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Research article

Modelling interactive effects of multiple disturbances on a coastal lake ecosystem: Implications for management

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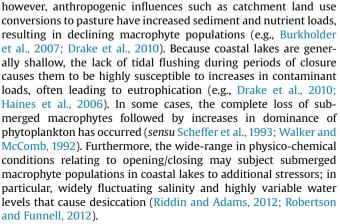
ABSTRACT

Coastal lakes, also known as temporarily open/closed estuaries or intermittently closed and open lakes and lagoons, are common worldwide, are typically sites of high biodiversity and often contain abundant macrophyte populations. Anthropogenic stressors such as increased nutrient and sediment loading have adverse effects on submerged macrophytes, and when closed, the lack of tidal flushing makes coastal lakes highly susceptible to eutrophication. Lake openings to the sea may occur naturally, but many coastal lakes are also opened artificially, often to reduce inundation of surrounding land. Here we used a coupled hydrodynamic-ecological model (DYRESM-CAEDYM), modified to include dynamic feedback between submerged macrophyte biomass and sediment resuspension, to explore the interactive effects of multiple disturbances (openings, eutrophication and climate change) on the dynamics of primary producers in a coastal lake (Waituna Lagoon) in South Island. New Zealand. Our results indicate that with exposure to high external nutrient loads, the frequent disturbances caused by artificial openings prevent sustained dominance by algae (algal biomass averaged 192 g C m^{-2} with artificial openings compared to 453 g C m^{-2} with no openings). However, under current nutrient loading, climate change is likely to enhance the effects of eutrophication on the system (algal biomass averaged 227 g C m⁻² with climate change compared with 192 g C m^{-2} for current climate). The model provides a decision-support tool to guide lake management in setting limits for nutrient loads and managing the opening regime, in order to prevent eutrophication and the potential collapse of the macrophyte community.

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1. Introduction

Coastal lakes are common worldwide, and are often highly valued for ecological, recreational and cultural reasons (Haines et al., 2006; Hume et al., 2007; Ticehurst et al., 2007). Also known as temporarily open/closed estuaries (TOCEs) or intermittently closed and open lakes and lagoons (ICOLLs), these ecosystems contain abundant and diverse submerged macrophyte communities that can sustain high levels of biodiversity (Schallenberg et al., 2010). In many estuaries and coastal lakes,



Management approaches for coastal lakes often encompass artificial opening to the sea when water levels are high, to reduce





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inundation of surrounding land (which is often used for agricultural purposes) or to flush nutrients from the lake (e.g. Schallenberg et al., 2010). This practice may be detrimental to ecosystem function however as openings can change entrance morphology, hydrodynamics, and cause desiccation of fringing wetlands (Haines et al., 2006). By contrast, artificial openings may reduce the effects of eutrophication, although the extent of water quality improvement is likely dependent on the degree of tidal flushing, which is generally not readily controlled (Schallenberg et al., 2010).

Regime shifts between macrophyte and phytoplankton dominated states have been observed in many coastal lakes, with unidirectional changes (i.e., permanent loss of submerged macrophytes) in some systems (e.g., Gerbeaux, 1993; Viaroli et al., 2008), and apparent multiple shifts in others (e.g., Mitchell, 1989; Riddin and Adams, 2012). In a number of coastal or shallow lake systems worldwide, long-term disturbances associated with catchment development (into agricultural land use, causing increased nutrient and sediment loading), water level fluctuations, manipulations of fish populations, and even the use of tributyltin (TBT), have been associated with such regime shifts (Blindow et al., 1993; Sayer et al., 2006; Schallenberg and Sorrell, 2009; Viaroli et al., 2008). For example, the East Kleinemonde and St Lucia estuaries in South Africa, both coastal lakes, exhibit shifts between macrophyte and macroalgae, or phytoplankton dominated states, dependent on opening status and salinity (Riddin and Adams, 2010; Taylor et al., 2006). In the South Island of New Zealand, submerged macrophytes in Te Waihora (Lake Ellesmere) were completely lost in 1968 following a severe storm that was preceded by long-term land use change in the catchment. The lake has been highly turbid and phytoplankton-dominated ever since (Gerbeaux, 1993). In contrast, Tomahawk Lagoon (also located in the South Island, New Zealand) has shifted between submerged macrophyte and phytoplankton dominance on an irregular cycle, with each phase lasting between 1 and 5 years (Mitchell, 1989). Similarly, Waituna Lagoon on the south coast of the Southland of New Zealand, which is the focus of the current study, has experienced cycles of submerged macrophyte and phytoplankton dominance due to recent variations in nutrient load from the catchment (Schallenberg et al., 2017). However, to what extent nutrient loads would have to be managed to maintain submerged macrophytes in these lakes before a complete collapse occurs is still poorly understood.

