Potential and timescale for on-shelf hypoxia in upwelling systems: and idealized model analysis

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Abstract

A maximally simple, coupled physical-biogeochemical box model is used to examine interactions controlling the potential and timescale for hypoxic levels of oxygen depletion over the shelf in an idealized eastern boundary upwelling system. Here near bottom oxygen drawdown is controlled by the balance between flushing with offshore source waters and the degree to which surface particulate organic carbon production and its subsequent sinking and remineralization are retained over the shelf and focused on the bottom. In the model, particle production is controlled by wind-driven upwelling of a generic nutrient to the surface, balanced by respiration and sinking. The degree to which this production occurs over shelf is a balance between the net particle growth rate $\eta$, and the upwelling driven shelf flushing rate $\lambda$, equivalent to the Ekman upwelling index scaled by the shelf width and surface layer depth. Initial oxygen drawdown follows this exponential rate of surface particle accumulation over shelf $(\alpha = \eta - \lambda)$, and so is slower for rapid upwelling (large $\lambda$) and slow particle growth (small $\eta$). An analytical approximation for the timescale of oxygen drawdown during the initial exponential surface particle growth stage under constant forcing is derived. Model steady states are used to characterize the potential for hypoxic levels of near-bottom oxygen drawdown over the model parameter space; this potential is greater for slower upwelling and wider shelf widths (smaller $\lambda$), and larger sinking rates up to the extent that sinking does not limit surface particle growth. A relatively complete characterization of the model system’s susceptibility to hypoxia can be obtained by combining these two diagnostics. If the sinking rate $s$ is comparable to or larger than the sum of the respiration rate $r$ and the constant shelf flushing
rate $\lambda_0$, then the system’s steady state will generally be hypoxic. For slower sinking rates, the system can never reach hypoxia, even for arbitrarily long upwelling seasons. Increased upwelling forcing reduces the potential for hypoxia, and also slows the timescale to hypoxia during the exponential growth stage, once nutrient limitation of the the surface growth is overcome. Fluctuations in the amplitude of the upwelling forcing can systematically reduce the potential for oxygen depletion below these estimates, especially when surface sinking export is rapid or forcing is strong.

1 Introduction

Episodes of low oxygen (hypoxia) in coastal waters can negatively affect fisheries and local ecosystem functioning by stressing and displacing vulnerable species, particularly benthic species such as commercially important groundfish and crustaceans (Bailey et al. 1985; Chan et al. 2008; Keller et al. 2015). In extreme cases low oxygen events lead to large areas of mortality or "dead zones" and thus have the potential to negatively affect regional ecosystems and economies. Recently in the Pacific Northwest, low oxygen events have been reported with increasing occurrence and associated with detrimental effects (Grantham et al. 2004; Chan et al. 2008; Keller et al. 2015), stimulating interest into what processes control hypoxia (Hales et al. 2006; Connolly et al. 2010; Adams 2014; Peterson et al. 2013; Siedlecki et al. 2015). It remains unclear how hypoxia develops in this region and upwelling systems in general, and specifically how hypoxia in upwelling systems is related to regional and basin scale processes (Hales et al. 2006; McClatchie et al. 2010; Deutsch et al. 2011).
The primary cause of oxygen drawdown in the ocean is bacterial respiration of decaying organic matter. Poorly ventilated waters will accumulate the respiration signal of any detrital flux into them, so that at both the gyre and regional scales the oxygen level is dependent on the accumulated respiration in that water mass. This respiration signal is mitigated by ventilation with surface waters, where oxygen is high due to phytoplankton activity and air-sea interaction (Wanninkhof et al. 2009). Thus in regions with poor ventilation or high detrital loading, oxygen can attain low levels and even become completely anoxic at depth, thus having a limiting effect on any heterotrophs that require oxygen (Levin 2003; Gruber 2011; Doney et al. 2012). Extensive regions of the Pacific, where ventilation is low and water residence times high, have large oxygen minimum zones (OMZs) associated with both the northern and southern subtropical gyres (Levin 2003; Stramma et al. 2010). In the sub-tropical north Pacific, variations in the oxygen level of the OMZ appear to be related to multi-decadal ventilation cycles due to tidal mixing in the East Pacific (Whitney et al. 2007; Falkowski et al. 2011) and variability in the respiration signal due to decadal scale changes in the nutricline depth in the tropics (Deutsch et al. 2011, 2014), though the details of these mechanisms and how exactly the associated water masses are transported remain relatively unknown. Additionally, OMZs are predicted to be larger and have lower oxygen levels associated with anthropogenic climate change, which would potentially drive more frequent and severe hypoxia events where water associated with OMZs is upwelled to the surface (Gruber 2011; Doney et al. 2012).

Along eastern boundaries of the subtropical gyres, intermittently persistent equator-
ward winds drive surface offshore Ekman flow throughout the spring and summer, upwelling nutrient-rich water to the surface and driving productive coastal ecosystems (Ryther 1969; Carr and Kearns 2003). Here bottom waters over the shelf can become hypoxic, with variability from year to year and over space (Bailey et al. 1985; Bailey 1991; Peterson et al. 2013; Adams 2014; Siedlecki et al. 2015). Coastal hypoxia in upwelling systems results from different processes than for dead zones in river-dominated systems such as the Mississippi delta region, where hypoxia is a direct result of high nutrient loading of coastal waters associated with wastewater and fertilizer runoff. Water brought onto the shelf in eastern boundary upwelling systems is already low in oxygen and high in nutrients due to the proximity of the OMZ (Chavez and MessiÁI 2009; Bograd et al. 2008; Pierce et al. 2012; Peterson et al. 2013). Oxygen is further depleted as detritus from the upwelling driven production is respired (Bailey 1991; Hales et al. 2006), especially in regions of low flushing (Adams et al. 2013). Thus hypoxia in coastal upwelling systems is the result of an interplay between physical and biogeochemical processes, driven by coastal production supported by the upwelling-driven nutrient flux to the surface.

In order to move toward prediction of coastal hypoxia it is critical to advance understanding of how shelf-scale physical-biological interactions lead to regional seasonal oxygen drawdown in upwelling systems, and in particular to separate shelf-processes from changes in oxygen levels in upwelled source water as drivers of coastal hypoxia. The relative roles of these two processes remain unclear. Recently, the role of source water has been highlighted as a potential driver of hypoxia in upwelling regions, as lower oxygen in upwelled water will
be more easily depleted to hypoxic levels (Bograd et al. 2008; McClatchie et al. 2010; Peterson et al. 2013). However, the role of shelf circulation and its interaction with particulate production, sinking and remineralization rates on oxygen drawdown has yet to be determined, though it appears the interplay between respiration and flushing is important (Adams et al. 2013; Adams 2014). Here we systematically explore the potential for an upwelling system to go hypoxic under variation of these key biogeochemical parameters. If the system is able to attain significant levels of oxygen drawdown, we then calculate the estimated timescale over which this de-oxygenation occurs. This analysis gives insights into the key processes driving on-shelf deoxygenation.

2 Methods

2.1 Box model geometry

The model presented and analyzed here is formulated to represent integral balances over a continental shelf under upwelling conditions, partitioned by depth into three volumes or boxes (Fig. 1). Motivated by observations in upwelling systems of elevated POC over the shelf in both the surface and bottom boundary layers (i.e. Hales et al. 2006), we divide the mid-shelf into three boxes. The top box, with thickness $H$, represents a surface boundary layer, where both wind-driven transport and photosynthetically driven production are confined. The bottom box, taken to have the same thickness $H$, represents the bottom boundary layer, in which onshore upwelling transport is confined and sinking particles accumulate. The interior water
column between the surface and bottom boundary layers forms a middle box, with thickness $H_{mid}$, so that the ratio between the middle and boundary layer boxes is $\delta_H = H/H_{mid}$. A single cross-shelf width $L$ is specified for all three boxes, and we assume that shelf-width does not vary alongshore, so that all modeled balances and quantities are computed per unit alongshore distance. For specific simulations and analysis, surface and bottom boxes are prescribed with $H = 20$ m, with the remainder of the water column (60 m for a nominal shelf depth of 100 m) assigned to $H_{mid}$, so that $\delta_H = 1/3$.

### 2.2 Physical forcing

The physical circulation is represented by wind-driven Ekman transport $U_E = \tau^y/\left(\rho_0 f\right)$ per unit alongshore distance, equivalent to an upwelling index (Schwing et al. 1996). Here $\tau^y/f < 0$ and $U_E < 0$ corresponds to upwelling conditions, with offshore transport out of the top box; here $\tau^y$ is poleward alongshore wind stress along an eastern boundary, $\rho_0$ is a reference density, and $f$ is the Coriolis parameter. The offshore Ekman transport is compensated by vertical upwelling transport $W_{up} = -U_E$ from the bottom box to the top box; in all cases $U_E \leq 0$ and $W_{up} \geq 0$, so that downwelling never occurs. After division by the box volume (per unit alongshore distance) $HL$, this volume flux translates to an upwelling volume-renewal, or cross-shelf flushing rate $\lambda$ (with units of inverse days, $d^{-1}$),

$$\lambda = -\frac{U_E}{LH} = -\frac{\tau^y}{\rho_0 f LH}.$$  

(2.1)

Conceptually, $\lambda$ is the average inverse shelf flushing time, or upwelling transport rate, so that $1/\lambda$ is the timescale for the upwelling circulation to completely flush out the top box.
Since we are assuming all offshore transport is compensated in the bottom box, \( \lambda \) is also the rate that the bottom box is flushed with off-shelf source waters. The upwelling rate is chosen such that we can examine a continuum of constant forcing levels, and ultimately include time variance, for two endmember biogeochemical cases defined below. This forcing level ranges from shelf flushing times of 50 days \((\lambda = 0.02 \text{ d}^{-1})\), corresponding to weak upwelling and slow flushing rates over a broad shelf, such as the Canary upwelling system, to shelf transport times of less than 3 days \((\lambda = 0.4 \text{ d}^{-1})\), corresponding to rapid upwelling and flushing over a narrow shelf, such as off Central California (Chavez and MessiÄl' 2009).

### 2.3 Biogeochemical model

The main objective of this study is to explore the dependence of near-bottom oxygen depletion on general characteristics of the upwelling system. Near-bottom oxygen is represented by the oxygen concentration in the bottom box, \( O_{bot} \) (mmol m\(^{-3}\)), equal to total dissolved oxygen divided by the bottom box volume. The rate of change of \( O_{bot} \) is proportional to the sum of respiration (remineralization) of bottom-box particles and the balance (onshore minus upward) of upwelling-driven advective oxygen fluxes,

\[
\frac{dO_{bot}}{dt} = -\frac{\nu}{\gamma} r C_{bot} + \lambda(O_s - O_{bot}). \tag{2.2}
\]

In (2.2), \( \nu = 10 \) and \( \gamma = 7 \) are stoichiometric (Redfield) ratios representative of the typical proportions of carbon and oxygen, respectively, to nitrogen in marine organic matter (e.g., Anderson and Sarmiento 1994), \( r \) (d\(^{-1}\)) is the carbon-specific particle respiration (remineralization) rate, \( C_{bot} \) is the particle (particulate organic carbon, or POC) concentration in the
bottom box, $\lambda$ is the upwelling transport rate defined above, and $O_s$ is the oxygen concentration of the deep offshore source waters advected into the bottom box by the upwelling circulation, here assumed constant in time. The equation (2.2) can be rewritten in terms of the oxygen drawdown relative to the offshore value, $\Delta O_{bot} = O_{bot} - O_s$:

$$\frac{d\Delta O_{bot}}{dt} = \frac{\nu}{\gamma} r C_{bot} - \lambda \Delta O_{bot}. \quad (2.3)$$

This relative drawdown is independent of $O_s$, which may differ between coastal systems, so the formulation (2.3) is used here. It is not necessary to consider or represent oxygen concentrations in the middle or top boxes, since downwelling and mixing between the boxes are not considered, so that oxygen enters the bottom box only from offshore. The neglect of mixing between boxes for all biogeochemical constituents is consistent with the focus on advectively driven upwelling systems. We do not attempt to simulate the biogeochemical functioning of the system after oxygen has been entirely depleted.

