A LARGE EDDY SIMULATION STUDY OF THE FORMATION OF DEEP
CHLOROPHYLL/BIOLOGICAL MAXIMA IN UN-STRATIFIED MIXED LAYERS: THE
ROLES OF TURBULENT MIXING AND PREDATION PRESSURE.

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Abstract

Recent experimental measurements of fluorescence values and turbulent energy dissipation rates, recorded in weakly stratified boundary layers in the open ocean, have highlighted a significant correlation between the formation of deep chlorophyll maxima (DCM) and turbulent mixing. Specifically, the depth of many DCM are observed to lie below, but within about one standard deviation, of the point at which the energy dissipation rate profile reaches its maximum. This correlation of DCM and turbulent mixing is both exciting and curious, as conventional thinking tends to see the latter as a destructive rather than a constructive agent in regards to the formation of deep biological maxima (DBM), for which DCM data is usually interpreted as a proxy. In order to investigate this phenomenon, a 3D Large Eddy Simulation (LES) of the ocean boundary layer was combined with a generic NPZ type biological model, in order establish what mechanisms might be driving the experimental observations.

Simulations of the LES-NPZ model, based upon various sets of generic biological parameters, demonstrate DCM/DBM formation occurs at normalised depths close to those seen in the experimental observations. The simulations support the hypothesis that the DBM are generated by a combination of zooplankton predation pressure curtailing phytoplankton growth near the surface, and a decline in the strength of the vertical mixing processes advecting nutrient through the boundary layer. In tandem these produce a region of the water column in which predation pressure is relatively low and nutrient aggregation relatively high, suitable conditions for DBM formation.
1. Introduction

The presence of deep (or sub-surface) chlorophyll/biomass maxima ($DCM/DBM$) observed in vertical fluorescence profiles is one of the most ubiquitous features of the world’s oceans (Macías et al. 2008), and much research effort has been devoted to understanding the mechanisms behind their formation and dynamics (see Cullen 2015 for a comprehensive review of the subject). Observations of $DCM$ are not just confined to the ocean boundary layer (e.g. Cullen 1982, Estrada et al. 1993, Letelier et al. 2004, Macías et al. 2013), but are a pervasive feature of the limnology of lakes too (Hamilton et al. 2010, White & Matsumoto 2012, Simmonds et al. 2015). Here the terminology $DCM$ specifies a broad (10-20m) region of relatively high chlorophyll concentrations (but weak concentration gradients), usually to be found at or somewhat below the mixed layer depth. This should not be confused with the concept of a rapidly varying biological ‘thin layer’, confined to vertical scales of just a few metres (e.g. Dekshenieks et al. 2001, McManus et al. 2003 & 2005, Johnston et al. 2009 Benoit-Bird et al. 2009, Durham et al. 2009), which are usually found residing within the top 10m or so of the water column.

A number of different postulates have been advanced to attempt to explain both the formation of $DCM$, and the reasons as to why they are observed so frequently under many different hydrodynamic conditions. These include the presence of a nutricline, giving rise to increases in phytoplankton growth rates in certain preferential layers of the water column (Simmonds et al. 2015), or the physical accumulation of phytoplankton cells at boundary layer interfaces (Ruiz et al. 2004, Huisman et al. 2006), such as the thermo/pycnocline (Dekshenieks et al. 2001). One possible mechanism by which aggregations could form at such boundaries would be through the action of intense levels of shear instabilities disrupting the swimming motions and effectively trapping gyrotatic micro-organisms (Durham et al. 2009, Hoeckner-Martinez & Smyth 2012). A further alternative, highlighted by the
observational and numerical work of Fennel & Boss (2003), emphasizes what they term the
“general compensation depth”, a level at which the local phytoplankton growth rate is
balanced out by losses due to zooplankton grazing and divergences of settling velocity. This
emphasis on predation pressure through zooplankton grazing is important because the upper
ocean mixing layer most conducive to high levels of phytoplankton growth (it usually
encompasses the euphotic zone in which light levels are sufficient for photosynthesis) is
turbulent, and turbulence levels significantly influence planktonic predation (e.g. Rothschild
Bala 2006 and references therein). Awareness of the rôle played by turbulence in the
formation and sustenance of biological layers has recently been heightened by the publication
of new observational evidence. This is derived from data recorded by sophisticated, next
generation, instrumentation, which shows that turbulent mixing rates and biological layers are
frequently correlated (Wang & Goodman 2010, Macías et al. 2013), highlighting that
background turbulence has a potentially creative, as well as a destructive capacity in regard to
biological aggregations. The observations of Macías et al. 2013 are particularly striking in
this regard, and are discussed in a little more detail in Section 2. They provide both
motivation and empirical support for the subsequent theoretical/computational analysis.

The question that now arises is how to go about investigating the creative and destructive
capacity of boundary layer turbulence in regards to DCM/DBM production? The recent
increase in instrumentation sophistication has been achieved hand-in-hand with ever
increasing advances in both computational speed and storage capacity. This in turns enables
one to contemplate the use of much more ambitious and extensive modelling methodologies
than have been attempted hitherto. The most common means of modelling planktonic
population dynamics has been through the utilization of some form of coupled nutrient-
phytoplankton-zooplankton (NPZ) system of differential equations (e.g. Franks 1995,
Edwards et al. 2000, Franks 2002). Usually such models contain various simplified descriptions of nutrient uptake, phytoplankton growth and zooplankton predation built into their equations. To study the effects of turbulence requires a more sophisticated, coupled, biophysical model. Previously this has been attempted by adding in a vertical eddy diffusivity term into the NPZ system, which in effect creates a one dimensional (vertical) biological boundary layer model (Baird & Emsley 1999, Denman & Peña 1999, Flierl & McGillicuddy 2002, Fennel & Boss 2003). However, the use of vertical eddy diffusivities in this way provides only a crude measure of the effects of water motion on the biology, particularly given that turbulence is, by definition, characterised by high levels of vorticity, which is fundamentally three dimensional in nature (Tennekes & Lumley 1972, McComb 1991, Lesieur 1997). Given the unquestioned advances in computational speeds in recent years, it seems reasonable to try and formulate something more powerful and sophisticated.

In Lewis (2005) the author attempted to devise such a model, building on ideas first formulated in the review article of Denman & Gargett (1995). This was achieved by employing a series of large-eddy simulations (LES) of ocean mixing layers, coupled together with a specially adapted NPZ model (specifically based upon the ideas of Baird & Emsley 1999) to describe the biological evolution in such an environment. LES captures the large scale features of a boundary layer flow extremely well and these are utilised to advect the biological fields in bulk. Although random, on small (planktonic) scales turbulent flows possess certain universal generic features, usually characterised by the local energy dissipation rate $\varepsilon(z)$ at a specified depth $z$. These generic features mean that the influence of the physical forcing on the population dynamics will conform to certain statistical norms, which can be estimated. Hence a knowledge of $\varepsilon$ allows one to parameterise the coupling of the LES to the NPZ, to create a fully integrated, three dimensional, bio-physical model across all scales. The main details of the adaptations necessary to produce a combined LES-NPZ
model of the mixing layer were presented in Lewis (2005). In that work the behaviour of the
(initially uniform) biological fields when subjected to a fixed level of wind forcing was
investigated. These results were generally satisfactory, but computational limitations
restricted the run times to no more than a day or so, severely restricting the interval during
which significant heterogeneities in the biological fields might develop. Subsequent advances
in computational capacity and processor speed now allow one to carry out runs over periods
of days and weeks, giving the opportunity to investigate the potential for the development of
aggregations over a number of biological cycles. In conjunction with the new experimental
results starting to become available, the LES-NPZ model now provides a means of
investigating the drivers of DCM/DBM production and dissipation to a much greater degree
of precision than hitherto. The results and analysis of a number of such investigations
(presented in Section 5) comprise the main body of this paper.

2. A brief summary of the observations of DCM recorded in the subsurface upper
ocean as discussed in the paper by Macías et al. (2013).

Briefly the paper of Macías et al. (2013) (denoted by M13 subsequently) describes an
extensive series of measurements recorded using a TurboMAP-L fast sampling (512Hz)
probe (Doubell et al. 2009), which is capable of measuring conductivity, sea temperature,
vertical shear and fluorescence on a resolution scale of the order of centimetres.
Measurements were taken at four different marine environments (specifically a coastal
upwelling region of the Alboran Sea off the east coast of Spain, in the tidally-dominated
Strait of Gibraltar (Macías et al. 2008), a region of open ocean in the North Atlantic situated
~34°30’N, 8°30’W, and at a site just off the tip of the Antarctic Peninsula.) by allowing the
probe to free-fall from the surface to a typical depth of 150m (so encompassing both the
upper wind driven mixed layer and the lower weakly stratified portion of the water column). The North Atlantic trials took place during the spring, but measurements from the other three sites were conducted during the summer months. At this time of year, DCM are very prevalent in polar and temperate latitudes. This is thought to be connected with the fact that in summer the levels of turbulent mixing are relatively low, leading to nutrient depletion and low phytoplankton growth in the upper mixed layer (Holm-Hansen et al. 2005). Estimates of (average) energy dissipation rate profiles $\varepsilon(z)$ were calculated from the vertical shear measurements recorded by the probe by means of the relation

$$\varepsilon(z) = \frac{15}{2} \nu \left( \frac{\partial u}{\partial z} \right)^2, \quad (1)$$

where $\nu$ is the kinematic viscosity (which is slightly temperature dependent but a value of $\nu = 10^{-6} \text{m}^2 \text{s}^{-1}$ will be assumed throughout this work). M13 do point out that the sampling within the highly turbulent near surface region (where wind stresses and wave effects are at their maximum) may be somewhat problematic, since the TurboMAP-L probe needs to be sinking at an almost constant speed through the water column. Such conditions are only reached at depths 10-15m below the surface. The prevailing vertical stratification conditions were summarised by means of an average buoyancy frequency $N(z)$, determined by

$$N^2(z) = -\frac{g}{\rho} \left( \frac{\partial \rho}{\partial z} \right), \quad (2)$$

where $\rho$ is the water density. Measurements of both fluorescence $F(z)$ (measured in relative fluorescent units) and energy dissipation rate were fitted to standard Gaussian curves to create model depth profiles. Four such profiles, one from each of the locations mentioned above, superimposed on the respective raw data are shown in Fig.1. (These profiles are reproduced from those of Fig. S1 of M13.)
Amongst the many interesting features of these datasets, the most pertinent to this particular study is the relative position of the deep chlorophyll maximum $DCM_{\text{depth}}$, to the position $peak_{\text{depth}}$ at which the energy dissipation rate reaches its recorded maximum. Some 73% of the analysed $\varepsilon(z)$ profiles were termed ‘positive’, in the sense that they exhibited a sub-surface $peak_{\text{depth}}$. Of these ‘positive’ profiles, two thirds (31 out of 46 profiles) exhibited a $DCM_{\text{depth}}$ situated below, but within one standard deviation of $peak_{\text{depth}}$. The average $DCM_{\text{depth}}$ for these ‘matching’ (M13) profiles was located some 18m deeper than the corresponding $peak_{\text{depth}}$ values. In other words, the maximum fluorescence measurements were significantly correlated with negative (decaying) $\varepsilon(z)$ gradients within the upper ocean mixed layer. In the remaining 15 profiles this correlation was absent. The main difference between these latter mixing layers was their relatively high degree of stratification ($N^2 = 3.21 \pm 1.82 \times 10^{-3} s^{-2}$), compared to the much lower values ($N^2 = 1.1 \pm 1.2 \times 10^{-3} s^{-2}$) associated with the ‘matching’ profiles. These results are important because many theoretical explanations of the formation of heterogeneous phytoplankton concentrations begin with the premise that significant stratification is already present, and such conditions are a prerequisite for biological aggregations (especially thin layer formation e.g. Durham et al. 2009, Hoeckner-Martinez & Smyth 2012). But here is experimental evidence of intense $DCM$ (typical values of the magnitude of $DCM_{\text{max}}$ are between 2-6 times the background) forming in the absence of strong stratification. Usually the presence of a $DCM$ correlates exactly with a corresponding deep biomass maximum $DBM$, although there is some experimental evidence (Longhurst & Harrison 1989, Pérez et al. 2006, Cullen 2015) that the latter can be displaced slightly below the former as the chlorophyll-to-carbon ratio increases with depth. However, this displacement usually occurs in relatively stable ocean boundary layers found in tropical waters, conditions which do not apply to any of the locations discussed in M13. Hence for these sites it is fair to assume that the measured $DCM$ is equivalent to the $DBM$. So
the question arises, what causes the formation of these aggregations in the absence of
significant stratification in the upper boundary layer?

