{-1}) are respectively the residual and maximum tidal currents spatially averaged over the 10 x 10 km spawning site, and $\alpha \sim 1159 \text{ m}^2 \text{ s}^{-1}$. In Eq. (1) U_R is multiplied by U_T because both U_R and U_T need to be small for the sticky effect to prevail (Fig. 1a). If the tidal currents are large, the site will flush swiftly even if the residual current is small. If the residual current is large, the site will also flush swiftly even if the tidal currents are small. The resulting self-seeding potential is never 100% (i.e. $T = \infty$) because water-born particles are dispersed out of the high reef density area by tidal diffusion. Eq. (1) fits the data in Table 2 under calm weather conditions with $r^2 = 0.69$ for simulations starting at neap tides under both calm weather and windy conditions. While for simulations starting at spring tides, $r^2 = 0.75$ and 0.69 under calm weather and windy conditions, respectively (Fig. 6). Eq. (1) could be used for predictions of connectivity at sites for which oceanographic data or a high resolution model is available to estimate both U_R and U_T .

The value of $\alpha \sim 1159 \text{ m}^2 \text{ s}^{-1}$ does not necessarily represent the value of the effective horizontal eddy diffusion coefficient K because in Eq. (1) T is proportional to α while in the classical diffusion theory T is proportional to K^{-1} following the formula (Fischer et al., 1979), i.e. $T = L^2/K$, where L is the domain length scale.

In most of the GBR matrix, however, and many other reef mosaics of the world, there are no field data or modelling to estimate U_R and U_T in Eq. (1). Then we propose the following simple, but less accurate, empirical formula that requires only a detailed bathymetry map,

$$T = 16 \text{ minimum}(A/(1-B), 1) \quad (2)$$

Eq. (2) fits the data in Table 2 with $r^2 = 0.66$ and 0.63 for simulations under calm weather, and starting under neap and spring tides, respectively. While under windy conditions $r^2 = 0.52$ and 0.48 for simulations starting at neap and spring tides, respectively (Fig. 6). It offers a simple way to estimate the likely degree of self-seeding of a reef matrix or an archipelago for which minimal oceanographic data are not available. The estimate is more robust for calm weather conditions than for windy conditions.

Preferred position for Figure 6

4. Discussion

This study shows that although self-seeding of reefs appeared unlikely based on historical models of water movement (Williams et al., 1984; Jones et al., 2009), our resolution of near reef oceanography has improved and biological evidence indicates that at least at some locations and for some taxa a high percentage of larvae can return to their natal reef (Jones et al., 1999; Almany et al., 2007).

Our models would be conservative for predicting levels of self-recruitment where larvae actively seek home (e.g. Gerlach et al., 2007). Variable mesh-sized models allow for a high resolution understanding of mainstream and near reef currents. It is clear that some scenarios of reef topography and tidal currents facilitate a high level of retention for times that equate with the PLD (Planktonic Larval Duration) of many larvae. PLD of 100 species of Pacific and Atlantic damselfish family was investigated by Wellington and Victor (1989), and the PLD was observed to change between 13 to 35 days. High mobility and strong navigational abilities are not required for high levels of self-recruitment where the sticky water effect prevails.

Our study demonstrated the importance of small-scale processes at a horizontal scale < 1 km in generating the sticky water effect in regions of high reef density. We have shown that trapping efficiency (i.e. self-seeding potential) increased with reef density (Table 2). Most particles were retained within the high reef density spawning sites after 12 days – regardless of tidal and wind-related conditions.

