'Sticky water' enables the retention of larvae in a reef mosaic

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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 directed 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 hot spots of high self-seeding, and these hot spots 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 kilometres to tens of kilometres 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 ∼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.

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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, 2005; Swearer et al., 1999; Carleton et al., 2001; Almany 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 (Crawford et al., 1990; Graber and Limouzy-Paris, 1997). 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; Almany 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 behaviour (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

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density of the reef matrix is high (i.e. reefs closely aggregated), the self-seeding potential may increase because the reef matrix directs the mean circulation away from and around the reef matrix (Fig. 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 increases, the sticky water effect should increasingly dominate, reducing expatriation and increase retention of waterborne larvae.

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

Fig. 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.

numerical model was crucial because the model must be able to cope with the complexity of the bathymetry. To model the GBR accurately one must cope with 2800 reefs scattered over its 2600 km length, with reefs ranging in area from $\sim 0.1 - \sim 100$ km^2 and often separated by narrow passages (i.e. tens to a few hundred metres). 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 modellers 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 (~ 150 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 (Fig. 2).

TOPEX data were 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 (Fig. 2) we applied 4 Sv to the open boundary, between $\sim 16.3°$ S and 17.4° S (1 Sv = 1 $\times 10^6$ m^3 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 (2.5×10^{-1} m$^{-1/3}$s) to simulate high roughness and lower values (2.5×10^{-3} m$^{-1/3}$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).

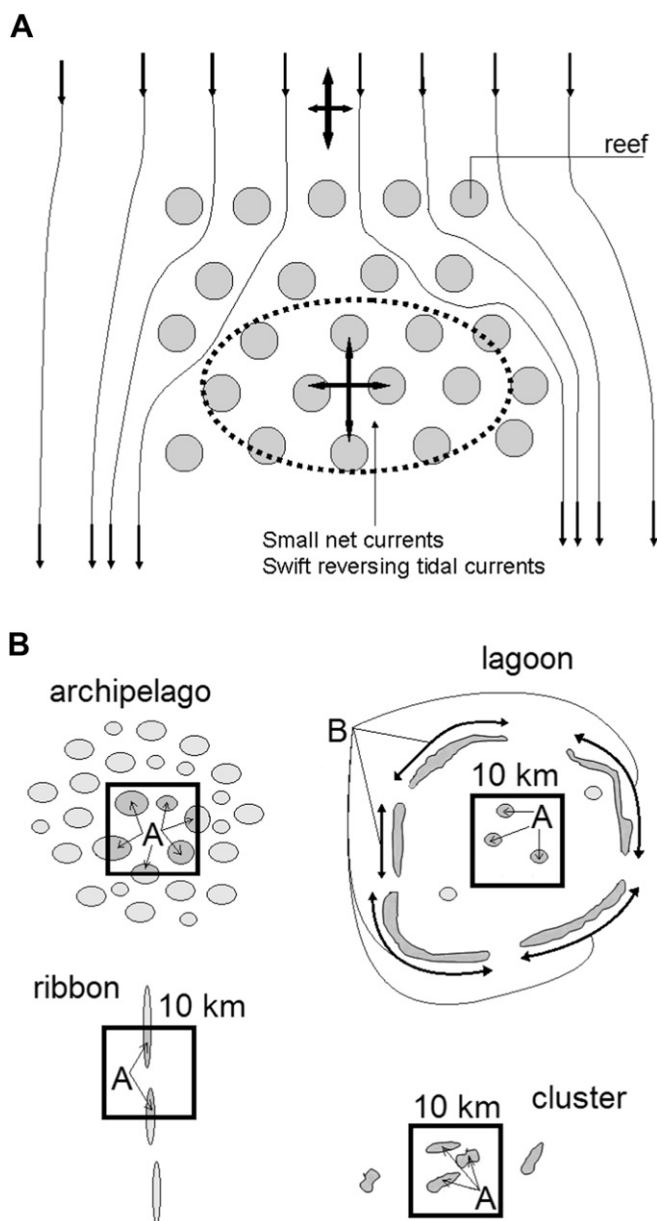To verify the model we used the data from tide gauges and moored current meters of Andrews (1983), Wolanski et al. (1989),