

On the upwelling-driven zonation of nitrogen, phytoplankton, and zooplankton in the eastern Great Australian Bight, Australia: A coupled physical-biological modelling study

Jochen Kämpf*

Abstract

This study uses a fully coupled physical-biological model to study nutrient enrichment and plankton dynamics in a seasonal coastal upwelling system. This upwelling system, located in the eastern Great Australian Bight, Australia, provides the feeding ground for a range of predatory species including tuna, sea lions, sharks, and whales. The biological model describes the interactions between dissolved nitrogen, phytoplankton, zooplankton, and detritus in response to changes in the physical environment predicted by a standard three-dimensional hydrodynamic model. This study tests a “zonation hypothesis” claiming that, in coastal upwelling systems, zones of maximum nitrogen, phytoplankton and zooplankton develop spatially separated along the coast due to the advective effect of coastal upwelling currents and biological delays in the formation of phytoplankton and zooplankton. While the physical process of wind-driven coastal upwelling is well understood and predictable, several aspects of the biological response simulated in this study are surprising. (i) During the upwelling phase, maximum phytoplankton and zooplankton production occurs in shallower waters alongside the upwelling zone of maximum surface nitrogen. In this upwelling shadow, recycled nitrogen contributes the same amount as physical processes to the local nutrient flux. (ii) Conversely, physical effects offset most of the local phytoplankton growth in the upwelling zone. After wind relaxation, the shutdown of the upwelling process eventually also triggers phytoplankton blooms in this zone. (iii) Wind relaxation creates a narrow coastal countercurrent that operates to maintain the plankton biomass near the upwelling center. For these reasons, the zonation hypothesis does not hold for the coastal upwelling system studied in this work.

Keywords

Coastal upwelling; Plankton dynamics; Numerical modelling; NPZD model; Coupled physical-biological interactions; Coastal oceanography

College of Science and Engineering, Flinders University, Adelaide, Australia

*Correspondence: jochen.kaempf@flinders.edu.au

Received: 23 May 2024; revised: 28 November 2024; accepted: 1 July 2025

1. Introduction

Coastal upwelling systems are among the world’s most productive regions in terms of the amount of organic carbon that is produced as phytoplankton via photosynthesis in the euphotic zone (Kämpf and Chapman, 2016). The combined effect of a vertical current that compensates for an offshore transport of surface waters, called upwelling, and the existence of nutrient-enriched shelf bottom water induced this high productivity if the associated vertical nutrient flux is sufficient to fuel the photosynthesis process. Phytoplankton blooms in upwelling regions attain

chlorophyll-*a* pigment concentrations of 1–15 mg m⁻³.

Under the influence of the Earth’s rotation (i.e., the Coriolis force), upwelling follows from alongshore winds that induce an offshore transport in the surface Ekman layer. Conversely, an onshore Ekman transport induces coastal downwelling (see Lentz, 2001; Kämpf, 2019). The wind-driven offshore surface flow induces an onshore pressure gradient due to the tilted sea level, which drives an energetic alongshore geostrophic flow known as the coastal upwelling jet. Upwelling jets are left-bounded (right-bounded) by the coast in the northern (southern hemisphere). On the other hand, coastal countercurrents (CCCs) often develop near the upwind side of bays after wind relaxation (Largier, 2020). CCCs are believed to contribute

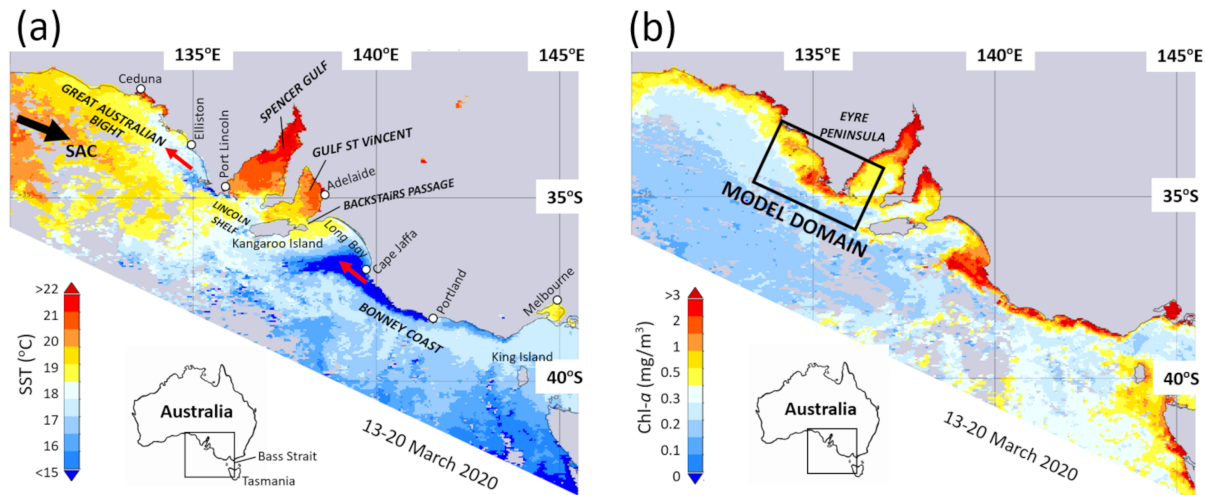


Figure 1. Composite satellite data of a) sea surface temperature SST ($^{\circ}\text{C}$) and b) chlorophyll-*a* (mg m^{-3}) during a major upwelling event for the period 13–20 March 2020. Red arrows show the direction of coastal upwelling jets. The black arrow in a) denotes the South Australian Current spreading southeastward along the shelf break. The rectangle in b) marks the upwelling center in the eastern Great Australian Bight and the spatial extent of the model domain. Data: MODIS-aqua provided by NASA's Giovanni data interface at <https://giovanni.gsfc.nasa.gov/giovanni/>.

to larvae retention in upwelling shadows (Kämpf, 2024a).

The transfers of nitrogen between seawater, phytoplankton and zooplankton are delayed due to their chemical-biological nature. Due to these delays and the adjective effect of the upwelling jet, Kämpf and Chapman (2016) argue that coastal upwelling systems are characterized by a zonation of trophic levels where the maxima of nutrients, phytoplankton, and zooplankton are spatially separated downstream along the upwelling jet. As far as the author is aware, this current-driven zonation, which has been demonstrated for equatorial upwelling systems (see Mann and Lazier, 1996), has not been verified for coastal upwelling systems.

South Australia's southern continental shelf accommodates a large seasonal coastal upwelling system, known as the Great Southern Australian Coastal Upwelling System (GSACUS) (Shute et al., 2022). Frequent southeasterly winds induce the upwelling of cold, nutrient-enriched water around the austral summer season (November–April). Upwelling events are highly variable due to the variability of weather patterns in the region. Regional sea surface temperature (SST) reductions due to upwelling are of the order of $1\text{--}3^{\circ}\text{C}$, noting that warmer water, formed in shallows of the Great Australian Bight arrives in the upwelling region by the end of austral summer (Figure 1a). Surface chlorophyll-*a* values of $1\text{--}3\text{ mg m}^{-3}$ (Figure 1b) are relatively modest compared to the world's largest upwelling systems (see Kämpf and Chapman, 2016). Nonetheless, the GSACUS plays an important role in the marine food web of the southern hemisphere. This is founded on a high abundance of sardine (*Sardinops sagax*) and anchovy (*Engraulis australis*) as keystone forage fish (Ward et al., 2006)

that serve as the diet for a range of predators including southern bluefin tuna (*Thunnus maccoyii*), sea lions, seals, sharks and seabirds. In addition, a range of whales including blue whales (*Balaenoptera musculus brevicauda*) and dolphins feed in the region supplemented by the appearance of swarms of the neritic krill (*Nyctiphanes australis*) (Gill, 2002, 2011, 2015; Möller et al., 2020).

This study focuses on the westernmost upwelling center in the eastern Great Australian Bight (GAB) that spreads from the southern headland of the Eyre Peninsula north-westward along the coast towards Elliston (Figure 1). This upwelling center, first described by Kämpf et al. (2004), has been affiliated with the high abundance of sardine and southern bluefin tuna in the eastern GAB (Ward et al., 2006), where the regional fishery authority undertakes regular survey-based sardine stock assessments. In this region, upwelling follows from the classical wind-driven upwelling process associated with southeasterly winds. Given the significant broadening of the shelf to $> 50\text{ km}$ in this region, the source of the upwelled water remained a mystery until the discovery of the Kangaroo Island Pool, described further below.

Several currents influence the water masses of the study region during summertime (Middleton and Cirano, 2002). One of these currents is the South Australian Current (SAC) that carries warm and nutrient-low surface waters eastward along the shelf break (Ridgway and Condie, 2004). The SAC typically starts to form in March spreading eastward across the shelf in a broad tongue through April and May (Rochford, 1986; Herzfeld, 1997). On the other hand, the Flinders Current transports cold and nutrient-rich water centered at a depth of $400\text{--}600\text{ m}$ westward along the

upper continental slope. In due course of the coastal upwelling process, the Flinders Current combines regionally with wind-driven circulation in support of upwelling from a depth of ~ 300 m (Kämpf, 2010; Richardson et al., 2020).

Most past oceanographic surveys focused on the Lincoln Shelf between Kangaroo Island and the southern headland of the Eyre Peninsula, not the actual upwelling plume in the eastern GAB (see Shute et al., 2022). Accompanied by CTD surveys and water sampling, a moored reference station of Australia's Integrated Marine Observing System (IMOS), located near the west coast of Kangaroo Island, has been providing physical and biological data since 2003. Given this data availability, most previous scientific studies focused on the Lincoln Shelf upstream from the upwelling center in the eastern GAB.

Based on a water-mass analysis, McClatchie et al. (2006) identified the Kangaroo Island (KI) Pool, which is a layer of dense, cold, and nutrient-rich shelf-bottom water that forms on the Lincoln Shelf during the upwelling season. Process-oriented hydrodynamic modelling suggests that the KI Pool forms through interaction of the Flinders Current with a localized group of shelf-incising submarine canyons (Kämpf, 2010). Based on hydrographic and stable isotope data, Richardson et al. (2018) analyzed the variability of water masses on the Lincoln Shelf. These authors identified five distinct water masses one of which stems from episodic upwelling. Using early IMOS data for the period 2009–2012, van Ruth et al. (2018) discovered significant interannual variations inherent in the formation of the KI Pool. These authors also reported vertical profiles of dissolved nitrate with maximum values of

$\sim 5\text{--}10\ \mu\text{M}$ on the Lincoln Shelf, which are adopted for this study. Shute et al. (2022) further discuss this variability in conjunction with calibrated chlorophyll-*a* profiles for the period 2003–2020. These authors also identified the existence of significant subsurface phytoplankton blooms with chlorophyll-*a* concentrations of up to $1\ \text{mg m}^{-3}$ in shallower waters around the KI Pool. In a purely biological study, Kämpf et al. (2023a) discussed the variability and composition of in situ sampled phytoplankton and zooplankton assemblages for the period 2009–2022. For completeness, it should be noted that Richardson et al. (2020) described the physical characteristics and nutrient enrichment of a smaller upwelling center formed regularly off Kangaroo Island's south coast.

Using a fully coupled physical-biological model, this study simulates the distributions of upwelled water in terms of temperature anomalies, dissolved nutrients, phytoplankton, zooplankton, and detritus in the eastern GAB on timescales of 1–2 months. The objective of this work is to determine factors that shape the zonation of trophic levels in a seasonal coastal upwelling region.