M13 postulate that the existence of a DCM may be explained by the juxtaposition of two
vertically opposing gradients of resources: light availability from the surface necessary for
photosynthesis and vertical mixing of nutrient rich deep waters into the euphotic zone,
creating an ‘optimal window’ for the formation of the DCM. This seems a highly plausible
hypothesis, albeit one that is likely to be modulated by other factors. M13 highlight the
possible rôle of cells sinking faster out of high turbulence zones and accumulating in low
vorticity regions situated below peak$_{depth}$, a hypothesis supported by the experiments of
Ruiz et al. (2004). Another potential regulatory factor is that of planktonic predation
(summarised, somewhat loosely, as that of a generic zooplankton species feeding on a
generic species of phytoplankton), which is known to be strongly dependent upon the level of
background turbulence (Rothschild & Osborn 1988). This is another vertical gradient that
augments those governing the availability of light and nutrients. Modern high speed
computing resources means it is now quite possible to investigate and test such postulates
much more systematically (and cheaply) than ever could be done using field trial data alone
(vital though that remains). A necessary pre-requisite is the existence of suitable bio-physical
models of the upper ocean boundary layer, which incorporate both the effects of wind-driven
and surface wave generated turbulence, coupled with the biological drivers of plankton
population dynamics. These are just the kind of bio-physical characteristics the LES-NPZ
model is able to replicate.

3. A description of the LES-NPZ model

Conceptually, the biological part of the LES-NPZ model is little different from other three
state NPZ models in the literature (e.g. Keifer & Atkinson 1984, Fasham et al. 1990, Edwards
& Brindley 1996, and previous references cited). Three, non-dimensional, scalar fields
denoted by \( N(x, t) = N^*/N_0, P(x, t) = P^*/P_0 \) and \( Z(x, t) = Z^*/Z_0 \), representative of nutrient (specifically nitrate), phytoplankton and zooplankton (where \( N_0 \) in kg m\(^{-3}\), \( P_0 \) and \( Z_0 \) in cells m\(^{-3}\) are suitable reference scales) are assumed to satisfy three advection diffusion equations of the general form

\[
\begin{align*}
\frac{DN}{Dt} + U_s \cdot \nabla N &= D_{TN} \nabla^2 N - N \text{ uptake by } P + N \text{ recycled from } P \text{ growth}, \quad (3) \\
\frac{DP}{Dt} + U_s \cdot \nabla P &= D_{TP} \nabla^2 P + P \text{ growth from } N - P \text{ grazing loss}, \quad (4) \\
\frac{DZ}{Dt} + U_s \cdot \nabla Z &= D_{TZ} \nabla^2 Z + Z \text{ growth grazing } P + Z \text{ mortality}. \quad (5)
\end{align*}
\]

Here \( D/Dt \equiv \partial/\partial t + \mathbf{u} \cdot \nabla \), and \( \mathbf{u}(x, t) = [u, v, w] = [u_1, u_2, u_3] \) is the (resolved LES) turbulent velocity field. This provides the first component of the physical coupling to the biology and is derived from a spatially and temporally (over one wave period) averaged version of the full three dimensional Navier-Stokes equations. First derived by Craik & Leibovich (1976), these consist of the equations of continuity \( \nabla \cdot \mathbf{u} = 0 \), momentum

\[
\frac{Du}{Dt} + f \mathbf{k} \times (\mathbf{u} + U_s) = -\nabla p_s \rho_0 - g \frac{\rho'}{\rho_0} + U_s \times \omega + SGS, \quad (6)
\]

and energy

\[
\frac{D\theta}{Dt} + U_s \cdot \nabla \theta = SGS. \quad (7)
\]

In (6) and (7), \( f \) is the Coriolis frequency, \( U_s \) the Stokes drift velocity, \( \omega = \nabla \times \mathbf{u} \) the vorticity, \( g \) is the acceleration due to gravity, \( \theta(x, t) = \theta_r + \theta'(x, t) \) the temperature field, \( \rho(x) = \rho_0 + \rho'(x) \) the fluid density and \( p_s = p + \rho_0[2\mathbf{u} \cdot U_s + |U_s|^2]/2 \) a generalized pressure term. The density is assumed to be proportional to the temperature, such that \( \rho'/\rho_0 = \theta'/\theta_r \) and details of the values of these parameters, including the reference density \( \rho_0 \) and temperature \( \theta_r \), are given in Table 1. The Stokes drift velocity was estimated by assuming that the ocean consists of steady, monochromatic deep-water waves (Philips 1977),
which (for convenience) are directed along the $x$-axis (easterly direction). In which case
\[ U_S = (U_S e^{2kx}, 0, 0), \]
where $U_S = \sigma k a^2$, $a$ being the wave amplitude, $k$ the wave-number and
\[ \sigma = \sqrt{gk} \] the wave frequency (see Table 1).

The sub-grid scales (SGSs) used to close the equations are based on a standard Smagorinsky (1963) scheme in which the unresolved Reynolds stresses $\overline{u'_i u'_j}$ (where the overbar denotes the filtering operation) and buoyancy fluxes $\overline{u'_i \theta'}$ are related to the spatial gradients of resolved flow field, so that
\[
\overline{u'_i u'_j} = -\nu_T S_{ij} = -\nu_T \left[ \left( \frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i} \right) - \frac{2}{3} S_{ij} \frac{\partial u_k}{\partial x_k} \right], \quad \overline{u'_i \theta'} = \nu_T \frac{\partial \theta}{\partial x_i},
\]
where $\nu_T$ is an eddy viscosity and $Pr$ is a turbulent Prandtl number. Details of the choice of the eddy viscosity in terms resolved strain rate $S_{ij}$ and a resolution scale $L_0$ (set to be 1m throughout) are discussed in Lewis (2005). Note the distinction between $q'$, the unresolved part of a scalar quantity $q_{total} = \bar{q} + q'$, and $q''$ used later to denote a fluctuation in the LES resolved part $q(x, t) = \overline{q(x, t)} = \langle q \rangle + q''(x, t)$, derived from eqs. 6-7. (In what follows $\langle q \rangle$ denotes $q(z, t) = \frac{1}{4XY} \int_{-X}^{X} \int_{-Y}^{Y} q(x, t) \, dx \, dy$, the instantaneous horizontal mean of a resolved quantity. Similarly $\langle q \rangle_T$ will denote $q(z) = \frac{1}{T} \int_0^T \langle q \rangle dt$, the time averaged horizontal mean, over a specified interval $T$.) For code verification purposes solutions of the velocity and temperature (pressure) fields were computed from equations (6-7) over a domain $120 \times 120 m^2$ horizontally and to a simulation base depth $z_S = 33(50)m$, utilising a basic grid of $40 \times 40 \times 75(114)$ nodes. This implies a regular resolution scale of $\Delta x = \Delta y = 3m$ and $\Delta z = 0.45m$ (although the vertical resolution is staggered to give greater resolution near the sea surface). In the course of these investigations many different turbulent boundary layers were generated. Their characteristics will be distinguished by the values of the Stokes drift...
velocity $U_S$, and the friction velocity $U_*$, which determines the strength of the wind forcing
applied at the surface

$$\nu \frac{\partial u}{\partial z} \bigg|_{z=0} = \frac{\tau}{\rho_0} = U_*^2. \quad (9)$$

Here $\tau$ is the surface wind stress, which was varied between simulations over a range of
2.25-25.0 \times 10^{-3} \text{kgm}^{-1}\text{s}^{-2}. This implies values of $U$, lying between 1.5-5.0 \times 10^{-3} \text{ms}^{-1},
roughly equivalent to windspeeds $U_{10} = 1.2-4.0$ \text{ms}^{-1} at a height of ten metres. The
corresponding values of $U_S$ are given in Table 1. All the boundary layers were made slightly
convective, with a turbulent buoyancy flux of $\overline{w'\theta'} = -1.2 \times 10^{-6}\text{Kms}^{-1}$ applied at the
surface. Other boundary conditions imposed on the flow are horizontal periodicity, $w = 0$ at
$z = 0$ and no slip at $z = -z_S$. Typically, the various boundary layers were spun up from rest
for a period $\tau_{spin} \sim 60000$s until a quasi-equilibrium state was reached, before any biological
fields were added. This marks time zero for the simulations proper. The physical
characteristics governing the generation of a particular simulation will be denoted by its
$(U_*, U_S)$ number. So the notation $(U_*, U_S) = (3.5, 3.9)$ specifies a simulation in which $U_*$ =
$3.5 \times 10^{-3} \text{ms}^{-1}$ and $U_S = 3.9 \times 10^{-2} \text{ms}^{-1}$ respectively. The corresponding Langmuir
number $La = \sqrt{U_* / U_S}$, as defined by McWilliams et al. (1997), can also be used to classify
the simulations.

