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A simple numerical model for predicting vertical distribution of phytoplankton on the continental shelf

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a r t i c l e i n f o

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A B S T R A C T

A simple one-dimensional ecosystem model of phytoplankton production and nitrogen recycling is used to predict the steady-state vertical distribution of phytoplankton on the continental shelf (i.e. water depths <100 m). For an homogenously mixed water-column, close-to-uniform profiles of phytoplankton biomass are simulated in the model at mixing rates greater than 3×10^{-3} m⁻² s⁻¹. When mixing is reduced, sub-surface maxima develop either in mid-water or at the seabed depending on the rate of light attenuation. Nitrogen exchange between the water-column and seabed drives a positive feedback in the model between settling velocity and surface phytoplankton productivity. The model is tested against observations made along the Western Australian shelf. Despite the model's simplicity, from 42 profiles in depths between 20 and 100 m, we are able to predict vertical distributions of phytoplankton and nitrate to within 1 standard deviation. The model is shown to reproduce observed cross-shelf gradients in depth integrated quantities.

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1. Introduction

The vertical distribution of phytoplankton in the ocean has a major influence on primary production and transfer of energy to higher trophic levels ([Lampert](#page--1-0) et [al.,](#page--1-0) [2003\).](#page--1-0) This vertical structure is invisible from space, meaning that estimates of ocean primary production based on remote sensing must rely on sparse (in space and time) vertical profiles, and an understanding of vertical phytoplankton dynamics [\(Morel](#page--1-0) [and](#page--1-0) [Berthon,](#page--1-0) [1989\).](#page--1-0) The exact shape of the vertical phytoplankton biomass profile is determined by a combination of the vertical gradient of light, the usually opposing vertical nutrient gradient, vertical mixing and gravitational settling ([Hodges](#page--1-0) [and](#page--1-0) [Rudnick,](#page--1-0) [2004\).](#page--1-0) In the simplest case, phytoplankton biomass follows the disappearance of light with depth. Vertical turbulent motions, gravitational settling and nutrient supply act to modify this simple situation, resulting in either an homogenous distribution of biomass, or in a sub-surface biomass maximum that is more difficult to predict ([Hodges](#page--1-0) [and](#page--1-0) [Rudnick,](#page--1-0) [2004;](#page--1-0) [Ryabov](#page--1-0) et [al.,](#page--1-0) [2010\).](#page--1-0) In fact, many regions of the open-ocean are characterised by a maximum chlorophyll concentration at, or below, the depth where photosynthetic production is balanced by respiration. The mechanisms behind the existence of these so called 'deep-maxima' have been discussed in previous studies ([Fennel](#page--1-0)

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[and](#page--1-0) [Boss,](#page--1-0) [2003;](#page--1-0) [Hodges](#page--1-0) [and](#page--1-0) [Rudnick,](#page--1-0) [2004;](#page--1-0) [Steele](#page--1-0) [and](#page--1-0) [Yentsch,](#page--1-0) [1960\).](#page--1-0)

Water-column conditions on the continental shelf differ from those in the open-ocean in several ways. Firstly, non-zero phytoplankton concentrations at the seabed are common [\(Chen](#page--1-0) et [al.,](#page--1-0) [2000;](#page--1-0) [Gong](#page--1-0) et [al.,](#page--1-0) 2000; Peña [and](#page--1-0) [Varela,](#page--1-0) [2007\),](#page--1-0) and bottom-water nutrient concentrations are known to be affected by fluxes between the water-column and sediment ([Rowe](#page--1-0) et [al.,](#page--1-0) [1975\).](#page--1-0) Secondly, spatial variations in turbidity occur at the scale of shelf topography [\(Shideler,](#page--1-0) [1979\),](#page--1-0) affecting the depth at which phytoplankton production becomes limited by light. Thirdly, variations from highly stratified to well-mixed conditions can occur over scales of a few kilometres in shelf waters, with variable mixing rates that may be orders ofmagnitude higher than those in the deep ocean [\(Haidvogel](#page--1-0) et [al.,](#page--1-0) [2000\).](#page--1-0) The emphasis here is on vertical, rather than horizontal, mixing because turbulence is much more effective in the vertical, as a result of the small vertical to horizontal aspect ratio of the coastal ocean (order 10−3) [\(Burchard](#page--1-0) et [al.,](#page--1-0) [2008\).](#page--1-0) Finally, physical processes such as upwelling, downwelling, and terrestrial run-off, can sometimes play a dominant role in shaping nutrient availability on the continental shelf, consequently affecting the vertical profile of phytoplankton.

Different-sized marine particles sink at different speeds. The smallest, and most abundant, particles consist of dead or living phytoplankton cells a few micrometres in diameter that sink at less than 1 m d−1, if at all. However, particle aggregates (0.5 mm or greater) are common in near-shore environments, and sink up to two orders of magnitude faster ([Alldredge](#page--1-0) [and](#page--1-0) [Gotschalk,](#page--1-0) [1988\).](#page--1-0)

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Particle size distribution may change as a result of aggregation, remineralisation or physical fragmentation, leading to large spatial and temporal variations in particle settling speed.

Spatial and temporal variations in vertical mixing, light penetration, phytoplankton settling velocity and nutrient supply make accurate prediction of the shape of the phytoplankton profile in continental shelf waters difficult. To demonstrate, and seek to understand, the consequences of some of this variability, we have applied a one-dimensional (1D) ecosystem model of phytoplankton and nitrate for coastal-water conditions (i.e. water depths less than 100 m). The model provides a means to investigate the relative influence of vertical diffusive mixing, gravitational settling and downward light attenuation on the steady-state depth distribution of phytoplankton in a 100 m water-column. The influence of advection is not included.