Warming temperatures and altered meteorological conditions caused by climate change may exert additional stress to these systems. Recent research indicates that the growth of cyanobacteria and filamentous algae will be enhanced by a warmer climate in shallow lake ecosystems (e.g., Trochine et al., 2011; Elliott, 2012; Paerl and Paul, 2012; Rolighed et al., 2016). These findings have important implications for the management of a range of aquatic ecosystems because proliferation of benthic and planktonic filamentous algae may influence transitions between alternate states (e.g. Genkai-Kato et al., 2012; Stevenson, 2014). In New Zealand, climate change may increase the potential for regime shifts in shallow or coastal lakes by enhancing the effects of eutrophication (e.g. increasing frequency of cyanobacterial blooms due to warmer water temperature), altering catchment-derived nutrient and sediment loading, and increasing wind-induced resuspension of bottom sediments which ultimately increases water column turbidity (Hamilton et al., 2012). Moreover, altered hydrology and warmer temperatures are likely to alter water levels in coastal lakes, disturbances already linked to regime shifts (Blindow et al., 1993; Scheffer and van Nes, 2007; Randsalu-Wendrup et al., 2016).

In this study, we used a deterministic model to explore drivers of ecological dynamics (i.e., the relationship between primary producers and their environment) in Waituna Lagoon, a coastal lake in South Island, New Zealand. Dynamic process-based ecological models are frequently used to provide guidance for sustainable management of aquatic ecosystems, particularly with regard to setting limits for nutrient loads and water levels (e.g., Marcé et al., 2010; Machado and Imberger, 2012; Parparov and Gal, 2012; Trolle et al., 2014). Moreover, these models can provide a useful tool for exploring ecological interactions across a broad suite of pressure gradients over long (decadal) time scales. Such complex models are rarely used to investigate the interactive effects of multiple disturbances on ecological dynamics in shallow aquatic ecosystems (Kuiper et al., 2014) and we are not aware of any application in this context on coastal lakes. Waituna Lagoon is especially well suited as a study site as it historically had large submerged macrophyte beds (Schallenberg et al., 2017), but has recently been subject to substantially increased nutrient loads following land-cover changes (McDowell et al., 2016). Observations of declining macrophyte populations and increased algal abundance have led to concern that the lagoon is at risk of shifting to a phytoplankton-dominated state (e.g., Robertson and Funnell, 2012).

For the purpose of this study, the model was primarily designed to further our understanding of the influence of, and interactions amongst, frequent disturbance (artificial lake openings) and chronic disturbance (increases in anthropogenic nutrient loading and climate change) on the potential for shifts in dominance of primary producers in coastal lakes. By utilizing a dynamic processbased ecological model, the insights gained in this study are likely to be applicable to similar systems. The application of the model to Waituna Lagoon may also be used as a decision-support tool to provide guidance on potential management options for the lagoon (involving managing nutrient loads and opening regimes) to prevent the further decline and collapse of the macrophyte population. Specifically, we asked the following questions: (i) what nutrient load reductions may be necessary to prevent long-term dominance of phytoplankton and prevent total collapse of submerged macrophytes in the system, and (ii) what are the potential interactive effects on ecosystem dynamics (with special emphasis on the biomass of primary producers) of artificial lake openings, climate change and nutrient loading? To answer these questions, we modified the coupled hydrodynamic-ecological model (DYRESM-CAEDYM; e.g., Gal et al., 2009) to include dynamic feedback between submerged macrophyte biomass and sediment resuspension. We then simulated a broad range of scenarios developed in consultation with other scientists, stakeholders, managers and iwi (indigenous Māori) with cultural connections to the lagoon, to explore the effects of multiple disturbances on the ecosystem. Given the value and occurrence of these ecosystems globally, the model framework presented here will be useful to inform management of such systems elsewhere.

2. Materials and methods

2.1. Study site

Waituna Lagoon (46° 34' S, 168° 36' E) is a small, shallow coastal lake in South Island, New Zealand (Fig. 1). Coastal lakes of this type have low to moderate freshwater surface inflows, are separated from the sea by a gravel barrier, and naturally remain closed for periods of many months to years (Kirk and Lauder, 2000). Although the barrier at Waituna Lagoon allows for some seepage between the lagoon and the sea, it is opened artificially usually once per year by the local environmental management agency (Environment Southland) to reduce inundation of surrounding farmland. When open, the mean depth in the lagoon is less than 1 m and the surface area is c. 8 km², but when closed the mean depth can increase to 1.6 m and the surface area to 16 km². Salinity in the lagoon ranges from <1 to 34 psu, depending on open/closed state, and opening

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