The performance of the LES code was extensively tested by comparing its output with that
of a similar code employed by McWilliams et al. (1997) to study Langmuir turbulence in the
upper ocean boundary layer. Comparison profiles of horizontal currents, shear stresses,
velocity variances and energy dissipation rates (Lewis 2005) showed excellent agreement
across the mixing layer $z \in [-z_{ML}, 0]$. Here $z_{ML}$ represents the mixing layer depth (e.g. de
Boyer Montégut et al. (2004), which varies according to both the strength of the wind forcing and the local hydrography (density and/or temperature differences, usually measured from the surface). The main difference between the two codes is the incorporation by McWilliams et al. (1997) of a stably stratified region below \( z_{ML} \) extending to a depth of \( z \approx -3z_{ML} \). By contrast, the LES-NPZ model does not feature any such stratification. This raises a problem with the use of the terminology ‘mixing-layer depth’ when applied to these simulations, since the hydrographical features that help regulate its position are absent. So for this work an alternative concept of turbulent or Ekman depth, will also be used. This depends purely on the mixing properties of the flow and is defined by Coleman et al. (1990) to be \( z_{TD} = U_*/f \). In practice \( z_{TD} \) will be larger than \( z_{ML} \), since the latter is constrained by the hydrographic features of the flow not incorporated into these simulations (Pearson et al. 2015). A rough equivalence would be closer to \( z_{ML} \sim z_{TD}/2 \). From a review of the relevant literature, Garratt (1992) suggests \( z_{ML} \sim 0.2 - 0.4z_{TD} \) for weakly stratified layers, but the inclusion of the Stokes drift term in (6) means that the mixing layer of these simulations is certain to be somewhat deeper than this. Since the velocity field is virtually zero below \( z_{TD} \), whilst the majority of M13’s measurements of DCM are found within weakly stratified mixed layers at depths significantly above \( z_{TD} \) (the turbulent mixing, although declining, is still a prevalent feature in Fig. 1), the lack of a stratified base to the computational domain is not a serious issue for this work.

Figs. 2-4 show some typical flow parameters derived from samples of these simulations. Fig. 2 shows the depth dependence of the mean (LES) velocities \( \langle u \rangle_T \) and \( \langle v \rangle_T \) derived from a \((U_x, U_y) = (3.5, 3.9)\) simulation after a time \( T = T_{sim} \sim 20-25 \) days. Typically, except very near the surface, the mean flow is directed in a south-southwest direction, with both \( \langle u \rangle_T \) and \( \langle v \rangle_T \) negative. The effect of the Stokes drift term is to deflect the mean current anticlockwise - away from the easterly wind direction - considerably beyond the 45° degrees predicted by
classical Ekman boundary layer theory (Lewis & Belcher 2004). Fig. 3a shows a comparison of the mean velocity variance profiles \((u''^2)_T, (v''^2)_T\) and \((w^2)_T\) taken from the same simulation. (N.B. \(w \equiv \bar{w}'\), since \(\langle w \rangle = 0\.) A feature of these results is the relatively large scale of the vertical \((w^2)_T\), as opposed to the horizontal \((u''^2)_T + (v''^2)_T\) turbulent mixing. Physically this is a manifestation of the formation of Langmuir cells, a series of counter rotating vortices aligned with the wind direction driven by the interaction of the wave field stretching and tilting the vertical vorticity field (Teixeira & Belcher 2002). From a biological point of view this enhanced mixing helps to ensure any nutrient resources, drawn from the deep ocean by large scale up-welling events, will be distributed quickly and uniformly throughout the mixing layer.

The other key physical parameter which encapsulates the mixing is the mean energy dissipation rate \(\varepsilon(z)\) highlighted earlier (q.v. eq. 1 and Fig. 1). Fig. 4 shows some profiles of \(\varepsilon(z)\), derived by balancing the (steady) resolved scale turbulent kinetic energy budget (McWilliams et al. 1997, Lewis 2005 eq.11, Polten & Belcher 2007), extracted from the \((2.0, 2.2), (3.5, 3.9)\) and \((5.0, 5.6)\) simulation datasets over a period of \(T \approx 1\) day. This involves combining terms such as Stokes, shear & buoyancy production, pressure working, turbulent transport and SGS dissipation. Near the surface \(\varepsilon(z)\) shows significant variation, by roughly a factor of five in magnitude as \(U_*\) increases, but at greater depths the differences are far less evident. Notice too that the \(\varepsilon(z)\) profiles often exhibit small secondary maxima, usually lying between about 5-15m below the surface. Such secondary maxima are a feature of these wind and wave driven Langmuir boundary layers. They can be explained by a comparison with the velocity variance profiles of Fig. 3a. Whilst the horizontal \((u''^2)_T + (v''^2)_T\) mixing component declines uniformly, this can sometimes be offset by vertical \((w^2)_T\) component which initially increases near the surface, giving rise to the small secondary maxima in \(\varepsilon(z)\). Comparing the profiles derived from these numerical simulations with the
experimental measurements of $\epsilon(z)$ recorded by M13 (see Fig. 1), one can see that the values all lie in a broadly similar $10^{-7} - 10^{-6}$ m$^2$s$^{-3}$ range. The main distinction is that for the numerical simulations the peak dissipation rate lies at the surface, where the wind and wave forcing are at their most intense, whilst in the experimental results the $peak_{depth}$ lies somewhat deeper. Careful inspection of all the low stratification profiles recorded off Spain and Gibraltar (e.g. Profiles 6 & 21 in Fig. 1) shows that the mean $peak_{depth}$ occurs at a relatively shallow 28.9m (M13 Table S1). In addition, most of these profiles exhibit dissipation values between $1 \times 10^{-7} - 2 \times 10^{-6}$ m$^2$s$^{-3}$ at depths 10-15m below the surface, similar to those seen in the numerical simulations. The profiles recorded at the North Atlantic and Antarctic Peninsula sites (e.g. Profiles 28 & 31 in Fig.1) are somewhat different, exhibiting much deeper values of $peak_{depth}$~70m. The probable reason for these large sub-surface peaks is an increase in the energy dissipation rate at the mixed layer/thermocline boundary. Observations of increased energy dissipation rates within the thermocline have been recorded (e.g. Moum & Osborn 1986) and are believed to be result of the action of internal wave scattering due to buoyancy fluctuations (Gregg 1989). However, the magnitude of this increased mixing generally lies within the range $10^{-10} - 10^{-9}$ m$^2$s$^{-3}$, which is rather too small to account for peaks shown in Fig. 1 and there may be other factors at work (see section 5a). In any event this should not distract from the main feature of all the profiles, namely the pattern of $DCM$ formation at depths where $\epsilon(z)$ is in sharp decline, which is motivation for this work.

The biological source/sink terms making up the right-hand sides of equations (3-5) are inspired by the work of Baird & Emsley (1999) and discussed in detail in Lewis (2005), so only a brief resumé is included here. Table 2 lists the main numerical values of the various biological parameters that appear in these terms. The nutrient uptake term in (3) is given by
\[ N \text{ uptake by } P = 4\pi r_p Sh(\varepsilon, z) D_N N(x, t) \left[ 1 - \frac{R_{N_0}(z)}{R_N^{\text{max}}} N(x, t) \right] P^*(x, t), \quad (10) \]

provided (10) is positive, otherwise it is set to zero. This reflects the balance between nutrient uptake by means of turbulent diffusion and the limitations brought about by the nitrate storage capacity of an average cell. Here \( r_p \) is a typical phytoplankton cell radius, \( Sh \) a non-dimensional turbulent Sherwood number, \( D_N \) the molecular diffusivity of nitrate and \( R_{N_0}(z)/R_N^{\text{max}} \) is the ratio of the nitrate storage capacity of the cell to its maximum potential storage capacity. The value of \( R_{N_0}(z) \), assuming a background ambient nitrate concentration level \( N_0 \) set to be \( 2.8 \times 10^{-5} \text{kg m}^{-3} \) (Fasham et al. 1990), can be established using a mass balance equation (Baird et al. 2001), as discussed in Lewis (2005). The \( R_N^{\text{max}} \) parameter was set to a value of \( 3s_N \) where \( s_N \) (kg cell\(^{-1}\)) is a nitrate stoichiometry coefficient quantifying the minimal amount of nitrate needed for a cell to be viable. Whenever the background concentration \( N(x, t) \) greatly exceeds \( N_0 \) then nutrient satiation sets in, at which point diffusion into the cell ceases. For the simulations results presented in Section 5 the value of \( R_{N_0}(z)/R_N^{\text{max}} \approx 0.5 \), which means that uptake ceases when the background nutrient concentration \( N(x, t) > 2 \). The physical forcing influences the scale of (10) in two ways. Directly, through the dependence of \( Sh \) on \( \varepsilon \), and indirectly through the effects of the turbulent mixing on the nutrient distribution. In practice the direct influence of \( \varepsilon \) on \( Sh \) is weak, since \( r_p \) is usually less than the Kolmogorov length scale \( (\nu^3/\varepsilon)^{1/4} \), meaning that \( Sh \) varies little from unity across the boundary layer. The indirect influence of \( \varepsilon \) on (10), as manifested through the nutrient distribution is far more important, and will form part of the investigation carried out in Section 5.
The nitrate recycled and phytoplankton growth terms employed in (3) and (4) are essentially analogues of each other and depend significantly on the scale of (10). In the model they are given by

\[
\text{Nitrate recycled} = (1 - \beta_E) \frac{s_N P^*(x, t)}{N_0} \mu_p^{\text{max}} e^{ax} \min \left[1, \frac{R_{N_0}(z)}{R_{N}^{\text{max}}} N(x, t) \right],
\]

(11)

\[
P \text{ growth} = \beta_E \min \left[1, \frac{R_{N_0}(z)}{R_{N}^{\text{max}}} N(x, t) \right] e^{ax} \mu_p^{\text{max}} p(x, t).
\]

(12)

Equation (12) encapsulates the fact that a phytoplankton species can potentially reproduce at its maximum growth rate \(\mu_p^{\text{max}}\) under ideal conditions; but this is regulated by the available light intensity for photosynthesis, which is assumed to decay exponentially with depth (\(\alpha\) is the light attenuation coefficient for water), and the cellular reserves of nitrate currently available (see Baird & Emsley (1999) for more on the details underpinning these terms).

Other factors can also inhibit phytoplankton growth efficiency and their effects are represented by the dimensionless parameter \(\beta_E \in [0, 1]\). These growth inefficiencies (cell death and decay) usually lead to a recycling of nitrate back into the water column, a process which is summarised by equation (11). The usual initial condition employed in these simulations will be to fix \(N(x, 0) = 1\), in which case the recycling term is about ten times smaller than the uptake term (10).