The choice of models in determining the location of self-seeding areas is critical because the models must be able to merge both the large scales and the small scales for the sticky water effect to be resolved (Wolanski et al., 2003). For a model to predict the self-seeding and connectivity potential within a large region such as the GBR, (1) the whole GBR (region) must be included in the model in order to include the correct forcing by the Coral Sea, and (2) a higher horizontal resolution is required because low resolution (cell size > 1 km) erases small reefs and most reef passages and does not yield the correct shear distribution near the edges of the remaining reefs and thus does not simulate correctly the advection-dispersion processes in a reef matrix (Wolanski et al., 1996 and 2003). To meet these criteria, ~ 10 millions of cells would be needed for a high-resolution, finite-difference model of the whole GBR. To avoid these numerical pitfalls a non-structured grid model is needed that requires only a few hundreds of thousands of cells (Legrand et al., 2006). This is the reason why we used the non-structured finite-element model of Lambrechts et al. (2008).

The water circulation in the Great Barrier Reef (GBR) was faithfully reproduced by the model (Table 1). Superimposed on the residual currents were tidal currents which, away from the reef matrix, were oriented mainly cross-shelf in areas of low reef density and long-shelf in areas of high reef density. This concurs with other field and finite-difference models with a coarse resolution (King and Wolanski 1996; Brinkman et al., 2001; Dight et al., 1990; Luick et al., 2007).

Our finite-element model has the advantage that it also provides details of the water circulation in the reef matrix. The model shows (e.g. see Fig. 3) that the water circulation in areas of high reef density is quite different to that around an isolated reef or island, which is dominated by reef-induced eddies; it is instead controlled by the reef architecture and the prevailing currents in surrounding waters that can create a stagnation or near-stagnation zone.

The residual currents were minimal in the high reef density areas independent of their location on the mid- or outer-shelf. The tidal currents were also reduced in areas of very high reef density, even when tidal amplitude was high. As a result the sticky water effect prevailed in areas of very high reef density, which promoted retention of the waterborne larvae. Most (~ 62%) of the larvae remained in spawning sites with high reef density after 12 days, while less than 3% of the larvae remained after 12 days near isolated reefs (see sites l and m, Table 2, Fig. 4B).

The distribution of the high self-seeding zones is patchy in a reef matrix but appears predictable. The GBR, and reef archipelagos elsewhere in the world, comprise a number of hot spots of high self-seeding reefs imbedded within a network of reefs that are replenished mainly by long-distance connectivity.

Wind affects currents, especially in shallow water (Wolanski, 1994). For coral reefs on the GBR, many organisms spawn in November and December when light winds generally prevail. We have studied two wind conditions, namely calm weather conditions and a Southeasterly wind at 6.67 m s^{-1} , which is the mean value for those months in the southern region. Our predictions apply to such conditions. In some years however strong winds may apply and at such times the wind may modify the spatial distribution of the self-seeding areas, and this remains unknown and research is needed. Oceanographic research in the GBR has historically focused on monitoring and modelling the circulation in the open waters of the GBR continental shelf and thus away from the dense reef matrix (Webster et al., 2008). However, reef ecological research is focused on reefs. Our findings call for a greater focus on the fine-scale circulation within the reef matrix itself.

This study has provided two simple analytical formulae for predicting the retention of passively drifting particles near reefs. These formulae can allow ecologists to make predictions on levels of connectivity among reefs and clusters of reefs for which the oceanography is unknown. Knowledge of this kind can be used to make structured sampling designs where predictions can be made on connectivity in ecological and evolutionary time (e.g. Taylor and Hellberg, 2003; Jones et al., 2005). We predict that relatedness (i.e. genetic panmixis), will be high in areas of sticky water and ‘spill over’ from these source areas may provide larvae to downstream reefs (Carr and Reed, 1993). Reefs of low retention time may depend on occasional changes of residual currents (Williams et al., 1984; Wolanski, 1994; Bode et al., 2006) and winds that alter levels of larval-subsidy from other reefs. The topography, tides and residual currents were a good predictor of stickiness and retention even when a representative wind was included in the model.