The bottom-box particle concentration $C_{bot}$ needed for (2.3) is derived from a maximally simple particle-nutrient model,

Particles (POC) :

$$\frac{dC_{top}}{dt} = \left( \frac{pN_{top}}{K+N_{top}} - r \right) C_{top} - sC_{top} - \lambda C_{top} \quad (2.4)$$

$$\frac{dC_{bot}}{dt} = -rC_{bot} + E_{bot}(t) \quad (2.5)$$

Nutrients :

$$\frac{dN_{top}}{dt} = -\gamma^{-1} \left( \frac{pN_{top}}{K+N_{top}} - r \right) C_{top} + \lambda (N_{bot} - N_{top}) \quad (2.6)$$

$$\frac{dN_{bot}}{dt} = \gamma^{-1} r C_{bot} + \lambda (N_s - N_{bot}) \quad (2.7)$$

The first term on the right-hand side of (2.4) represents net top-box particle concentration (POC) growth deriving from the excess of photosynthetically-driven productivity over part-
cle respiration. Production proceeds via a particle-specific rate constant, $p \, (d^{-1})$, scaled by a Monod-form dependence on a top-box generic nutrient concentration ($N_{top}$; mmol m$^{-3}$). The production rate is essentially independent of $N_{top}$ when $N_{top} \gg K$ for a given value of the half-saturation constant $K$ (mmol m$^{-3}$); for $N_{top} \approx K$, $N_{top}$ becomes limiting. Top-box particles are lost in proportion to their concentration by respiration at the rate $r$ and by vertical sinking export, or settling, at the specific settling rate $s = S/H \, (d^{-1})$, which can be considered the ratio of the physical sinking velocity $S$ (m d$^{-1}$) to the box thickness $H$ (m). Top-box particles are also lost by offshore advection at a rate given by their concentration multiplied by the shelf flushing rate $\lambda \, (d^{-1})$, and are assumed to sink faster than the upwelling velocity so that there is no upwelling of POC. Bottom-box particles are supplied by the incoming sinking flux $E_{bot}(t)$ and lost by respiration. Since most studies show that essentially all particles incorporated in surficial sediments are respired very near the sediment-water interface, with respiration products returned to overlying waters (e.g., ?, also see Siedlecki et al. (2015)), sediment respiration is assumed to be incorporated in the bottom-box respiration, so no explicit term is included that would separately represent loss of $C_{bot}$ through long-term sediment burial. The nutrient balances include the same terms corresponding to particle growth and respiration seen in (2.4) and (2.5), differing only in sign (production consumes nutrient, respiration releases it) and a scaling by the stoichiometric ratio $\gamma$. Bottom onshore and surface offshore nutrient transport terms are as for bottom-box oxygen and top-box particles, respectively, with $N_s$ the constant nutrient concentration of the upwelling source waters.

The incoming particle flux $E_{bot}$ in the bottom-box particle balance (2.5) would be equal
to the outgoing sinking export flux from the top box $E_{top} = sC_{top}$ if the middle box were absent. More generally (Sec. A.1), the particle flux is attenuated and spread out in time by respiration and sinking through the middle box, so that

$$E_{bot}(t) = \delta s \int_0^t e^{-(r+s')(t-t')} E_{top}(t') \, dt' ,$$  \hspace{1cm} (2.8)

and where $s' = S'/H_{mid}$ is the specific settling rate for the middle box, and $\delta = s'/s$. Here $S' > S$ would allow for the amplification of particle sinking velocities by aggregation or biological scavenging and repackaging, but we generally take $S' = S$, so that $\delta = \delta_H$. The incoming sinking flux $E_{bot}$ will differ most from the outgoing sinking flux $E_{top}$ for high respiration rates (large $r$) and long settling transit times (small $s'$), i.e. when the respiration length scale is much shorter than the shelf depth (Sec. A.1).

### 2.4 Total nutrient budget

A diagnostic of model behavior is the degree to which the on-shelf nutrient flux $\lambda N_s$ is retained over the shelf, i.e., summed over the model boxes, and quantification of the pathways with which it is lost (Fig. 1). The total model nutrient equivalent per unit alongshore distance, $\mathcal{N}$, is the sum of the particle and nutrient content of the top and bottom boxes multiplied by the corresponding box volume:

$$\mathcal{N} = LH[(C_{top} + C_{bot})/\gamma + N_{top} + N_{bot}] .$$  \hspace{1cm} (2.9)
The total nutrient flux budget is defined by summing equations (2.4) - (2.7) and multiplying by the box volume, to compute the rate of change of N:

\[
\frac{dN}{dt} = LH[\lambda N_s - \lambda C_{top}/\gamma - \lambda N_{top} - rC_{mid}(\gamma\delta_H)^{-1}].
\]  

(2.10)

where POC concentrations are converted to nutrient units through scaling by \(1/\gamma\). Sinking flux and respiration terms cancel in the summation as total nutrients are moved through the system and converted from POC back into nutrients, etc. Here total nutrients enter the model through onshore transport of nutrients into the bottom box (\(\lambda N_s\)), and leave the model both through offshore transport of particles and nutrients in the top box (\(\lambda C_{top}/\gamma + \lambda N_{top}\)), and through effective remineralization loss of POC in the middle box \([-rC_{mid}(\gamma\delta_H)^{-1}]\). As the system approaches steady state (2.10) will become zero, so that the on-shelf nutrient flux will will be exactly balanced by surface and mid-water column losses.

2.5 Model parameter space

As basic points of reference, two contrasting sets of parameter values are considered (Tables 1-3), denoted by "Fast Particles" (FP) and "Slow Particles" (SP). These cases were chosen to contrast the bottom oxygen drawdown behavior for fast growing, fast sinking particles, and slow growing, slow sinking particles. The FP case, with relatively large values of \(p\), \(s\), and \(K\), represents a system characterized, for example, by a dominance of rapidly growing and sinking plankton with a higher nutrient half-saturation, such as coastal diatoms, which are observed to dominate the biomass of the initial production response to coastal upwelling (e.g., ?). The SP case, with relatively small values of \(p\), \(K\), and \(s\), represents a system with a slower
biological response to upwelled nutrients and much slower particle sinking velocities. These two sample cases are intended to be illustrative of key biogeochemical-physical interactions and not representative of specific physiology or ecosystem states.

For the initial analysis, the respiration rate is taken to be constant and uniform in all boxes, and the upwelling parameter $\lambda_0$ is set to 0.1 d$^{-1}$. For definiteness and to aid discussion, we focus on two bottom-oxygen drawdown levels $\Delta O_{\text{bot}} = \Delta O_{\text{hyp}} = \{40, 100\}$ mmol m$^{-3}$. These thresholds represent the oxygen drawdown required for the system to reach commonly defined levels of moderate hypoxia (60 mmol m$^{-3}$ $\approx$ 1.3 mL L$^{-1}$) and extreme hypoxia (0 mmol m$^{-3}$) given an offshore source water oxygen concentration of $O_s = 100$ mmol m$^{-3}$($\approx$ 2.24 mL L$^{-1}$).

3 Results

3.1 Two example cases

The FP and SP cases described above are used to construct a simple representation of the long-term evolution of the system over an upwelling season. Here the model is initialized with conditions representative of the onset of the upwelling season (Tables 1,2). The system is then forced for 150 days (comparable to the maximal extent of a mid-latitude eastern boundary upwelling season) with constant upwelling-favorable winds, so that $\lambda = \lambda_0 > 0$, where $\lambda_0$ is a constant. In this scenario the time-evolution of the model system (Figs. 2,3) is characterized by two distinct stages: (i) an initial phase, during which the time-evolution
is approximately exponential, followed by (ii) approach toward a long-term, steady-state balance. The initial, exponential phase lasts roughly 20 d for FP (Fig. 2, dotted line) and over 50 d for SP (Fig. 3, dotted line), ending when the surface reaches nutrient limitation ($N_{top} \approx K$).

The two cases FP and SP have widely differing bottom oxygen responses. For FP, oxygen depletion is rapid and sustained, reaching $\Delta O_{bot} = 40 \text{ mmol m}^{-3}$ (hypoxia) after only 20 d, within the exponential stage, and $\Delta O_{bot} = 100 \text{ mmol m}^{-3}$ (anoxia) after 30 d (Fig. 2a). For the SP case, oxygen decline is slow and limited, so that $\Delta O_{bot}$ reaches only 9 mmol m$^{-3}$ after 100 d (Fig. 3a). These differences motivate exploration and comparison of the processes driving benthic oxygen drawdown in each of the two cases.

### 3.1.1 Initial exponential growth phase

As given by (2.2), bottom oxygen drawdown is driven by a balance between the supply and respiration of sinking particles and flushing with off-shelf source waters. Thus oxygen depletion depends heavily on the temporal evolution of surface production over the shelf, and in particular and how much of this production settles out over the shelf and accumulates at the shelf bottom. For both example cases, at the initiation of upwelling surface nutrient levels rise so that nutrients are not limiting production ($N_{top} >> K$), and nutrient levels initially continue to rise even as surface particle levels grow (Figs. 2,3). In this unlimited regime surface particle growth occurs at the net saturated rate $\eta = p - r - s$, a balance of production, remineralization and particle settling. This growth is balanced by off-shelf loss of surface particles at the same
rate as upwelling, so that $C_{top}$ accumulates exponentially at a rate $\alpha = \eta - \lambda$:

$$C_{top}(t) \approx C_{top0}e^{\alpha t} = C_{top0}e^{(p-r-s-\lambda)t}. \quad (3.1)$$

For the two sample cases, $\alpha$ is 0.3 d$^{-1}$ for FP and 0.1 d$^{-1}$ for SP (Table 3). The factor of three difference in $\alpha$ causes more rapid surface particle accumulation in FP relative to SP: after 25 days of continuous forcing FP has reached its maximum $C_{top}$ value, subsequently declined and is under nutrient limitation (Fig. 2), while SP surface POC levels are still low and growing exponentially (Fig. 3). This exponential growth stage ends when surface particle levels are high enough to efficiently uptake the upwelled nutrient flux, nutrients become limiting, production declines, with $\eta$ and $\alpha$ following.

Oxygen depletion at depth requires export of particles from the surface to the shelf bottom. While the surface particle concentration ($C_{top}$) is growing exponentially, the export of particles ($E_{top} = sC_{top}$) follows. This settling export reduces particle accumulation in the top box, but it is the sole factor driving accumulation in the bottom box. Thus, as $C_{top}$ increases exponentially, particle sinking drives corresponding exponential growth in the bottom particle accumulation $C_{bot}$ (Figs. 2,3), with both bottom nutrients and oxygen depletion increasing as these particles are respired. Thus the approximate exponential rate of both bottom nutrient accumulation and oxygen drawdown is also $\alpha$, following the surface particle accumulation during the initial exponential growth phase (Fig. 2a,3a, dashed line). However, the amplitude of the bottom nutrient and oxygen response has an additional dependence on parameters, including the sinking, respiration and upwelling rates, as these affect the supply of surface particles to the bottom box and set the flushing rate of the bottom with off-shelf waters.
Although the exponential rate of growth \( \alpha \) for FP is only three times that for SP, the delivery of particles to depth is far more pronounced for FP due to two effects. The first is that the product of faster particle production and higher settling rate drives a greater sinking flux for FP than for SP, so that the fraction of upwelled nutrients converted to sinking flux in the top box is higher. The second effect is that more rapid sinking through the middle box for FP results in less attenuation by respiration and a higher rate of particle delivery to the bottom box, so that respiration is focused in the bottom box. The dependence of oxygen drawdown on the model parameters during the exponential stage is presented in more detail in Sec. 3.2.2.

### 3.1.2 Long-term steady-state response

While both the FP and the SP oxygen drawdown both initially follow an exponential evolution, the two cases differ fundamentally in the amplitude of oxygen drawdown that is ultimately achieved. A drawdown of 100 mmol m\(^{-3}\), which would correspond to anoxic conditions for a nominal offshore (source) oxygen value \( O_s = 100 \text{ mmol m}^{-3} \), is reached for FP in 30 d. In contrast, the SP drawdown never reaches 10 mmol m\(^{-3}\), an order of magnitude less. The difference in this long term behavior can be understood by analysis of the steady state response of the system.

Steady states are achieved for both FP and SP, and in general for any parameter space under constant forcing, after the exponential growth stage and nutrient limitation. In the long term, a steady-state balance results from this limitation, in which the \( C_{top} \) growth rate is precisely zero, and total nutrients \( \mathcal{N} \) within the system remain constant (Figs. 2cd,3cd). In the FP
case, the steady-state balance has a large oxygen drawdown, which is not reached until well after the hypoxic thresholds are passed. For SP, however, the steady state has only a small oxygen drawdown, never approaching hypoxia. The immediate reason for the smaller steady-state value of oxygen drawdown for SP, relative to FP, is the same as the in the exponential stage: slow sinking in the SP case limits delivery of upwelled nutrients back to the bottom box as sinking particle flux. The constant-forcing steady states, the associated particle-nutrient-oxygen balances, and their general dependence on the physical and biogeochemical controls are explored more fully in the next section.

