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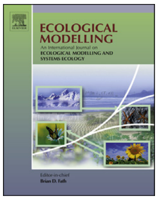

A biophysical representation of seagrass growth for application in a complex shallow-water biogeochemical model

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ABSTRACT

Seagrasses are a critical component of the healthy functioning of many coastal marine ecosystems. Capturing the dynamics of seagrass communities requires both a detailed representation of processes such as seagrass nutrient uptake and photosynthesis, as well as models of light penetration, water column and sediment biogeochemical processes and other ecosystem characteristics that determine the environmental state. Here we develop a new two-state, 13-parameter seagrass model with the aim of providing sufficient detail to represent light and nutrient limitation, but simple enough to be coupled into a 60 state variable biogeochemical model. The novel formulation is built around a nitrogen-specific leaf area parameter, Ω, that is well-constrained and is used in calculating both the rate of photosynthesis and the fraction of the seafloor covered by seagrass, A_{eff}, where $A_{eff} = 1 - \exp(-\Omega SG_A)$ and SG_A is the aboveground areal seagrass biomass. The model also contains terms for the uptake of nutrients from multiple layers of varying-porosity sediments, translocation of organic matter between leaves and roots, respiration and simple mortality terms. The model is applied to Gladstone Harbour, a macro-tidal sub-tropical estuary in northeast Australia, and is able to simulate realistic spatial seagrass distributions. A simplified form of the model is derived, which can be used to predict seagrass light-limited growth based on five measurable species-specific parameters (maximum growth rate, mortality rate, compensation irradiance, leaf blade angle and nitrogen-specific leaf area). The steady-state percent coverage of seagrass achieved at varying light levels and mortality intensity is calculated as a means of understanding the dynamics of the new seagrass model.

1. Introduction

Mathematical modelling is an important tool for assessing the effect of different anthropogenic impacts on coastal habitats, and how to invest resources most effectively for resource management and conservation. Seagrass ecosystems are economically and ecologically valuable, and are threatened by stressors such as water quality decline that act across a range of scales (Orth et al., 2006; Grech et al., 2012). The reason seagrasses provide so many valuable ecosystem services is that they act not only as a source of food but also as ecosystem engineers, creating structures and modifying environmental conditions which support a wide range of other trophic processes (Hastings et al., 2007).

Strong feedbacks between seagrass processes and environmental conditions (including water column nutrients, water clarity and sediment resuspension) suggest that incorporating seagrass in ecosystem models can be important for accurate predictions of water column processes in shallow-water coastal ecosystems (Webster and Harris, 2004). Conversely, modelling seagrass in isolation without accounting for interactions with water quality and sediment resuspension, may fail to capture important drivers of seagrass communities (van der Heide et al., 2007; Carr et al., 2012).

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The availability of photosynthetically active radiation is a key requirement for seagrass growth, and a limiting resource in many seagrass habitats (Ralph et al., 2007; Collier et al., 2012). Seagrass photosynthesis responds to light according to a classical photosynthesis-irradiance saturating curve (Touchette and Burkholder, 2000), and this process has been modelled by fitting empirical data to various equations, e.g. hyperbolic tangent function, adjusted to account for maximum seagrass densities (Burd and Dunton, 2001), Monod function (Elkalay et al., 2003), or asymptotic exponential function (Zimmerman et al., 1995; Newell and Koch, 2004; da Silva and Asmus, 2001). However, photosynthesis–irradiance curves are strongly affected by preceding environmental conditions, such as long and short-term light history, and temperature (Kehoe et al., 2015; O'Brien et al., 2009). Some phytoplankton photosynthesis models use measurable mechanistic parameters (Han, 2002) or allometric relationships to address this challenge (Baird and Suthers, 2007). There is a strong need for similar mechanistic relationships in seagrass models (Baird et al., 2003; Macreadie et al., 2014).

Explicit seagrass processes have been included within coupled hydrodynamic – biogeochemical or ecosystem models. Early biogeochemical studies (Harris et al., 1996; Cerco and Moore, 2001; Newell and Koch, 2004; Webster and Harris, 2004) focused on the role seagrass played in the proportion of pelagic to benthic productivity, and in particular the negative impact of coastal eutrophication on seagrass stocks. Ecosystem models tend to have less physiological detail, but are able to look at longer term dynamics (Carr et al., 2012). More recently researchers have improved the physiological realism of seagrass models, by, for example, considering above- and below-ground biomass in order to better resolve the role of seagrass in ecosystem function (Cerco et al., 2013; Plus et al., 2015). In each study a compromise between physiological detail and manageable model complexity is made, with the level of detail depending on the complexity and number of other components of the ecological model, and the particular application of the study.

