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A numerical model of wave- and current-driven nutrient uptake by coral reef communities

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ABSTRACT

We developed a numerical model capable of simulating the spatial zonation of nutrient uptake in coral reef systems driven by hydrodynamic forcing (both from waves and currents). Relationships between nutrient uptake and bed stress derived from flume and field studies were added to a four-component biogeochemical model embedded within a three-dimensional (3-D) hydrodynamic ocean model coupled to a numerical wave model. The performance of the resulting coupled physical-biogeochemical model was first evaluated in an idealized one-dimensional (1-D) channel for both a pure current and a combined wave-current flow. Waves in the channel were represented by an oscillatory flow with constant amplitude and frequency. The simulated nutrient concentrations were in good agreement with the analytical solution for nutrient depletion along a uniform channel, as well as with existing observations of phosphate uptake across a real reef flat. We then applied this integrated model to investigate more complex two-dimensional (2-D) nutrient dynamics, firstly to an idealized coral reef-lagoon morphology, and secondly to a realistic section of Ningaloo Reef in Western Australia, where nutrients were advected into the domain via alongshore coastal currents. Both the idealized reef and Ningaloo Reef simulations showed similar patterns of maximum uptake rates on the shallow forereef and reef crest, and with nutrient concentration decreasing as water flowed over the reef flat. As a result of the cumulative outflow of nutrient-depleted water exiting the reef channels and then being advected down the coast by alongshore currents, both reef simulations exhibited substantial alongshore variation in nutrient concentrations. The coupled models successfully reproduced the observed spatial-variability in nitrate concentration across the Ningaloo Reef system.

1. Introduction

Coral reefs are highly productive ecosystems with high biodiversity typically found in the high-light, low-nutrient waters of the tropics (Odum and Odum, 1955). As natural resources, coral reefs provide valuable economic services and products worldwide (Moberg and Folke, 1999). Over the past century stresses, such as overfishing, increased terrestrial runoff from land-use changes, global warming, ocean acidification, and physical disturbance, have resulted in numerous deleterious impacts ranging from increased coral bleaching, increased instances of disease, and decreased rates of coral growth (Hoegh-Guldberg et al., 2007; Hughes, 1994; Nystrom et al., 2000).

Among coral reef ecosystem modelling studies, two types of models have received the most attention: box models and spatially explicit models. Box models focus on resolving the complexity of the trophic interactions within a defined ecosystem domain (e.g., Polovina, 1984; Porter et al., 1999; Tanner et al., 1996). These models normally assume zero mass flux across the model boundaries (i.e., they internally conserve mass) and that the properties inside the domain are spatially homogeneous (i.e., zero-dimensional in space). The structure and parameters used in these models are often based on historical data rather than on mechanistic processes describing the relationship between material fluxes, rate kinetics, and environmental forcing variables (e.g., Meesters et al., 1998; Porter et al., 1999). Box models are very effective in describing complex ecological processes that involve a large number of state variables, especially when the intrinsic interactions between these variables are poorly understood. Conversely, spatially explicit models extend the dimensionality of a model to reflect the more realistic spatial variation in environmental conditions, such as water depth, benthic rugosity, temperature, light, waves, currents, and water chemistry; all factors that are well-

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known for driving the spatial zonation in rates of reef growth and metabolism (Atkinson and Falter, 2003; Hatcher, 1997; Kinsey, 1985; Monismith, 2007). Spatially explicit models of pelagic reef communities (e.g., phytoplankton) typically couple physical transport models with biogeochemical reaction models of carbon, nitrogen, and phosphorus (e.g., Pinazo et al., 2004), thus providing the link to ecological processes operating at multiple spatial scales (Hatcher, 1997). Both types of models have been effectively applied to understand and manage reef ecosystems; the choice between the models depends on the complexity of the ecological structure and the required resolution of the time and spatial scales (Hatcher et al., 1987).

As in many ecosystems, nutrients play a particularly critical role in the dynamics of coral reef communities. Nutrient availability limits the growth of reef algae (Carpenter and Williams, 2007; Hatcher and Larkum, 1983; Schaffelke and Klumpp, 1998) which, in turn, provides an important food source for grazing fish and invertebrates (Carpenter, 1986; Odum and Odum, 1955). Rates of nutrient loading can affect the sensitivity of coral growth to changes in aragonite saturation state (Langdon and Atkinson, 2005). Any changes in nutrient loading can subsequently have an indirect but important impact on coral reef communities: high levels of nutrient loading coupled with reduction in herbivore biomass or other stressors (e.g., bleaching) can cause reef communities to shift from coral- to algal-dominated (Naim, 1993; Pastorok and Bilyard, 1985; Walker and Ormond, 1982). To properly assess the complex impacts that human activities and environmental changes have on coral reef ecosystems, we therefore must first understand the factors that control the spatial and temporal variability in nutrient dynamics across entire coral reef systems.