3.2 Potential and timescale for bottom de-oxygenation

3.2.1 The potential for hypoxia: Steady states under constant forcing

In the constant forcing scenario, the asymptotic behavior for all variables is a constant steady state. In reality, neither physics or biogeochemistry in upwelling systems ever reach steady state, either because of the variability of forcing or the long timescales necessary to approach steady state relative to the duration of the upwelling season. Further, as will be shown, the steady-state deoxygenation can be quite large: in much of the parameter space the drawdown is greater than the highest observed oxygen levels. Nonetheless, the model steady states can be used to examine the maximum deoxygenation potential over a wide range of the parameter space. This allows analysis of the system’s response to key parameters, and of the factors that can drive the system to hypoxia and anoxia.

Under constant forcing, the exponential growth stage ends with nutrient limitation in
the top box, slowing the growth of $C_{top}$, resulting, for a given value of $s$, in a constant delivery of particles to the bottom box and a steady-state for the bottom oxygen drawdown $\Delta O_{bot}$ that equates the flushing of the bottom box with offshore water and consumption of oxygen by carbon degradation. Explicit expressions for these steady-state solutions can be obtained by setting the time derivatives in (2.4)–(2.8) to zero; these are given in the Appendix [equations (A.8)–(A.13)]. The steady states prove always to be stable: small perturbations from them decay, so that the perturbed solution evolves back toward the steady state. The rate of approach to the steady state is controlled by the parameter $\sigma = \lambda_0 r (r + \delta \lambda_0) / [\delta s (r + \lambda_0)]$. For FP $\sigma = 0.09 \text{ d}^{-1}$, while for SP $\sigma = 0.93 \text{ d}^{-1}$, so the SP system adjusts much more rapidly toward steady state after the initial exponential phase terminates, with the factor of 10 difference arising from the order of magnitude difference in the settling rate $s$ between the two cases.

The surface particle balance comes into steady state when either (i) there are no seed particles to initiate growth ($C_{top} = 0$) or (ii) the intrinsic particle production rate is exactly balanced by the total particle loss rate from respiration, sinking, and offshore transport. From (2.7), the latter balance requires that $p N_{top} / (K + N_{top}) = r + s + \lambda_0$, which determines the surface nutrient steady state $\overline{N_{top}}$ in terms of the rate parameters and half-saturation constant,

$$\overline{N_{top}} = \frac{r + s + \lambda_0}{p - r - s - \lambda_0} K = \frac{p - \alpha}{\alpha} K,$$

where the overline on $N_{top}$ denotes a steady state. The remaining equations describe a system containing a closed loop, and must be solved simultaneously: $C_{top}$ depends on the upwelling source nutrient $N_{bot}$ and determines the sinking flux, which in turn determines $C_{mid}$ and then $C_{bot}$, while $C_{bot}$ provides the respiration source for $N_{bot}$, closing the loop. The resulting steady-
state solution for the bottom oxygen depletion is:

\[
\Delta \bar{O} = \frac{\delta s^2}{r_s + (r + \delta_s)\lambda_0} v (N_s - \overline{N_{top}}) \quad (3.3)
\]

\[
= \frac{\delta s^2}{r_s + (r + \delta_s)\lambda_0} v (N_s - \frac{p - \alpha}{\alpha} K), \quad (3.4)
\]

with the second expression using (3.2) above. Here the bottom oxygen depletion $\Delta \bar{O}$ is the product of two factors, with the first dependent only on remineralization $r$, sinking $(s, \delta)$ and the physical forcing $\lambda_0$, while the second depends on all these (through $\alpha$), as well as the off-shelf nutrient source level $N_s$, the production rate $p$, half-saturation $K$, and trivially on the stoichiometry $v$. The second factor is a linear function of $N_s$, so that increased deep offshore nutrient concentration will result in increased steady-state bottom-oxygen depletion, given that all other parameters are fixed.

Provided that production is large enough to support production of $C_{top}$ (i.e., $\alpha$ significantly greater than zero), variations in the intrinsic surface particle production $p$ rate have almost no effect on bottom oxygen depletion, when all other system parameters, including the sinking rate $s$, are held fixed. This can be seen by rewriting the second factor in (3.4) as

\[
N_s - \overline{N_{top}} = \left(1 - \frac{pK_s}{\alpha}\right) \frac{N_s}{N_s} \approx \left(1 - \frac{pK_s}{\alpha}\right) N_s. \quad (3.5)
\]

Where $K_s = K/(K + N_s)$ and $N_s = N_s/(K + N_s)$ are, respectively, a dimensionless half-saturation constant and a dimensionless source nutrient level, which satisfy $K_s + N_s = 1$ with, generally, $K_s \ll 1$ and $N_s \approx 1$. The factor $1 - pK_s/\alpha$ in (3.5) is nearly constant and approximately equal to one for all $p$ except those near the limiting value of $p$ (Fig. 4).

The primary control on steady state bottom-oxygen depletion with respect to variations
in the model parameter space is therefore exerted by the first factor on the right-hand side of (3.4). Of particular interest is the dependence on the upwelling parameter \( \lambda_0 \), which may vary widely under different physical circumstances, and on the settling rate \( s \), which is poorly constrained from observations. In contrast, the respiration rate \( r \) is relatively well constrained to be roughly in the range \( 0.1 - 0.2 \, \text{d}^{-1} \), at least at depth (see Siedlecki et al. 2015). Discussion of the dependence on the relative-sinking-rate parameter \( \delta \) is deferred to the next section.

For both the FP and SP cases, the steady-state response has a similar dependence on the upwelling timescale \( \lambda_0 \) when all other FP and SP parameters are held fixed (Fig. 5ab). Here steady-state oxygen depletion is always reduced when \( \lambda_0 \) is greater, i.e. upwelling stronger or shelf width smaller, and on-shelf oxygen drawdown ceases when completely when \( \lambda_0 \) is above a case-dependent threshold, \( \lambda_0 = \eta_\ast \approx \eta \), where \( \eta_\ast = \rho N_s - r - s \). This reduction in deoxygenation with increasing \( \lambda \) is primarily due to shunting of production off-shelf, so that particle accumulation at depth will not occur. As \( \lambda_0 \) approaches the net growth rate \( \eta \), particle concentration growth over the shelf ceases; consumption of nutrients by particle production cannot keep up with the nutrient supply, surface nutrient levels increase, which in turn causes increased offshore transport of total nutrients at the surface (Fig. 5gh). Thus despite the increased nutrient supply to the system with stronger upwelling, particle production is not retained over the shelf, limiting accumulation at depth and the associated oxygen drawdown.

Similarly, the potential for oxygen drawdown is greatest at low upwelling rates or when the shelf is wide, i.e. when \( \lambda_0 \) is small (Fig. 5ab). However, the system takes relatively much longer to reach the steady state values as upwelling declines. For the steady states, the
increase of oxygen drawdown with decreasing upwelling extends all the way to the limit of zero upwelling. In the limit of small $\lambda_0$ (i.e., as $\lambda_0 \to 0$), the steady-state solution (A.4) for bottom-box oxygen drawdown is

$$\Delta O_{bot} = \frac{\delta s}{r} v(N_s - \bar{N}_{top}) \approx \frac{\delta s}{r} vN_s. \quad (3.6)$$

This is also the maximum steady-state value of $\Delta O_{bot}$ with respect to variations in $\lambda_0$ with all other parameters held fixed. The timescale $1/\sigma$ for approach to this steady state diverges as $1/\lambda_0$ as $\lambda_0 \to 0$, so that this theoretical limiting steady-state solution will never be reached from general initial conditions. However, the result (3.6) emphasizes that rapid subsurface sinking (large $\delta$) increases oxygen drawdown. It also suggests that drawdown is large for slow respiration (small $r$), but this interpretation is less robust, as the large drawdown for small $r$ and $\lambda_0$ is realized only after an extremely long, slow approach toward the steady state, with timescale diverging as $1/(\lambda_0 r)$ as $\lambda_0 \to 0$ and $r \to 0$.

The steady-state solutions also show a strong dependence on the sinking rate $s$ (Fig. 6). The sinking rate affects both the vertical export from the top box and the attenuation through the middle box, so that for both small and large values of $s$ particle accumulation and remineralization in the bottom box is limited and oxygen drawdown is low, and in between these extremes there a sinking rate that maximizes oxygen drawdown. Low values of $s$ decrease the settling rate from the surface, in turn increasing the surface particle accumulation rate $\alpha$, resulting in a high surface $C_{top}$ steady state, allowing greater loss of particles off-shelf. Additionally, because of the slow sinking rate, the small settling fraction of this high particle load is substantially reduced by mid-depth respiration, so that particle levels are low in both the
middle and bottom boxes. This results in weak bottom oxygen drawdown for small $s$, while the offshore flux of total nutrients is dominated by surface particle transport.

In general rapid surface sinking (high $s$) slows the surface particle accumulation rate $\alpha$, shutting down accumulation completely when the settling rate $s$ reaches the critical value $s_{\text{max}} = p - r - s$ making the accumulation rate $\alpha = 0$. At this limit, the system is flushed out and all variables decay to their offshore source water values. For the steady states, the maximum sinking rate for deoxygenation to occur is further reduced by nutrient limitation to $s_\ast = pN_\ast - r - \lambda_0$, where $N_\ast = N_s/(K + N_s)$. For intermediate values of $s$, the exported fraction of surface particle production increases with $s$, while the surface POC accumulation rate $\alpha$ decreases; here particle concentrations decline at the surface as more production is exported, but increase in the bottom box as a result of more effective transport through the middle box, and the enhanced particle export to the bottom box drives increased bottom oxygen depletion. The effect of oxygen drawdown increasing with sinking rate is large when the remaining parameters are fixed to their values for the FP example, so that $s \gg r$ over a wide range of allowable $s$ values and middle box attenuation is accordingly limited (Sec. A.1). When the remaining parameters are instead fixed to their values for the SP case, all allowable sinking rates are relatively small (e.g., $s_\ast < r$), leading to low levels of sinking export out of the surface and relatively high levels of respiration loss in the middle box, in turn limiting both particle flux to the bottom and oxygen drawdown.

As the sinking rate $s$ increases toward the maximum value for steady state production to occur ($s_\ast$), a sinking level is reached which simultaneously maximizes both deoxygenation
\( \Delta \bar{O} \), the bottom nutrient concentration \( N_{\text{bot}} \), and the bottom POC concentration \( C_{\text{bot}} \). This “optimal” sinking rate \( s = s_{\text{opt}} \) results in much different levels of potential oxygen drawdown for the FP and SP cases: FP can attain extreme hypoxia (\( \Delta \bar{O} > 100 \text{ mmol m}^{-3} \)) for a range of sinking rates, while the most hypoxic sinking rate for SP results only in a nominal amount of oxygen reduction (17.3 mmol m\(^{-3} \)), so that the SP case never attains hypoxia or anoxia for any sinking level. This maximizing sinking rate \( s_{\text{opt}} \) is used in Sec. 3.3.2 to explore the potential for hypoxia for the entire \((p, r, s, \lambda_0, K)\) constant-forcing parameter space.

The steady-state oxygen depletion defines the potential for the system to become hypoxic. However, the timescale for approach to hypoxia or anoxia may be much longer than an upwelling season, in which case the steady state depletion would never be realized. In order to determine whether the system could achieve the potential level of oxygen drawdown given by the steady states, it is useful to determine the timescale to hypoxia during the initial exponential growth phase.

### 3.2.2 Timescale to hypoxia: exponential phase

As shown in Sec. 3.1.1, the model’s initial response in the top box is well-approximated by a first-order exponential rise during the intervals when the nutrient is non-limiting, i.e. when \( N_{\text{top}} \gg K \). This analytical approximation has appeal in two ways: First, it offers guidance on the parameter dependences that shape the system response time, much as the steady-state analysis, above, did, and so guide our examination of the full model solutions. Second, if it can offer reasonable approximations of the de-oxygenation time without full model solutions,
approximations can be made more readily with only knowledge of a few parameterizations. We will examine the first of these here, supplemented by comparisons to numerical solutions of the model equations.

The exponential character of the initial response is inherent in the initial bottom-box de-oxygenation evolution, although delayed and dampened by the transfer through the water column. The existence of the analytical solution for the \( C_{top} \) (3.1) while \( N_{top} \gg K \) leads to subsequent analytical solutions for \( C_{mid}, C_{bot}, \) and \( \Delta O_{bot} \) such that:

\[
\Delta O_{bot}(t) \approx \frac{\nu C_{top0}}{\gamma G} (e^{\alpha t} - 1). \quad (3.7)
\]

As previously, \( \alpha = p - r - s - \lambda_0 \) is the net saturated exponential rate of surface particle accumulation under constant forcing, and \( G \) is a function of the parameter \( \alpha \), modified by \( r, s, \lambda_0 \) and \( \delta \),

\[
G = \frac{(\alpha + \lambda_0)(\alpha + r)(\alpha + r + \delta s)}{\delta rs^2}, \quad (3.8)
\]

that captures the factors that ultimately link export of \( C_{top} \) to input to, respiration in, and flushing of the bottom box.