The model is kept as simple as possible, to isolate the most fundamental mechanisms that control the ecosystem. Coupling simple biological models to a 1D (vertical) representation of ocean physics, has contributed greatly to theoretical and heuristic understanding ofthe marine ecosystem ([Franks,](#page--1-0) [2002\).](#page--1-0) Of most relevance here, are several studies published over the last 10 years used to investigate the mechanisms behind the deep maxima in chlorophyll and phytoplankton in the open ocean [\(Beckman](#page--1-0) [and](#page--1-0) [Hense,](#page--1-0) [2007;](#page--1-0) [Fennel](#page--1-0) [and](#page--1-0) [Boss,](#page--1-0) [2003;](#page--1-0) [Hodges](#page--1-0) [and](#page--1-0) [Rudnick,](#page--1-0) [2004\).](#page--1-0)

Applied to a range of water-column depths between 20 and 100 m depth, and compared with observations along a cross-shelf gradient in phytoplankton biomass on the Western Australian (WA) shelf, the model provides a reasonable representation of the vertical phytoplankton structure and dynamics. Separate elements of the WA field data are used for both model parameterisation and validation, and for convenience the field measurements are described before the model.

2. Materials and methods

2.1. Field measurements

For comparison with our model we use a set of chlorophyll a and nitrate profiles collected in 2007 during a shelf-scale survey of the Western Australian (WA) continental shelf between 22 and 34S [Thompson](#page--1-0) et [al.,](#page--1-0) [2011\).](#page--1-0) A total of 41 daytime profiles of chlorophyll a (derived from in situ fluorescence) and 33 profiles of nitrate collected between the 20 and 110 m depth contour are used (Fig. 1). Profiles of chlorophyll and nitrate collected at the same shelf-depth $(\pm 5 \,\mathrm{m})$ are averaged to provide a set of long-shore averaged profiles for shelf depths of 20, 30, 40, 50, 60, 70, 80, 100, and 110 m. Nitrate profiles were not available for either the 40 or 60 m shelf depth. Chlorophyll a (mg Chl a m−3) is converted to phytoplankton nitrogen biomass (mmol N m−3) by assuming a chlorophyll to nitrogen ratio of 2.0 (c.f. [Fennel](#page--1-0) [and](#page--1-0) [Boss,](#page--1-0) [2003\).](#page--1-0) Matching temperature and salinity profiles are also examined, along with 18 daytime profiles of photosynthetically active radiation (PAR). Methods for the collection and analysis of these data are described in [Thompson](#page--1-0) et [al.](#page--1-0) [\(2011\).](#page--1-0)

The observations were made during a shelf-wide phytoplankton bloom that occurs annually in this region during the austral autumn, limited by the availability of nitrogen [\(Koslow](#page--1-0) et [al.,](#page--1-0) [2008;](#page--1-0) [Thompson](#page--1-0) et [al.,](#page--1-0) [2011\).](#page--1-0) The bloom coincides with de-stratification of the water-column, which is maintained throughout the winter months by convective mixing and storm winds [\(Feng](#page--1-0) et [al.,](#page--1-0) [2003;](#page--1-0) [Koslow](#page--1-0) et [al.,](#page--1-0) [2008\).](#page--1-0) Well-mixed conditions are commonly observed on the continental shelf $(0-100 \text{ m})$ in this region throughout the autumn and winter, with surface mixed layer depths that typically extend all the way to the seabed ([Pearce](#page--1-0) et [al.,](#page--1-0) [2006\).](#page--1-0)

Fig. 1. Sample location of field data used in this study (black circles). Contour lines show bathymetry at 100, 200, 500 and 1000 m.

2.2. Model description

We follow the general approach of [Fennel](#page--1-0) [and](#page--1-0) [Boss](#page--1-0) [\(2003\),](#page--1-0) [Hodges](#page--1-0) [and](#page--1-0) [Rudnick](#page--1-0) [\(2004\),](#page--1-0) [Riley](#page--1-0) et [al.](#page--1-0) [\(1949\),](#page--1-0) [Steele](#page--1-0) [and](#page--1-0) [Yentsch](#page--1-0) [\(1960\),](#page--1-0) and [Taylor](#page--1-0) [\(1988\),](#page--1-0) who have used simple 1D ecosystem models to study the steady-state vertical distribution of phytoplankton in the ocean. For completeness, we note that others [\(Ryabov](#page--1-0) et [al.,](#page--1-0) [2010;](#page--1-0) [Beckman](#page--1-0) [and](#page--1-0) [Hense,](#page--1-0) [2007\)](#page--1-0) have used timevarying model simulations, based on the same basic phytoplankton and nutrient equations used in the steady-state approach. In these time-varying cases, the emphasis is still placed on the steady-state distribution of phytoplankton after a period of constant forcing. In all of these studies, vertical mixing is assumed to be constant throughout the surface mixed layer. This has proved to be a useful simplification in other model studies of ocean phytoplankton dynamics [\(Anderson](#page--1-0) [and](#page--1-0) [Williams,](#page--1-0) [1998;](#page--1-0) [Oguz](#page--1-0) et [al.,](#page--1-0) [2001;](#page--1-0) [Taylor](#page--1-0) et [al.,](#page--1-0) [1993\).](#page--1-0)

The model is nitrogen-based, to suit the nitrogen-limited WA ecosystem, and for simplicity consists of only two compartments, phytoplankton P and nitrate N (Fig. 2). The time dependent rate of

Fig. 2. Conceptual 1D ecosystem model. Nitrate is represented by N, phytoplankton by P, and the depth of the water column by h. The major fluxes and forcing are depicted by arrows.

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