Predictions on connectivity can assist in the planning of site and placement of MPA for sources and sink reefs as well as areas where retention is likely to be high (Palumbi, 2004). Cowen et al. (2006) used an oceanographic model of the Caribbean to identify areas with high and low potential for self-recruitment. Our study adds value to Cowen et al.’s conclusions in that we have made specific predictions on tide and topographic categories and metrics that facilitate retention as well as conditions where population subsidies from other reefs are likely.

Currents alone do not describe levels of connectivity as some larvae have excellent swimming ability and sensory systems that provide directionality, potentially allowing them to stay near or search for natal reefs (Kingsford et al., 2002); this capability has sometimes been included in models (e.g. Wolanski et al., 1997; Cowen et al., 2006). The larvae of some taxa have limited mobility and short larval duration (e.g. corals; Kingsford et al., 2002; Connolly and Baird, 2010). In this case, the larvae may behave similarly to as passive particles. In contrast, fishes and some invertebrates are capable of minimising dispersal from natal reefs through strong swimming, directionality and behaviourally altering depth of distribution. Despite this, even fishes have very limited mobility early in life. Many fishes only have strong swimming ability during the last 0.25 of their planktonic larval duration (Fisher et al., 2000; Fisher, 2005); hence the levels of passive drift explained in our study are relevant.

References

- Almany, G.R., Berumen, M.L., Thorrold, S.R., Planes, S., Jones, G.P., 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316, 742–744.
- Andrews, J.C., 1983. Water masses, nutrient levels and seasonal drift on the outer central Queensland shelf (Great Barrier Reef). *Australian Journal of Marine and Freshwater Research* 33, 717–722.
- Andrews, J.C., Furnas, M.J., 1986. Subsurface intrusions of Coral Sea Water into the central Great Barrier Reef—I. Structures and shelf-scale dynamics. *Continental Shelf Research* 6, 491–514.
- Andrews, J.C., Clegg, S., 1989. Coral Sea circulation and transport from modal information models. *Deep-Sea Research* 36, 957–974.
- Andutta, F.P., Ridd, P.V., Wolanski E., 2011. Dynamics of hypersaline coastal waters in the Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 94, 299–305.
- Ayre, D.J., Hughes, T.P., 2000. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54, 1590–1605.
- Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.L., Wallace, C.C., Willis, B.L., 1986. Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar. Biol.* 90, 379–394.
- Black, K.P., Gay, S.L., 1987. Eddy formation in unsteady flows, *Journal of Geophysical Research* 92(C9), 9514–9522.
- Black, K.P., Gay, S.L., Andrews, J.C., 1990. Exposure times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. *Coral Reefs* 9, 105–114.
- Black, K.P., 1993. The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. *Coral Reefs* 12, 43–53.
- Bode, M., Bode, L., Armsworth, P., 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series* 308, 17–25.
- Brinkman, R., Wolanski, E., Deleersnijder, E., McAllister, F., Skirving, W., 2001. Oceanic inflow from the Coral Sea into the Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 54, 655–668.
- Burgess, S.C., Kingsford, M.J., Black, K.P. 2007. Influence of tidal eddies and wind on the distribution of presettlement fishes around One Tree Island, Great Barrier Reef. *Marine Ecology Progress Series* 341, 233–242.
- Carleton, J.H., Brinkman, R., Doherty, P.J., 2001. The effect of water flow around coral reefs on the distribution of pre-settlement fish (Great Barrier Reef, Australia). pp. 209–230