The above approximation captures the temporal evolution of near-bottom oxygen well during the exponential stage (Figs. 2a, 3a, dashed lines). For the FP case an oxygen drawdown of \( \Delta O = 40 \text{ mmol m}^{-3} \) is reached in 21 days, soon after nutrient limitation, with (3.7) predicting 18 days, so that the exponential approximation provides a useful estimate of the time to moderate hypoxia. For the SP case where deoxygenation is minimal, a drawdown of \( \Delta O = 4 \text{ mmol m}^{-3} \) is reached is after 60 days, with (3.7) predicting 58 days. Here and for all parameter choices, the exponential approximation overestimates the oxygen drawdown, pro-
viding a faster timescale to achieve a given oxygen level. After nutrient limitation, the model diverges from the exponential solution as particle growth slows and the system approaches steady state.

Thus for regions of the model parameter space where hypoxia is possible, an approximate timescale for hypoxia $t_{exp}$ can be found by rearranging (3.7) to solve for the time at which a specific oxygen drawdown value $\Delta O_{hyp}$ is reached:

$$t_{exp} = \frac{1}{\alpha} \ln \left( 1 + \frac{\gamma \Delta O_{hyp} G}{\nu C_{top0}} \right) \approx \frac{1}{\alpha} (G_1 + G_2),$$

(3.9)

where $G_1$ depends on the initial conditions and stoichiometry, while $G_2$ depends on the model parameters such that

$$G_1 = \ln \frac{\gamma \Delta O_{hyp}}{\nu C_{top0}}, \quad G_2 = \ln G.$$ 

(3.10)

In (3.9) the initial surface particle accumulation rate $\alpha$ determines the basic exponential timescale of the oxygen drawdown response, while the logarithmic factor $G_1 + G_2$ scales the deep-box parameter-dependent relationship to the surface accumulation. The factor $G_1$ captures the time-scale dependence related to the magnitude of the specific deoxygenation target relative to the respiratory potential of the initial-condition $C_{top}$, while the factor $G_2$ captures the parameter-timescale dependence of the transfer and retention of surface particle driven respiratory potential to the bottom box.

Since the timescale to hypoxia during the exponential phase follows the surface particle accumulation timescale $\alpha^{-1}$, it is dependent on both the forcing and the biogeochemical parameters (Fig. 7). As the upwelling parameter $\lambda_0$ increases, the particle accumulation rate $\alpha$ decreases as more production is shunted off-shelf, so that oxygen drawdown slows in turn, and
totally ceases for forcing levels that severely limit surface accumulation, i.e. as \( \lambda_0 \) approaches \( p - r - s \). Hence strong upwelling or narrow shelves decrease oxygen drawdown in the exponential stage, just as they do in the steady states (Fig. 5), and the net saturated particle growth rate \( \eta = p - r - s \) sets the limit on how much forcing the system can tolerate before production over the shelf (and the associated oxygen drawdown at depth) ceases completely. However, the trend of oxygen drawdown being more severe with weaker forcing breaks down at small values of \( \lambda_0 \); here slow upwelling relative to the shelf width leads to nutrient limitation, so that production is stunted and oxygen drawdown is reduced. In this limit of sluggish upwelling, the exponential approximation does not give a good estimate of the oxygen drawdown time, as the assumption of \( N_{top} \gg K \) is violated.

The timescale to hypoxia is also dependent on the inverse sinking timescale \( s \) (Fig. 7b). For the FP case with sinking varied, deoxygenation is limited for both rapid and slow sinking, similar to the steady state analysis (Fig. 6). For slow sinking rates, the potential for oxygen drawdown is limited, since the exponential stage ends before significant oxygen drawdown is realized, as in the SP case (Fig. 3); here \( t_{exp} \) is much shorter than the realized time to moderate and severe hypoxia, if these levels of deoxygenation occur at all. For more rapid sinking the realized oxygen drawdown timescale follows \( \alpha^{-1} \), so that deoxygenation takes longer as sinking increases. This increase in the time to hypoxia with increased sinking is due to the limiting effect of \( s \) on the net accumulation rate \( \alpha \); as surface export increases, it slows the net accumulation rate, with deoxygenation slowing in turn. Thus oxygen drawdown ceases completely as \( s \) approaches \( p - r - \lambda_0 \) and \( \alpha \) approaches zero. For the FP case, \( t_{exp} \)
gives a useful estimate of the time to hypoxia for a wide range of sinking rates for which this drawdown potential is possible. Thus in general the \( t_{\text{exp}} \) approximation gives a useful estimate for the timescale to hypoxia when the system has a strong potential for hypoxia, as determined by the steady state analysis, and such that oxygen drawdown is reached within or shortly after the exponential stage.

### 3.2.3 Combining the potential and timescale criteria for oxygen drawdown

A relatively complete characterization of the system’s susceptibility to hypoxia under constant forcing can be obtained by combining the two basic diagnostic approaches described in the previous sections. The analysis of the basic dependence of the steady-state oxygen-drawdown responses on the control parameters allows a broad characterization of the system’s steady-state susceptibility to hypoxia, but provides no information on the timescale required to approach the steady state, and so will be fundamentally misleading as an indicator of potential hypoxia in cases in which the approach timescale proves to be very long. On the other hand, the exponential timescale estimate is only significant if the steady state is hypoxic. These two perspectives are each separately incomplete, but are also complementary and can be usefully combined.

The combined perspective relies on a simple, two-step logical unfolding. The steady-state hypoxic susceptibility is first considered. If the steady state is not hypoxic for a given threshold \( \Delta O_{\text{hyp}} \), then it can be inferred that the time-dependent response is uninteresting or irrelevant. However, if the steady state is hypoxic, then the timescale of the exponential
response (3.7)-(3.10) is computed, and this determines whether the hypoxic regime can be reached during an upwelling season of given length. Thus, for parameters for which hypoxia cannot be reached, a maximal oxygen drawdown is computed, while for parameters for which hypoxia can in principle be reached, a timescale for onset of hypoxia is computed.

A quantitative summary of this combined characterization is conveniently formulated as a contour plot, in which the steady-state oxygen drawdown is contoured in those regions where it does not reach the predetermined hypoxic level, and the exponential timescale for drawdown is contoured in those regions where the steady-state drawdown exceeds the hypoxic criterion. For example, consider the dependence of on the production rate $p$ and sinking rate $s$, with all other parameters ($K, r, \lambda_0, \delta, N_s$) held fixed as in the FP or SP examples (Fig. 8). The resulting summary plots are nearly identical for FP and SP, because the oxygen drawdown depends only weakly on $K$, the only fixed parameter distinguishing the two cases. If $p$ and $s$ for SP were both increased to the FP values, the resulting SP oxygen drawdown response would be very similar to the FP response.

Here for both cases the system does not have the potential for hypoxia ($\Delta O_{bot} = \Delta O_{hyp}$) below a critical sinking level, here $s \approx 0.3$ d$^{-1}$, and for these slow sinking cases, the steady state oxygen level is essentially independent of the production rate $p$. For sinking rates greater than the critical sinking level, the exponential timescale estimate $t_{exp}$ indicates that extreme hypoxia will be reached rapidly, within 20 days from the onset of the steady upwelling forcing. Only for a very narrow range of $p$ values does the hypoxia timescale approach the nominal 150-day upwelling season length, occurring as $p$ decreases toward the minimum production
level needed to achieve net particle growth. From this point of view, the primary role that intrinsic productivity $p$ plays in controlling the system’s susceptibility to hypoxia is to control the amplitude of the settling rate that can be supported without shutting down production, while the settling rate directly controls the intensity of the potential oxygen drawdown. The production rate $p$ plays a secondary role through its influence on the exponential drawdown timescale, but this is not a limiting factor, relative to the nominal length of an upwelling system, unless $p$ is very close the critical value for limiting net growth.

3.3 Classifying potential for hypoxia and anoxia: parameter space reduction

3.3.1 Normalized production and sinking rates

Summary figures such as Fig. 8 succinctly describe the hypoxic susceptibility, as a function of $p$ and $s$, of a system with given, fixed values of the remaining parameters: $K, r, \lambda_0, \delta$ and $N_s$. The dependence on $\Delta O_{bot}$ on $N_s$ can be seen from (3.4)–(3.5) to be essentially a proportionality, but this leaves still six independent parameters on which the oxygen drawdown response depends. The steady-state solution for bottom-oxygen depletion can be seen from (3.4) to depend only on the ratios of the fundamental rates, and consequently one of these six parameters can be effectively removed simply by choosing one rate to define a master timescale, and normalizing the others by that master rate. The sum of the respiration and upwelling rates, $r + \lambda_0$, describes the non-sinking fraction of surface particle loss, and proves to be a convenient choice for the master rate.
With the master rate chosen as \( r + \lambda_0 \), the normalized sinking rate \( \tilde{s} = s/(r + \lambda_0) \) represents the ratio of sinking to non-sinking fractions of surface particle loss, while the steady-state bottom-oxygen drawdown \( (3.4) \) becomes

\[
\overline{\Delta O_{bot}} = \frac{\delta (1 + \Lambda)^2 \tilde{s}^2}{\Lambda + (1 + \Lambda)(1 + \delta \Lambda)\tilde{s}} \left( 1 - \frac{\bar{p}K_s}{\bar{\alpha}} \right) \frac{N_s}{N_*},
\]

where \( \Lambda = \lambda_0/r, \ (\bar{p}, \bar{\alpha}) = (p, \alpha)/(r + \lambda_0), \) and \( K_* \) and \( N_* \) as in \((3.5)\). Thus, \( \overline{\Delta O_{bot}} \) is seen to depend only on \( \delta, K_* \) and the three relative rate parameters \( \Lambda, \tilde{s} \) and \( \bar{p} \) (with \( \bar{\alpha} = \bar{p} - 1 - \tilde{s} \) and \( N_* = 1 - K_* \)), as well as on \( N_s \).

An immediate consequence of this scaling is that summary figures identical to Fig. 8, but expressed now in terms of the scaled production and sinking rates, \( \bar{p} \) and \( \tilde{s} \), can be seen to apply for all systems with the same values of \( \Lambda, \delta \) and \( K \). That is, the dependence of oxygen drawdown and exponential drawdown timescale on the biogeochemical parameters \( p \) and \( s \) can be determined from Fig. 8 for all systems that have the same ratio of upwelling to respiration rates (fixed \( \Lambda = \lambda_0/r; \) and also fixed \( \delta \) and \( K \)) by converting the dimensional \( p \) and \( s \) to their equivalent scaled values \( \bar{p} \) and \( \tilde{s} \). The net accumulation rate \( \alpha \) may be used in place of the intrinsic production rate \( p \) in these summary figures, and \( \bar{\alpha} = \alpha/(r + \lambda_0) \) can be used in place of \( \bar{p} \) (Fig. 9). The scaled exponential drawdown timescale \( \tilde{t}_{exp} = (r + \lambda_0)t_{exp} \) is also a function only of the scaled rates, and consequently the entire summary figure can be seen to be a function only of the scaled rates (and \( \Lambda, \delta \) and \( K \)). The dependence on \( K \) is more apparent in this comparison, as is the lengthening of the exponential timescale for small \( \tilde{\alpha} \).

It follows immediately from this scaling and from Fig. 9 that, for \( \delta = 1/3 \) and \( \Lambda = 0.5 \) (and for both the FP and SP values of \( K_* \)), the critical sinking rate for susceptibility to hypoxia
(anoxia) is $\tilde{s} \approx 1$: for $\tilde{s} < 1$, the system can never reach anoxia, even for arbitrarily long upwelling seasons, while for $\tilde{s} > 1$, hypoxia (anoxia) is possible if the exponential timescale for drawdown is sufficiently short. This result implies that for these parameters, the hypoxic (anoxic) threshold is reached when the sinking fraction of particle loss is approximately equal to the non-sinking fraction of particle loss, i.e., $s \approx r + \lambda_0$. It is for this reason that the critical value of $s$ for the FP and SP values $r = 0.2 \text{ d}^{-1}$ and $\lambda_0 = 0.1 \text{ d}^{-1}$ was seen to be $s \approx 0.3 \text{ d}^{-1}$ (Fig. 8). The dimensional timescale $t_{exp}$ is equal to the product of the normalized timescale $\tilde{t}_{exp}$ and the non-sinking loss fraction timescale $1/(r + \lambda_0)$, so, in general, the dimensional drawdown timescale will be shorter when $r + \lambda_0$ is larger.