2. Model description

2.1 Overview

This study applies a fully coupled physical-biological model to predict the nutrient enrichment and phytoplankton production in coastal waters of the eastern Great Australian Bight under the action of upwelling-favorable winds. The model domain (Figure 2) has been rotated by 25 degrees counterclockwise, such that the deeper isobaths are aligned

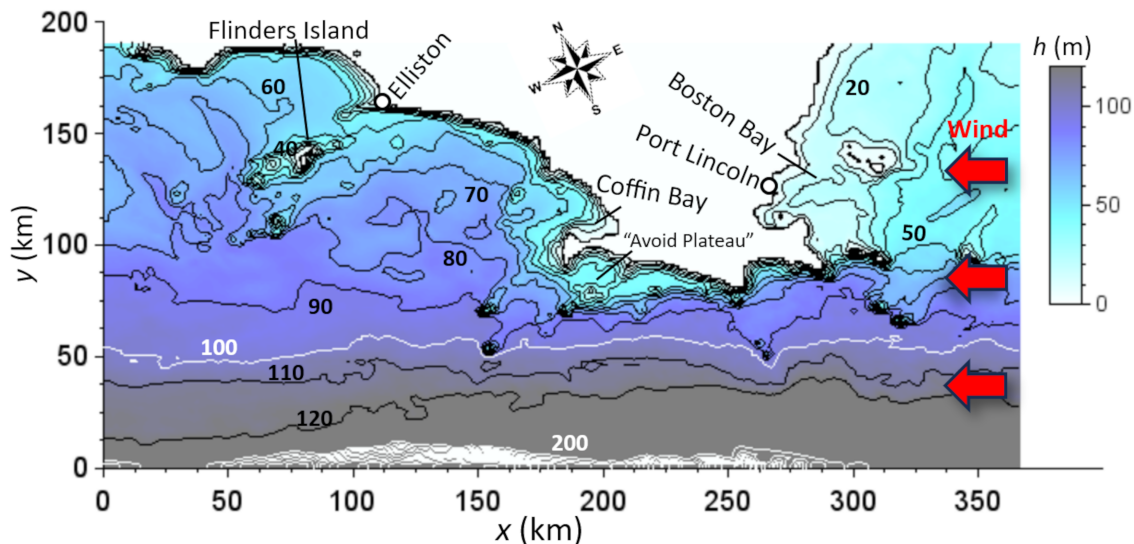


Figure 2. Model domain derived from the latest gridded GEBCO data provided on a 15 arc-second interval grid. The bathymetry is represented by color shading and isobaths ($CI = 10$ m for black lines, 100 m for white lines). Minimum and maximum water depths are set to 5 m and 120 m, respectively. Red arrows illustrate the direction of upwelling-favorable wind (southern hemisphere). The model domain has been rotated by 25 degrees counterclockwise relative to north.

with the rotated x direction of the Cartesian coordinate system.

COHERENS (Luyten et al., 1999) serves as a three-dimensional hydrodynamic model for this study. The governing equations are the finite-difference forms of conservation equations for momentum, heat, volume, and scalars (salinity) for an incompressible fluid on the f plane cast in terrain-following sigma coordinates. COHERENS is based on the same physical laws and coordinate transformation, and similar numerical algorithms that govern other sigma coordinate models such as POM (Blumberg and Mellor, 1987) or ROMS (Shchepetkin and McWilliams, 2005).

The biological model is directly coupled with the physical model sharing the same numerical grid and time step. It is based on a full Nitrogen-Phytoplankton-Zooplankton-Detritus (NPZD) model, described by Ji et al. (2008). Kämpf et al. (2023b) and Kämpf (2024b) applied a similar model (neglecting zooplankton and detritus effects) in studies of wind-induced upwelling and phytoplankton production near reef islands. Kämpf (2025) applied the full NPZD model to study plankton production in the Bonney Coast upwelling.

2.2 Physical model

The physical model is driven by a uniform wind stress that is aligned with the orientation of the southern headland of the Eyre Peninsula. The wind stress component aligned with the model's x direction is calculated from the conventional bulk formula:

$$\tau_x = \rho_{air} C_D U |U| \quad (1)$$

where $\rho_{air} = 1.24 \text{ kg m}^{-3}$ is air density, and $C_D = 0.0013$ is a typical wind drag coefficient, and $U \text{ (m s}^{-1}\text{)}$ is the x -component of the wind velocity. The y -component of the wind-stress is set to zero. The wind forcing is linearly blended in during the first simulation day to avoid the generation of unwanted surface gravity waves and inertial oscillations.

The Coriolis parameter is set to a constant value of $f = -0.895 \times 10^{-4} \text{ s}^{-1}$, corresponding to a geographical latitude of 38°S . Meridional variation of f is irrelevant for the predominantly zonal water circulation in the GAB and can be ignored.

Horizontal turbulence is parameterized using the closure scheme by Smagorinsky (1963). Vertical turbulence is parameterized with the k - ϵ turbulence closure using standard parameter settings (see Luyten et al., 1999). Eddy viscosities are assumed to be the same magnitude as eddy diffusivities. Bottom friction is parameterized using a quadratic approach in which the bottom friction coefficient, c_D , can be related to a roughness length, δ , via the relationship (see Luyten et al., 1999):

$$c_D = [\ln(z^*/\delta)/\kappa]^{-2} \quad (2)$$

where z^* is the distance of the bottom-nearest horizontal velocity grid point to the seafloor and $\kappa = 0.4$ is the von Kármán constant. A uniform roughness length of $\delta = 2 \text{ mm}$ is used in this study. Variations of turbulence parameters had no significant influence on the results.

Seawater density is calculated from a linearized equation of state according to:

$$\rho(T, S) = \rho_o [1 - \alpha(T - T_o) + \beta(S - S_o)] \quad (3)$$

where T is temperature, S is salinity, $\rho_o = 1026 \text{ kg m}^{-3}$, $T_o = 19^\circ\text{C}$ with $\alpha = 1.8 \times 10^{-4} \text{ }^\circ\text{C}^{-1}$ and $S_o = 35.8$ with $\beta = 7.6 \times 10^{-4}$. The use of the full equation of state for seawater did not significantly alter the results.

COHERENS includes a sophisticated Lagrangian particle tracking module, in which the gridded velocity field is interpolated to the particle location to calculate particle movements from accurate logarithmic displacement laws (see Luyten et al., 1999). Non-buoyant Lagrangian particles are used here to illustrate the dominant advective flow paths of the upwelling circulation. Particle displacements are based on maximum turbulent velocity components calculated from (Maier-Reimer, 1980):

$$(u_T, v_T, w_T) = \sqrt{6(A_h, A_h, A_z)/\Delta t} \quad (4)$$

where A_h and A_z are horizontal and vertical eddy viscosity, respectively, derived by the model's turbulence closure schemes, and Δt is the numerical time step. The turbulent velocities are then determined for each particle with the Monte-Carlo method which involves multiplying each maximum current component by a randomly generated number between -1 and 1 . These diffusive velocity components are then added to the advective velocity components before the calculation of particle displacements.

2.3 Biological model

The conservation equations for dissolved nitrogen (N), phytoplankton (P), zooplankton (Z), and detritus (D) can be formulated as (see Ji et al., 2008):

$$\frac{\partial N}{\partial t} = \text{adv}(N) + \text{diff}(N) - S_1 + \beta S_2 + S_4 \quad (5)$$

$$\frac{\partial P}{\partial t} = \text{adv}(P) + \text{diff}(P) + S_1 - S_2 - S_3 \quad (6)$$

$$\frac{\partial Z}{\partial t} = \text{adv}(Z) + \text{diff}(Z) + \alpha S_2 - S_5 \quad (7)$$

$$\begin{aligned} \frac{\partial D}{\partial t} = & \text{adv}(D) + \text{diff}(D) + (1 - \alpha - \beta) \times \\ & \times S_2 + S_3 + \gamma S_5 - S_4 \end{aligned} \quad (8)$$

where t is time, $\text{adv}(\cdot)$ and $\text{diff}(\cdot)$ are three-dimensional advection and diffusion operators, S_1 represents the nutrient uptake by phytoplankton, S_2 zooplankton grazing on phytoplankton, S_3 phytoplankton mortality, S_4 remineralization of detritus, and S_5 zooplankton mortality. Eddy diffusivities are the same as those used in the prognostic temperature and salinity equations. For simplicity, both phytoplankton and detritus are considered non-buoyant relative to the ambient fluid; that is, sinking effects are ignored. Figure 3 illustrates the transfer of nitrogen between the components of the nitrogen cycle that commences once sufficient dissolved nitrogen becomes available in the euphotic zone. Concentrations of components of the nitrogen cycle are expressed in units of μM of dissolved nitrate. Forcing and parameter settings of the NPZD model are the same as in the modelling study of the adjacent Bonney Coast upwelling (Kämpf et al., 2025).

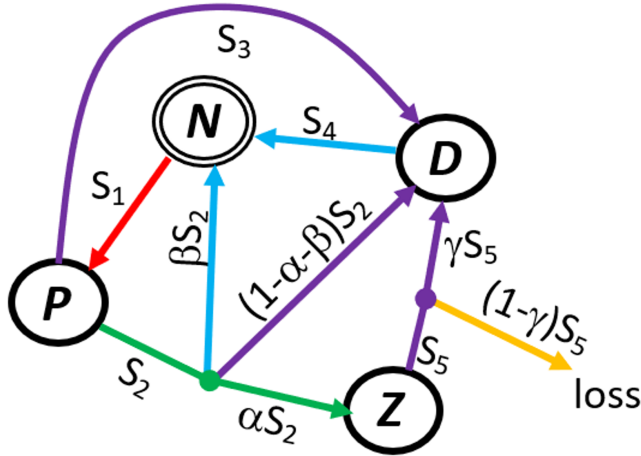


Figure 3. Schematic of the transfer of nitrogen between components of the simplified nutrient cycle considered in this study. N: Nitrogen; P: Phytoplankton; Z: zooplankton; D: detritus; S1 to S6: transfer functions (not to confused with salinity) including the parameters α , β and γ . See the text for more information.

The NPZD model is partially driven by photosynthetically active radiation (PAR), I , that is approximated by the classical exponential light-attenuation curve:

$$I(t, z) = I_o(t) e^{-a_w z} \quad (9)$$

where I_o is surface radiance, z is depth, and a_w is the light attenuation coefficient, set to $a_w = 0.1 \text{ m}^{-1}$. Effects due to self-shading by particles are ignored. Surface radiance is a function of the day-night sunlight cycle, which depends on location and time of year, and cloud coverage. This is expressed in this study by a simplified day-night cycle according to:

$$I_o(t) = \max[I_{oo} \sin(2\pi t/T), 0] \quad (10)$$

where I_{oo} is set to 500 W m^{-2} , t is time, and T is the duration of a day. This gives an average value of $I_{oo}/\pi \approx 159 \text{ W m}^{-2}$.

The nitrogen use by phytoplankton S_1 is formulated as:

$$S_1 = f(I) \mu_{\max} \left[\frac{N}{K_N + N} \right] P \quad \text{with} \quad (11)$$

$$f(I) = (1 - e^{-\hat{\alpha} I}) e^{-\hat{\beta} I}$$

where $\hat{\alpha} = 0.025 (\text{W m}^{-2})^{-1}$ and $\hat{\beta} = 0.001 (\text{W m}^{-2})^{-1}$, the maximum possible phytoplankton growth rate is set to $\mu_{\max} = 1.5 \text{ day}^{-1}$, and the half-saturation constant to $K_N = 1 \mu\text{M}$.

The zooplankton grazing term S_2 can be expressed as:

$$S_2 = g_{\max} \left[\frac{P^2}{(K_P)^2 + P^2} \right] Z \quad (12)$$

where $g_{\max} = 0.3 \text{ day}^{-1}$ and $K_P = 0.3 \mu\text{M}$. Only a fraction ($\alpha = 0.3$) of this term appears as a source in the zooplankton equation (7), while another fraction ($\beta = 0.3$) is recon-verted to dissolved nitrogen via excretion. The remainder fraction of $1 - \alpha - \beta = 0.4$ of S_2 appears as detritus. The other terms in (5)–(8) are given by:

$$S_3 = \lambda P, \quad S_4 = \varepsilon D, \quad S_5 = m Z^2 \quad (13)$$

where the phytoplankton mortality rate is set to a constant value of $\lambda = 0.5 \text{ day}^{-1}$, the detritus remineralization rate to $\varepsilon = 0.1 \text{ day}^{-1}$, and the zooplankton-density dependent mortality rate to $m = 0.2 (\mu\text{M})^{-1} \text{ day}^{-1}$.