- in Wolanski E (Editor), *Oceanographic Processes of Coral Reefs. Physical and Biological Links in the Great Barrier Reef*. CRC Press, Boca Raton, Florida.
- Carr, M.H., Reed, D.C., 1993. Conceptual issues to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Science* 50, 2019–2028.
- Christie, M.R., Johnson, D.W., Stallings, C.D., Hixon, M.A., 2010. Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. *Molecular Ecology* 19, 1042–1057.
- Christie, M.R., Tissot, B.N., Albins, M.A., Beets, J.P., Jia, Y., Ortiz, D.M., Thompson, S.E., Hixon, M.A., 2010. Larval connectivity in an effective network of Marine Protected Areas. *Plos One* 5, e15715.
- Connolly, S.R., Baird, A., 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology* 91, 3572–3583.
- Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. *Science* 311, 522–527.
- Crawford, W.R., Tyler, A.V., Thomson, R.E., 1990. A possible eddy retention mechanism for ichthyoplankton in Hecate Strait. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 1356–1363.
- Deleersnijder, E., Campin, J.M., Delhez, E.J.M., 2001. The concept of age in marine modeling. I. Theory and preliminary model results. *Journal of Marine Systems* 28, 229–267.
- Delhez, E. J. M., 2006. Transient residence and exposure times. *Ocean Science* 2, 1-9.
- Dight, I.J., James, M.K., Bode, L. 1990. Modelling the larval dispersal of *Acanthaster planci*. II. Patterns of reef connectivity. *Coral Reefs* 9, 125–134.
- Fischer, H.B., List, J.E., Koh, C.R., Imberger J., Brooks, N.H., 1979. Mixing in inland and coastal waters. Elsevier, Amsterdam, 302 pp.
- Fisher, R., Bellwood, D.R., Job, S.D., 2000. Development of swimming abilities in reef fish larvae. *Marine Ecology Progress Series* 202, 163–173.
- Fisher, R., 2005. Swimming speeds of larval coral reef fishes: impacts on self-recruitment and dispersal. *Marine Ecology Progress Series* 285, 223–232.
- Ganachaud, A., Kessler, W., Wijffels, S., Ridgway, K., Cai, W., Holbrook, N., Bowen, M., Sutton, P., Qiu, B., Timmermann, A., Roemmich, D., Sprintall, J., Cravatte, S., Gourdeau, L., Aung, T., 2007. Southwest Pacific Ocean Circulation and Climate

- Experiment. Part I. Scientific Background. NOAA OAR Special Report / International CLIVAR Project Office. C. P. S. N. 111.
- Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P., Miller-Sims, V., 2007. Smelling home can prevent dispersal of reef fish larvae. PNAS 104, 858–863.
- Gladstone, W., Westoby, M., 1988. Growth and reproduction in *Canthigaster valentini* (Pisces, Tetradontidae): a comparison of a toxic reef fish with other reef fishes. Environ. Biol. Fishes. 21, 207–221.
- Graber, H.C., Limouzy-Paris, C.B., 1997. Transport patterns of tropical reef fish larvae by spin-off eddies in the straits of Florida. Oceanography 10, 68–71.
- Hamann, M., Grech, A., Wolanski, E., Lambrechts, J., 2011. Modeling the fate of marine turtle hatchlings. Ecological modeling 222, 1515–1521.
- Hutchings, P., Kingsford, M., Hoegh-Guldberg, O., 2008. The Great Barrier Reef. CSIRO Publishing and Springer, Collingwood and Dordrecht, 392 pp.
- Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C., 1999. Self-recruitment in a coral reef fish population. Nature 402, 802–804.
- Jones, G.P., Planes, S., Thorrold, S.R., 2005. Coral reef fish larvae settle close to home. Current Biology 15, 1314–1318.
- Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S., van Oppen, M.J.H., Willis, B.L., 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28, 307–325.
- King, B.A., Wolanski, E., 1996. Tidal current variability in the Central Great Barrier Reef. Journal of Marine Systems 9, 187–202.
- Kingsford, M.J., Leis, J., Shanks, A., Lindeman, K., Morgan, S., Pineda, J., 2002. Sensory environments, larval abilities and local self-recruitment. Bull Mar Sci. Suppl. 70, 309–340.
- Lambrechts, J., Harnet, E., Deleersnijder, E., Bernard, P.E., Legat, V., Remacle, J.F., Wolanski, E., 2008. A multi-scale model of the hydrodynamics of the whole Great Barrier Reef. Estuarine, Coastal and Shelf Science 79, 143–151.
- Lee, T.N., Rooth, C., Williams, E., McGowan, M., Smant, A.F., Clarke, M.E. 2002. Influence of the Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. Continental Shelf Research 12, 971–1002.
- Legrand, S., Deleersnijder, E., Hanert, E., Legat, V., Wolanski, E., 2006. High-resolution unstructured meshes for hydrodynamics models of the Great Barrier Reef, Australia. Estuarine, Coastal and Shelf Science 68, 36–46.