Thus, for values of $\Lambda$, $\delta$, $K_*$, and $N_s$ as in the FP and SP cases, and for $\Delta O_{hyp}$ equal to the nominal offshore oxygen level $O_s = 100 \text{ mmol m}^{-3}$, the transition toward anoxic steady states – or high potential for bottom oxygen depletion – occurs for $\tilde{s} \approx 0.5 - 1.0$, provided that $\tilde{\alpha} > 0.1 - 0.2$ (Fig. 8). These values of normalized sinking rate correspond to dimensional sinking rates that are comparable to the sum of the respiration and upwelling shelf flushing rates. For smaller sinking rates, the system can never reach anoxia, even for arbitrarily long upwelling seasons. Typically, $\tilde{t}_{exp} \approx 10$ for $\tilde{\alpha} \approx 0.25$ (Fig. 9); thus, if the dimensional net saturated production rate $\alpha = p - r - s - \lambda_0$ is at least one-fourth the sum $r + \lambda_0$ of the respiration and upwelling rates, the dimensional time to hypoxia will be of order $10/(r + \lambda_0)$ or less. The latter will in turn be less than 100 d if the sum of the respiration and upwelling rates is greater than $0.1 \text{ d}^{-1}$, as it is for the value of $r + \lambda_0$ for FP and SP ($0.3 \text{ d}^{-1}$). This implies that hypoxia can be reached within the upwelling season even with relatively small net saturated particle
production rates $\alpha \approx 0.03 \text{ d}^{-1}$, if the physical forcing is relatively steady and sinking rates are large enough. Fluctuations in the amplitude of the upwelling forcing can systematically reduce the potential for oxygen depletion below these steady state estimates, especially when sinking rates are large or forcing is strong (see Discussion).

### 3.3.2 Optimal sinking and susceptibility to hypoxia

Additional progress toward a more general characterization of susceptibility to hypoxia within this modeling framework can be made by restricting attention to solutions with values of $\bar{s} = s / (r + \lambda_0)$ for which the steady-state oxygen drawdown $\overline{\Delta O_{bot}}$ is maximum, with all other parameters held fixed. Previously we found that the bottom steady state oxygen drawdown is maximized for a value of the settling rate $s$ that is close to $s_*$, the maximum settling rate for steady-states with particle accumulation, and defined this value as the optimal sinking rate $s_{opt}$. In general, the corresponding maximal oxygen drawdown $\overline{\Delta O_{bot}}(s_{opt})$ that is obtained for the optimal sinking rate proves to be a useful proxy for the drawdown over a much wider range of $s$: typically, the drawdown is half or more of the maximal drawdown over roughly half of the full range $0 < s < s_*$ of settling rates that support particle concentration growth. For example, when $s$ is varied while other parameters are held fixed as in the FP or SP example, drawdowns of over 100 mmol m$^{-3}$ and over 15 mmol m$^{-3}$ respectively, roughly half the maximal values at the corresponding values of $s_{opt}$, are obtained throughout the respective ranges $0.25 < s < 0.75 \approx s_*$ and $0.06 < s < 0.13 \approx s_*$ (Fig. 6ab).

The optimal $s$ is the sinking rate $s_{opt}$ that gives the maximal value of $\overline{\Delta O_{bot}}$ in (3.4),

31
under variations of $s$ with all other parameters fixed, and can be accurately approximated as (see Appendix)

$$
\tilde{s}_{\text{opt}} = \tilde{s}_{\text{max}} \left[ 1 - \left( \frac{\tilde{p} K_s}{\tilde{s}_{\text{max}}} \right)^{1/2} \right] = \tilde{p} - 1 - [(\tilde{p} - 1)\tilde{p} K_s]^{1/2},
$$

(3.12)

where $s_{\text{max}} = p - r - s$ is the maximum sinking rate for surface particle accumulation ($\alpha > 0$). This optimal sinking rate depends only on $\tilde{p}$ and $K_s$; it does not depend on $\delta$, $\Lambda$, or $N_s$. An optimal net accumulation rate can be obtained from (3.12),

$$
\tilde{\alpha}_{\text{opt}} = \tilde{\alpha} - 1 - \tilde{s}_{\text{opt}} = [(\tilde{p} - 1)\tilde{p} K_s]^{1/2}.
$$

(3.13)

This is the net accumulation rate that the system exhibits at the optimal sinking rate $\tilde{s}_{\text{opt}}$.

Both the optimal sinking rate $\tilde{s}_{\text{opt}}$ and the net production rate $\tilde{\alpha}$ increase monotonically with $\tilde{p}$, for any $K$ with $0.02 < K < 2 \text{ mmol m}^{-3}$ (Fig. 10). It was seen above that, when other parameters are held fixed, increasing the production rate $p$ had little effect on oxygen drawdown potential. However, changes in $p$ can affect the drawdown indirectly, by supporting growth for larger sinking rates $s$. The near linear increase of $\tilde{s}_{\text{opt}}$ with $\tilde{p}$ reveals again the primary role that intrinsic productivity plays in controlling the system’s susceptibility to hypoxia: it sets the maximum sinking velocity that can be supported without shutting down production. The accumulation rate $\tilde{\alpha}_{\text{opt}}$ also increases, with $\tilde{p}$. The dependencies of $\tilde{s}_{\text{opt}}$ and $\tilde{\alpha}_{\text{opt}}$ on $K_s$ are opposite, with the former decreasing and the latter increasing with $K_s$. Thus, a system with smaller $K$ will support a larger optimal sinking rate, with a smaller corresponding net accumulation rate, than an otherwise identical system with larger $K$. The primary dependence revealed by this analysis, however, is the indirect control of drawdown potential by the production rate $p$ (or $\tilde{p}$), through its effect on allowable sinking rates.
3.3.3 Oxygen drawdown dependence on δ and K

The optimal sinking rate $\tilde{s}_{opt}$ can be substituted into (3.4) to obtain the corresponding maximal oxygen drawdown value $\Delta O_{\text{bot}}(s_{opt})$ for given values of $\tilde{\rho}$ and $K_s$. With the dependence on $s$ removed in this way, attention can be focused on the dependence of the steady-state response on the remaining parameters, $\Lambda$ and $\delta$. For the FP values of $\tilde{\rho}$ and $K$, increasing $\delta$ past 0.5 gives uniformly large steady-state oxygen drawdowns, regardless of the value of $\Lambda$; small oxygen drawdowns are obtained only for small $\delta$ (Fig. 11a). The corresponding exponential drawdown timescales are all short, and shorter for small $\Lambda$ than for large $\Lambda$. For the SP values of $\tilde{\rho}$ and $K$, increasing $\delta$ past 1.0 gives potentially anoxic steady-state oxygen drawdowns, especially for small $\Lambda$ (Fig. 11b). However, the corresponding exponential drawdown timescales are all relatively long ($\tilde{t}_{\text{exp}} > 45$); for example, for $r + \lambda_0 = 0.3 \text{ d}^{-1}$, they are longer than the nominal 150-day upwelling season length.

3.3.4 General criteria for hypoxic susceptibility

Scaling time by $(r + \lambda_0)^{-1}$ and setting $\tilde{s} = \tilde{s}_{opt}$ removes two of the six independent parameters that remain after the proportionality of $\Delta O_{\text{bot}}$ to $N_s$ is recognized, leaving the four parameters $\tilde{\rho}, \delta, \Lambda$ and $K_s$. The dependence of the maximal oxygen drawdown $\Delta O_{\text{bot}}(s_{opt})$ on $\Lambda$ can then be examined for fixed $\tilde{\rho}, \delta$ and $K_s$. This approach yields two simple criteria on $\tilde{\rho}$ that broadly express the susceptibility to hypoxia as functions of the two remaining parameters, $\delta$ and $K_s$. Consequently, each of these criteria can be completely summarized in a single contour plot. The result is a compact description of the intrinsic susceptibility of a given system to
hypoxia, which assumes only that the steady-state bottom-oxygen drawdown is comparable to
that obtained at the optimal sinking rate.

The criteria show that the susceptibility to hypoxia depends on the values of two con-
stants, \( P \) and \( P' \), relative to the ratio \( \tilde{\rho} = p/(r + \lambda_0) \) of the production rate to the sum of
respiration and upwelling rates. For a given oxygen drawdown value \( \Delta O_{hyp} \) that is speci-
fied as the hypoxic level, these constants divide the steady-state response into three regimes
(Fig. 10a): if \( \tilde{\rho} < P \), then the steady-state response will not be hypoxic; if \( P < \tilde{\rho} < P' \), then
hypoxic steady states occur for some sinking rates and some values of the ratio \( \Lambda = \lambda_0/r \) of
upwelling and respiration timescales; and if \( \tilde{\rho} \geq P' \), then all steady states with sinking rate
equal to the optimal rate \( s_{opt} \) are hypoxic, regardless of the value of \( \Lambda \):

\[
\begin{align*}
\tilde{\rho} < P & : \text{ no hypoxic steady states exist} \quad (3.14) \\
P \leq \tilde{\rho} < P' & : \text{ hypoxic steady states exist} \quad (3.15) \\
\tilde{\rho} \geq P' & : \text{ all } s = s_{opt} \text{ steady states are hypoxic.} \quad (3.16)
\end{align*}
\]

From (3.13), the criteria may be expressed also in terms of critical values \( P_{\tilde{\alpha}} \) and \( P'_{\tilde{\alpha}} \) of \( \tilde{\alpha} \),
where

\[
P_{\tilde{\alpha}} = \left[ (P - 1)PK_s \right]^{1/2}, \quad P'_{\tilde{\alpha}} = \left[ (P' - 1)P'K_s \right]^{1/2},
\]

and a set of inequalities similar to (3.14)–(3.16) apply to \( \tilde{\alpha} \) (Fig. 10b). For simplicity, we
take \( \Delta O_{hyp} = O_s = 100 \text{ mmol m}^{-3} \), so that the hypoxic level corresponds to anoxia, but for
generality we continue to refer to the criteria in terms of hypoxia rather than anoxia.

The criteria for hypoxic susceptibility (3.14)–(3.16) indicate that the potential for high
levels of oxygen drawdown in the steady states is generally favored for rapid production (large
slow remineralization (low \( r \)) and slow upwelling (small \( \lambda_0 \)), which will yield relatively large normalized growth parameters \( \tilde{p} = p/(r + \lambda_0) \) that will be more likely to satisfy the corresponding inequalities. Additionally, the potential for hypoxia increases as the constants \( P \) and \( P' \) decrease toward unity, reducing the value of \( \tilde{p} \) that will satisfy the criteria: the minimal value of \( \tilde{p} \) for steady-state growth is \( \tilde{p} = \tilde{p}_s = 1/N_s \approx 1 + K_s \approx 1 \), so when \( P = 1 \) or \( P' = 1 \), all values of \( \tilde{p} \) that support growth will satisfy the corresponding criteria. Note that only the sum \( r + \lambda_0 = p - s_{\text{max}} \) enters into these criteria, not \( \lambda_0 \) and \( r \) separately, which effectively couples, or entangles, the physical and biogeochemical controls. For the SP and FP values of \( \delta, K, N_s \) (Table 2) and for \( \Delta O_{\text{hyp}} = 100 \text{ mmol m}^{-3} \), the values of \( (P, P') \) are \((1.54, 2.39)\) for FP and \((1.40, 2.12)\) for SP, while the values of \( \tilde{p} \) are 3.67 for FP and 1.50 for SP (Table 3). Thus, the strictest inequality (3.16) is easily satisfied for the FP values, while the weaker inequality (3.15) is narrowly satisfied for the SP values (Fig. 10). Although neither the SP nor the FP value of the sinking rate \( s \) is equal to the corresponding optimal rate \( s_{\text{opt}} \), it can therefore be inferred from the criteria (3.14)-(3.16) that the drawdown for FP is likely to be sufficient to produce an anoxic steady state (for \( O_s = 100 \)), while that for SP is much less likely to be sufficient to produce anoxia.

Expressions for the two dimensionless constants \( P \) and \( P' \), based on the approximation (3.12) are provided in the Appendix. For fixed ratios \( \Delta O_{\text{hyp}}/N_s \), these constants depend only on \( \delta \) and \( K_s \), with both \( P \) and \( P' \) decreasing with decreasing \( K_s \) and with increasing \( \delta \), except for \( \delta < 1 \), where \( P \) is independent of \( \delta \) (Fig. 13; see also Fig. 10b). States with \( \Lambda \approx 1 \) tend not to be optimally hypoxic: the most-hypoxic steady states are reached as \( \Lambda \to \infty \) for
δ < 1, and as Λ → 0 for δ > 1 (Fig. 11). In addition, they are based on the optimal sinking assumption, whereas general sinking rates will tend to be sub-optimal. For these reasons, the criteria (3.14)–(3.16) will in general imply stricter limits on ˜p and a greater degree of hypoxic susceptibility than is likely to be realized. For example, the actual transition to hypoxia for Λ and (δ, K∗) as in the FP and SP examples occurs near ˜p = P′ rather than ˜p = P (Fig. 9). These considerations provide additional motivation to regard the criteria obtained with ΔOhyp = Os as indicators for hypoxia, rather than anoxia.

