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A dynamic growth model of macroalgae: Application in an estuary recovering from treated wastewater and earthquake-driven eutrophication

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ABSTRACT

A dynamic growth model of macroalgae was developed to predict growth of the green macroalga *Ulva* sp. in response to changes in environmental variables. The model is based on common physiological behaviour of macroalgae and hence has general applicability to macroalgae. Three state variables (nitrogen, carbon and phosphorus) were used to describe physiological processes and functional differences between nutrient and carbon uptakes. Carbon uptake is modelled as a function of temperature, light, algal internal state and water current, while nutrient uptake depends on internal state, temperature and environmental nutrient level. Growth can only occur when nutrients in the environment and in the internal storage pools (N-quota and P-quota) reach threshold levels. Physiological rates follow the Arrhenius relationship and increase exponentially with increasing temperature within the temperature tolerance range of a species. When parameterised and applied to *Ulva* sp. in the eutrophic Avon-Heathcote Estuary, New Zealand, the model generally reproduced field observations of *Ulva* sp. growth and abundance. Growth followed a clear seasonal cycle with biomass increasing from early-middle summer, reaching peak values in early autumn and then decreasing. Conversely, N-quotient levels were maximal during the winter months, declining during summer peak growth. These seasonal patterns were collectively driven by temperature, light intensity and nutrients. The model captured the N-quota and growth responses of *Ulva* sp. to the N-reduction arising from diversion of treated wastewater from the Avon-Heathcote Estuary to an offshore outfall in 2010, and of raw sewage N-discharges resulting from wastewater infrastructure damage caused by the Canterbury earthquakes in 2011. Sensitivity analyses revealed that temperature-related parameters and maximum uptake rate of C were among the most sensitive parameters in predicting biomass. In addition, the earthquake-derived changes in reduction of immersion time and decrease in the start biomass prior to summer blooms were shown to drive considerable declines in summer growth and biomass of *Ulva* sp.

1. Introduction

Blooms of nuisance macroalgae occur frequently in coastal ecosystems driven by eutrophication (Hull, 1987; Franz and Friedman, 2002; Niu et al., 2010; Hu et al., 2010). Primary species among these macroalgae is *Ulva*, which is an opportunistic green macroalgal genus with potentially high growth rates leading to rapid biomass accumulation in response to excessive nutrient loading from wastewater or riverine sources (e.g. Raffaelli et al., 1998; Thornber et al., 2008). In estuaries and other sheltered environments, these blooms or their detached drift can form dense beds and generate hostile physico-chemical environments in underlying sediments (Raffaelli et al., 1991; Valiela et al., 1997). This biomass can present a significant environmental hazard when it decomposes, as underlying sediments become organically enriched, turn sub-oxic/anoxic and sulphate-reducing bacteria produce toxic concentrations of hydrogen sulphide (Raffaelli et al., 1998). Consequently, estuarine eutrophication mitigation undertaken by environmental managers often has a target for the reduction of *Ulva* and other nuisance macroalgal blooms (Bricker et al., 1999; Paerl, 2009).

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Ulva sp. is commonly distributed around New Zealand in a variety of environments ranging from rock pools, estuaries and harbours, to exposed coasts and offshore islands (Barr et al., 2008). Large nuisance *Ulva* sp. populations have existed in the Avon-Heathcote Estuary, near Christchurch city (Fig. 1) for many years, supported by discharge of tertiary-treated wastewater into the estuary (Knox and Kilner, 1973; Bolton-Ritchie and Main, 2005; Murphys, 2006). To mitigate this problem, local government in Christchurch invested *ca* NZ$80 million to divert the wastewater offshore, by building an ocean outfall commissioned in March 2010. We initiated a research programme 3 years prior to this, to determine the efficacy of the diversion in restoring estuarine health (Vopel et al., 2012). A key programme objective was to determine if the reduction in allocthonous estuarine nitrogen loading (predicted to be 90% in dissolved inorganic nitrogen) as a consequence of the outfall would be sufficient to significantly reduce macroalgal growth and biomass in the estuary, or if residual loadings from the urban Avon and Heathcote Rivers and/or from 'legacy' nutrient fluxes from the sediments, would continue to sustain nuisance algal growth.