The loss of phytoplankton to zooplankton grazing and the zooplankton growth rate terms used in (4) and (5) are also analogous. In the model they appear as

\[
P \text{ grazing loss} = Z^*(x, t) P(x, t) I(R, T_R, \epsilon, \sigma_Z),
\]

(13)

\[
Z \text{ growth} = \min[\mu_Z^{\text{max}}, Y P^*(x, t) I(R, T_R, \epsilon, \sigma_Z)]Z(x, t).
\]

(14)

Here \(I(R, T_R, \epsilon, \sigma_p)\) is representative of a predation rate integral (units m\(^3\)s\(^{-1}\)) defined explicitly in Lewis & Pedley (2001 eqs. 16-17), evaluated over a range \([0, R]\), where \(R\) is the
contact radius of the zooplankton predator. This parameter is the maximum distance over
which it can perceive its prey ($R \sim 1-40 \times 10^{-3} \text{m}$) and in Lewis & Pedley (2001) it is
assumed to be spherically symmetric for mathematical simplicity. In reality, most predators
possess a much narrower conical perception field, the ramifications of which are discussed in
Lewis (2003), Lewis & Bala (2006 & 2008). Loosely $I(R, T_R, \varepsilon, \sigma_Z)$ estimates the predation
rate of the predator from its encounter rate (Rothschild & Osborn 1988), times its capture
efficiency. The latter is governed by parameters such as a predator’s reaction time $T_R$, its
swimming or pursuit speed $\sigma_Z$ and level of turbulence summarised by $\varepsilon$. Turbulence always
enhances encounter rates by advecting more prey particles into the predator’s vicinity, but in
certain instances can lead to the suppression of the predation rate, because it makes the act of
actually capturing prey more problematic. In this work the zooplankton predators are
relatively small $r_Z \sim 10^{-5} - 10^{-4} \text{m}$, and their corresponding swimming speeds $\sigma_Z \sim 5 - 20 \times
10^{-4} \text{m s}^{-1}$ are an order of magnitude smaller than the mixing velocity scales found in the
upper boundary layer (Fig. 2). Consequently swimming is not included directly into the
advection terms in (5) because it would be too small to influence the spatial distribution of
the zooplankton. Potentially, swimming could make a significant impact at depths close to
the mixing layer boundary where $\varepsilon$ falls off rapidly and DBM are observed. This is
particularly true of the predation term, which falls to zero in the absence of any advective or
swimming motions. On balance this would a fairly unlikely scenario, but for illustrative
purposes non-swimming predators will feature in some of the simulations (cf. Figs. 14 & 16)
carried out here. The specific ideas as to how these competing factors are formulated into the
integrand of $I(R, T_R, \varepsilon, \sigma_Z)$, are discussed in Lewis & Pedley (2001). Fig. 5a shows some
profiles of the predation rate $I(R, T_R, \varepsilon, \sigma_Z)$ for a relatively efficient ($T_R = 5 \text{s}$) non-swimming
predator, possessing a contact radius $R = 2 \times 10^{-3} \text{m}$, over a range of windspeeds ($U_* =$
2.0-5.0 $\times 10^{-3} \text{m s}^{-1}$). Generally an efficient predator benefits from increasing levels of
turbulent mixing, since its encounter rate goes up leading to more prey captures. This is
reflected in Fig. 5a which exhibits a steady increase of predation rate with windspeed. The
benefit is particularly marked near the surface where $\epsilon$ is at its largest, q.v. Fig. 4. By contrast
increased turbulent mixing can be detrimental to the predation rate of an inefficient predator
($T_R = 15s$), such as the one illustrated by the profiles in Fig. 5b. In these instances, the
comparatively high relative velocities found near the surface means the predator has to react
faster than $T_R$ in order to capture prey moving into its vicinity. This it is unable to do, leading
to a drop in its overall predation rate. The predation rate determines both the decline in the
general phytoplankton population through grazing (13), and the zooplankton growth rate
(14). The latter is regulated by the yield $Y$ of new predator cells per prey cell captured, and is
also restricted never to exceed a fixed maximum zooplankton growth rate $\mu_z^{\text{max}}$, theoretically
attainable under ideal conditions.

The biological part of the model is closed by assuming that the zooplankton growth rate is
limited by a simple constant mortality term of the form

$$ Z \text{ mortality} = \mu_z^{\text{death}} \frac{Z'(x, t)}{Z_0}. \quad (15) $$

The mortality rate $\mu_z^{\text{death}}$ is a purely biological parameter independent of $\epsilon$. Its importance
stems from the fact that it regulates the period of oscillations of the planktonic $P/Z$
populations within the model (see Section 4). The diffusion coefficients in (3-5) are
calculated from the eddy viscosity by means of a turbulent Schmidt number

$$ D_{\Gamma} = \frac{v_T(x)}{S_{\text{turbulent}}} \quad (\Gamma = N, P, Z). \quad (16) $$

The Schmidt number cannot be too large as it is regulated by the LES resolution scale and
one cannot expect to resolve the scalar fields down to a finer level than that can be achieved
for the velocity fields. A proposal made by Sullivan et al. (1994) and adopted in Lewis
(2005) was to prescribe $S_{c_{turbulent}}$ in the form

$$S_{c_{turbulent}} = \frac{1}{(1 + 2L_0/\Delta)^\gamma},$$

(17)

where $\Delta^2 = (3\Delta x/2)(3\Delta y/2)\Delta z$. For the simulations discussed here $S_{c_{turbulent}} \approx 1/2$, a
value compatible with $L_0$ scale which prescribes the resolution of the LES velocity field.

Equations (3-5) are solved subject to certain prescribed boundary conditions on the
biological fields. Horizontally, periodic boundary conditions were imposed. Vertically, zero
surface flux conditions are (usually) imposed for each field, whilst at $z = -z_s$ certain
prescribed fluxes into the simulation domain were enforced. For the majority of the
simulations presented here the vertical boundary conditions satisfied

$$\frac{\partial \Gamma}{\partial z} \bigg|_{z=0} = 0, \quad \frac{u_T}{S_{c_{turbulent}}} \frac{\partial \Gamma}{\partial z} \bigg|_{z=-z_s} = \langle w\Gamma \rangle, \quad (\Gamma = N, P, Z).$$

(18)

In the case of the planktonic fields, $\Gamma = P$ and $Z$, deceased cells were assumed to sink, under
gravity, out of the simulation domain at a rate governed by a settling velocity $U_{sink}$ (Lewis
2005). This fixes $\langle w\Gamma \rangle = U_{sink} \phi^d \Gamma_{z=-z_s}$, where $\phi^d$ is the (small) proportion of deceased
cells out of the total population. The boundary conditions imposed on the nitrate field were
more flexible. In general wind, tidal and other driving forces instigate upwelling motions that
circulate nutrient rich water from the deep ocean through the mixing layer. So one would
expect nitrate levels in the mixing layer to remain relatively constant, as losses through
uptake by the phytoplankton for photosynthesis will be quickly replenished via this source.
Hence a positive flux of nitrate into the simulation domain was invariably imposed. Williams
and Follows (1998) suggest this background flux should be $\sim 2 \times 10^{-8}$ mol N m$^{-2}$s$^{-1}$,
which is roughly equivalent to $\langle wN^* \rangle = -2.8 \times 10^{-10}$ kg m$^{-2}$s$^{-1}$. This figure was taken as
representative of the background nutrient replenishment flux from the deep ocean into the boundary layer. However, in instances where \( z_D \gg z_T \), introducing replenishment nutrient at the base is not very useful, since there is little or no mixing to advect it through the boundary layer. To overcome this problem, simulations were also conducted in which the replenishment flux was imposed at the surface \( (z = 0) \) instead. Such a surface nutrient surge could be driven by a significant river run off event, iron seeding experiments or even ash from a volcanic eruption (Frogner et al. 2001). This allows one to investigate what changes (if any) occur to the DCM/DBM characteristics when the replenishment nutrient is added at alternative depths subject to radically different turbulent mixing regimes.

4. Model verification and the influence of boundary layer structure on the Biological Dynamics

The full version of the LES-NPZ model seeks to summarise the effects of a number of different physical and biological drivers on the planktonic populations. It depends upon many different parameters, not all of which are critical in determining the evolution of the biology. To determine which terms are important and explore a suitable parameters space for the biological variables, a greatly simplified version of the NPZ model described above was developed with all the advection/diffusion terms and boundary layer structure removed. This simplified NPZ model reduces to the formulism

\[
\frac{dN}{dt} = e P(t) \min(1, hN(t)) - d[1 - hN(t)] N(t) P(t) \times H[1 - hN(t)],
\]

\[
\frac{dP}{dt} = a \min(1, hN(t)) P(t) - b P(t) Z(t),
\]

\[
\frac{dZ}{dt} = Z(t) \min(\mu_z^{\text{max}}, cP(t)) - \mu_z \text{death} Z(t), \tag{19\ a,b,c}
\]
where \(H(x)\) is the Heaviside step function \((H(x) = 1 \text{ if } x \geq 0 \text{ and zero if } x < 0)\) and the
other constants are given by

\[
a = \beta E \mu_p^{\text{max}}, \quad b = I(R, T_R, \sigma_Z)Z_0, \quad c = YP_0 I(R, T_R, \sigma_Z),
\]

\[
d = 4\pi r_p S h D_N P_0, \quad e = (1 - \beta_E) \frac{s_N P_0}{N_0} \mu_p^{\text{max}}, \quad \& \quad h = \frac{R_{N_0}}{R_N^{\text{max}}}. \tag{20}
\]

These terms no longer exhibit any dependency on depth \(z\) or turbulent mixing \(\varepsilon\), which are features of the full LES-NPZ model. In this reduced form equations (19-20) are sufficiently simplified to allow some qualitative analysis of their behaviour. Assuming \(hN(t) < 1\) and \(cP(t) < \mu_z^{\text{max}}\), (the most common scenario) the equations possess a single co-existence equilibrium point in positive phase space, situated at

\[
(N_{EQ}, P_{EQ}, Z_{EQ}) = \left(\frac{1}{b} - \frac{e}{d}, \frac{\mu_z \text{ death}}{c}, \frac{d h}{b} \left(\frac{1}{h} - \frac{e}{d}\right)\right) \approx \left(\frac{1}{b} - \frac{\mu_z \text{ death}}{c}, \frac{a}{b}\right). \tag{21}
\]

Employing some fairly typical biological parameters, as listed in Table 2, one finds \(h^{-1} > 10ed^{-1}\), hence the approximation made in (21). Linearised stability analysis of the community matrix of partial derivatives at this equilibrium point yields three eigenvalues of the form

\[
(\lambda_1, \pm \lambda_2) \approx \left(\frac{d \mu_z \text{ death}}{c}, \pm \sqrt{a \mu_z \text{ death}}\right). \tag{22}
\]

These eigenvalues give rise to three solution branches near \((N_{EQ}, P_{EQ}, Z_{EQ})\), one of which is an exponentially increasing on a time scale of \(\tau_{\text{exp}} = c/d\mu_z \text{ death}\), whilst the remaining two associated branches give rise to oscillatory solutions for the \((P, Z)\) fields on a timescale

\[
\tau_{\text{oscil}} = 2\pi/\sqrt{a \mu_z \text{ death}}. \tag{23}
\]
(specifically for those used in Fig. 6) one finds that $\tau_{oscit} \approx 10.5$ days whilst $\tau_{exp} \approx 43$
days. So this analysis suggests that if the initial populations happen to lie close to

$\begin{pmatrix} N_{EQ}, P_{EQ}, Z_{EQ} \end{pmatrix} \approx (1.56, 0.43, 0.85)$, then $(P, Z)$ will oscillate regularly about their
equilibrium values at a relatively rapid frequency $\sim 1/\tau_{oscil}$, whilst growing relatively slowly
over the longer time scale $\tau_{exp}$. However, this conclusion is slightly deceptive because the
nutrient uptake term will shut down if ever $N$ gets too large and cells become satiated (when
$hN > 1$ in 19a). In such circumstances the predicted growth branch actually manifests itself
as a decay branch, over the same long timescale $\tau_{exp}$. This means that the $(P, Z)$ populations
simply oscillate regularly, whilst the nutrient concentration exhibits a net depletion, brought
about by funding of the new $P$ growth. Qualitatively, this kind of behaviour is illustrated in
Fig. 6, which shows the evolution, over a period of 25 days, of the normalised
Phytoplankton-Zooplankton-Nitrate fields, starting from initial values of
$\begin{pmatrix} N, P, Z \end{pmatrix} t=0 = (1.0, 0.5, 0.5)$. Oscillations in the $(P, Z)$ fields over a timescale close to the predicted $\tau_{oscit} \approx$
10.5 days are apparent, whilst the $N$ field decays relatively slowly from its initial value, since
there is no mechanism for nutrient replenishment in the simplified NPZ model. Note too how
the peaks in the $Z$ field always lag a few days behind those of the phytoplankton
concentration. This kind of behaviour is generic to other NPZ models, e.g. Baird & Emsley