While the NPZD model seems intrinsically complex, the phytoplankton response can be elegantly summarized by the daily average of the largest possible phytoplankton growth rate under saturated nutrient conditions, that is:

$$\langle \mu_* \rangle(z) = \mu_{\max} \left\langle (1 - e^{-\hat{\alpha} I}) e^{-\hat{\beta} I} \right\rangle \quad (14)$$

where $\langle \cdot \rangle$ stands for the averaging. The vertical profiles of μ_* and λ (Figure 4) reveal that phytoplankton production is only possible above the compensation depth of 47 m (where $\langle \mu_* \rangle = \lambda$). Note that $\langle \mu_* \rangle$ attains a maximum of 0.55 day^{-1} at a depth of $\sim 10 \text{ m}$ which slightly exceeds the surface value of 0.5 day^{-1} .

A conversion ratio of 1.59:1 can be used to convert chlorophyll-*a* concentrations in units of mg m^{-3} from phytoplankton concentrations in units of $\mu\text{M-N}$. This conversion is based on an average C:chl-*a* ratio of 50:1 (see Jakobsen and Markager, 2016) and a Redfield ratio of C:N of 106:16.

2.4 Model domain and experimental design

The model domain (Figure 2) is 366 km long, resolved by a grid spacing of $\Delta x = 1.833$ km, and 190 km wide, resolved by a grid spacing of $\Delta y = 1.588$ km. Overall the continental shelf of the eastern GAB is relatively shallow (~ 80 – 120 m) compared with other continental shelves. The shelf is the narrowest (~ 80 km) off the southern headland of the Eyre Peninsula and significantly widens to ~ 200 km westwards. Coffin Bay is located on the western side of the headland. It consists of a series of small, connected bays (see Kämpf and Ellis, 2015) noting that only the outer bay can be spatially resolved here. The shallow waters of Spencer Gulf are

located on the eastern side of the headland. Moreover, the coastal bathymetry varies greatly along the southern headland. Along the eastern side, the ocean rapidly deepens to > 80 m within a few kilometers from the coast. The western side features a submarine plateau with depths < 50 m that widens westward to ~ 20 km. The bay adjacent to this plateau is called the Avoid Bay. Henceforth, this region, which plays a significant role in coupled physical-biological dynamics in the eastern GAB (as will be shown with the findings of this study), is referred to as the Avoid Plateau. While the study region contains multiple smaller islands, only a few, like Flinders Island, are spatially resolved in this study.

The model bathymetry has been derived from the gridded GEBCO 2024 data set provided on a 15 arc-second interval grid. The data are averaged onto a coarser model grid to maximize model efficiency while still resolving key dynamical features. The original data array is rotated by 25° anti-clockwise, such that the shelf break is largely aligned with the rotated x coordinate. The minimum and maximum water depths are set to 5 m and 120 m, respectively. 20 equidistant sigma levels are used in the vertical; that is, the maximum vertical grid spacing is 6 m. The limit to 120 m avoids biases associated with the steep (up to 1°) continental slope of the region (illustrated by the white contours in Figure 2). This limit also allows for the use of a relatively large numerical timestep of 21 s (which is constrained by the phase speed of long surface gravity waves) and a total simulation time of 60 days.

The initial vertical profiles of temperature and salinity (Figure 4a) assumed horizontally uniform, are based on data taken near Kangaroo Island in the absence of upwelling, as reported by Richardson et al. (2020). The surface mixed layer, 40 m thick, contains the warmest ($T = 19^\circ\text{C}$) and saltiest ($S = 35.8$) water. Both temperature and salinity then linearly decrease from the base of the surface mixed layer to values of $T = 14^\circ\text{C}$ and $S = 35.3$ at a depth of 100 m. Below, temperature and salinity continue to decrease slightly toward the depth of 120 m. Accordingly, the depth range 40–100 m marks the seasonal pycnocline characterized by a vertical density change $\Delta\rho$ of ~ 0.55 kg m^{-3} (Figure 4b). The internal deformation radius, $r = c/|f|$, can be estimated at ~ 4.5 km with $c^2 = \Delta\rho/\rho_0 gh$, where $g = 9.81$ m s^{-2} is vertical acceleration due to gravity, and $h = 40$ m.

The initial vertical profile of N is based on observational evidence from van Ruth et al. (2018) associated with the formation of the KI Pool. Here, surface layers of the water column are devoid of nitrogen to a depth of 40 m (Figure 4c). Starting from this depth, N increases linearly, reaching 5 μM at 100 m and continuing to rise slightly below that depth. Note that the compensation depth is located just below the base of the mixed layer (see Figure 3d). Experiments start with a small uniform ambient chl- a concentration of 0.1 mg m^{-3} , corresponding

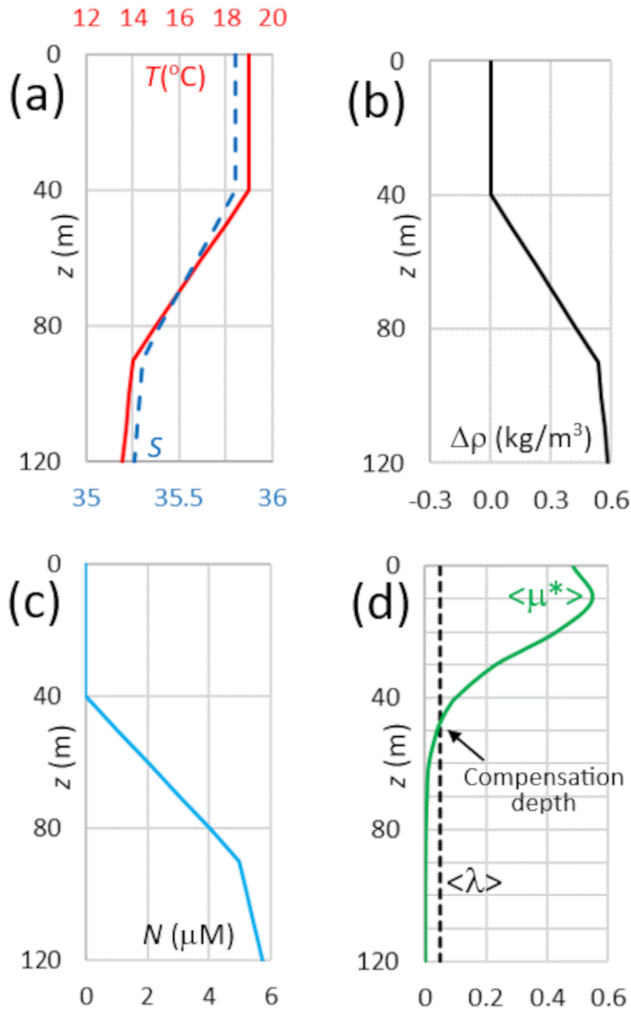


Figure 4. Vertical distributions of initial values of a) temperature (red full curve, $^\circ\text{C}$) and salinity (blue dashed curve, no unit), b) the seawater density excess $\Delta\rho$ (kg m^{-3}) relative to $\rho_0 = 1026$ kg m^{-3} , calculated from (3), and (c) nitrogen (μM). Panel d) shows the daily averaged vertical profiles of the largest possible growth rate under saturated nutrient conditions $\langle\mu^*\rangle$ (green curve, day^{-1}) together with the phytoplankton mortality rate λ (black dashed curve, day^{-1}).

to $P = 0.1/1.59 \approx 0.063 \mu\text{M}$. Initial values of both Z and D are set to $0.1 \mu\text{M}$. A variation of these values did not significantly alter the results.

Except for sea-surface elevation, zero gradient conditions are used for all variables at all open boundaries. The Rayleigh damping method is applied to sea-level elevation within 10 grid points from all open boundaries, except for the eastern boundary, with a damping coefficient of a value of $\varepsilon = 0.05$. This implies that sea-level anomalies are reduced by 5% in these damping zones after each simulation step. This method effectively eliminates the generation of unwanted boundary effects.

The simulation of the main experiment begins with a state at rest. Based on the analysis of regional wind data (not shown), the model is forced by a constant x -component of wind velocity of $U = -5 \text{ m s}^{-1}$, which corresponds to a low-wind-forced upwelling regime (Nieblas et al., 2009). The total simulation time of the main experiment is 60 days.

Additional experiments use the output of the main experiment after 40 days as initial conditions and then apply a transient wind forcing of either $U = -10 \text{ m s}^{-1}$ (strong upwelling) or $U = +10 \text{ m s}^{-1}$ (strong downwelling). After 4 days of the up/downwelling forcing, the wind speed linearly decreased to zero within a day for the remainder of 30 days. Objectives of these additional experiments are to (a) compare the results for an average wind forcing with that and a short and strong transient upwelling event on a similar timescale (1 month), and (b) to test the effects of a transient strong downwelling event on the plankton productivity in the region.

3. Results and discussion

3.1 Surface distributions (main experiment)

The wind forcing operates to lower the sea level by $\sim 2 \text{ cm}$ along the entire coast (Figure 5a). Satellites cannot detect such small sea-level anomalies. Offshore Ekman transport directly causes this drop in the sea level in regions where the coast is parallel to the wind. However, in some regions such as Coffin Bay, the coastline is perpendicular to the wind direction. Coastal Kelvin waves pass along the negative sea level across these regions. This effect also explains the existence of negative sea-level anomalies along the west coast of Spencer Gulf despite onshore winds.

Sea-level contours tend to follow the bathymetric contours, which implies a topographic steering of the geostrophic flow. The strongest cross-isobath gradients in sea level occur along the 50–60 m bathymetric contours. This implies that the geostrophic flow is steered around and not across shallow-water regions of the Avoid Plateau or the ridge of slightly elevated seafloor between Flinders Island and the mainland. The trajectories of non-buoyant Lagrangian floats confirm this topographic steering of sea-water which largely bypasses the shallow-water regions (Figure 5b). Due to turbulent diffusive processes, some

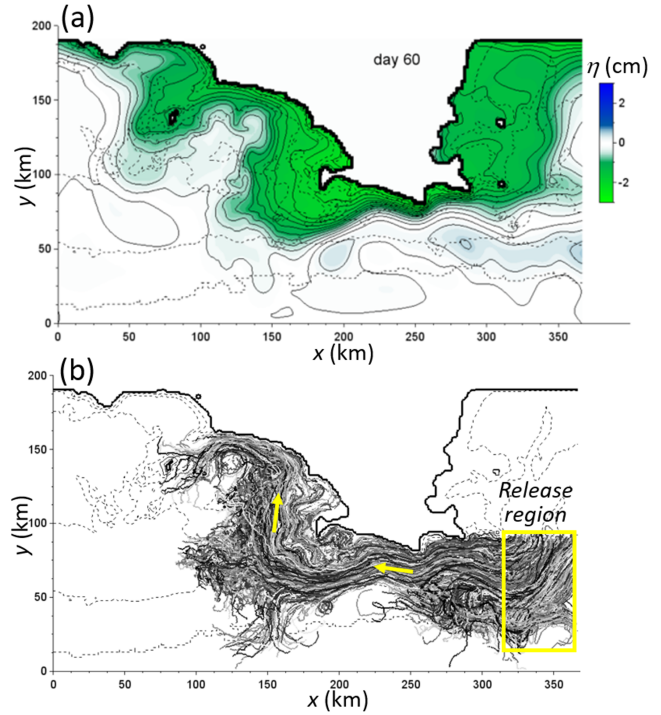


Figure 5. Horizontal distributions after 60 days of a) sea-level anomaly η (cm) (color shading and contours, $CI = 0.2 \text{ cm}$) and b) the trajectories of 1000 Lagrangian particles released at random locations within 20 m from the seafloor in total water depths between 50 and 100 m. The yellow rectangle shows the release region. Yellow arrows illustrate the dominant flow path. Dashed lines are isobaths ($CI = 20 \text{ m}$).

particles still make it into the shallow-water regions including the Avoid Plateau and Coffin Bay, which form a classical upwelling shadow (see Kämpf and Chapman, 2016).