- 1 Lobel, P.S., Robinson, A.R., 1986. Transport and entrapment of fish larvae by mesoscale
2 eddies and currents in Hawaiian waters. *Deep Sea Research* 33, 483–500.
- 3 Lucas, L.V., Thompson, J.K., Brown, L.R., 2009. Why are diverse relationships observed
4 between phytoplankton biomass and transport time? *Limnology and Oceanography*
5 54, 381–390.
- 6
7
8
9 Luick, J.L., Mason, L., Hardy, T., Furnas, M.J., 2007. Circulation in the Great Reef Barrier
10 Lagoon using numerical tracers and in situ data. *Continental Shelf Research* 27, 757–
11 778.
- 12
13
14 Middleton, J.H., Cunningham, A., 1984. Wind-forced continental shelf waves from a
15 geographical origin. *Continental Shelf Research* 3, 215–232.
- 16
17
18 Monsen, N.E., Cloern, J.E., Lucas, L.V., Monismith, S.G., 2002. A comment on the use of
19 flushing time, residence time, and age as transport time scales. *Limnology and*
20 *Oceanography* 47, 1545–1553.
- 21
22
23 Munday, P.L., Leis, J.M., Lough, J.M., Paris, C.B., Kingsford, M.J., Berumen, M.L.,
24 Lambrechts, J., 2009. Climate change and coral reef connectivity. *Coral Reefs* 28,
25 379–395.
- 26
27
28
29 Oliver, J., King, B., Willis, B., Babcock, R., Wolanski, E., 1992. Dispersal of coral larvae
30 from a coral reef. Comparison between model predictions and observed
31 concentrations. *Continental Shelf Research* 12, 873–891.
- 32
33
34
35 Palumbi, S.R., 2004. Marine reserves and ocean neighborhoods: The spatial scale of marine
36 populations and their management. *Annual Review of Environment and Resources*
37 29, 31–68.
- 38
39
40 Paris, C.B., Chérubin, L.M., Cowen, R.K., 2007. Surfing, spinning or diving from reef to
41 reef: effects of population connectivity. *Marine Ecology Progress Series* 347, 285–
42 300.
- 43
44
45
46 Reyns, N., Sponaugle, S., 1999. Patterns and processes of brachyuran crab settlement to
47 Caribbean coral reefs. *Marine Ecology Progress Series* 185, 155–170.
- 48
49
50 Robertson, D.R., Petersen, C.W., Brawn, J.D., 1990. Lunar reproductive cycles of benthic
51 brooding reef fishes: reflections of larval biology or adult biology? *Ecological*
52 *Monographs* 60, 311–329.
- 53
54
55 Smagorinsky, I., 1963. General Circulation Experiment with Primitive Equations. *Monthly*
56 *Weather Review* 91, 91–164.
- 57
58
59
60
61
62
63
64
65