In the simulations of the full LES-NPZ model which follow, the evolution of the $P$ and $Z$-
fields exhibits qualitatively similar oscillatory behaviour to that illustrated in Fig. 6. The
period of the oscillations in the mixing layer always lies close to the value set by $\tau_{oscil}$,
except in those instances when the initial conditions $(P, Z) t=0$ differ significantly from the
equilibrium values $(P_{EQ}, Z_{EQ})$. The default values of $(P, Z) t=0 = 0.5$ usually employed are
close enough to equilibrium for oscillatory behaviour to commence immediately. The
incorporation of turbulent mixing brings about some quantitative changes in the biological dynamics. Firstly the peak concentrations are somewhat reduced and smoothed out compared to those shown in Fig. 6 (typically by around 40% or so). The biological parameters in the simplified model are set appropriately for conditions at the surface $z = 0$, but in reality no phytoplanktonic cell will reside so close to the surface all the time and as a result its growth will be retarded by a lack of light when carried deeper into the boundary layer. This is counter-acted, to some extent, by the reduction in zooplankton predation pressure as one descends deeper into the boundary layer. The combination of these effects reduces the peak concentration scales. Secondly, as will be seen in many of the simulations, the turbulent mixing does not extend uniformly across the entire simulation domain. This means a cell initially situated somewhere near the top of the mixing layer has a higher probability of residing near the surface for longer periods and replicating more frequently than a cell initially residing below the mixing depth. (Since it experiences greater exposure to elevated light levels.) This effect gradually manifests itself in a visible lag in the intervals separating successive concentration peaks at different depths. The nutrient flux boundary condition (18) is sufficient to replenish nutrient losses due to phytoplankton growth, so the decline in nutrient concentration exhibited in Fig. 6 is not a feature of the full LES-NPZ model.

5. Studies of DCM/DBM formation and characteristics using the LES-NPZ model

Before looking in more detail at those bio/physical parameters which most influence the formation of DCM/DBM, it is worth pointing out some generic features common to all the LES-NPZ simulations results reported here. Each boundary layer is generated by means of the fixed wind forcing boundary condition (9), summarised by its $(U_*, U_S)$ parameters. Typically a boundary layer is spun up from rest and the respective $(U_*, U_S)$ forcing applied so that it relaxes into a state of quasi equilibrium, a process which takes about $\tau_{spin} \sim 60000$s. It
is at this point the mean $\varepsilon(z)$ profiles are estimated and these appear alongside the biological profiles in the figures that follow. Knowledge of $\varepsilon(z)$ allows one to calculate the biophysical coupling terms that appear in (3-5). The whole process is then repeated, but this time the onset of quasi-equilibrium is the signal for the biological fields to be introduced into the boundary layer. Biological evolution (usually) commences from an initial distribution $(N, P, Z)_{t=0} = (1.0, 0.5, 0.5)$, uniformly applied both horizontally and vertically. The biological fields are then allowed to evolve for a period $T_{\text{sim}} \sim 20-25$ days, in accordance with the biological parameterisations set out in Table 2.

The choice of simulation time period $T_{\text{sim}} \sim 20-25$ days is driven primarily by biological considerations. One needs to allow the biological fields to replicate through at least a couple of reproductive cycles. These values of $T_{\text{sim}}$ are somewhat larger than $\tau_{\text{pred}}$ the predictability timescale of the LES. The latter is the time by which imperfections brought about by not resolving down to the smallest scales propagate through the eddy hierarchy to produce significant contamination of the large scale motions (see Lesieur 1997 Chapter XI-XII). For this work $\tau_{\text{pred}} \approx 25T_E = 25 \times$ large-eddy turnover scale $\approx 1.5$ days. This does not invalidate the methodology, because a LES computed over times $T_{\text{sim}} > \tau_{\text{pred}}$ is still a statistically realistic representation of an actual flow, but one that is in the process of being advected as a complete body of water from its original position (as would happen under the action of a large scale current encompassing a much greater volume than the typical $120 \times 120 \times 33$ or $50m^3$ domains used here). It is important that the flow statistics generated by the LES remain roughly stable over a simulation time period. Fig. 3b shows the evolution of the mean velocity variance $\langle u''^2 \rangle_T$ profile over a $T_{\text{sim}} = 23$ day period, taken from a representative $(U_*, U_S) = (5.0, 5.6)$ simulation. As one can see the variance remains almost
constant throughout, and this scenario applies for both the $(v''^2)_{\tau}$ and $(w^2)_{\tau}$ variances too. So the basic statistics are sufficiently robust for meaningful conclusions to be drawn.

5a) Sensitivity to wind forcing.

The first set of simulations were designed to investigate the sensitivity of DCM/DBM formation to wind forcing. To achieve this, three different wind driven boundary layers (each with a simulation depth $z_S = -50m$) were spun up, with parameter settings $(U_*, U_S) =$ (2.0, 2.2), (3.0, 3.3) & (4.0, 4.4). These values are representative of low, intermediate and strong wind forcing regimes respectively (the terminology ‘strong’ is only comparative, since it represents a windspeed of only around 4ms$^{-1}$). Figs. 7a-c show the energy dissipation rate profiles for each of the three boundary layers in turn, alongside the corresponding profiles of zooplankton predation. Derived from the initial spin up run, these average profiles remain fixed throughout the subsequent biological simulation. The dissipation profiles show a progressive increase in the near surface maximum dissipation rates (0.65-2.0× $10^{-7}$m$^2$s$^{-3}$) with wind forcing, and a corresponding deepening of the mixing layer. In each case the dissipation rate falls to (almost) zero around about half the turbulent depth $\approx z_{TD}/2$ , equivalent to 10, 15, & 20m respectively. The predation rate profiles $I(R, T_R, \varepsilon, \sigma_Z)$ are calculated for a relatively large predator (length scale $r_Z = 3 \times 10^{-4}m$), possessing a spherical perception field of radius $R = 1.3 \times 10^{-2}m$, with an average swimming speed $\sigma_Z = 2 \times 10^{-4}ms^{-1}$, reacting in a time $T_R = 5s$ (see Table 2). These profiles are all fairly similar near the surface (as $T_R$ is only moderately fast, the predator cannot benefit from the increase in prey contacts brought about by the highest surface dissipation rates), falling away at different rates, before levelling off $\sim 10^{-7}$m$^3$s$^{-1}$ near $z_{TD}/2$. Since $\varepsilon(z < z_{TD}/2) \approx 0$ and the flow is relatively quiescent, the predator is forced to rely on its swimming capabilities alone in order to find prey. This means the predation rate is almost constant for $z < z_{TD}/2$. 
Figs. 8a-c show the corresponding evolution of the biological \((N, P, Z)\) profiles over the simulation time \(T_{sim}\), assuming a maximum (surface) phytoplankton growth rate of \(\mu^\text{max}_P = 5 \times 10^{-5}\) s\(^{-1}\). In these simulations nutrient losses through biological growth were compensated for by a nutrient flux \(\langle wN^+ \rangle\) into the boundary layer through the base \(z_S\) of the simulation domain. Since losses from the former are easily outweighed by gains from the latter, the effect over time is to create a nutricline, with significantly higher nutrient concentrations at the base of the layer compared to the surface. Consider the \((U_s, U_S) = (2.0, 2.2)\) case Fig. 8a first. The mixing layer of \(z_{ML} \approx z_{TD}/2 = 10\) m is relatively shallow, insufficient for any of the extra nutrient added at the base to be vertically mixed into the surface region. So it simply accumulates, uselessly, in the lower layers. However, this is of little import since the initial nutrient level \(N = 1.0\) is already sufficient to support immediate \(P\) growth. However, this growth is not uniformly distributed across the boundary layer. Instead a DBM forms at a depth \(z = 8 - 15\) m, at or just below the point \(z_{ML} \approx z_{TD}/2\) where \(\varepsilon(z) \approx 0\). The position and form of the simulated DBM is strikingly similar to those recorded in the experimental datasets shown in Fig.1 (which are for DCM). This illustrates the importance of M13’s results, since most other observational reports on DCM do not include any corresponding measure of turbulent mixing. This numerical modelling work strongly supports M13’s observations that the two are indeed correlated. Notice too that DBM is not brought about by the presence of the nutricline, because that has not had time to form as yet. The numerical DBM is a transient feature, lasting about 5 days or so because, just as in the simplified model illustrated in Fig. 6, the growth in the \(P\) concentration promotes a corresponding surge in the zooplankton concentration. A numerical DZM forms at a similar depth but somewhat after the DBM, consuming the latter before itself dies off. This restores the biological fields to a uniform (not the initial) state after about 20 days. One would anticipate the cycle would be repeated roughly in accordance with the dynamical properties
discussed for the simplified model (for these parameters $\tau_{oscit} \approx 12$ days at a depth of $z \approx 7$ m), although this has not happened by the end of the simulation. For the $(U_*, U_z) = (3.0, 3.3)$ simulation shown in Fig. 8b, the results are broadly similar. Again the $z_{ML} \approx z_{TD}/2 = 15$ m depth is still too shallow for much of the replenishment nutrient added at $z_S = 50$ m to be mixed into the surface region. But with initial nutrient levels already high across the simulation domain, a DBM still forms relatively quickly. As before the DBM forms just below $z_{TD}/2$, between $z = 17 - 23$ m, persists for about 5 days, before being consumed by the numerical DZM, which itself dies out through lack of food after about 15 days. Notice the initial DBM is thicker than in Fig. 8a but less intense. This fits with statistical analysis of M13 (specifically Fig. 4 of that paper) that within the $DCM_{depth} \pm 0.5DCM_{thick}$ range, the highest fluorescence values are associated with smaller values of $\epsilon(z)$. However, for the strongest wind forcing case (Fig. 8c) the results are quite different. In this instance no DBM forms. Instead the $P$ profile grows almost uniformly across the whole of the simulation domain, before being consumed by the growth in zooplankton it has stimulated.

It is worth looking more closely at why no DBM forms for the $(4.0, 4.4)$ case, when based on the other less windy simulations, one might expect a somewhat less intense maxima to occur somewhere about $z = 25$ m. There are two possible reasons. First the $\epsilon(z)$ profiles derived turbulent kinetic energy budget equation, have a tendency to underestimate the extent of the vertical mixing lower down in the boundary layer. This can be seen by examining the horizontally averaged vertically velocity variance profiles $\langle w^2 \rangle_T$ for the three simulation regimes (Figs. 9a-c). For the low wind case $(2.0, 2.2)$, the $\langle w^2 \rangle_T$ profile closely matches the corresponding $\epsilon(z)$ profile (cf. Figs. 7a & 9a), but for the higher wind cases the $\langle w^2 \rangle_T$ profile decays more slowly and penetrates to a deeper level than the corresponding $\epsilon(z)$ profiles.