The upwelling process induced by the offshore Ekman transport draws colder waters to the surface (Figure 6a). After 20 days of simulations in the main experiment, SST anomalies of -2°C have developed within 20 km from the southern headland of the Eyre Peninsula (Figure 6a, top panel) in regions where nutrient-enriched shelf bottom water is located relatively close to the shore (see Figure 2). This upwelling plume of cold water separates from the coast and is topographically steered around the Avoid Plateau. During this initial phase, the nearshore shallow-water regions of the plateau and Coffin Bay remain unaffected by the upwelling. Another, less pronounced upwelling plume of SST anomalies of -1°C has formed along the coast upstream from Elliston with an offshore diversion towards Flinders Island.

During the following 40 days, the upwelling plumes intensified in terms of temperature anomalies, the upwelling jet distributes colder waters downstream, and colder water eventually also penetrates the shallower re-

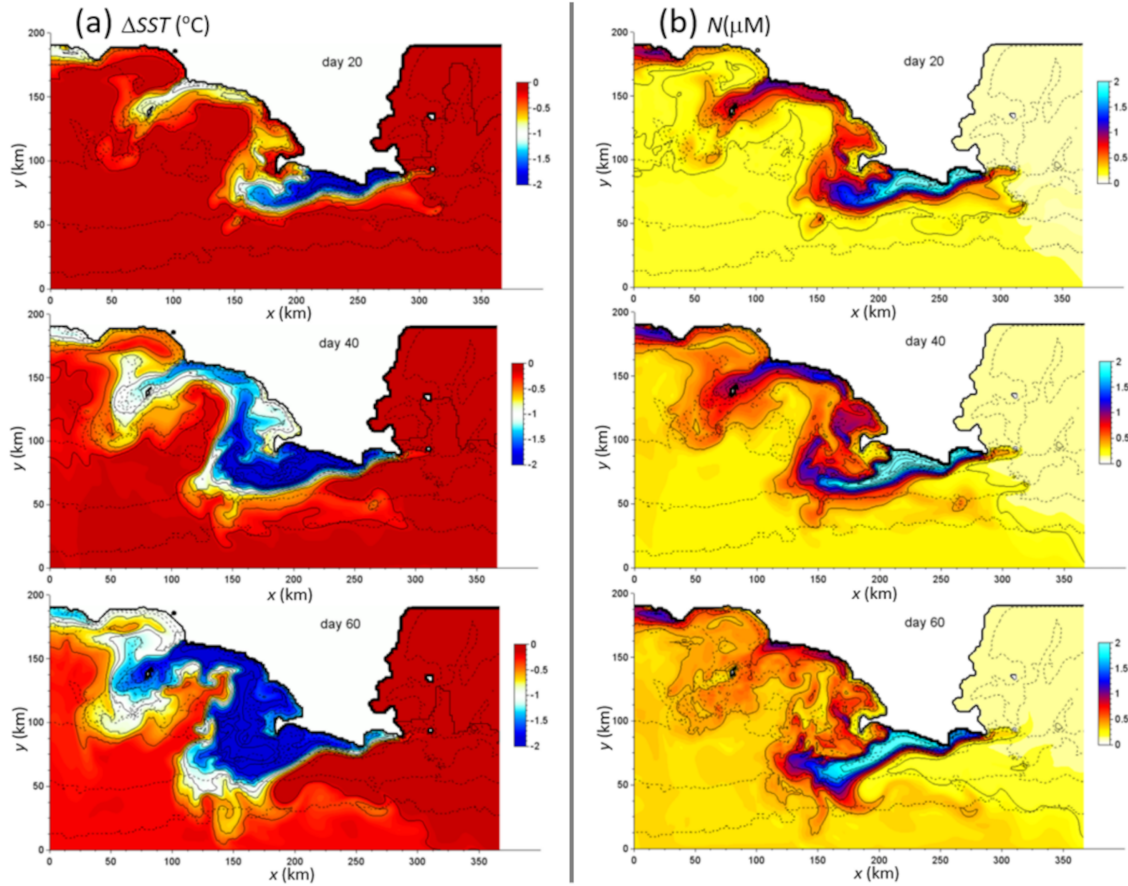


Figure 6. Horizontal distributions after 20, 40, and 60 days of a) SST anomalies (colors shading and contours, $CI = 0.2^{\circ}C$), and b) surface values of dissolved nitrogen N (μM). Dashed lines are isobaths ($CI = 20$ m).

gions (Figure 6a, middle and bottom panels). The simulated SST pattern agrees well with satellite data (see Figure 1).

The newly upwelled water brings nutrient-rich water to the sea surface (Figure 6b). After 20 days, a nutrient plume with nitrogen concentrations of $\sim 2 \mu M$ has formed in the upwelling zone (Figure 6b top level). Note the second upwelling plume near Elliston with nitrogen concentrations of $\sim 1 \mu M$. At this point in time, the temperature and nitrogen distributions are still strongly (negatively) correlated.

As time progresses, the temperature plume continues to expand due to the advective effect of currents. In contrast, the nutrient plume remains static which implies that the advective effect is offset by biological processes in the nutrient budget (Figure 6b, middle and bottom panels). Hence, pronounced differences between temperature and nitrogen distributions develop over time downstream from the upwelling center. For instance, cold upwelled water has appeared with relatively low dissolved nitrogen levels ($< 0.8 \mu M$) in Coffin Bay after 60 days of simulation (Figure 6b, bottom panels). On the other hand, a stand-alone nutrient front (not mirrored by a temperature front)

has formed along the eastern flank of the Avoird Plateau. The formation of this nutrient front cannot be explained by physical processes alone.

Phytoplankton growth occurs delayed after the initial nutrient enrichment in surface waters. During the first 20 days, phytoplankton concentrations have slowly risen to $\sim 0.4 \mu M$ in shallower waters of the Avoird Plateau (Figure 7a, top panel). After 40 days, phytoplankton concentrations have increased to values $1\text{--}1.5 \mu M$ in a V-shaped plume emanating from the Avoird Bay on the western side of the southern headland (Figure 7a, middle panel).

The phytoplankton plume, which has a width of 10–20 km, is located inshore from the nutrient plume (compare with Figure 6b, middle panel). While the phytoplankton plume continues to exist after 60 days, phytoplankton blooms have also appeared in other regions including Coffin Bay and the upwelling zones near Elliston and Flinders Island (Figure 7a, bottom panel). Peak phytoplankton concentrations of $1\text{--}1.5 \mu M$ correspond to chlorophyll-*a* concentrations of $1.6\text{--}2.4 \text{ mg m}^{-3}$, which agrees with observational evidence (Kämpf et al., 2004; see Figure 1b).

After 60 days, the surface zooplankton distribution (Figure 7b) strongly resembles the phytoplankton distri-

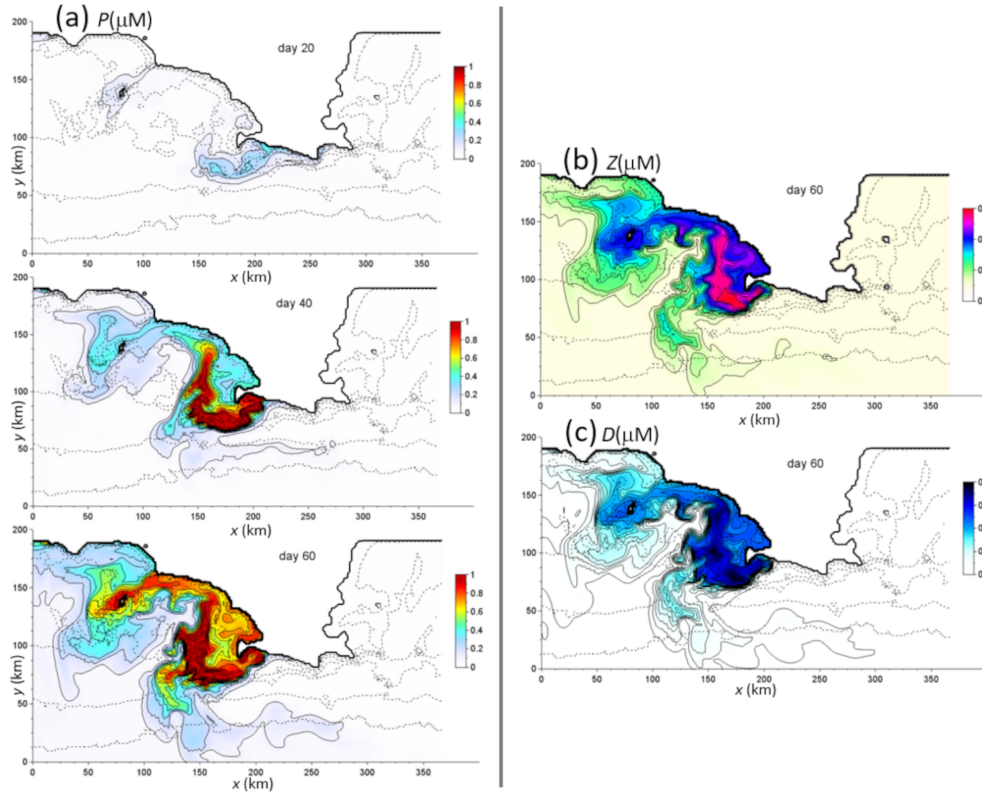


Figure 7. a) Same as Figure 6, but for surface phytoplankton P (μM). Panels b) and c) display the surface distributions of zooplankton Z (μM) and detritus D (μM) after 60 days. The contours in panels a), b) and c) use $CI = 0.1 \mu\text{M}$, $0.02 \mu\text{M}$, and $0.04 \mu\text{M}$, respectively.

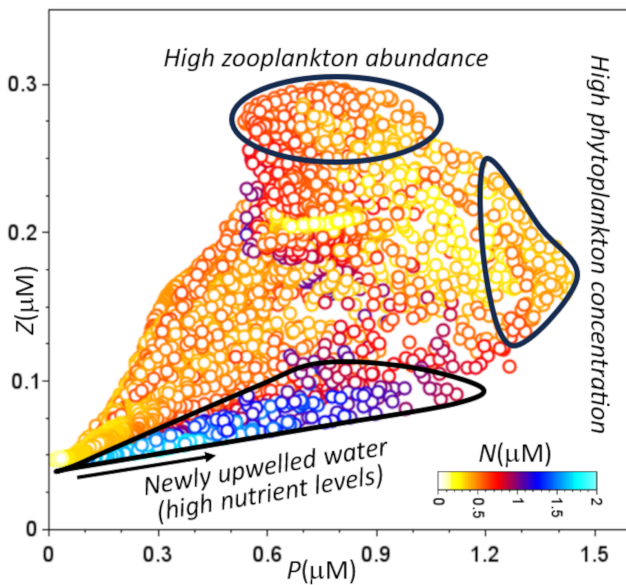


Figure 8. Scatterplot of surface values of zooplankton Z (μM) versus phytoplankton P (μM), color-coded with nitrogen concentration N (μM). Zones of high values of each parameter are highlighted.

tribution because zooplankters graze directly on phytoplankton. Another factor is that the zooplankton abundance is still relatively small $\sim 0.3 \mu\text{M}$ and cannot decimate the phytoplankton assemblages on timescales of 2 months. The surface detritus distribution (Figure 7c) also largely matches the phytoplankton and zooplankton distributions. While detritus has several sources (i.e., phytoplankton and zooplankton mortalities and excretion by zooplankters), these sources overlap in the same region. Note that detritus attains maximum concentrations of $\sim 0.8 \mu\text{M}$ which is only 20% less than the nitrogen content of surface phytoplankton. Over time, remineralization of this detritus will support further phytoplankton growth beyond the 60 days simulated here.