- 1 Spagnol, S., Wolanski, E., Deleersnijder, E., 2001. Steering by coral reef assemblages. pp.
2 145-160 in Wolanski E (Editor), *Oceanographic Processes of Coral Reefs: Physical*
3 *and Biological Links in the Great Barrier Reef*. CRC Press, Boca Raton, Florida.
- 4 Spagnol, S., Wolanski, E., Deleersnijder, E., Brinkman, R., McAllister, F., Cushman-Roisin,
5 B., Hanert, E., 2002. An error frequently made in the evaluation of advective
6 transport in two-dimensional Lagrangian models of advection-diffusion in coral reef
7 waters. *Marine Ecology Progress Series* 235, 299–302.
- 8 Sponaugle, S., Cowen, R.K., Shanks, A., Morgan, S.G., Leis, J.M., Pineda, J., Boehlert,
9 G.W., Kingsford, M.J., Lindeman, K.C., Grimes, C., Munro, J.L., 2002. Predicting
10 Self-recruitment in marine populations: biophysical correlated and mechanisms.
11 *Bulletin of Marine Science* 70, 341–375.
- 12 Swearer, S.E., Caselle, J.E., Lea, D.W., Warner, R.R., 1999. Larval retention and recruitment
13 in an island population of coral-reef fish. *Nature* 402, 799–802.
- 14 Taylor, M.S., Hellberg, M.E., 2003. Genetic evidence for local retention of pelagic larvae in a
15 Caribbean reef fish. *Science* 299, 107–109.
- 16 Valle-Levinson, A., 2010. *Contemporary Issues in Estuarine Physics*. Cambridge University
17 Press, United Kingdom, 315pp.
- 18 van Oppen, N.J.H., Lutz, A., De'ath, G., Peplow, L., Kininmonth, S., 2008. Genetic traces of
19 recent long-distance dispersal in a predominantly self-recruiting coral, *PLoS One*
20 3(10), E3401.
- 21 Webster, I., Brinkman, R., Parslow, J., Prange, J., Steven, A., Waterhouse, J., 2008. Review
22 and Gap Analysis of Receiving-Water Water Quality Modelling in the Great Barrier
23 Reef. Report to Environment and Water Resources. *Water for a Healthy Country*
24 Flagship, Canberra, 146 pp.
- 25 Wellington, G.M., Victor, B.C., 1989. Planktonic larval duration of one hundred species of
26 Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology* 101, 557–567.
- 27 Williams, D.M., Wolanski, E., Andrews, J.C., 1984. Transport mechanisms and the potential
28 movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral*
29 *Reefs* 3, 229–236.
- 30 Wolanski, E., van Senden, D., 1983. Mixing of Burdekin River flood waters in the Great
31 Barrier Reef. *Australian Journal Marine Freshwater Research* 34, 49–63.
- 32 Wolanski, E., Burrage, D., King, B., 1989. Trapping and diffusion of coral eggs near Bowden
33 Reef, Great Barrier Reef following mass coral spawning. *Continental Shelf Research*
34 9, 479–496.

- 1 Wolanski, E., 1994. Physical Oceanographic Processes of the Great Barrier Reef. CRC Press,
2 Boca Raton, Florida, 194 pp.
- 3 Wolanski, E., Asaeda, T., Tanaka, A., Deleersnijder, E., 1996. Three-dimensional island
4 wakes in the field, laboratory and numerical models. Continental Shelf Research 16,
5 1437–1452.
6
- 7 Wolanski, E., Doherty, P., Carleton, J., 1997. Directional swimming of fish larvae
8 determines connectivity of fish populations on the Great Barrier Reef.
9 Naturwissenschaften 84, 262–268.
- 10 Wolanski, E., Spagnol, S., 2000. Sticky waters in the Great Barrier Reef. Estuarine, Coastal
11 and Shelf Science 50, 27–32.
12
- 13 Wolanski, E., Brinkman, R., Spagnol, S., McAllister, F., Steinberg, C., Skirving, E.,
14 Deleersnijder, E., 2003. Merging scales in models of water circulation: Perspectives
15 from the Great Barrier Reef. pp. 411–427 in Lakhan, V.C. (Editor), Advances in
16 Coastal Modeling. Elsevier, Amsterdam.
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Text for figures

Figure 1. (a) Sketch of the sticky water effect in a reef matrix over a continental shelf, showing (lines) streamlines of the residual current and (crosses) the tidal ellipses. (b) Definition of the reef architecture.