This behaviour is also a feature of other LES ocean boundary layer codes (e.g. McWilliams et al. 1997, Pearson et al. 2015) which incorporate Langmuir circulations. It is also evident
from M13 experimental measurements of $\varepsilon(z)$ (Fig.1) that energy dissipation does not abruptly cease at one particular depth, but rather there is evidence of intermittent turbulent bursts extending below $\text{peak}_{\text{depth}} - \text{peak}_{\text{thick}}$. Polten and Belcher (2007) point out that in contrast to classic shear driven boundary layers, inclusion of significant wave effects characterised by the Stokes drift term $U_S$, results in increased vertical transport associated with the formation of down-welling jets carrying fluid down as far as the turbulent depth $z_{TD}$. This feature is probably a factor underlying the strong sub-surface peaks observed in the $\varepsilon(z)$ profiles recorded at the North Atlantic/Antarctic sites. For the strong wind/wave (4.0, 4.4) simulation this enhanced vertical mixing penetrates to $z_{TD} = 40\text{m}$, preventing the formation of a DBM in this instance. The other possible reason is that in this instance the setting of $z_S = 50\text{m}$ is too small, and if the simulation domain were to be extended to say $z_S = 75\text{m}$ it would be large enough facilitate the generation of a weak DBM. M13’s observations show that DBM can occur at depths down to 100m or so, in boundary layers subject to genuinely strong $U_* > 5.0 \times 10^{-3}\text{ms}^{-1}$ wind forcing conditions.

Figs. 10a-c show the evolution of the biological $(N, P, Z)$ profiles for the same three boundary layers as before, only this time the replenishing nutrient flux is applied at the surface rather than the base. So unlike in the previous examples, this extra nutrient is mixed throughout the mixing layer, eventually reaching depths close to $z_{TD}$ for the (4.0, 4.4) simulation. Although a surface flux is a somewhat unrepresentative of how nutrient replenishment typically occurs within ocean mixing layers, it provides a means, within the model constraints, of making the extra nourishment readily available to the biological populations in those regions of the water column where DBM formed previously. For the low and intermediate wind simulations (2.0, 2.2) & (3.0, 3.3) the initial behaviour is much as before, with transient DBM forming at around $z_{ML} \approx z_{TD}/2$ (the extra surface nutrient means the DBM form slightly closer to the surface and are more intense). However, the main
effect of adding replenishment nutrient at the surface is to stimulate the appearance of a
secondary DBM, about 15 days after the primary DBM was consumed by the zooplankton
population. The secondary DBM develop at the same depths as the primary and last about the
same time, but are slightly less intense. For the strong wind (4.0, 4.4) simulation the extra
vertical mixing prevents the formation of either a primary or secondary DBM, much as
before. Two points come out of this. First, DBM formation is clearly a fairly robust process,
which operates independently of changes in the nutrient distribution within the boundary
layer. Provided enough nutrient is present initially and the mixing is not too strong, DBM are
very likely to form. Second, if background nutrient levels remain fairly high through some
effective means of replenishment as in Fig. 10, there is a tendency for the characteristic
biological timescales to manifest themselves over and above the homogenising tendencies of
the physical boundary layer drivers. Hence the formation of the secondary DBM, seen in the
low wind simulations, occurs after about 15 days, close to the predicted $\tau_{oscit} \approx 12$ days
timescale derived from the biological parameters alone. By contrast, secondary DBM had not
formed by the end of the base flux simulations, because not enough nutrient was present to
stimulate them.

5b) Sensitivity to predation pressure and nutrient initial conditions

The simulations presented in the previous section assumed a relatively large ($r_Z = 3 \times$
$10^{-4}$ m) zooplankton predator, with a correspondingly large contact radius $R = 1.2 \times 10^{-2}$ m
and swimming capabilities $\sigma_Z = 2 \times 10^{-4}$ ms$^{-1}$. It is interesting to investigate what happens
if the predator were made somewhat smaller, reduced in size to $r_Z = 5 \times 10^{-5}$ m, with the
other parameters rescaled accordingly (see Table 2, e.g. $\sigma_Z = 5 \times 10^{-5}$ ms$^{-1}$ and $R = 2 \times$
$10^{-3}$ m). The effect of these basic size reductions is to dramatically slow down the predation
rate for an individual predator. This is illustrated in Fig. 11, which shows the corresponding
predation rate calculated from a $\varepsilon(z)$ profile taken from a $(U, U_2) = (3.0, 3.3)$ simulation
(with $z_S = -33\text{m}$ rather than $z_S = -50\text{m}$). Compared to the corresponding profile for the
large predator (Fig. 7b), the individual capture cross section has fallen by a factor of ~200.
However, smaller predators tend to be more numerous than larger ones. In these illustrative
examples the background concentration for the large predator was set to $10^2 \text{cells m}^{-3}$,
increasing to $2 \times 10^4 \text{cells m}^{-3}$ for the smaller predator. This effectively offsets the drop in
capture cross section, meaning the overall predation pressure on the $P$ field is little changed.

Fig. 12 shows the evolution of the biological ($N, P, Z$) profiles based upon the small
zooplankton predator with replenishment nutrient added at the base. Compared to the
corresponding evolution profiles $(U_*, U_S) = (3.0, 3.3)$ for the large predator, shown in Fig.
8b, a couple of distinctive features are obvious. On this occasion the initial $DBM$ forms at just
below $z = z_{TD}/2$ between about 15-20m much as before, but then two secondary $DBM$
evolve, after about 10 and 20 days respectively. The reason for this much faster evolution lies
in the fact that the death rate of the small predator has increased by a factor of 10/3
compared to that of the large predator (smaller organisms tend to have shorter life-spans).
From the analysis of Section 4 this reduces $\tau_{oscil} = 2\pi/\sqrt{a\mu_{Z,death}}$ to about 6.5 days,
leading to the production of two secondary $DBM$ over the $T_{sim}$ interval. The other distinctive
feature is that the secondary $DBM$ are almost as intense as the primary and form a little
deeper in the water column. This can be put down to the fact that the simulation domain is
somewhat shallower than previously, which means that it is easier for nutrient added at the
base to reach the regions where $DBM$ formation occurs. So it is more easily accessible for the
phytoplankton, producing a strong response in the secondary growth phases. Looking at the
 corresponding results for a surface nutrient flux in Fig. 13 (cf. Fig. 10b for the large predator)
the results are broadly similar to the base flux results, with the formation of two secondary
$DBM$, although on this occasion they are slightly less intense than the primary. Since nutrient
entering at the surface is mixed more thoroughly throughout the mixing layer, the background
concentration never reaches the levels seen in the base flux results, reducing the intensity of
the secondary growth surge. Notice too that the mixing has the effect of gradually merging
the secondary maxima together, so the $DBM$ becomes a more permanent feature of the
boundary layer. Overall, these results show that phytoplankton populations residing in the
turbulent boundary layer will tend to evolve to form $DBM$ a little below $z_{TD}/2$, provided the
boundary layer contains enough nutrient to stimulate them. These $DBM$ are robust features of
the biological dynamics, and form independently of the finer details of the predation
pressures imposed by different zooplankton species. So observations of $DBM$ formation in
real biophysical boundary layers, which may contain a myriad of co-existing/competing
planktonic species, should not be surprising.

These conclusions lead to the question what would happen if the initial nutrient conditions
were not conducive to $DBM$ formation? To this end a simulation was carried out with
$(N,P,Z)_{t=0} = (0.1, 0.5, 0.5)$, to see what effect a very small initial nutrient concentration
would have on the development of the biological fields. In this simulation the wind forcing
was relatively low $(U_s, U_S) = (2.5, 2.8)$, and nutrient replenishment was added through the
surface. The phytoplankton field was subject to a predation pressure term similar to that
shown in Fig. 11, except that in this case the swimming contribution was switched off $\sigma_Z =
0.0\text{ms}^{-1}$. This was compensated for by a reduction in the reaction time to $T_R = 1\text{s}$. Since the
predator can no longer swim, it means that the phytoplankton field is not actually subject to
any predation pressure below the turbulent depth $z_{TD} \approx 25\text{m}$, because in this region there are
neither advective nor swimming motions to bring a predator/prey pair into close proximity.
The corresponding $(N,P,Z)$ profiles are shown in Fig. 14. The outstanding feature of these
results is the formation not of a $DBM$, but instead a near uniform biological profile extending
across nearly all the turbulent depth. But the circumstances of the evolution of this feature are
significant. Since $N_{t=0} = 0.1$ is so low, the initial behaviour of both the $(P,Z)$ fields is to die
off through lack of food resources. As the boundary layer is replenished with nutrient (notice
it never quite reaches the starting value of $N = 1.0$ for the previous simulations) the
phytoplankton is able to respond with renewed growth after about 15 days. However, at this
time the zooplankton population is still virtually extinct, so there is no predation pressure to
retard the phytoplankton growth in the upper regions of the mixing layer. Consequently the
growth is close to uniform across the mixing layer and no significant DBM forms. The
decline in the phytoplankton growth rate due to reductions in the ambient light level across
the mixing layer is insufficient, in itself, to generate a DBM. (There is some variation due to
the light. After 18 days, when the global concentration of $P$ reaches a maximum, $\langle P \rangle = 1.78$
at the surface, increasing to $\langle P \rangle = 2.06$ at $z = -0.65z_T$, a difference of 14%. But this is
small amount compared to the 50–300% differences seen in the experimental results of Fig. 1
and the simulations in which predation pressure is significant.) Instead the strength of the
vertical mixing ensures that all the different $P$ cells are exposed to roughly the same amount
light, and consequently they all grow at the roughly the same rate. After 20 days or so the
zooplankton population starts to recover in response to the new food resource now available.
It too grows uniformly across the boundary layer. One would anticipate that if the simulation
were to be run for a longer period of time, then on the next population cycle a situation more
akin to the previous simulations would pertain and DBM formation would occur. This is
because the nutrient conditions would no longer be so extreme as to force both planktonic
fields to near extinction and hence the higher predation pressure near the surface would again
manifest itself. It also suggests that the observational DBM recorded by M13 formed as they
did because a) their boundary layers were either well stocked, or recently replenished, with
significant amounts of nutrient and b) the low fluorescence measurements found in the
surface regions are a consequence of high predation pressure in those localities. To
investigate these points further, Fig. 15 shows what happens in the scenario when the
predation term is switched off altogether. Starting from a standard, nutrient rich

\[(N, P, Z)_{t=0} = (1.0, 0.5, 0.5)\] initial profile, the zooplankton population starves and quickly
dies out. Unrestrained by predation, the phytoplankton population grows rapidly to very high
concentrations, almost uniformly across those parts of the boundary layer where there is
sufficient nutrient to support the excess growth (in the top layers for the surface flux, Fig.
15a; at or below \(z_{TF}\) for the base flux, Fig. 15b). Again there is little sign that the decline in
the ambient light level with depth is a sufficient stimulus (by itself) to initiate significant
\(DBM\) formation in these wind driven boundary layers.