The uptake of dissolved inorganic nutrients (e.g., ammonium, nitrate, and phosphate) by reef corals and algae is limited by the convective mass transfer of nutrients across concentration boundary layers adjacent to the surfaces of reef coral and algae (Atkinson and Bilger, 1992; Badgley et al., 2006; Falter et al., 2004; Thomas and Atkinson, 1997). This is due primarily to the high rates of carbon fixation being driven by high light levels and the low availability of nutrients in the water column (Atkinson and Falter, 2003). The kinetics of nutrient uptake by coral reef communities is thus dictated not only by nutrient concentrations, but also by local flow and mixing rates near the benthos, as well as the morphological roughness of the community itself (Bilger and Atkinson, 1992). Local flow and mixing rates (occurring over scales of meters) depend on large-scale spatial and temporal variations in waves and currents (occurring over scales of hundreds of meters to kilometres). Over even larger scales (several kilometres or more), regional ocean current systems and coastal upwelling can bring nutrient-rich water from far offshore, thereby directly impacting the nutrient uptake of the coral reef communities living in shallow nutrient-poor water in the nearshore (Leichter et al., 2003; Palter et al., 2005; Williams and Follows, 2003). The spatial and temporal zonation of nutrient uptake rates is thus mechanistically linked to physical processes operating at multiple spatial and temporal scales. Due to this inherent multi-scale dependency, the only feasible way to accurately resolve and predict nutrient dynamics in coral reef communities is through the development and application of spatially and temporally explicit coupled physical–biogeochemical numerical models.

Recently, the individual components required to develop a coupled hydrodynamic–biogeochemical model for benthic coral reef communities have been tested and made available in the literature. Modern coupled wave-circulation numerical models capable of simulating nearshore ocean hydrodynamics, including over reefs (e.g., Haas et al., 2003; Lowe et al., 2009; Warner et al., 2008a), can provide the hydrodynamic foundation for such models. For many decades, biogeochemical models coupled to hydrodynamic models have been tested and applied extensively to study plankton communities in pelagic systems (see review by Jørgensen, 2010), though similar numerical models have not yet been rigorously developed for communities of benthic primary producers. Robust functional relationships relating the nutrient uptake kinetics by coral and algal communities to benthic boundary layer dynamics have been well-established for nearly 20 years (e.g., Bilger and Atkinson, 1992; Falter et al., 2004). Nevertheless, to our knowledge, these physical–biological relationships have not yet been coupled with a numerical hydrodynamic model to simulate the uptake of dissolved nutrients in coral reef systems.

In this study, we describe the development of a new benthic nutrient uptake module to simulate rates of nutrient uptake by coral reef communities within the popular, community-based, coastal 3-D ocean modelling system ROMS (Regional Ocean Modelling System). This integrated model is capable of simulating the complex temporal and spatial variability in nutrient uptake rates across real reefs, driven by waves, currents, and turbulent mixing in a deterministic way. While the focus of the model application in this present study is on nutrient uptake by shallow coral reef communities, the modelling framework developed here can easily be extended to investigate benthic nutrient uptake processes in other coastal environments (e.g., seagrass systems).

This paper is organized as follows. In Section 2, we describe the numerical ocean circulation and wave models that served as the foundation for this study, detail the development of a new benthic nutrient uptake module, and investigate the enhancement of nutrient uptake rate by wave-driven oscillatory flow. In Section 3, results from three separate model applications are presented, firstly to evaluate the model performance under idealized conditions, and secondly to examine the ability of the model to simulate the spatial variability of nutrient concentrations in a real fringing reef system with complex bathymetry. Potential applications and the scope for further development with this new modelling framework are discussed in Section 4.

2. Methods

We developed the integrated numerical model using a 3-D ocean circulation model two-way coupled to a spectral wave model. The circulation model also includes a reactive tracer module capable of simulating pelagic biogeochemical cycling, in which we inserted our new benthic nutrient uptake model. This benthic uptake module is driven by currents, waves, and turbulent mixing processes simulated by the two hydrodynamic (wave and circulation) models. A benthic boundary layer model, embedded in the circulation model, calculates wave- and current-induced bottom stresses, which predicts the nutrient uptake rate coefficient. A schematic of the modelling framework and the linkages between its various components are summarized in Fig. 1 (for descriptions of model variables, *see* Table 1). Each component in Fig. 1 is described in detail in the following Sections 2.1–2.4.

2.1. Ocean circulation and wave models

We based the hydrodynamic modelling on a version of the open-source, community ocean circulation model ROMS (release 3.2) coupled to the spectral wave model SWAN (Simulating Waves Nearshore, release 40.51). ROMS is a 3-D model that solves the primitive hydrostatic equations for momentum on a horizontal curvilinear Arakawa C grid, with terrain-following coordinates in the vertical, using a stable split-explicit time-stepping scheme (Haidvogel et al., 2008; Shchepetkin and McWilliams, 2005). The model incorporates the effects of density stratification due to temperature and salinity fields, air-sea fluxes and tidal forcing, and has been designed to take advantage of shared-memory, parallel computing architectures. The ROMS code is flexible by providing