Modelling of algal growth was considered an important part of the study because of the known complexity of drivers and responses of nuisance algal growth in estuaries. Estuarine environments suffering macroalgal blooms are often characterised by substantial fluctuations in abiotic and biotic variables that change over different time scales (Hughes et al., 2011). Nitrogen is usually the limiting nutrient for algal growth in marine coastal waters (Ryther and Dunstan, 1971; Thornber et al., 2008; Paerl, 2009), but its concentration is often an unreliable predictor of eutrophic conditions (Bricker et al., 1999), as N may be drawn down to low levels during bloom events. Algal growth also shows seasonal variation, mediated by complex physiological responses involving interactions of limitation by nutrients, temperature and light. The importance of temperature on growth in *Ulva* was demonstrated by Henley and Ramus (1989) who concluded that temperature changes of 2 or 3 °C had a much greater effect on growth than did the constant addition of 8–12 μM NH_4^+. Moreover, several studies have highlighted the importance of interactions between light, temperature and nitrogen supply (Duke et al., 1989; Rivers and Peckol, 1995; Altamirano et al., 2000; Taylor et al., 2001). As suggested by Duke et al. (1989) "the proximal mechanism for seaweeds' accumulation of N at low light and temperatures may be that N uptake is less limited by light and temperature than is growth". In addition, water motion is also known to influence the growth and physiology of macroalgae (Parker, 1981; Hurd, 2000; Barr et al., 2008). Finally, it has been suggested that seasonal accumulation of *Ulva* biomass in Avon-Heathcote Estuary is at least partially set by the initial overwintering biomass (Hawes and O'Brien, 2000). Thus, algal growth and biomass accumulation may be limited by one set of factors at a certain time of year and by another at a different time (e.g. Peckol et al., 1994), mediated and integrated by physiological processes. This complexity means that an internally consistent physiological model of macroalgal growth is an important tool for understanding and predicting nuisance macroalgal growth and potential responses to management actions to reverse eutrophication.

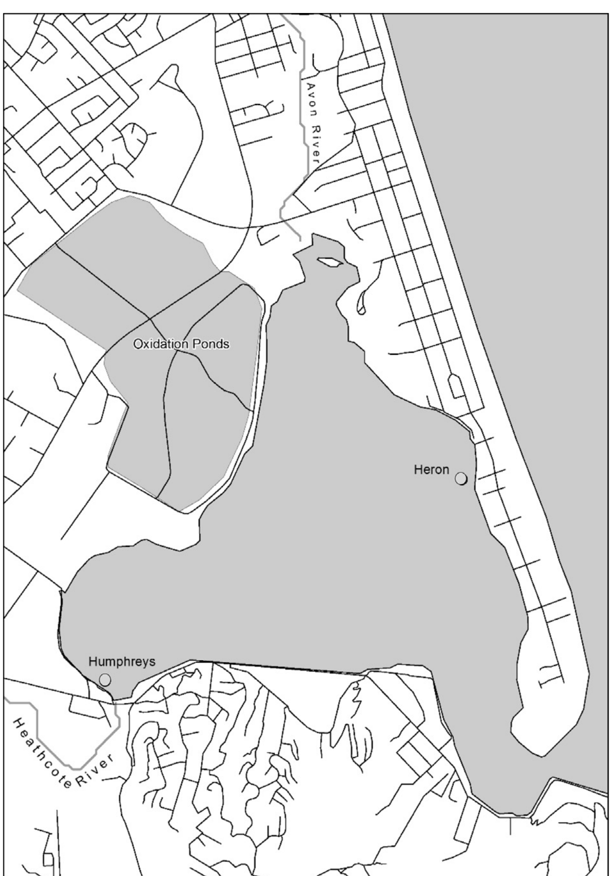

Fig. 1. Study sites in Avon-Heathcote Estuary, New Zealand.

Macroalgal growth models have been increasingly used for management of coasts and estuaries (e.g. Bendoricchio et al., 1994; Solidoro et al., 1997; Martins and Marques, 2002; Aveytua-Alcázar et al., 2008). Earlier types of model development for predicting macroalgal growth were useful in understanding the growth response of algae to change of environmental conditions. Because these simple models do not consider the effect of internal state on growth (e.g. Bendoricchio et al., 1994), their application is limited. The extension of earlier models to incorporate the internal state of algae (e.g. N-quota) has considerably improved their applicability (e.g. Solidoro et al., 1997; Aveytua-Alcázar et al., 2008), but carbon uptake is still not explicitly described in these models. Without separately describing the difference of uptakes between carbon and nutrients, the application of such models to wide range of environmental systems would be compromised, particularly in estuaries with a large variation of environmental variables including the Avon-Heathecote Estuary. The present model represents an advance on previously published *Ulva* models (i.e., Solidoro et al., 1997; Aveytua-Alcázar et al., 2008) primarily in the functional responses of carbon and nutrient uptakes.

Our primary objective is to develop a generic model of macroalgae to predict its physiological behaviour in response to changes of environmental conditions. The model was parameterised for *Ulva* sp. and validated in Avon-Heathecote Estuary with time-series of environmental data from 2008 to 12. These data encompass the March 2010 outfall commissioning and a much less expected series of events: the sequence of earthquakes of 2010–11 which devastated much of Christchurch (http://en.wikipedia.org/wiki/2011_Christchurch_earthquake). The earthquakes had multiple effects on the Avon-Heathcote Estuary including morphological uplift of much of the estuary bed (by up to 0.5 m: Measures et al., 2011), and ecological effects arising from liquefaction and damaged wastewater infrastructure, which caused sediment and raw sewage overflows into the estuary (Zeldis et al., 2011; Barr et al., 2012). We use the model to explore these effects on growth and biomass of *Ulva* in the estuary, to contribute to future management of the estuary including Avon and Heathcote River loads. We also explore the potential effect of earthquake-derived factors on growth and