The preceding analysis can be used to classify any upwelling system’s potential susceptibility for hypoxia. For a given system with given characteristic values of p, r, λ0, δ, and K∗, the normalized productivity ˜p may be computed and compared with the corresponding critical values P and P′, to provide a simple quantitative estimate of the system’s susceptibility to hypoxia. A subsequent estimate of the timescale to hypoxia, based on the analytical expression (3.9) can be made to determine whether a hypoxic state can be reached in a nominal upwelling season length.

4 Discussion

A maximally simple, coupled physical-biogeochemical box model has been used to examine carbon cycling and oxygen drawdown near the shelf bottom in eastern boundary upwelling systems. It was found possible to achieve a relatively complete characterization of the bottom oxygen depletion response in this model (Fig. 9). The major biogeochemical control on the overall potential susceptibility of the system was found to be the sinking rate s: for sufficiently
small sinking rates, the system can never reach hypoxia even for arbitrarily long upwelling seasons, while the critical sinking rate allowing the system to approach hypoxia is nearly independent of the net saturated production and accumulation rates, $\eta$ and $\alpha$. For sinking rates large enough that hypoxia could in principle be reached, the net saturated surface particle accumulation rate $\alpha$ (or, more precisely, the normalized rate $\tilde{\alpha} = \alpha/(r + \lambda_0)$) was found to be the major control on the timescale of approach to hypoxia: for sufficiently large accumulation rates, hypoxia can be reached in typical upwelling seasons, while for very small accumulation rates, the time to hypoxia can exceed the length of typical upwelling seasons, and hypoxia – although possible in principle – cannot be reached.

For both the steady state and exponential timescale analysis, oxygen drawdown decreases with stronger upwelling forcing (Figs. 5, 7). More specifically, in order for severe hypoxia to potentially occur (a drawdown of 100 mmol/m$^3$, or $\approx 2.25$ ml/L), the sinking rate must be greater than the sum of the remineralization and upwelling rates ($s > r + \lambda_0$). Thus if the forcing parameter $\lambda_0$ is made larger, either by stronger upwelling forcing or for a narrow shelf, sinking must be more rapid for hypoxia to potentially occur, even under arbitrarily long upwelling seasons. Additionally, if hypoxia can occur and the system is forced sufficiently to overcome nutrient limitation, then the timescale to get to a hypoxic state lengthens with increased forcing, since particle production is shunted off-shelf, particle accumulation decreases (smaller $\alpha$), in turn lightening the remineralization load at depth, slowing oxygen drawdown. Together these results suggest that if upwelling winds intensify with climate change (Sydeman et al. 2014; Bakun et al. 2015), the increased forcing could offer a mitigating effect on future
coastal deoxygenation events, even as the oxygen levels in upwelled source waters decline (Doney et al. 2012; Bakun et al. 2015).

Here we have restricted the forcing to be constant in time, while in reality upwelling is inherently intermittent during the upwelling season (Carr 1998; Bane et al. 2007). In this study the addition of an oscillatory component to the upwelling forcing, so that the system varies between strong and weak upwelling, can significantly reduce the potential for oxygen drawdown over the shelf relative to the constant forcing case, even when the cumulative mean upwelling is equivalent. For example, if the forcing in the FP case is modified to

$$\lambda(t) = \lambda_0 \left[1 - \cos(\omega t)\right],$$

(4.1)

so that upwelling oscillates between $2\lambda_0$ and zero, but the mean forcing over an upwelling period is still $\lambda_0$, then the steady state oxygen drawdown is reduced by over 50 mmol m$^{-3}$ (Fig. 14). This reduction is accomplished by moving upwelled nutrients and production off-shelf, so that export to depth over the shelf is diminished, reducing oxygen drawdown. Production can be shunted off-shelf under variable forcing in two possible ways: either by a matching of the surface particle combined growth and decay timescale with the upwelling period, or with forcing faster than the net surface particle production rate for a significant duration of the upwelling period ($\lambda > \eta$ so that $\alpha < 0$). In both cases there is a correlation of strong forcing with high surface nutrient levels, enhancing off-shelf nutrient loss (e.g., Fig. 14d), reducing the fraction of nutrients retained and converted to sinking particles that may subsequently deplete bottom oxygen. Details of this effect, and the role of retention in controlling oxygen drawdown, are presented in detail in Harrison et al (in prep.).
The analytical characterization of the physical-biogeochemical upwelling system made here is possible only because of the many simplifications and idealizations in the model formulation. Some aspects of the response of a more generalized model have been explored, including the effects of elevated subsurface sinking rates \((\delta > 1/3 \text{ or } \delta_S > 1)\), upwelling through the middle box, and upwelling of particles from the bottom box (Appendix). Fast subsurface sinking, achieved for example through particle aggregation (Alldredge and Gotschalk 1989; Karaka et al. 2009), increases particle flux to the bottom layer by reducing particle respiration loss in the middle box, resulting in enhanced remineralization and oxygen depletion in the bottom box, thus increasing both the rate and amplitude of bottom oxygen depletion there. In this way a small change in the surface export rate can be compensated by increased subsurface sinking to achieve a similar level of oxygen drawdown at depth. Middle-box nutrient upwelling results in less flushing of the bottom box with offshore oxygen, and similarly enhances oxygen depletion (Sec. A.5). The role of the depth of return flow in controlling the development of hypoxia may be relevant in comparisons of oxygen depletion in different upwelling systems, where higher rates of mid-depth return flow have been observed, for example, in Oregon and Peru relative to California and NW Africa (Smith 1981; Lentz and Chapman 2004), and also across all upwelling systems, since source water depth may shallow over the upwelling season, driven by changes in thermocline structure (Jacox and Edwards 2011; Peterson et al. 2013). Upwelling of productively active particles from the bottom box, for example representing upwelling of diatom resting spores (Smetacek 1985), affect the potential for hypoxia similarly to reducing the settling rate \(s\), so that growth of surface particles
$C_{top}$ can continue for much greater rates of surface export (Sec. A.5). A non-uniform respiration rate (larger $r$ in the surface box) can be approximately simulated by modifying the production rate $p$ accordingly, so that when the difference $p - r$ maintains the same value, the potential for hypoxia is largely unchanged; this interpretation can be improved by also modifying the effective rate constant $K$ (Sec. A.6).

Many other influences on oxygen drawdown, including effects of three-dimensional circulation and downwelling, and all the many complications of the biological and chemical transformations that are implicit in the model conversions between nutrients and particles, cannot be addressed within the framework of the present model, and require more sophisticated approaches with substantially more complex models. Achieving a similar level of general understanding of these more complex models remains an outstanding scientific challenge. The present work is intended as a preliminary step toward that broader understanding.

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A Appendix

A.1 Middle-box particle concentration

The equation for the middle-box particle concentration is:

\[ \frac{dC'_\text{mid}}{dt} = -rC'_\text{mid} - s'C'_\text{mid} + s'C_{\text{top}} \quad \text{where} \quad C'_\text{mid} = \delta S C_{\text{mid}}, \quad (A.1) \]

where \( s' = S'/H_{\text{mid}} \) is the subsurface sinking speed scaled by the height of the middle box \( H_{\text{mid}} \).

It is convenient to use here the scaled concentration \( C'_\text{mid} = \delta S C_{\text{mid}} \), because the box thickness ratio \( \delta_H = H/H_{\text{mid}} \) then enters the model equations only through the ratio \( \delta \). Multiplication of (A.1) by the integrating factor \( \exp[-(r + s')t] \) and integration, using \( C'_{\text{mid}}(0) = 0 \) and \( E_{\text{bot}} = s'C_{\text{mid}} \), then gives (2.8) directly. The steady solutions for \( C'_\text{mid} \) and \( E_{\text{bot}} \) may be obtained either by setting the time-derivative equal to zero in (A.1) or letting \( t \to \infty \) in (2.8). The equations (A.1) and \( E_{\text{bot}} = s'C_{\text{mid}} \) can be convenient to retain in place of (2.8) for numerical solution.

For an impulsive sinking flux from the top box \( E_{\text{top}}(t) = sC_{\text{top}} = E_0 \delta_D(t - t_0) \) at \( t = t_0 \), where here \( \delta_D \) is the Dirac-\( \delta \) impulse function, the incoming sinking flux to the bottom is \( E_{\text{bot}}(t > t_0) = s'E_0 \exp[-(r + s')(t - t_0)] \) and its total time-integral is \( \int_0^\infty E_{\text{bot}}(t) \, dt = E_0/(1 + r/s') \), illustrating that attenuation of the sinking flux from the top to the bottom boxes is largest for large \( r \) and small \( s' \).

A.2 Parameter dependence of \( t_{\text{exp}} \) constant \( G \)

The constant \( G(p, r, s, \lambda_0, \delta) \) in (3.7)-(3.10) is:

\[ G(p, r, s, \lambda_0, \delta) = \frac{(p - r - s)(p - s - \lambda_0)(p - s - \lambda_0 + \delta s)}{\delta rs^2}. \quad (A.2) \]
With \( p \) replaced by \( \eta = p - r - s \), this may be written equivalently as:

\[
G(\eta, r, s, \lambda_0, \delta) = \frac{\eta(\alpha + r)(\alpha + r + \delta s)}{\delta rs^2}. \tag{A.3}
\]

### A.3 Steady states

The explicit (non-trivial) steady state solutions of (2.3)–(2.7) and (2.8) [with (A.1) and \( E_{bot} = s'C_{mid} \)] are:

\[
\Delta O_{bot} = \nu r \gamma \lambda_0 C_{bot}, \tag{A.4}
\]

\[
\overline{C}_{top} = \frac{(r + \delta s)\lambda_0 \gamma}{r s + (r + \delta s)\lambda_0} (N_s - N_{top}) \tag{A.5}
\]

\[
\overline{C}_{mid} = \frac{\delta s}{r + \delta s} \overline{C}_{top} \tag{A.6}
\]

\[
\overline{C}_{bot} = \frac{s}{r} \overline{C}_{mid} \tag{A.7}
\]

\[
N_{top} = \frac{r + s + \lambda_0}{p - r - s - \lambda_0} K = \frac{p - \alpha}{\alpha} K \tag{A.8}
\]

\[
N_{bot} = N_s + \frac{r}{\lambda_0 \gamma} \overline{C}_{bot}, \tag{A.9}
\]

From (A.5), it follows that \( N_{top} < N_s \) for all states with \( \overline{C}_{top} > 0 \). Note that the exponential growth rate \( \alpha \) from the analysis of the initial transient response appears again in (A.8). In (A.5), from (A.8)-(A.9),

\[
N_s - N_{top} = \left(1 - \frac{pK_s}{\alpha}\right)(1 + K_s)N_s, \tag{A.10}
\]

so that \( N_{top} = N_s \) and \( \overline{C}_{top} = \overline{C}_{mid} = \overline{C}_{bot} = 0 \) when \( pK_s = \alpha \), or \( s = s^* \). The quantities \( N_s = N_s/(K+N_s) \) and \( K_s = K/(K+N_s) = 1 - N_s \) may be regarded as dimensionless saturated-growth and growth-limitation nutrient levels, respectively, computed from \( N_s \) and \( K \). In general, \( K \ll N_s \), so that \( K_s \ll 1 \) and \( N_s \approx 1 \).
A.4 Optimal sinking

The special steady solution at which $\overline{\Delta O}$, $\overline{N_{bot}}$ and $\overline{C_{bot}}$ are maximum (i.e., where $d\overline{\Delta O}/ds = d\overline{N_{bot}}/ds = d\overline{C_{bot}}/ds = 0$, with all other parameters fixed) can be obtained as a solution $s = s_{opt}$ of the cubic equation

$$s^3 + as^2 + bs + c = 0,$$

(A.11)

where

$$a = 2(\lambda_0 R - s_{max}), \quad b = s_{*}s_{max} - \lambda_0 R (s_{*} + 3s_{max}), \quad c = 2\lambda_0 R s_{*}s_{max},$$

(A.12)

and

$$R = \frac{r}{r + \delta \lambda_0} = \frac{1}{1 + \delta \Lambda}. \quad \text{(A.13)}$$

To obtain the cubic equation (A.11), it is helpful to use (3.4) or to write the solution for $\overline{C_{bot}}$ in the form

$$\overline{C_{bot}} = \frac{\delta \lambda_0 (K + N_s) R}{r^2} \frac{s^2(s_{*} - s)}{(s + \lambda_0 R)(s_{max} - s)}. \quad \text{(A.14)}$$