Figure 2. (A) Location map showing the grid over the whole GBR; the high resolution near reefs is highlighted by a zoom on the Swain reef area where were located three virtual spawning areas namely, (a) large dense archipelago, (b) large medium density archipelago and (c) large low density archipelago. (B) Map of the southern and central regions of the Great Barrier Reef, Australia. Field data sites of tidal currents (red dots), residual currents (green dots) and the salinity transect (blue line); (NCJ) North Caledonia Jet; (EAC) Eastern Australian Current; (NQC) North Queensland Current. Residual circulation indicated by the black arrows, and the dominant direction of the tidal currents is indicated by the double pointed brown arrows. The Coral Sea inflow was applied along the orange line. The squares (a) to (q) indicate the location of the virtual spawning sites in areas of different architecture. (C) Location of current meters in the sticky water experiment of Wolanski and Spagnol (2000) and used in this study to demonstrate that the mean currents are deflected around a high reef density area.

Figure 3. Predicted residual currents and the peak tidal currents during flood and ebb in the Swain reef area.

Figure 4. (A) Distribution of the virtual larvae plume after 12 days originating from three spawning sites in the Swain reef area, namely, (a) high-density archipelago, (b) medium-density archipelago and (c) low-density archipelago. (B) Time-series plot of the percentage of larvae remaining in the (10 by 10 km box) of the areas a, b, c and l (area characteristics see Table 2), and the simulation started at 1st of August 2006. The mean residence time is the time needed for the number of larvae inside the box to decrease to 0.37 its initial value (Deleersnijder et al., 2001).

Figure 5. MODIS chlorophyll-a image on of the central and southern GBR showing oceanic (blue) water intruding in the central GBR and flowing southward inshore of the high reef density area. Red is high Chlorophyll-a or turbid water; blue is low Chlorophyll -a water; and black is land and cloud (Steinberg, 2007). The Swain reef area is indicated, and shows hot spots of high chlorophyll concentration in high reef density areas in agreement with our estimates of the sticky water effect.

Figure 6. Scatter plot of the residence time T2 predicted by the SLIM model against the residence time T1 predicted by Eq. (1) for (A) calm weather (no wind) and (B) southeasterly wind of 6.67 m s^{-1} . Residence time T2 predicted by the SLIM model against the residence time T1 predicted by Eq. (2) for (A) calm weather (no wind) and (B) southeasterly wind of 6.67 m s^{-1} . The figure indices (n) and (s) denotes simulations starting at neap (1st of August 2006) and spring tides (8th of August 2006), respectively.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Table 1. Observed (U_o) and predicted (U_p) longshore residual currents ($m\ s^{-1}$, >0 if northward, <0 if southward) and peak tidal currents (U_T , in $m\ s^{-1}$) at mooring sites. The location of the current meter mooring sites is shown in Figure 2. The data sources A, B, C and D refer respectively to Andrews (1983), Wolanski et al. (1989), Spagnol et al. (2001) and Middleton and Cunningham (1984). The root mean square error RMSE ($m\ s^{-1}$) is shown in the last row.

Currents ($m\ s^{-1}$) in the GBR at mooring sites						
Site name	Latitude (°S)	Longitude (°E)	U_o	U_p	U_T	Source
Lizard Island	-14.7406	145.4253	0.05	0.07	0.23	C
Cape Upstart	-19.6253	147.9142	-0.11	-0.10	0.63	C
Old Reef	-19.4071	148.0197	-0.10	-0.09	0.59	
near shelf break	-18.8311	148.2896	-0.25	-0.20	0.36	A
Myrmidon Reef	-18.2452	147.4100	-0.18	-0.25	0.52	A
Bowden Reef	-19.0600	147.9597	-0.02	-0.02	0.47	B
Rattray Island	-19.9826	148.5833	-0.08	-0.09	0.47	
Hook	-19.9400	149.1100	-0.15	-0.16	0.71	D
Bushy	-20.8900	150.1600	-0.13	-0.13	0.32	D
Bell	-21.8200	151.1400	-0.06	-0.06	0.45	D
RMSE	-	-	-	0.03	-	-