A variation on this theme is to initiate a simulation with a non-uniform \(N_{t=0}\) profile. Two
such examples are shown in Fig. 16. Fig. 16a shows a run beginning with a moderately high
\(N = 1.4\) nutrient concentration near the surface, declining uniformly to a minimum value of
\(N = 0.2\) at \(z = z_S\). The subsequent behaviour of the \((N, P, Z)\) profiles from this initial state is
interesting. Near the surface the abundance of nutrient promotes rapid growth in the
phytoplankton population, but this in turn is rapidly consumed by the zooplankton. Since the
reaction time \(T_R = 1\)s of this small predator is rapid, it is able to feed very efficiently near the
surface. Consequently the phytoplankton population has hardly any time to establish itself
before it is consumed and hence the \(P\) concentration falls away. One can infer its transient
presence by the small predator characteristic \(\tau_{oscit} \approx 6.5\) day period still to be seen in the
upper zooplankton profiles. Lower down one sees the formation of a very intense \(DBM\) at a
depth of about 20m, somewhat deeper than those shown in Figs. 8, 10 & 12. Formation at this
depth is brought about by the juxtaposition of the relatively high nutrient levels from the
initial profile, remaining in situ due to the lack of mixing, in combination with a rapid decline
in predation pressure to near zero, again caused by the lack of any mixing or swimming to
bring about predator/prey contacts. This \(DBM\) also lasts longer than those generated in other
simulations and is not subject to the \(\tau_{oscit} \approx 6.5\) day period which pertains in the upper layers
where strong predation pressure is a factor. The initially imposed nutricline in effect creates two somewhat disconnected boundary layers, in which the biological dynamics evolves at different rates. Fig. 16b shows what happens if the initial nutrient profile is inverted from high-low to low-high. As in Fig. 15b, the low level of predation at depths \( z < z_{TD} \) combined with easily availability of nutrients (as distinct from Fig. 16a), initially produces very high phytoplankton concentrations. But in this scenario, unlike in Fig. 15b, there is sufficient predation pressure to regulate this growth after just a few days. Higher up (and somewhat overshadowed by the growth near \( z_s \)) a DBM again develops around 20m as in Fig. 16a. The higher ambient nutrient concentration in this case means it is actually twice as intense (cf. the contrasting \( P \) concentration scales in Fig. 16) as the DBM which develops from the high-low nutricline.

The intensity scales of both DBM shown in Fig. 16 would indicate that they are somewhat artificial constructs (none of the observed DBM recorded by M13 show such a high level of intensity), brought about by an extremely favourable correlation between the initial nutrient profiles and the rapid decline in both mixing and predation levels below \( z_{TD}/2 \). Nevertheless, they serve to highlight the hypothesis that those regions of the water column which are most favourable to DBM formation are those that exhibit a), sufficiently high nutrient and light levels to promote growth in combination with b), a significant fall off in the ambient predation pressure. Since sharp reductions in \( \varepsilon(z) \) bring about a corresponding easing in predation pressure at or just below \( z_{ML} \approx z_{TD}/2 \), it is not surprising that simulated DBM are seen to develop around this depth. It would also explain the strong observational correlations, manifest in M13’s datasets, between the location of real DBM and those regions of the water column where the energy dissipation rate is in decline (Fig. 1).

5c) Horizontal Distribution
Since the LES-NPZ model carries out three dimensional simulations, it is worth trying to discern any significant patterns in the evolution of the biological fields when viewed across a horizontal plane. Periodically during the course of each simulation, instantaneous snapshots of the horizontal distribution of the biological fields are recorded at various different depths. These can then be processed to create ‘movies’ of the biological fields as they evolve during a simulation (copies of these ‘movies’ are available from the authors on request). Some examples of these snapshots, taken from the \((U_*, U_\delta) = (3.0, 3.3)\) surface nutrient flux simulation (q.v. Fig. 10b for the corresponding vertical profiles), are shown Figs 17-19. Fig. 17 is taken at a depth of 10m after 4.7 days, whilst Figs. 18 & 19 are for a depth of 20.4m after 4.7 and 5.9 days respectively. The significance of these latter two selections is that they represent samples taken from the primary \(DBM\), which from Fig. 10b is seen to reach its maximum intensity at \(~20m\) after around four days. But first it is interesting to consider why the \(DBM\) does not form at a shallower depth, at say 10m for example. Fig.17 shows the instantaneous vertical velocity field \(w\) at the same moment as the corresponding biological correlations. The \(w\) field exhibits the characteristic Langmuir turbulence pattern of up and down-welling zones (McWilliams et al. 1997, Lewis 2005, Polten & Belcher 2007, Teixeira & Belcher 2010), in this case rotated clockwise (~\(40^\circ\)) from the wind direction (the \(x\)-axis) by a combination of the Coriolis forcing and the Stokes drift term (see Lewis & Belcher 2004). This ‘streakiness’ pattern of elongated up and down-welling zones is replicated (but to a lesser extent) in the biological fields. It is particularly noticeable in the distribution of the \(P\) field, which exhibits a correlation between high phytoplankton concentrations and vertical down-welling. Since nutrient is being added at the surface in this instance, the down-welling regions act, in effect, as richer local food environs for the phytoplankton, providing the spur they need for significant extra growth (~up to 7% more than the horizontal mean concentration). Notice that this all happens relatively quickly, because the \(N\) field shows a
significant absence of nutrient in the down-welling zones, presumably because the excess has
already been utilised to boost the growth of the local phytoplankton population. Assuming an
average down-welling velocity of \( w \approx 2 \times 10^{-3} \text{ms}^{-1} \) around this depth, it would take about
500s for any excess nutrient to be advected a distance of 1m. This would be time enough to
produce differentials in the \( P \) concentration field of between \( \sim 1-2\% \) (assuming a light
reduced \( P \) growth rate of \( \sim 3.3 \times 10^{-5} \text{s}^{-1} \)], roughly what is observed. The much slower
growing zooplankton \( (\mu_z^\text{max} = 2.9 \times 10^{-6} \text{s}^{-1}) \) are not sensitive enough to respond to stimuli
over as (relatively) short a time period as 500s, and hence the distribution of the \( Z \) field is
almost completely uniform in the horizontal (cf. the small colour-scale changes in Fig. 17d).

Looking at the corresponding horizontal distributions recorded at the exact same point in
time, but at a depth of 20m (Fig. 18), one is immediately struck by the fact that the vertical
mixing is somewhat weaker and the ‘streakiness’ pattern of elongated up and down-welling
zones is less pronounced. As a result those regions of the \( P \) field distribution exhibiting
higher than average growth (shown in yellow), now cover a broader area than in Fig. 17.
What seems to be happening is that by the time one reaches a depth of \( z \approx 20\text{m} \), the excess
nutrient is no longer being confined to the strictly defined down-welling zones that
transported it from the surface. This idea is supported by the velocity variance data shown in
Fig. 3a (from a simulation with comparable wind forcing) which shows that at \( z \approx 10\text{m} \) the
vertical \( \langle w^2 \rangle_T \) velocity component is dominant, but by \( z \approx 20\text{m} \) the horizontal combination
of \( \langle u''^2 \rangle_T + \langle v''^2 \rangle_T \) exceeds that of \( \langle w^2 \rangle_T \). This would produce a pooling effect, caused by
the replenishment nutrient spreading out (horizontally) from the disintegrating down-welling
zones. This pooling of nutrient, \textit{in combination with} the reduced zooplankton predation
pressure at this depth, then promotes the formation of the primary \( DBM \) in this region. Notice
that the pooling of nutrient is not directly apparent from the \( N \)-field itself because on arrival it
would be quickly absorbed by the phytoplankton based on the timescales mentioned above.
Rather it manifests itself in the relatively uniform excess growth seen in the $P$ field distribution. In future it would be interesting to test this pooling hypothesis quantitatively, by carrying out simulations to monitor the average horizontal flux of nutrients at different depths to see if $DBM$ formation corresponds to increased levels of horizontal mixing. Fig. 19 shows values of the biological fields at this depth after about 6 days, just as the primary $DBM$ is starting to break down. Over the interval of 1.3 days between Figs. 18 & 19, the zooplankton has had the opportunity to generate excess growth in response to the increased higher $P$ field concentrations, increasing the local predation pressure, which ultimately destroys the $DBM$ feature.

6. Conclusions

The study of the formation and the underlying factors that drive $DCM/DBM$ formation has a long history (Cullen 2015 and reference therein). The literature would seem pretty much exhaustive. However, the recent publication by M13 of various open ocean datasets which unequivocally link $DCM$ formation and levels of background turbulent mixing (something previously that has only been speculated on), provides a new slant and calls for a more detailed investigation of this phenomena. Advances in computing power and resources allow one, using the LES methodology, to simulate three dimensional, wind and wave driven turbulent boundary layers in great detail. By coupling such simulations to a generic type of NPZ model specially adapted to reflect the influence of background turbulence levels on growth and predation rates, one has the means to carry out just such an investigation. The results reported here largely corroborate the findings of M13. Provided the wind forcing is not too strong (q.v. Figs. 8c & 10c) and the boundary layer is relatively nutrient rich, the simulations predict $DCM/DBM$ formation at depths at or just below half the
turbulent depth $\approx z_{tp}/2$, the level at which the upper mixing layer starts to peter out, very similar to the observational data. This depth is a robust feature, as the $DCM/DBM$ continue to form here irrespective of whether the nutrient profile is uniform (primary $DBM$), or develops in the presence of a nutricline (either bottom up or top down) as seen in the secondary $DBM$ (Figs. 10a-b, 12, 13 & 16). The simulations also support the idea that $DCM/DBM$ are generated primarily in response to predation pressure (Figs. 14-16). Starting the simulations from a very low nutrient base (see Fig. 14) effectively switches off the predation pressure by starving the zooplankton population to near extinction. In its absence, when phytoplankton growth was re-initiated by replenishment of nutrient through the surface, growth resumed uniformly and no $DBM$ formed. Removing the predation term altogether from the model, also inhibited $DBM$ formation (Fig.15). Taken together, these results indicate that whilst the vertical mixing is sufficiently vigorous to circulate phytoplankton cells throughout the upper mixing layer so that they all get to experience pretty much the same amount of light, it is not vigorous enough to offset the retardation in growth experienced near the surface through increased levels of predation pressure (see the various predation rate profiles). This is not too surprising because increases in turbulent mixing generate corresponding increases in predation pressure (provided the predator can react fast enough to capture the extra prey contacts it makes), but has relatively little influence on the amount of light penetrating the mixing layer. It is also significant that the $DBM$ formed irrespective of the type of predator (large or small) was used. This conclusion concerning the importance of predation pressure in $DCM/DBM$ formation was also reached by Fennel & Boss (2003) in their (somewhat simpler) mathematical modelling work. It is just possible that $DCM/DBM$ formation could be initiated by a combination of retarded light level growth and a strong positive nutricline (low nutrient at the surface, high at the base) without the need for any predation pressure (this hypothesis is not specifically tested here). However given the results shown in Fig. 14, such a combination
of stimuli does not seem sufficient to produce the intense DBM observed in Fig. 1. Rather this work tends to support the ideas expressed by Banse (2013) of the importance of “top-down” processes in DCM/DBM formation, since phytoplankton growth is usually matched or exceeded by grazing losses.