The cubic equation (A.11) can be written,

$$s^3 + as^2 + bs + c = (s^2 - 2s_{max}s + s_{*}s_{max})(s + 2\lambda_0 R + \lambda_0 R p K_s), \quad \text{(A.15)}$$

where $p K_s = s_{max} - s_{*}$. For $\lambda_0 R p K_s$ sufficiently small (for example, if $N_s \gg K$), a solution of the quadratic part of (A.15) gives the approximation (3.12) for $s_{opt}$. This solution for $s_{opt}$ may be substituted into (A.14) and (A.9) to obtain the corresponding estimates of the maximum
values $\bar{C}_{\text{bot, max}}$ and $\bar{N}_{\text{bot, max}}$ of the steady $\bar{C}_{\text{bot}}$ and $\bar{N}_{\text{bot}}$,

\[
\bar{C}_{\text{bot, max}} \approx \frac{\lambda_0 \gamma \delta (K + N_s) R}{r^2} \frac{s_{\text{opt}}^3}{(s_{\text{opt}} + \lambda_0 R) s_{\text{max}}} \tag{A.16}
\]

\[
\bar{N}_{\text{bot, max}} \approx N_s + \frac{\delta (K + N_s) R}{\phi_B R} \frac{s_{\text{opt}}^3}{(s_{\text{opt}} + \lambda_0 R) s_{\text{max}}} \tag{A.17}
\]

where the maxima have been taken with respect to $s$ while holding other parameters fixed. Here it has been used that the approximate value $s_{\text{opt}}$ satisfies

\[
\left( s^* - s_{\text{opt}} \right) / \left( s_{\text{max}} - s_{\text{opt}} \right) = s_{\text{opt}} / s_{\text{max}}. \tag{s}
\]

The steady states with $\Delta \bar{O}_{\text{bot}} = \Delta O_{\text{hyp}}$ at the optimal sinking rate $s = s_{\text{opt}}$ satisfy

\[
\Delta O_{\text{hyp}} \approx \frac{\nu \lambda_0 \delta (K + N_s) R}{r \lambda_0} \frac{s_{\text{opt}}^3}{(s_{\text{opt}} + \lambda_0 R) s_{\text{max}}}. \tag{A.18}
\]

The sinking rate $s_{\text{opt}}$ is optimal over $s$ for fixed $r$ and $\lambda_0$. For fixed $p$ and $s_{\text{max}}$, the optimal $r$ can be found by substituting $\lambda_0 = p - s_{\text{max}} - r$ in (A.18) and optimizing over $r$. Then $\Delta O_{\text{hyp}} \propto 1/F(r)$, where

\[
F(r) = \delta s_{\text{opt}} (p - s_{\text{max}}) + [p - s_{\text{max}} + (1 - \delta)s_{\text{opt}}] r - r^2. \tag{A.19}
\]

For steady-state hypoxic drawdown $\Delta O_{\text{hyp}} > 0$, $F(r) > 0$ is required, and because $d^2 F / dr^2 < 0$, the maximum value of $\Delta O_{\text{hyp}}$ must obtain at one of the endpoints $r = \{0, p - s_{\text{max}}\}$, while the minimum value may obtain at the point $r = r_q = [p - s_{\text{max}} + (1 - \delta)s_{\text{opt}}]/2$, where $dF / dr = 0$, provided that $0 < r_q < p - s_{\text{max}}$. The values of $F(r)$ at these three points are

\[
F(0) = \delta s_{\text{opt}} (p - s_{\text{max}}) \tag{A.20}
\]

\[
F(r_q) = \delta s_{\text{opt}} (p - s_{\text{max}}) + \frac{1}{4} [p - s_{\text{max}} + (1 - \delta)s_{\text{opt}}]^2 \tag{A.21}
\]

\[
F(p - s_{\text{max}}) = s_{\text{opt}} (p - s_{\text{max}}). \tag{A.22}
\]
Thus, the minimum of $F$ and the maximum of $\Delta O_{hyp} \propto 1/F$ are at $r = 0$ for $\delta < 1$, and at $r = p - s_{max}$ for $\delta > 1$. The resulting sufficient condition for the existence of anoxic states (for some $r$, with fixed $p - s_{max}$ and $s = s_{opt}$) is

$$p - s_{max} = r + \lambda_0 \leq p/P, \quad \text{(A.23)}$$

where, for $\delta < 1$,

$$P = \frac{\xi^2}{\xi^2 - 1}, \quad \xi = \frac{(1 + N_s A)^{1/2} - K_s^{1/2}A}{1 - K_s A}, \quad A = \frac{\nu(K + N_s)}{\Delta O_{hyp}}. \quad \text{(A.24)}$$

Conversely, a sufficient condition for the non-existence of anoxic steady states is

$$p - s_{max} = r + \lambda_0 > p/P. \quad \text{(A.25)}$$

For $\delta > 1$, $A$ is replaced by $\delta A$ in the definition of $P$:

$$P = \frac{\xi^2_{\delta}}{\xi^2_{\delta} - 1}, \quad \xi_{\delta} = \frac{(1 + N_s \delta A)^{1/2} - K_s^{1/2}A}{1 - K_s A}. \quad \text{(A.26)}$$

Thus, the expression for the optimal criterion constant $P$ in (3.15) is:

$$P = \frac{\xi^2}{\xi^2 - 1}, \quad \xi = \frac{(1 + N_s A\delta)^{1/2} - K_s^{1/2}A\delta}{1 - K_s A\delta}, \quad A_\delta = \max\{1, \delta\}A. \quad \text{(A.27)}$$

Substituting $r = r_q$ into (A.19) and (A.18) gives a quartic in the variable $q = (p/s_{max})^{1/2}$, one solution of which gives the condition (3.16)

$$p - s_{max} = r + \lambda_0 \leq p/P' \quad \text{(or} \quad p - s_{max} = r + \lambda_0 > p/P') \quad \text{(A.28)}$$

analogous to (A.23) and (A.25) that describes the regions where hypoxic states do (or do not) exist for $r = r_q$, and therefore for any $r$, since $r_q$ is the least hypoxic $r$ for the given $p$, $s_{max}$. 45
and optimal sinking $s_{opt}$. The quartic equation for $q$ is

$$q^4 + a_q q^3 + b_q q^2 + c_q q + d_q = 0,$$

where

$$a_q = 2K^* \frac{1}{2}[2K^* \delta A - (1 + \delta)]$$

$$b_q = 2\delta + K^*(1 - \delta)^2 - 12K^* \delta A$$

$$c_q = 2K^* \frac{1}{2} \delta (3 - \delta + 6A)$$

$$d_q = 1 - 2(1 + \delta) + (1 - \delta)^2 - 4\delta A,$$

and $A$ is defined in (A.27). A solution $q = \xi$ of a quadratic equation in the same variable $q$ is the origin of the previous conditions (A.23) and (A.25). The additional special steady state with $C_{top} = C_{bot}$ occurs when $s = s_{bt}$, where

$$s_{bt} = \frac{r}{2} \left[ 1 + \left( 1 + \frac{4}{\delta} \right)^{1/2} \right].$$

**A.5 Upwelling of $C_{bot}$ ($\beta > 0$) or $N_{mid}$ ($\phi_M > 0$)**

The model equations may be modified to allow upwelling of particles from the bottom to the top box, through a term proportional to the bottom-box particle concentration $C_{bot}$, the shelf flushing rate $\lambda$, and a dimensionless parameter $\beta$ that controls the fraction of bottom particles
to be upwelled:

\[
\frac{dC_{\text{top}}}{dt} = \left( \frac{pN_{\text{top}}}{K + N_{\text{top}}} - r \right) C_{\text{top}} - sC_{\text{top}} - \lambda C_{\text{top}} + \beta \lambda C_{\text{bot}} \quad \text{(A.35)}
\]

Middle:

\[
C_{\text{mid}} = \frac{1}{\delta s} C'_{\text{mid}} \quad \text{where} \quad \frac{dC'_{\text{mid}}}{dt} = -rC'_{\text{mid}} - s' C'_{\text{mid}} + s' C_{\text{top}} \quad \text{(A.36)}
\]

Bottom:

\[
\frac{dC_{\text{bot}}}{dt} = -rC_{\text{bot}} + sC'_{\text{mid}} - \beta \lambda C_{\text{bot}}. \quad \text{(A.37)}
\]

For \( \beta = 1 \), the steady-state equations (A.7) and (A.8) for \( \overline{C}_{\text{bot}} \) and \( \overline{N}_{\text{top}} \) are modified to

\[
\overline{C}_{\text{bot}} = \frac{s}{r + \beta \lambda_0} \overline{C}_{\text{mid}} \quad \text{(A.38)}
\]

\[
\overline{N}_{\text{top}} = \left( \frac{p}{s_{\text{max}} - \Sigma} - 1 \right) K \quad \text{(A.39)}
\]

where

\[
\Sigma = s \left( 1 - \beta' \delta s r + \delta s \right), \quad \beta' = \frac{\beta \lambda_0}{r + \beta \lambda_0} \quad \text{(A.40)}
\]

while the other expressions in (A.4)–(A.9) are unchanged. Consequently, the qualitative structure of the solutions is similar to that obtained for \( \beta = 0 \), but the effective sinking rate \( \Sigma \) in (A.39) is reduced relative to \( s \) in (A.8). Thus, growth of \( C_{\text{top}} \) can be sustained for much larger values of \( s \) when \( \beta = 1 \), as the "no-growth" limit for \( s \) increases from \( s_\ast \) to \( s_\beta \), where

\[
s_\beta = \max \left\{ \frac{1}{2} \left( \frac{s_\ast - r/\delta}{1 - \beta'} \right) \left[ 1 \pm \left( 1 + \frac{4(1 - \beta')s_\ast r/\delta}{(s_\ast - r/\delta)^2} \right)^{1/2} \right] \right\}.
\quad \text{(A.41)}
\]

For FP and SP, \( s_\beta = \{1.54, 0.11\} \), respectively, relative to \( s_\ast = \{0.57, 0.10\} \).

If a fraction \( \phi_M > 0 \) of the upwelling volume flux is taken to come from the middle box, so that a reduced, complementary fraction \( \phi_B = 1 - \phi_M \) comes from the bottom box, there are two main effects on the system. First, the equation (2.3) for the bottom oxygen drawdown
is modified to

\[
\frac{d\Delta O_{\text{bot}}}{dt} = -\nu rP_{\text{bot}} - \lambda_0 \phi_B \Delta O_{\text{bot}},
\]

(A.42)

so that the flushing of bottom oxygen for a given value of \(\lambda_0\) is reduced by the factor \(\phi_B < 1\).

Second, the middle box receives and supplies, respectively, fractions \(\phi_M\) of the onshore and upward upwelling fluxes of nutrients, so that all three nutrient equations are modified, and the middle-box nutrient equation becomes coupled to the other variables:

**Top:**

\[
\frac{dN_{\text{top}}}{dt} = -\gamma^{-1} \left( \frac{pN_{\text{top}}}{K + N_{\text{top}}} - r \right) C_{\text{top}} + \lambda (\phi_B N_{\text{bot}} + \phi_M N_{\text{mid}} - N_{\text{top}})
\]

(A.43)

**Middle:**

\[
\frac{dN_{\text{mid}}}{dt} = \gamma^{-1} r C_{\text{mid}} + \lambda \phi_M (N_s - N_{\text{mid}})
\]

(A.44)

**Bottom:**

\[
\frac{dN_{\text{bot}}}{dt} = \gamma^{-1} r C_{\text{bot}} + \lambda \phi_B (N_s - N_{\text{bot}}).
\]

(A.45)

This also modifies the total nutrient budget, so that (2.9)-(2.10) are replaced by

\[
\mathcal{N} = LH \left[ (C_{\text{top}} + C_{\text{mid}}/\delta_H + C_{\text{bot}})/\gamma + N_{\text{top}} + N_{\text{mid}}/\delta_H + N_{\text{bot}} \right].
\]

(A.46)

and

\[
\frac{d\mathcal{N}}{dt} = LH \{ \lambda [N_s - (\gamma^{-1} C_{\text{top}} + N_{\text{top}})] \},
\]

(A.47)

as particle respiration or storage in the middle box no longer represents a loss of total model nutrient equivalent.

### A.6 \(p - r\) equivalence (large surface \(r\))

Suppose that a solution with given \((p, K, r)\) is also intended to represent a solution with the same subsurface \(r\) but a larger respiration rate \(\hat{r} = r + \delta r\) in the top box. Then for \(N_{\text{top}} \gg K\),
the same net difference $p - r$ of production and respiration is obtained if $p$ is replaced by $\hat{p} = p + \delta r$:

\[
p \frac{N_{\text{top}}}{K + N_{\text{top}}} - r \approx p - r; \quad (A.48)
\]

\[
\hat{p} \frac{N_{\text{top}}}{K + N_{\text{top}}} - \hat{r} = (p + \delta r) \frac{N_{\text{top}}}{K + N_{\text{top}}} - (r + \delta r) \quad (A.49)
\]

\[
\approx (p + \delta r) - (r + \delta r) = p - r. \quad (A.50)
\]

Thus, if $\delta r = 0.4$, for example, the FP and SP cases $(p, K, r) = \{(1.1, 1, 0.2), (0.45, 0.25, 0.2)\}$ can also represent $(\hat{p}, \hat{K}, \hat{r}) = \{(1.5, 1, 0.6), (0.85, 0.25, 0.6)\}$. This works well for $N_{\text{top}} \gg K$.