Table 2. Location, reef architecture characteristics, and the reef cover parameter A and the lagoon closure parameter B of the 10 x 10 km spawning sites shown in Figure 2. The residence time T_1 (in days) under calm weather, is estimated for simulations starting and neap (1st of August 2006) and spring tides (8th of August 2006). During calm weather conditions and for a simulation starting under neap tides, the table shows the relative number N_1 and N_2 (in %) of larvae remaining in the spawning sites after 12 and 24 days respectively. During windy conditions and for a simulation starting at neap tides, the residence time T_2 (in days) of the spawning sites. U_{R1} and U_{R2} ($m s^{-1}$) are the residual currents in the spawning sites under calm weather and windy conditions, respectively. U_T ($m s^{-1}$) is the peak tidal current averaged spatially in the spawning sites.

Site	Lat. (° S)	Long. (° W)	Reef architecture	(A)	(B)	(neap) T_1	(spring) T_1	N_1 (12 d)	N_2 (24 d)	T_2	U_{R1}	U_T	U_{R2}
a	21.95	152.45	large dense archipelago	0.95	0	20.6	20.5	62.4	29.8	18.4	0.01	0.08	0.01
b	21.45	151.85	large medium density archipelago	0.55	0	7.5	5.4	16.1	4.3	8.7	0.06	0.55	0.04
c	21.25	152.15	large and low density archipelago	0.3	0	3.0	3.8	2.7	0.0	4.8	0.10	0.48	0.02
d	21.15	151.25	highly restricted lagoon	0.3	0.95	22.8	22.0	63.1	37.2	27	0.01	0.09	0.01
e	20.75	150.75	highly restricted lagoon	0.7	0.8	14.8	10.5	46.0	21.4	8	0.01	0.14	0.02
f	20.35	150.45	partially restricted lagoon	0.1	0.8	13.0	11.1	42.5	11.5	15	0.01	0.13	0.01
g	19.95	150.05	low restricted lagoon	0.1	0.6	5.2	2.8	7.5	0.0	5.3	0.02	0.23	0.02
h	19.85	149.30	reef cluster shielded but with swift tidal currents	0.1	0.3	1.5	2.3	3.8	0.0	2.2	0.04	0.30	0.04
i	19.55	149.15	cluster with small reefs	0.1	0.5	10.1	6.7	31.4	19.2	8.1	0.02	0.35	0.02
j	19.55	148.85	cluster of reefs with side shielded and swift tidal currents	0.1	0.3	1.8	0.8	0.0	0.0	1.9	0.01	0.55	0.01
k	19.25	148.65	cluster with large reef > 10 km	0.95	0.3	6.6	6.8	7.7	0.4	8.1	0.01	0.20	0.01
l	19.05	148.75	open area at shelf break	0	0	1.0	1.1	0.0	0.0	1.1	0.12	0.23	0.07
m	19.85	148.65	open inshore area	0	0	1.3	1.6	0.0	0.0	1.8	0.11	0.49	0.01
n	19.35	148.15	cluster with large reef, shielded upstream with moderate tidal currents	0.1	0.3	4.7	1.8	0.0	0.0	4.4	0.01	0.35	0.06
o	18.75	147.55	small low density archipelago	0.1	0	2.8	5.4	7.9	0.9	6.9	0.03	0.16	0.01
p	18.35	146.75	cluster with front and back areas of the small reef shielded	0.3	0.2	4.3	5.1	4.9	0.6	5.7	0.02	0.09	0.02
q	15.25	145.75	ribbon reef	0.1	0	1.1	2.0	0.3	0.0	1.0	0.03	0.14	0.04