The motivation for the seagrass model developed here is twofold: firstly to develop a biophysical formulation for seagrass response to light, which depends on measurable, transferable parameters, and overcomes some of the limitations of standard photosynthesis–irradiance formulations. Secondly, to represent seagrass processes as they impact on ecosystem function in shallow-water coastal environments, in a complex ecosystem model that also quantifies other water column (phytoplankton), benthic (macroalgae, corals) and sediment (microphytobenthos) primary producers. Where differences exist in the supply of nutrients and light between different primary producers represented in the model, these differences are given greater attention in the model parameterisation (Baird et al., 2003, 2014). Thus, the seagrass model component investigated here has nutrient uptake from multiple sediment layers (distinguishing it from macroalgae that has nutrient uptake from the water column), geometric calculations of light uptake that consider the 2 dimensionality of leaves (to distinguish it from 3-dimensional microalgae, Baird and Middleton (2004)), and a C:N:P stoichiometry characteristic of benthic plants (Atkinson and Smith, 1983). However many other details, such as light scattering within a seagrass canopy (Zimmerman, 2003), or detailed seagrass photophysiology, that are justifiable in a model of a single-species seagrass meadow, have not been included in order to keep the complexity of the ecosystem model manageable for a 3-dimensional model implementation.

Seagrass communities can be split into shallow- and deep-water species, with deeper-water seagrass species recovering faster from disturbance than those present in shallow water (Rasheed et al., 2014). As this dynamic is important in our study location of Gladstone Harbour, we have configured the model with two seagrass groups, with the contrasting behaviour of the two groups providing insights into the model behaviour.

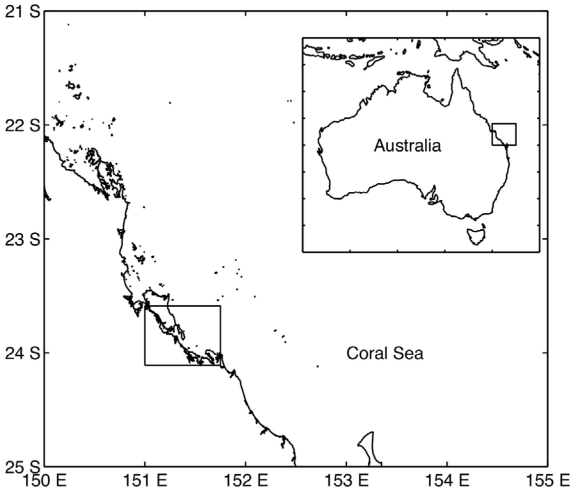

Fig. 1. Geographic location of the study site, Gladstone Harbour, on the northeast coast of Australia. Boxed region on larger panel is the geographical extent of Fig. 2.

In this paper, a seagrass model is derived that introduces new parameterisations to include geometrically-derived constraints of leaf anatomy and depth-resolved root structure, and is forced by spectrally-resolved downwelling light. The model is applied with two seagrass types in a highly-impacted estuarine environment with strong tides in which light is the dominant limiting factor to seagrass growth. The general behaviour of the model is assessed against spatially-resolved biomass of the seagrass collected over a decade from Gladstone Harbour, Australia (Fig. 1). Finally, analytical calculations are undertaken to understand the behaviour of the new model parameterisations.

2. Study site and observations

Gladstone Harbour (Fig. 2) is a macro-tidal, sub-tropical estuary with large barotropic tides of amplitudes of up to 4 m (Herzfeld et al., 2015). The tides undergo a neap-spring cycle with a period of approximately 14 days, with a spring tide range of ~4 m and neap tide range of ~1 m, with maximum currents of ~2 m s^{-1}). The Calliope, and to lesser extent the Boyne, rivers discharge into the estuary. Additional fresh water may propagate through the Narrows as a result of flooding from the nearby Fitzroy River to the north. The large tides ensure that the water column is vertically well-mixed most of the time, and are also responsible for significant resuspension of fine sediment, resulting in a generally turbid water column. The region is characterised by extensive areas of tidal flats that become exposed at low tide and large areas of mangroves fringing the estuary.

Seagrass distribution in Gladstone Harbour has been intensively monitored and studied (Petrou et al., 2013; Rasheed et al., 2013; Chartrand et al., 2012; Petus et al., submitted for publication; Bryant et al., 2014). Seagrass biomass, area and species composition data is available from monitoring performed between 2002 and 2013 inclusive as part of the long-term monitoring in Gladstone Harbour and Rodds Bay (Rasheed et al., 2005, 2006, 2008, 2014; Taylor et al., 2007; Chartrand et al., 2009; Thomas et al., 2010; Davies et al., 2013). This data, collected in the period between October and December, consists of biomass estimates (g DW m^{-2}, DW – dry weight) for the species *Zostera muelleri*, *Halophila ovalis*, *Halophila decipiens*, *Halophila spinulosa* and *Halodule uninervis*, and qualitative description of sediment type (e.g. fine sand, sand, mud, shell or a combination thereof).