However, the two production-respiration differences are not the same in the range $N_{\text{top}} \approx K$, which is important for the steady-state response. Better agreement can be obtained if $K$ is also replaced by $\hat{K}$, where $\hat{K}$ is chosen to make the slopes agree for $N_{\text{top}} \gg K$:

\[
\frac{d}{dN_{\text{top}}} \left( p \frac{N_{\text{top}}}{K + N_{\text{top}}} - r \right)_{N_{\text{top}} \gg K} = \frac{d}{dN_{\text{top}}} \left( \hat{p} \frac{N_{\text{top}}}{\hat{K} + N_{\text{top}}} - \hat{r} \right)_{N_{\text{top}} \gg \hat{K}} \Rightarrow \hat{K} = \frac{p}{\hat{p}} K. \quad (A.51)
\]

Then the FP and SP cases can be more accurately taken also to represent, again with $\delta r = 0.4$ for example, $(\hat{p}, \hat{K}, \hat{r}) = \{(1.5, 0.73, 0.6), (0.85, 0.13, 0.6)\}$.

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Time Series of the Northeast Pacific.
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<th>Parameter</th>
<th>Value</th>
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<tr>
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<td>remineralization rate [d(^{-1})]</td>
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<tr>
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<td>shelf flushing rate [d(^{-1})]</td>
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<td>( \delta = s'/s )</td>
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<tr>
<td>( \delta_H = H/H_{mid} )</td>
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<td>source nutrient concentration [mmol m(^{-3})]</td>
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<td>( \Delta O_{hyp} )</td>
<td>{40,100}(^\dagger)</td>
<td>moderate and extreme hypoxia criteria [mmol m(^{-3})]</td>
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<tr>
<td>( H )</td>
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<td>top and bottom box height [m]</td>
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<tr>
<td>( L )</td>
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<td>( U_E = -\lambda_0 H L )</td>
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<tr>
<td>( \tau^v = \rho_0 f U_E )</td>
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<td>alongshore windstress [N m(^{-2})]</td>
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\(^\dagger\) 1 mL L\(^{-1}\) ≈ 44.7 mmol m\(^{-3}\)

\(^\ddagger\) \( \tau^v \) is computed using \( \rho_0 = 1025 \text{ kg m}^{-3} \) and \( f = 10^{-4} \text{ s}^{-1} \)
<table>
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<td>$P'$</td>
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Figure 1: Schematic of box model and total nutrient cycling. Upwelling favorable wind stress $\tau^y$ drives offshore surface transport, parameterized by $\lambda$, the inverse shelf-transit or volume-renewal time, a function of the wind stress, the shelf width $L$, and the depth of the surface and bottom layer $H$. Upwelling brings nutrients ($N$) to the surface, driving particle ($C$) production. Some of the upwelled nutrient flux is lost offshore ($\lambda N_{top}, \lambda C_{top}$), some exported to the bottom as sinking particle flux ($E_{bot}$), and some remineralized in the mid-watercolumn ($-rC_{mid}$). Offshore surface transport is compensated by onshore transport in the bottom box, bringing source nutrients ($N_s$) and oxygen ($O_s$) into the system.
Figure 2: Model solutions vs. time \( t \) (days) for fast growing, fast sinking parameter case FP. (a) Bottom oxygen drawdown \( \Delta O_{\text{bot}} \), with the exponential approximation (3.7; grey dash) and the hypoxic and anoxic levels \( \Delta O_{\text{hyp}} = \{40, 100\} \) (dotted). (b) Particle (POC) distributions: \( C_{\text{bot}} \) (solid), \( C_{\text{mid}} \) (dash-dot), \( C_{\text{top}} \) (dash). (c) Nutrient distributions: \( N_{\text{bot}} \) (solid), \( N_{\text{top}} \) (dash-dot), and total nutrients \( \mathcal{N} \) (2.9; grey). (d) Total nutrient flux budget (2.10) scaled by \( LH \): on-shelf flux \( (\lambda N_s; \text{blue}) \), surface POC loss \( (\lambda_0 C_{\text{top}}/\gamma; \text{green}) \), surface nutrient loss \( (\lambda_0 N_{\text{top}}; \text{yellow}) \), middle remineralization \( (-\frac{r C_{\text{mid}}}{\delta H \gamma}; \text{dash-dot}) \), sum \( ((LH)^{-1} d\mathcal{N}/dt; \text{grey}) \). Steady state values are shown at \( t = 150 \) d (large dots). The end of the exponential growth stage is marked by nutrient limitation \( (N_{\text{top}} < 5K, \text{vertical dotted lines}) \).
Figure 3: Model solutions as in Fig. 2, but for slow growing, slow sinking parameter case SP.
Figure 4: The ratio \( \frac{N_s - N_{top}}{K + N_s} = \left(1 - \frac{pK_s}{\alpha}\right) \) vs. \( p \), with \( \alpha = p - r - s - \lambda_0 \), for \( (r, \lambda_0) = (0.2, 0.1) \) d\(^{-1}\), \( \delta = 1/3 \) and \( N_s = 35 \) mmol m\(^{-3}\). The ratio is shown for \((p, s) = (1.1, 0.5)\) d\(^{-1}\) and \( K = 1 \) mmol m\(^{-3}\) (solid line) and \((p, s) = (0.45, 0.05)\) d\(^{-1}\) and \( K = 0.25 \) mmol m\(^{-3}\) (dashed), and the FP \((p = 1.1)\) and SP \((p = 0.45)\) example values are marked (large dot).
Figure 5: Steady state solutions vs. shelf transit rate $\lambda_0$ with other parameters as in the (left) FP and (right) SP cases. (a,b) Bottom oxygen drawdown $\Delta O_{\text{bot}}$, with the hypoxic/anoxic levels $\Delta O_{\text{hyp}} = \{40, 100\}$ indicated (dotted lines). (c,d) Particle (POC) distributions: $C_{\text{bot}}$ (solid), $C_{\text{mid}}$ (dash-dot), $C_{\text{top}}$ (dashed). (e,f) Nutrient distributions: $N_{\text{bot}}$ (solid), $N_{\text{top}}$ (dash-dot), and total nutrients $N$ (2.9; grey). (g,h) Total nutrient budget $(LH)^{-1}dN/dt$ with terms as in Fig. 2. The FP and SP ($\lambda_0 = 0.1 \text{ d}^{-1}$) steady state solutions (as in Figs. 2-3) are indicated (large dots).
Figure 6: Steady state solutions vs. \( s \) with other parameters as in the FP (left) and SP (right) cases, and panels otherwise as in Fig. 5. The FP \((s = 0.5)\) and SP \((s = 0.05)\) solutions are indicated (large dots). The quantities \( s_*, s_{bt} \), and the hypoxic-optimal values \( s_{opt}, \Delta O_{bot}(s_{opt}), C_{bot}(s_{opt}), N_{bot}(s_{opt}) \) are also indicated (dotted lines)
Figure 7: Timescale to moderate ($\Delta O = 40 \text{ mmol/m}^3$, grey) and extreme ($\Delta O = 100 \text{ mmol/m}^3$, black) hypoxia vs. forcing $\lambda_0$ (top) and sinking $s$ (bottom) rates for the FP case. Full model solutions are shown in solid lines, approximate exponential solutions in dashed. The basic exponential timescale $\alpha^{-1}$ is also shown (dotted).
Figure 8: Steady state bottom-oxygen values $O_{bot} = O_s - \Delta O_{bot}$ (mmol m$^{-3}$; contours) or estimated time to anoxia $t_{exp}$ (d; color) vs. $(p, s)$ (d$^{-1}$) for $O_s = 100$ mmol m$^{-3}$, $(r, \lambda_0) = (0.2, 0.1)$ d$^{-1}$, $\delta = 1/3$, $N_s = 35$ mmol m$^{-3}$ and (a) $K = 1$, (b) $K = 0.25$ mmol m$^{-3}$. $O_{bot}$ is shown where $\Delta O_{bot} < O_s$ and $t_{exp}$ is shown where $\Delta O_{bot} > O_s$. The FP and SP values of $(p, s)$ are indicated (black dots). The critical lines $s = s_* = pN_s - r - \lambda_0$ are also shown (solid); for $s > s_*$, there is no growth or retention ($C_{top} = C_{bot} = \Delta O_{bot} = 0$).
Figure 9: Steady state solutions $\overline{O}_{bot} = O_s - \Delta O_{bot}$ (mmol m$^{-3}$; contours) or estimated dimensionless time to anoxia $\tilde{t}_{exp} = (r + \lambda_0) t_{exp}$ (color) vs. $(\tilde{\alpha}, \tilde{s})$ for $O_s = 100$ mmol m$^{-3}$, $N_s = 35$ mmol m$^{-3}$, $(\delta, \Lambda) = (1/3, 0.5)$ and (a) $K_s = 0.028$, (b) $K_s = 0.007$. $O_{bot}$ is shown where $\Delta O_{bot} \leq O_s$ and $\tilde{t}_{exp}$ is shown where $\Delta O_{bot} > O_s$. The FP and SP values of $(\tilde{\alpha}, \tilde{s})$ are indicated (black dots). The critical lines $\tilde{s} = \tilde{s}_* = (N_s/K_s) \tilde{\alpha} - 1$ (solid) and $\tilde{s} = \tilde{s}_{opt}$ (dashed; blue: $\tilde{\alpha} < P_\alpha$, green: $P_\alpha < \tilde{\alpha} < P_\alpha'$, red: $\tilde{\alpha} > P_\alpha'$) are also shown. The dimensionless time $\tilde{t} = 45$ corresponds to 150 d for the FP and SP value of $r + \lambda_0 = 0.3$ d$^{-1}$. 
Figure 10: Optimal (a) sinking rate \( \bar{s} = \bar{s}_{\text{opt}} \) and (b) net accumulation rate \( \bar{\alpha}_{\text{opt}} = \bar{\rho} - 1 - \bar{s}_{\text{opt}} \) vs. \((\bar{\rho}, K_*)\). In both, the FP (black dot) and SP (white dot) values of \((\bar{\rho}, K_*)\) are indicated. The hypoxia criteria \( \bar{\rho} = P \) (green solid line) and \( \bar{\rho} = P' \) (red solid line) are shown and the corresponding regimes from (3.14)–(3.16) are indicated (white, green, red labels) for \( \delta = 1/3 \). In (b), the criteria are also shown for \( \delta = 5/3 \) (dotted green, red).
Figure 11: Steady-state oxygen drawdown $\Delta O_{\text{bot}}$ (mmol m$^{-3}$) at the optimal sinking rate $\tilde{s} = s_{\text{opt}}$ vs. ($\delta, \log_{10} \Lambda$), with $\tilde{p}$ and $K$ as for the (a) FP and (b) SP examples. The 100 mmol m$^{-3}$ contour (white) and the (a) FP and (b) SP values of ($\delta, \log_{10} \Lambda$) (white dot) are indicated.
Figure 12: Exponential drawdown timescale $\bar{t}_{\text{exp}}$ at the optimal sinking rate $\bar{s} = \bar{s}_{\text{opt}}$ vs. $(\delta, \log_{10} \Lambda)$, with $\bar{p}$ and $\bar{K}$ as for the (a) FP and (b) SP examples. The (a) FP and (b) SP values of $(\delta, \log_{10} \Lambda)$ (white dot) are indicated. For the FP and SP value $r + \lambda_0 = 0.3 \text{ d}^{-1}$, a nominal upwelling season length of 150 d corresponds to a dimensionless time $\bar{t} = 45$. 

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Figure 13: Steady-state hypoxia-criteria (3.14)–(3.16) constants (a) $P$ and (b) $P'$ vs. $(\delta, K_*)$. The FP and SP values of $(\delta, K_*)$ are indicated (black dots).
Figure 14: Solutions for FP as in Fig. 2 but for oscillatory forcing as in (4.1). The constant forcing steady state values (large dots at \( t = 150 \) d) and time-dependent solutions (thin) for (a) \( \Delta O_{\text{bot}} \) and (b) \( C_{\text{bot}} \) and (c) \( \mathcal{N} \) are also shown, all of these have been significantly reduced with the inclusion of periodic forcing.