Figure 8 summarizes the relationships between dissolved nitrogen levels, phytoplankton concentrations, and zooplankton abundance after 60 days of simulation. Three different functional regimes can be deduced from this. The first regime represents newly upwelled water which has high values of N and low levels of P and Z . The second regime has high levels of P in conjunction with reduced levels of N , representing the nitrogen uptake by phytoplankton growth, and small levels of Z . The third regime represents waters of the highest zooplankton abundance Z in conjunction with reduced levels of P , reflecting zoo-

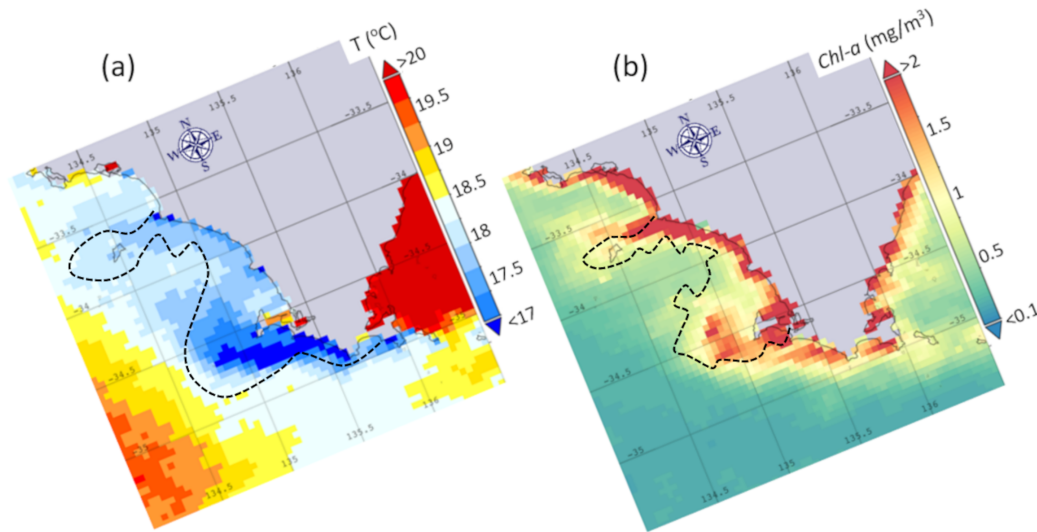


Figure 9. Satellite-derived monthly mean near-surface distributions of a) SST ($^{\circ}\text{C}$) and b) chlorophyll-*a* for March 2020. The dotted lines illustrate the extents of the temperature and phytoplankton plumes after 60 days of simulation (see Figures 6a and 7a). Data source: NASA Giovanni (<https://giovanni.gsfc.nasa.gov/giovanni/>).

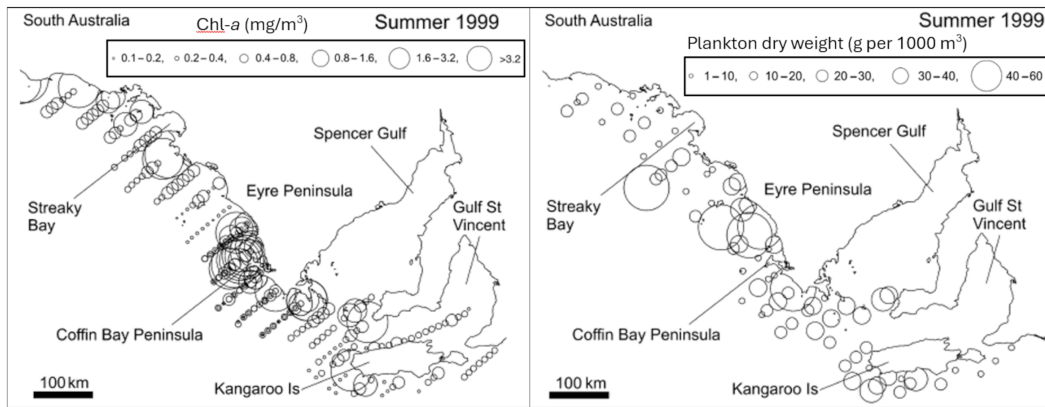


Figure 10. Seasonal distribution of in situ sampled values of a) near-surface chl-*a* concentration (mg m^{-3}) and b) relative zooplankton biomass ($\text{g per } 1000 \text{ m}^3$) in the eastern GAB in summer 1999. Approximately 300 stations were sampled along 25 transects aligned perpendicular to the shelf break. Red ellipses highlight the upwelling zone. Adapted from Ward et al. (2006).

plankton grazing on phytoplankton, and relatively low levels of *N*. But there are anomalies. For instance, there are regions of moderate values of both *P* and *Z*, but with either elevated or reduced nitrogen levels, reflecting strong variations along the inner shelf (see Figure 6b).

3.2 Comparison against observational evidence (main experiment)

Predicted SST and phytoplankton distributions agree well with satellite observations (Figure 9, compare with Figures 6a and 7a), both in magnitude and distribution. With anomalies of -2°C the cold-water plume starts to develop along most of the southern headland of the Eyre Peninsula. In agreement with the prediction, the satellite SST data (Figure 9a) indicate that the cold-water plume

separates from the coast near the Avoid Plateau before returning coastward again in the lee of Coffin Bay. On the other hand, the MODIS ocean color data reveal high chl-*a* levels $> 2 \text{ mg m}^{-3}$ over the Avoid Plateau and a distinct nearby chl-*a* plume that separates from the coast (Figure 9b). In agreement with this distribution, the simulated phytoplankton distribution corresponds to maximum chl-*a* levels of $\sim 1.5\text{--}2 \text{ mg m}^{-3}$ (see Figure 7a), using a chl-*a*:*P* conversion ratio of 1.59:1. The satellite data also indicate upwelling effects along the coast between Coffin Bay and Ellison, and around Flinders Island (see Figure 2), noting that satellite chl-*a* data can be significantly biased in optically shallow ($< 20\text{--}30 \text{ m}$) water (e.g., Staehr et al., 2022), such as in Coffin Bay. Obvious discrepancies between the simulated and satellite chl-*a* data exist along the

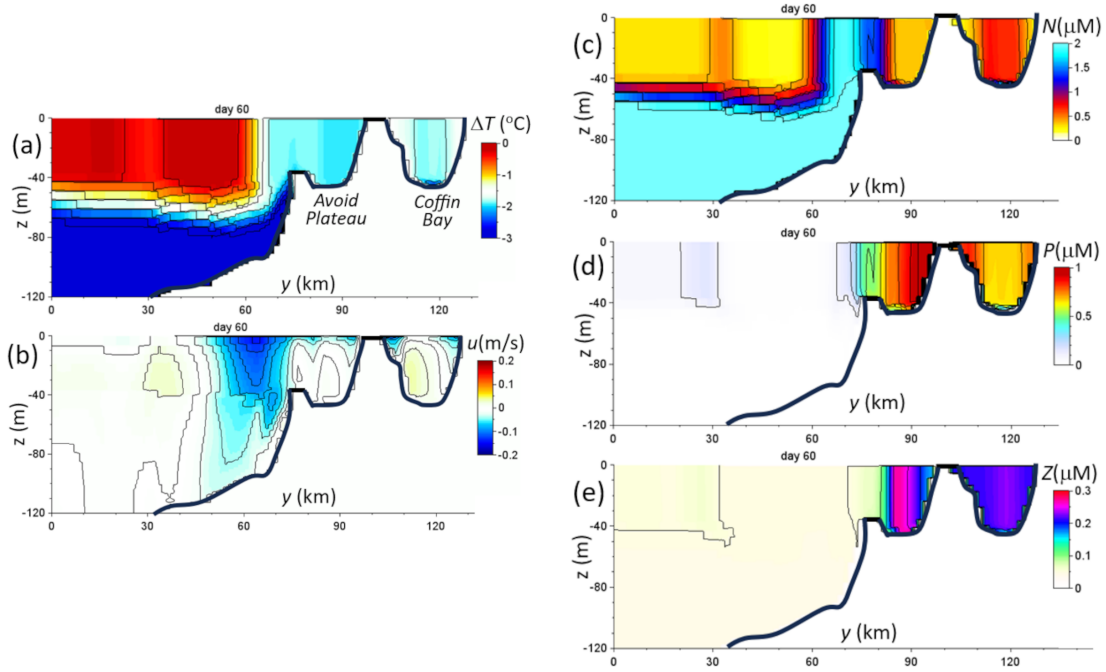


Figure 11. Vertical transects (color shading and contours) at $x = 192$ km after 60 days of a) temperature anomalies ΔT [$^{\circ}\text{C}$] ($CI = 0.3^{\circ}\text{C}$), b) the u -velocity component [m s^{-1}] ($CI = 0.02 \text{ m s}^{-1}$), c) dissolved nitrogen concentration N [μM] ($CI = 0.2 \mu\text{M}$), d) phytoplankton concentration P [μM] ($CI = 0.1 \mu\text{M}$), and e) zooplankton abundance Z [μM] ($CI = 0.05 \mu\text{M}$). Fields were transformed from σ - to z -coordinates with a vertical grid spacing of 1 m.

southern headland of the Eyre Peninsula, which marks the tail of the upwelling plume. Here, the cold, nutrient-rich upwelled water has already relatively high chlorophyll- a levels $\sim 1.5 \text{ mg m}^{-3}$, which is not replicated by the model. This feature cannot be explained via (unrealistically) rapid phytoplankton growth. Observational evidence from the Lincoln Shelf (Shute et al., 2022) reveals the existence of subsurface chlorophyll- a maxima of similar levels along the entrance of Spencer Gulf, not represented in the model. Hence, it is likely that the upwelling along the southern headland already contains elevated chl- a levels. However, this missing feature does not influence the simulated phytoplankton productivity farther west in the main upwelling plume, which agrees well with satellite data.

Both the predicted and satellite-derived chl- a distributions are consistent with in-situ data (Figure 10a). The sampled zooplankton distribution for summer 1999 (Figure 10b) indicates a high abundance around the Avoid Plateau, which agrees with the prediction (see Figure 7b), but the zooplankton distributions can differ in other years (see Ward et al., 2006). The good agreement between model predictions and observational data allows us to analyze the model results in greater detail, as discussed in the following.

3.3 Vertical transects (main experiment)

To explore the high spatial variability of the biological response to the nutrient upwelling, the focus is here placed

on a transect at $x = 192$ km that shows physical and biological data after 60 days in different regions of the upwelling jet, the Avoid Plateau, and Coffin Bay (Figure 11). The temperature transect shows a marked temperature/density front at $y \approx 60$ km just ~ 10 km south of the edge of the plateau (Figure 11a). This front extends to a depth of ~ 50 m and separates cold upwelled near-shore water from ambient warmer surface water. Negative temperature anomalies of -2°C are found on the shoreward side of this front including the shallow waters of the Avoid Plateau and Coffin Bay, where the water column is well mixed. This temperature transect also displays the active phase of upwelling in terms of upward sloping isotherms near the plateau.

The temperature front coincides with the core of the upwelling jet that attains speeds of up to 0.2 m s^{-1} (Figure 11b). The upwelling jet is a surface-intensified feature that extends to a depth of 40–50 m. The upwelling jet does not reach into shallower nearshore waters where the currents are relatively sluggish.

The upwelling process lifts nutrient-enriched water to the sea surface in the region between the temperature front and the southern edge of the Avoid Plateau where it marks a nutrient front (Figure 11c). The nutrient front separates newly upwelled water of high nitrogen levels ($N \approx 2 \mu\text{M}$) from shallower nearshore water of low concentrations ($N \approx 0.5 \mu\text{M}$). The waters of Coffin Bay attain a dissolved nitrogen level of $N \approx 0.7 \mu\text{M}$.

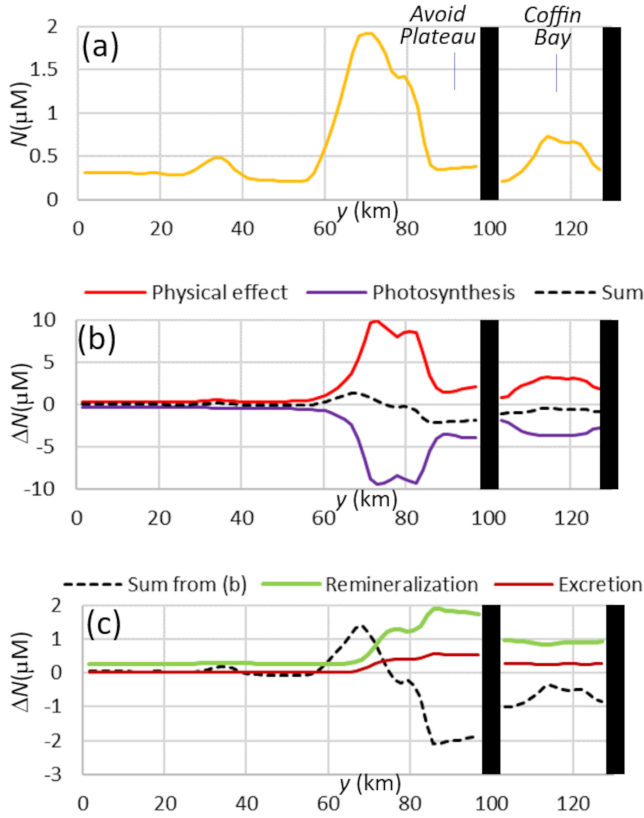


Figure 12. Nutrient budget. Transects at $x = 192$ km of a) surface values of dissolved nitrogen N after 60 days, and the amounts that b) the physical effect (advection and diffusion) and nutrient uptake by phytoplankton (photosynthesis), and c) remineralization of detritus and excretion by zooplankton have contributed to the N value. All values in μM . Black bars denote land.

A phytoplankton bloom has evolved shoreward from the nutrient plume (Figure 11d). Shallow waters over the Avoid Plateau are characterized by $\approx 1 \mu\text{M}$, whereas slightly lower values ($\sim 0.7 \mu\text{M}$) are predicted for Coffin Bay. Driven by grazing on phytoplankton, zooplankton abundance increases to values of $0.2\text{--}0.3 \mu\text{M}$ in the waters over the plateau and Coffin Bay (Figure 11e).

3.4 Nitrogen and phytoplankton budgets (main experiment)

This section focuses again on the transect at $x = 192$ km for an analysis of the local nitrogen and phytoplankton budgets and how these differ between the different biological regimes. To this end, the individual terms on the right-hand of equations (5) and (6) are integrated over the entire simulation time to determine their contributions to the final values of N and P .

The distribution of N shows a clear maximum of up to $2 \mu\text{M}$ in the range $y = 65\text{--}85$ km (Figure 12a) corresponding to the upwelling zone (see Figure 11c). Values

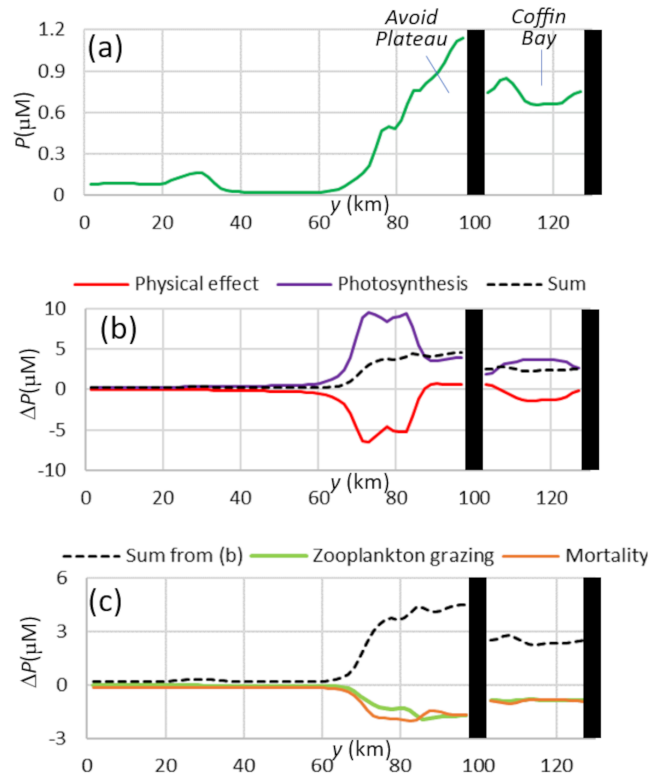


Figure 13. Phytoplankton budget. y-transects at $x = 192$ km of a) surface values of phytoplankton concentration after 60 days, and the amounts that b) the physical effect (advection and diffusion) and photosynthesis, and c) zooplankton grazing and phytoplankton mortality have contributed to the P value. All values in μM . Black bars denote land.

of $N \sim 0.35 \mu\text{M}$ are found in the waters over the Avoid Plateau, whereas slightly higher values of up to $0.7 \mu\text{M}$ are developed in Coffin Bay.

The largest terms in the nitrogen equation (5) are the nutrient supply from physical effects (advection and diffusion) and the nutrient uptake by phytoplankton (Figure 12b). The physical effect peaks with $\Delta N \sim 8\text{--}10 \mu\text{M}$ in the upwelling zone. The physical effect is also positive with values of $\Delta N \sim 1\text{--}3 \mu\text{M}$ in the shallower nearshore regions. The sum of the two terms is positive in the region $y = 60\text{--}75$ km, where the upwelling process dominates. In contrast, the sum is negative over the Avoid Plateau and Coffin Bay, where photosynthesis takes up more nitrogen than is supplied by physical processes alone. This missing nitrogen of $\sim 1 \mu\text{M}$ is supplied primarily via the remineralization of detritus and to a minor degree from excretion by zooplankton (Figure 12c).

In the following the total nitrogen gain is defined as the sum of all positive terms in (5); that is, the physical process, remineralization of detritus, and excretion by zooplankton. After 60 days, Coffin Bay has received a total of

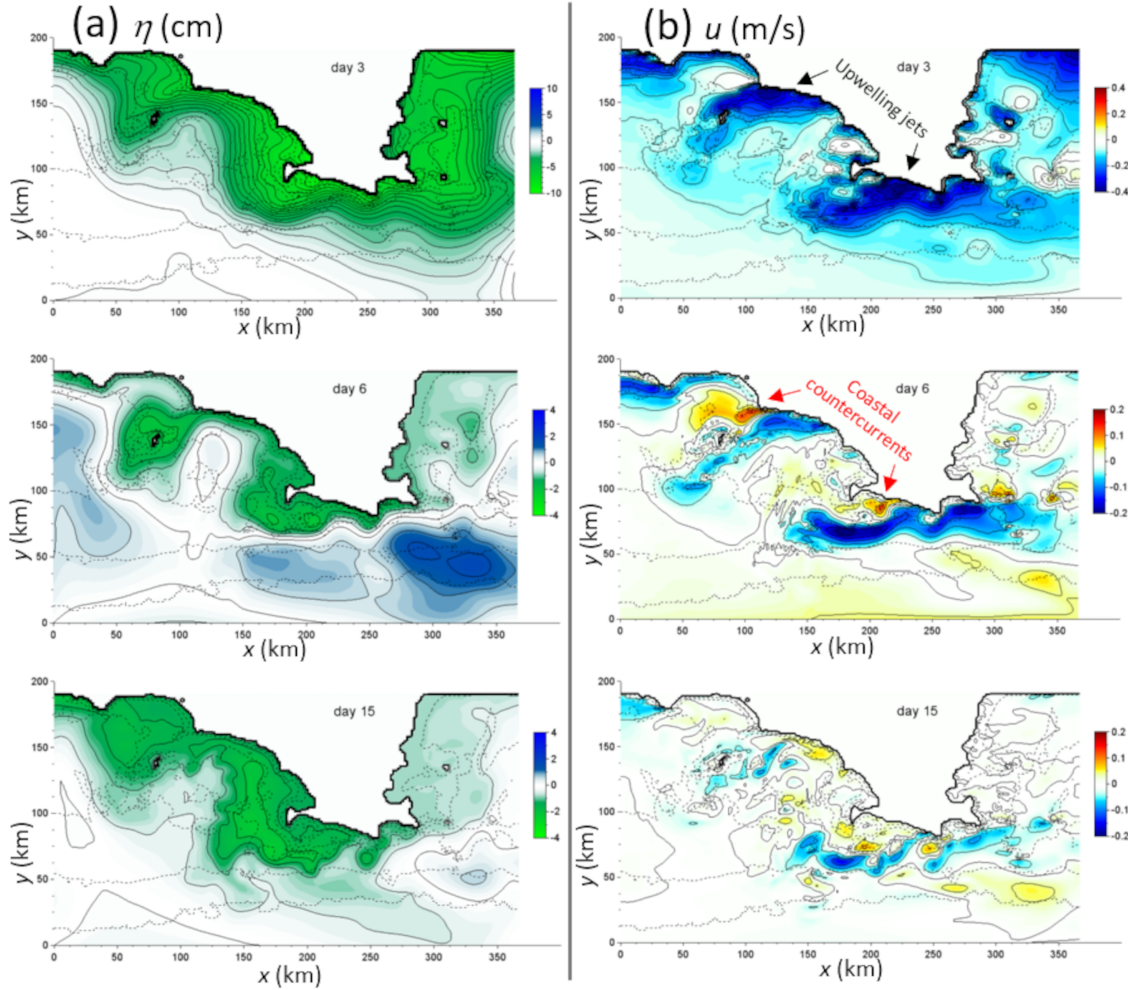


Figure 14. Case study with strong transient upwelling-favorable winds. Horizontal distributions of sea level anomalies η [cm] (color shading and contours) after a) 3 days ($CI = 0.5$ cm) and c) 6 days ($CI = 0.2$ cm), and the u -velocity components of surface flows [m s^{-1}] (color shading) after b) 3 days and d) 6 days, both with $CI = 0.05$ cm). Dashed lines are isobaths ($CI = 20$ m).

$\sim 4.3 \mu\text{M}$ in nitrogen with $\sim 73\%$ provided by the physical process, 20% from remineralization and 7% from excretion. Around 80% of this total gain has been consumed by phytoplankton. Waters on the Avoid Plateau received a similar total, but physical processes contributed a smaller fraction (43%), remineralization a larger fraction (45%), and excretion $\sim 11\%$ of the total. Here, photosynthesis has consumed $\sim 90\%$ of the total gain. In contrast, the physical process contributed $\sim 90\%$ to the total nitrogen gain of $\sim 10 \mu\text{M}$ near the upwelling front, where only 8% and 2% came from remineralization and excretion, respectively. In the upwelling zone, the nutrient uptake by phytoplankton ranges between 50% and 90% of the total.

After 60 days of simulation, the surface phytoplankton concentration along the transect has maximum values $> 0.6 \mu\text{M}$ in shallower waters of the Avoid Plateau and Coffin Bay (Figure 13a). Like in the nitrogen budget, physical effects and nitrogen use by photosynthesis are

the largest terms in the phytoplankton budget (6) (Figure 13b). However, here the roles are reversed. While photosynthesis is the source of phytoplankton, the physical process operates as a sink via the removal of phytoplankton from the region. This sink is most pronounced near the upwelling front, where seawater of low phytoplankton content is upwelled to the surface. This sink vanishes in shallower, nearshore waters, where photosynthesis is the dominant process. Hence, the physical process operates to reduce phytoplankton growth in the upwelling zone, and the largest net local phytoplankton production occurs in adjacent waters. In addition, zooplankton grazing and phytoplankton mortality operate to remove 70–90% of the net phytoplankton production, at roughly the same proportions (Figure 13c).

Similar relationships (not shown) hold for the upwelling plume on the continental shelf downstream from Coffin Bay. In this region, phytoplankton production takes up

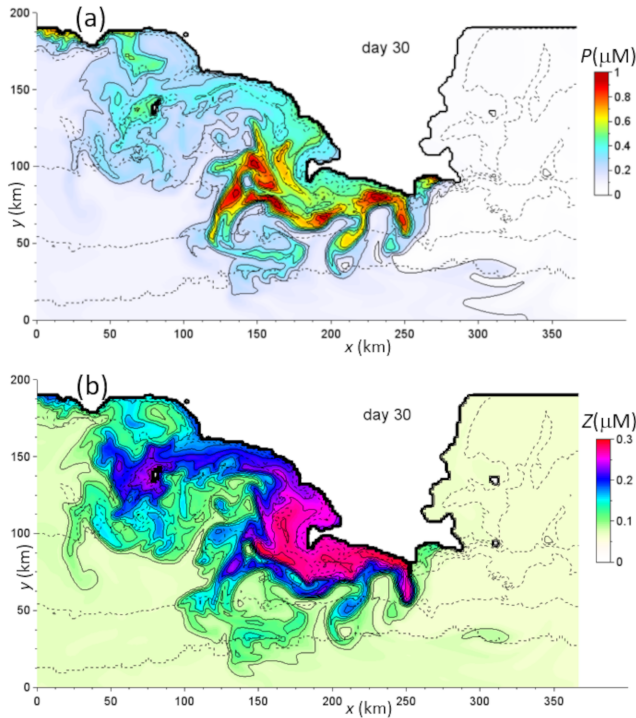


Figure 15. Case studies with a transient upwelling-favorable wind event. Horizontal surface distributions after 30 days of additional simulation of a) phytoplankton concentration [μM] (color shading and contours, $CI = 0.1 \mu\text{M}$), and b) zooplankton abundance [μM] (color shading and contours, $CI = 0.02 \mu\text{M}$). Dashed lines are isobaths ($CI = 20 \text{ m}$).

most of the nutrient enrichment from physical processes and remineralization of detritus. Remineralization accounts for around 30% of the total nitrogen gain. On the other hand, zooplankton grazing, phytoplankton mortality and physical effects, in roughly equal proportions, remove $\sim 80\%$ of the phytoplankton produced.

3.5 Effects of transient strong-wind events (additional experiments)

This section explores the impacts of transient strong-wind events on the coupled physical-biological dynamics in the eastern GAB. The results of the main experiment after 40 days (see Figures 6 and 7) are used as an initial condition for two case studies. A transient event of either upwelling- or downwelling-favorable wind of 10 m s^{-1} speed is used as forcing. Again, the wind field is taken as spatially uniform. Wind speed is linearly increased to the final value over 1 day, kept constant for the next 3 days, and then reduced to zero over another day. The total simulation time of both case studies is 30 days.

The upwelling-favorable wind event lowers the coastal sea level by $\sim 8 \text{ cm}$ within 3 days (Figure 14a, top panel). The sea-level response is more pronounced than in the main experiment (compare with Figure 5a). Again, the as-

sociated onshore pressure gradient leads to the formation of westward upwelling jets that attain a maximum speed of 0.4 m s^{-1} (Figure 14b, top panel). The upwelling jets are the strongest along the southern headland of the Eyre Peninsula and the coastline near Ellison.

After wind relaxation, the sea level adjusts such (Figure 14a, middle panel) that coastal countercurrents develop along the western side of the southern headland and near Ellison (Figure 14b, middle panel). The coastal countercurrents attain speeds of $0.1\text{--}0.2 \text{ m s}^{-1}$. Upwelling jets continue to exist farther offshore.

Sea-level anomalies of $\sim -2 \text{ cm}$ still exist after 15 days (i.e., more than 10 days after the wind calmed down) (Figure 14a, bottom panel), and surface currents still contain remnant features of coastal countercurrents and offshore upwelling jets (Figure 14b, bottom panel).

The intensified wind transiently enhances the nutrient flux in the upwelling zone. In addition, changes in the hydrodynamics after wind relaxation have two major biological effects. Firstly, significant phytoplankton growth with $P \approx 0.8\text{--}1 \mu\text{M}$ is apparent in a band that marks the former nutrient upwelling plume (Figure 15a, compared with Figure 6b). While the physical effect constituted a loss term in the local phytoplankton budget during the upwelling phase (see Figure 13b), the absence of this effect after wind relaxation facilitated the new phytoplankton bloom. Secondly, the coastal countercurrent operates to transport phytoplankton-rich (and zooplankton-rich) surface waters eastward along the southern headland. To this end, the relaxation of strong upwelling-favorable wind events has created a vast marine zone of increased zooplankton abundance of $\sim 0.2\text{--}0.3 \mu\text{M}$ that, contrary to expectation, also extends eastward along the southern headland of the Eyre Peninsula (Figure 15b). This zone also covers the shallower waters of Coffin Bay and the Avoid Plateau.

The downwelling-favorable wind event creates offshore Ekman transport along parts of the coastline that are oriented parallel to the wind. Under the additional action of coastal Kelvin waves, this wind forcing operates to raise the sea level by $\sim 8 \text{ cm}$ along the coast within 3 days (Figure 16a, top panel). The associated offshore pressure gradient leads to the formation of eastward coastal currents, known as downwelling jets, of a maximum speed of 0.4 m s^{-1} (Figure 16b, top panel). Downwelling jets are the strongest along the southern headland of the Eyre Peninsula and the coastline near Ellison. After wind relaxation, sea-level anomalies reduce over time (Figure 16a, middle and bottom panels) and so does the speed of downwelling jets (Figure 16b, middle and bottom panels). Significant coastal countercurrents do not form after wind relaxation.

The transition to downwelling-favorable winds almost immediately shuts down the nutrient upwelling process. After 30 days of additional simulation, surface phytoplankton levels of $\sim 0.5 \mu\text{M}$ are lower than in the upwelling case (Figure 17a, compare with Figure 13a). However, like the

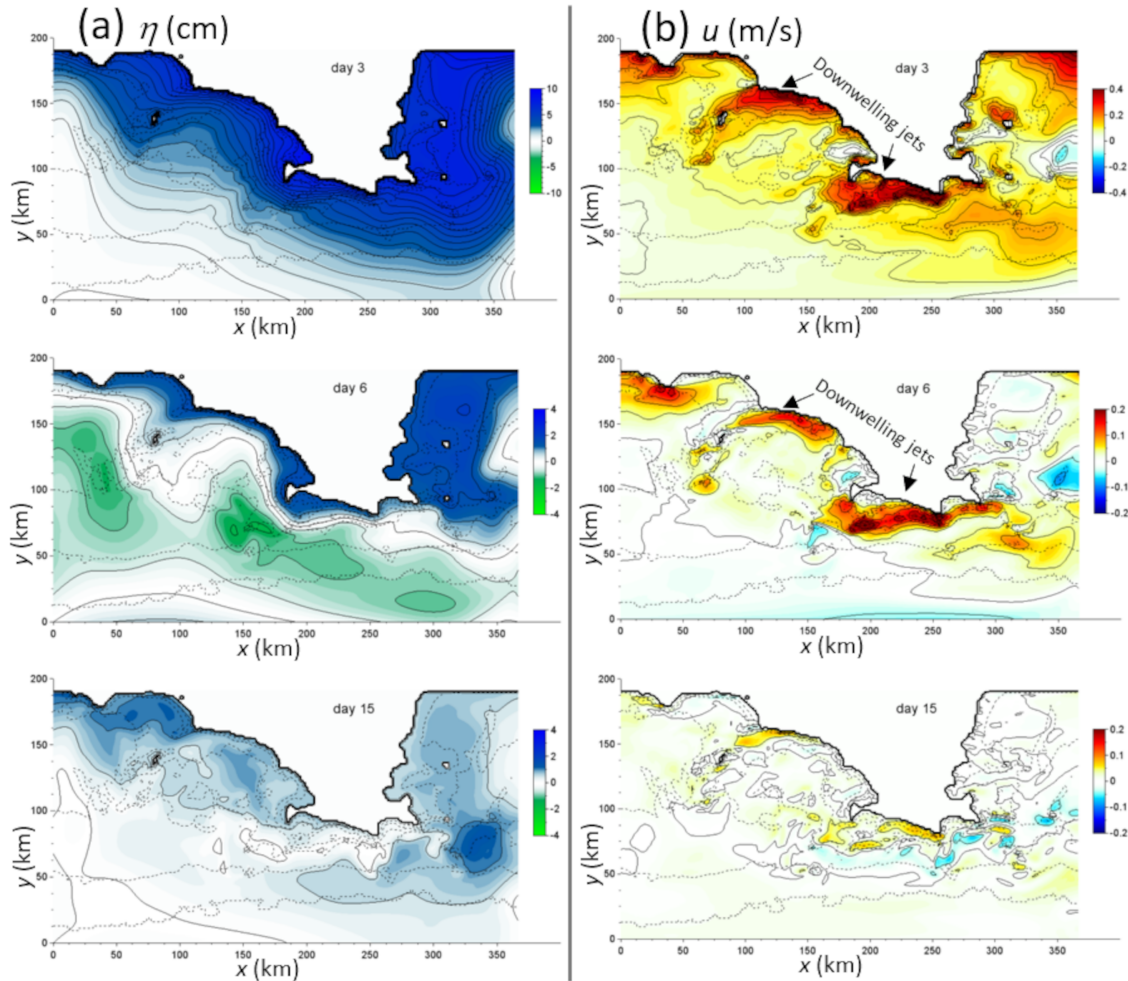


Figure 16. Same as Figure 14 but for the case study with downwelling-favorable winds.

coastal countercurrent, the downwelling jet also operates to transport phytoplankton- and zooplankton-rich waters eastward along the southern headland of the Eyre Peninsula. To this end, the surface zooplankton distribution after a downwelling-favorable wind event strongly resembles that after the upwelling-favorable wind event (Figure 17b, compare with Figure 15b). It should be noted that most of the biological response seen here is the result of the initial, 40-day long upwelling event that precedes the transient upwelling/downwelling events.

4. Final discussion and conclusions

Based on observational evidence from equatorial upwelling regions in the Pacific, Kämpf and Chapman (2016) stated that, in coastal upwelling regions, the zones of maximum nitrogen, phytoplankton and zooplankton are found spatially separated along the coastal upwelling jet. Findings, presented here for the eastern Great Australian Bight suggest that the zone of maximum phytoplankton can also form in shallower water alongside the upwelling zone of

maximum nitrogen. Moreover, since this region forms an upwelling shadow of reduced flows, zooplankton can feed directly on the phytoplankton in the same region without being swept away by the upwelling flow. This suggests that shallower inshore waters alongside the upwelling jet can form larval retention zones that also benefit from enhanced phytoplankton and zooplankton production.

There are two main reasons why the zonation hypothesis by Kämpf and Chapman (2016) may not apply to all coastal upwelling systems. Firstly, bathymetry controls can lead to the separation of the upwelling jet from the coast and the formation of a plankton-productive zone alongside rather than downstream from the nitrogen maximum. Here, zooplankton can directly graze on phytoplankton in the absence of advective effects. Secondly, significant phytoplankton production also occurs directly in the zone of maximum nitrogen once the upwelling process has ended. Thirdly, relaxation of upwelling-favorable wind can induce a coastal countercurrent that transports waters back towards the upwelling center. Because of these coupled physical-biological interactions, regions of maximum

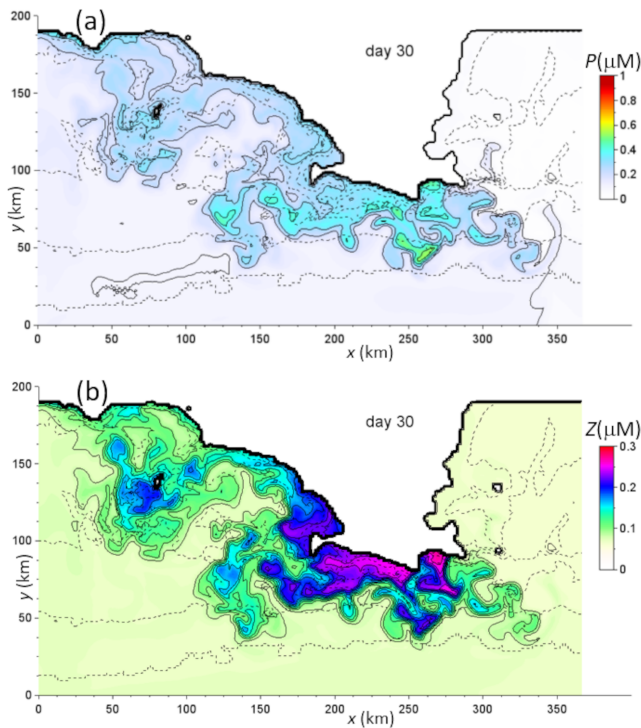


Figure 17. Same as Figure 15, but for the case study with downwelling-favorable winds.

nitrogen, phytoplankton, and zooplankton form in close vicinity of each other. The locations of these regions are predominantly controlled by physical processes as a robust feature of the simulations. Variations of parameters of the biological model do not make much difference to the results.

Future studies of upwelling in the eastern Great Australian Bight should focus on how the South Australian Current and coastally trapped waves influence the plankton dynamics. This study demonstrates the usefulness of coupled physical-biological modelling for the understanding of the functioning of coastal upwelling systems. Similar studies should be undertaken in other upwelling regions.

Acknowledgements

This study did not receive external research support. Model simulations were run on a standard laptop computer using the GFORTRAN compiler. Scilab (<https://www.scilab.org/>) was used to prepare most graphs of this paper. Figure 1 uses MODIS-Aqua satellite data made available via the NASA Giovanni data interface (<https://giovanni.gsfc.nasa.gov/giovanni/>).

Conflict of interest

None declared.

Declarations

- The author has not made any use of AI technology in this research, neither in the generation of the results nor in the writing of the text.
- This work has not received any funding from external sources.
- This work has not been published before and it is not considered for publication elsewhere.
- The single author of this work was responsible for conceptualization, investigation, generation of data, formal analysis, validation, interpretation, and all writing and reviewing roles.

References

- Blumberg, A.F., Mellor, G.L., 2013. *A description of a three-dimensional coastal ocean circulation model*. Three-Dimensional Coastal Ocean Models Coastal and Estuarine Sciences Ser. Vol. 4, AGU.
- Gill, P., 2002. *A blue whale (*Balaenoptera musculus*) feeding ground in a southern Australian coastal upwelling zone*. J. Cetacean Res. Manage. 4 (2), 179–184. <https://doi.org/10.47536/jcrm.v4i2.854>
- Gill, P.C., Morrice, M.G., Page, B., Pirzl, R., Levings, A.H., Coyne, M., 2011. *Blue whale habitat selection and within-season distribution in a regional upwelling system off southern Australia*. Mar. Ecol. Progr. Ser. 421, 243–263. <https://doi.org/10.3354/meps08914>
- Gill, P.C., Pirzl, R., Morrice, M.G., Lawton, K., 2015. *Cetacean diversity of the continental shelf and slope off southern Australia*. J. Wildl. Manage. 79, 672–681. <https://doi.org/10.1002/jwmg.867>
- Herzfeld, M., 1997. *The annual cycle of SST in the Great Australian Bight*. Prog. Oceanogr. 39, 1–27. [https://doi.org/10.1016/S0079-6611\(97\)00010-4](https://doi.org/10.1016/S0079-6611(97)00010-4)
- Jakobsen, H.H., Markager, S., 2016. *Carbon-439 to-chlorophyll ratio for phytoplankton in temperate coastal waters: seasonal patterns and relationship to nutrients*. Limnol. Oceanogr. 61, 1853–1868. <https://doi.org/10.1002/lno.10338>
- Ji, R., Davis, C., Chen, C., Beardsley, R., 2008. *Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: a 3-D biological–physical modeling study*. J. Marine Syst. 73 (1–2), 31–47. <https://doi.org/10.1016/j.jmarsys.2007.08.002>
- Kämpf, J., 2010. *On the preconditioning of coastal upwelling in the eastern Great Australian Bight*. J. Geophys. Res.-Oceans 115, C12071. <https://doi.org/10.1029/2010JC006294>
- Kämpf, J., 2019. *Extreme bed shear stress during coastal downwelling*. Ocean Dynam. 69 (5), 581–597. <https://doi.org/10.1007/s10236-019-01256-4>

- Kämpf, J., 2024a. *On the retroflexion of upwelling jets near coastal bends*. Cont. Shelf Res. 279, 105276. <https://doi.org/10.1016/j.csr.2024.105276>
- Kämpf, J., 2024b. *On the wind-driven formation of plankton patches in island wakes*. J. Mar. Sci. Eng. 12 (1), 193. <https://doi.org/10.3390/jmse12010193>
- Kämpf, J., 2025. *Phytoplankton and zooplankton production in the Bonney Coast upwelling, Australia: A coupled physical-biological model investigation*. Cont. Shelf Res. 285, 105373. <https://doi.org/10.1016/j.csr.2024.105373>
- Kämpf, J., Chapman, P., 2016. *Upwelling System of the World*. Springer Nature, New York. <https://doi.org/10.1007/978-3-319-42524-5>
- Kämpf, J., Doubell, M., Griffin, D., Matthews, R.L., Ward, T.M., 2004. *Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia*. Geophys. Res. Lett. 31, L09310. <https://doi.org/10.1029/2003GL019221>
- Kämpf, J., Ellis, H., 2015. *Hydrodynamics and flushing of Coffin Bay, South Australia: A small tidal inverse estuary of interconnected bays*. J. Coast. Res. 31 (2), 447–456. <https://doi.org/10.2112/JCOASTRES-D-14-00046.1>
- Kämpf, J., Möller, L., Baring, R., Shute, A., Cheesman, C., 2023b. *The island mass effect: a study of wind-driven nutrient upwelling around reef islands*. J. Oceanogr. 79, 161–174. <https://doi.org/10.1007/s10872-022-00673-2>
- Kämpf, J., Newman, M., Doubell, M., Möller, L., Baring, R., Shute, A., Rodriguez, A.R., 2023a. *A study of the seasonal and interannual variability of phytoplankton and zooplankton assemblages in a significant marine ecosystem*. Oceanologia 65 (2), 434–451. <https://doi.org/10.1016/j.oceano.2022.12.003>
- Largier, J.L., 2020. *Upwelling bays: How coastal upwelling controls circulation, habitat, and productivity in bays*. Annu. Rev. Mar. Sci. 12, 415–447. <https://doi.org/10.1146/annurev-marine-010419-011020>
- Lentz, S.J., 2001. *The influence of stratification on the wind-driven cross-shelf circulation over the North Carolina shelf*. J. Phys. Oceanogr. 31, 2749–2760. [https://doi.org/10.1175/1520-0485\(2001\)031<2749:TIOSOT>2.0.CO;2](https://doi.org/10.1175/1520-0485(2001)031<2749:TIOSOT>2.0.CO;2)
- Luyten, P.J., Jones, J.E., Proctor, R., Tabor, A., Tett, P., Wild-Allen, K., 1999. *COHERENS – A Coupled Hydrodynamical-Ecological Model for Regional and Shelf Seas: User Documentation*. MUMM Report, Management Unit of the North Sea, Brussels, 914 pp.
- Maier-Reimer, E., 1980. *On the formation of saltwater wedges in estuaries*. Lect. Notes Coast. Estuar. Stud. 1, 91–101.
- Mann, K.H., Lazier, J.R.N., 1996. *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*. 2nd Edn., Blackwell Science, Oxford, xii, 394 pp.
- McClatchie, S., Middleton, J.F., Ward, T.M., 2006. *Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight*. J. Geophys. Res. 111, C08007. <https://doi.org/10.1029/2004JC002699>
- Middleton, J.F., Cirano, M., 2002. *A northern boundary current along Australia's southern shelves: The Flinders Current*. J. Geophys. Res.-Oceans 107 (C9), 3129. <https://doi.org/10.1029/2000JC000701>
- Möller, L.M., Attard, C.R.M., Bilgmann, K., Andrews-Goff, V., Jonsen, I., Paton, D., Double, M.C., 2020. *Movements and behaviour of blue whales satellite tagged in an Australian upwelling system*. Sci. Rep. 10, 21165. <https://doi.org/10.1038/s41598-02078143-2>
- Nieblas, A.E., Sloyan, B.M., Hobday, A.J., Coleman, R., Richardson, A.J., 2009. *Variability of biological production in low wind-forced regional upwelling systems: a case study off southeastern Australia*. Limnol. Oceanogr. 54, 1548–1558. <https://doi.org/10.4319/lo.2009.54.5.1548>
- Richardson, L.E., Middleton, J.F., James, N.P., Kyser, T.K., Opdyke, B.N., 2018. *Water masses and their seasonal variation on the Lincoln Shelf, South Australia*. Limnol. Oceanogr. 63, 1944–1963. <https://doi.org/10.1002/lno.10817>
- Richardson, L.E., Middleton, J.F., James, N.P., Kyser, T.K., Opdyke, B.N., 2020. *Upwelling characteristics and nutrient enrichment of the Kangaroo Island upwelling region, South Australia*. Cont. Shelf Res. 200, 104111. <https://doi.org/10.1016/j.csr.2020.104111>
- Ridgway, K.R., Condie, S.A., 2004. *The 5500-km-long boundary flow off western and southern Australia*. J. Geophys. Res.-Oceans 109, C04017. <https://doi.org/10.1029/2003JC001921>
- Rochford, D.J., 1986. *Seasonal changes in the distribution of the Leeuwin Current waters off southern Australia*. Aust. J. Mar. Freshwater Res. 37, 1–10. <https://doi.org/10.1071/MF9860001>
- Shchepetkin, A.F., McWilliams, J.C., 2005. *The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model*. Ocean Model. 9 (4), 347–404. <https://doi.org/10.1016/j.ocemod.2004.08.002>
- Shute, A., Kämpf, J., Doubell, M., Rodriguez, A.R., Möller, L., Baring, R., Newman, M., 2022. *Variability of surface and subsurface phytoplankton blooms in a seasonal coastal upwelling system*. Cont. Shelf Res. 246, 104832. <https://doi.org/10.1016/j.csr.2022.104832>
- Smagorinsky, J., 1963. *General circulation experiments with the primitive equations. I: the basic experiment*. Mon. Weather Rev. 91, 99–164. [https://doi.org/10.1175/1520-0493\(1963\)091%3c0099:GCEWTP%3e2.3.CO;2](https://doi.org/10.1175/1520-0493(1963)091%3c0099:GCEWTP%3e2.3.CO;2)
- Staehr, S.U., Van der Zande, D., Staehr, P.A.U., Markager, S., 2022. *Suitability of multisensory satellites for long-*

term chlorophyll assessment in coastal waters: A case study in optically complex waters of the temperate region. *Ecol. Indic.* 134, 108479.

<https://doi.org/10.1016/j.ecolind.2021.108479>

van Ruth, P.D., Patten, N.L., Doubell, M.J., Chapman, P., Rodriguez, A.R., Middleton, J.F., 2018. Seasonal- and event-scale variations in upwelling, enrichment and primary productivity in the eastern Great Australian Bight. *Deep Sea Res Pt. II*, 157–158, 36–45.

<https://doi.org/10.1016/j.dsr2.2018.09.008>

Ward, T.M., Mcleay, L.J., Dimmlich, W.F., Rogers, P.J., McClatchie, S., Matthews, R., Kämpf, J., Van Ruth, P.D., 2006. Pelagic ecology of a northern boundary current system: effects of upwelling on the production and distribution of sardine (*Sardinops sagax*), anchovy (*Engraulis australis*) and southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. *Fish. Oceanogr.* 15, 191–207.

<https://doi.org/10.1111/j.1365-2419.2006.00353.x>