The question as to why the DBM form at the depth they do is intriguing. From the investigations here, the depth $z_{TD}/2$ marks the point at which the coherence of the Langmuir cells driven by the wind and wave generated turbulence starts to break down. The vertical velocity component, which up that point is the dominant feature of the boundary layer turbulence, weakens (see Fig. 3a) and the horizontal components become more prevalent. This leads to a rapid increase in the vertical nutrient gradient as $\langle w^2 \rangle_T$ declines (see Fig. 10), and a smoothing out of the horizontal gradients as the relative strength $\langle u''t^2 \rangle_T + \langle v''t^2 \rangle_T$ increases (cf. Figs. 16 & 17). In combination this would tend to lead to a pooling of nutrient at around this depth, initiating a strong phytoplankton growth in response. If so, this work indicates that DCM/DBM formation can actually be influenced by the surface wave characteristics driving the Langmuir turbulence regime. A surprising connection, given that in the past it has been assumed that surface wave effects were simply too small to significantly influence even the ocean boundary layer dynamics, let alone the associated biology.

This effect could also be brought about by other features of the flow, such as the presence of shallow thermo/pycnocline acting to restrict the extent of the vertical transport. Since the boundary layers generated in these simulations are unstratified, it is difficult to definitively rule this out. However, in their observations M13 found that the position of the $DCM_{depth}$ lay some ~18m (on average) below the corresponding $\epsilon(z)$ peak$_{depth}$ when stratification was relatively low (Section 2). This strongly suggests that their $DCM$ were not brought about by
the presence of a pycnocline. Indeed Fennel and Boss (2003) argue that in contrast to
relatively small lakes (e.g. Simmonds et al. 2015), the density changes associated with
shallow pycnoclines found in the open ocean would be too small to disrupt vertical transport
very significantly. This idea is supported by the experimental $\varepsilon(z)$ profiles of M13 (Fig. 1)
and the numerical vertical velocity profiles shown in Fig. 9, which both show that vertical
mixing does not shut off abruptly at around $z_{TD}/2$ but continues to exert an influence to a
least twice this depth. This would tend to disrupt and deepen pycnoclinic formation, making
it unlikely this is the cause of M13’s observed DCM.

The DCM/DBM generated in these simulations are transient, lasting no more than a few
days. However, this is due to the fact that the biological $P-Z$ fields are two generic
representations of many different planktonic species. In reality DCM/DBM found in the
ocean will contain many different species each subject to their own specific growth and
predation cycles. So in the absence of any very strong mixing events, observed DCM are
likely to be longer lasting than those generated here, although their species composition may
change over time. This idea could be tested in more detail by introducing more separate
biological species (e.g. by having the large predator feeding directly on the small predator
which in turns feeds on the $P$ field) into the simulations, provided suitable biological
coupling terms could be introduced into the model equations (3-5). Future developments of
this kind should enable better parameterizations for the simpler, but very much faster 1D
biophysical models most commonly in use. And if experimental development is such that the
recording of physical measurements (e.g. more $\varepsilon(z)$ sampling) in conjunction with biological
ones becomes the norm, then there is scope to develop specialised LES-NPZ models in order
to study very specific planktonic ecosystems.
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Figure Captions

Figure 1. Four illustrative fluorescence (left) and energy dissipation rate profiles taken from Fig. S1 of the paper by Macías et al. 2013, showing how DCM are to be found just below $z = \text{peak}_\text{depth}$, where $\langle \varepsilon(z) \rangle$ reaches its maximum value $\varepsilon_{\text{max}}$. The measurements are taken from four different sites. Profile 6 is from the Alboran Sea; Profile 21 is from the Strait of Gibraltar; Profile 28 is near the Antarctic peninsula; Profile 31 is from the North Atlantic. Full details of these sites, along with many further similar profiles are presented in Macías et al. 2013.

Figure 2. Time (over a period $T = T_{\text{sim}}$) and spatially averaged velocity profiles $\langle u \rangle_T \quad \text{and} \quad \langle v \rangle_T \quad \text{(units ms}^{-1})$. Data derived from a $(U_s, U_S) = (3.5, 3.9)$ simulation.

Figure 3. a) Time (over a period $T = T_{\text{sim}}$) and spatially averaged velocity variance profiles $\langle u'' \rangle_T \quad \text{and} \quad \langle v'' \rangle_T \quad \text{and} \quad \langle w^2 \rangle_T \quad \text{normalised by} \quad U_s^2$. Data derived from the $(U_s, U_S) = (3.5, 3.9)$ simulation. b) Evolution of $\langle u'' \rangle_T$, over periods of $T = 5, 8, 12, 16 \& 19$ days. Data derived from the $(U_s, U_S) = (5.0, 5.6)$ simulation.

Figure 4. Time (over a period $T \approx 1$ day) and spatially averaged kinetic energy dissipation rate profiles $\varepsilon(z)$. Data derived from the $(U_s, U_S) = (2.0, 2.2) \quad \text{and} \quad (3.5, 3.9) \quad \text{and} \quad (5.0, 5.6) \quad \text{simulations}.$

Figure 5. Illustrative profiles of the variation of the predation rate integral $I(R, T_R, \varepsilon, 0)$ for a non-swimming predator and contact radius $R = 2 \times 10^{-3}$ m. Data derived from the $(U_s, U_S) = (2.0, 2.2) \quad \text{and} \quad (3.5, 3.9) \quad \text{and} \quad (5.0, 5.6) \quad \text{simulations with 5a) } T_R = 5s \quad \text{and 5b) } T_R = 15s.$
Figure 6. Evolution of the mean concentrations of Nutrient, Phytoplankton & Zooplankton derived from the simplified NPZ model for $\mu_p^{\text{max}} = 2.5 \times 10^{-5} \text{s}^{-1}$ with other biological parameters as in Table 2.

Figure 7. Energy dissipation profiles (left) and the corresponding zooplankton predation rate profiles (right) taken from three LES-NPZ model simulations subject to a) low wind $(U_*, U_S) = (2.0, 2.2)$, b) intermediate wind $(U_*, U_S) = (3.0, 3.3)$ & c) high wind $(U_*, U_S) = (4.0, 4.4)$ forcing. The predation profiles are based upon data for the large predator (Table 2) with $\sigma_Z = 2 \times 10^{-4} \text{ms}^{-1}$, $T_R = 5s$ and $R = 1.2 \times 10^{-2} \text{m}$.

Figure 8. Evolution profiles of the normalised $\langle N \rangle$, $\langle P \rangle$ & $\langle Z \rangle$ concentrations, starting from initial values of $(1.0, 0.5, 0.5)$ respectively. An inward nutrient flux boundary condition is implemented at the base $z_s = -50\text{m}$ of the simulation domain. a) low wind $(U_*, U_S) = (2.0, 2.2)$, b) intermediate wind $(U_*, U_S) = (3.0, 3.3)$ & c) high wind $(U_*, U_S) = (4.0, 4.4)$ forcing. Biological data as given in Table 2, incorporating the large zooplankton predator.

Figure 9. Evolution of the (normalised) vertical velocity variance $\langle w^2 \rangle_T$ profile recorded during different stages of a typical set of simulations. a) low wind $(U_*, U_S) = (2.0, 2.2)$, b) intermediate wind $(U_*, U_S) = (3.0, 3.3)$ & c) high wind $(U_*, U_S) = (4.0, 4.4)$ forcing. Note the greater penetration depths compared to the corresponding energy dissipation profiles shown in Fig. 7.

Figure 10. Evolution profiles of the normalised $\langle N \rangle$, $\langle P \rangle$ & $\langle Z \rangle$ concentrations, starting from initial values of $(1.0, 0.5, 0.5)$ respectively. An inward nutrient flux boundary condition is implemented at the surface $z_s = 0\text{m}$ of the boundary layer. a) low wind $(U_*, U_S) = (2.0, 2.2)$, b) intermediate wind $(U_*, U_S) = (3.0, 3.3)$ & c) high wind $(U_*, U_S) = (4.0, 4.4)$ forcing. Biological data as given in Table 2, incorporating the large zooplankton predator.
Figure 11. Energy dissipation profile (left) and the corresponding zooplankton predation rate profile (right) taken from the intermediate wind \((U_*, U_S) = (3.0, 3.3)\) forced simulation. The predation profiles are based upon data for the small predator (Table 2) with \(\sigma_Z = 5 \times 10^{-5} \text{ms}^{-1}, T_R = 5 \text{s} \) and \(R = 2 \times 10^{-3} \text{m}\).

Figure 12. Evolution profiles of the normalised \(\langle N \rangle, \langle P \rangle \) & \(\langle Z \rangle\) concentrations, starting from initial values of \((1.0, 0.5, 0.5)\) respectively for intermediate wind \((U_*, U_S) = (3.0, 3.3)\) forcing. An inward nutrient flux boundary condition is implemented at the base \(z_s = -33 \text{m}\) of the simulation domain. Biological data as given in Table 2, incorporating the small zooplankton predator.

Figure 13. Evolution profiles of the normalised \(\langle N \rangle, \langle P \rangle \) & \(\langle Z \rangle\) concentrations, starting from initial values of \((1.0, 0.5, 0.5)\) respectively for an intermediate wind \((U_*, U_S) = (3.0, 3.3)\) forcing. An inward nutrient flux boundary condition is implemented at the surface \(z_s = 0 \text{m}\) of the boundary layer. Biological data as given in Table 2, incorporating the small zooplankton predator.

Figure 14. Evolution profiles of the normalised \(\langle N \rangle, \langle P \rangle \) & \(\langle Z \rangle\) concentrations, starting from initial values of \((0.1, 0.5, 0.5)\) respectively for an intermediate wind \((U_*, U_S) = (2.5, 2.8)\) forcing. An inward nutrient flux boundary condition is implemented at the surface \(z_s = 0 \text{m}\) of the boundary layer. Biological data as given in Table 2, incorporating the small zooplankton predator, except here it is non-swimming \(\sigma_Z = 0.0 \text{ms}^{-1}\) and fast reacting \(T_R = 1 \text{s}\).

Figure 15. Evolution profiles of the normalised \(\langle N \rangle, \langle P \rangle \) & \(\langle Z \rangle\) concentrations, starting from initial values of \((1.0, 0.5, 0.5)\) respectively, for an intermediate wind \((U_*, U_S) = (2.5, 2.8)\) forcing. In this instance the zooplankton predation term is switched off. Fig. 15a is for a
surface nutrient flux; whilst in 15b it is imposed at the base of the simulation domain. Other
data as in Fig. 14.

Figure 16. Evolution profiles of the normalised $\langle N \rangle$, $\langle P \rangle$ & $\langle Z \rangle$ concentrations for an
intermediate wind $(U_*, U_S) = (2.5, 2.8)$ forcing. In Fig. 16a, the initial nutrient profile forms
a nutricline, ranging from $0.2 - 1.4$ for $z = -33$ to $z = 0$ m respectively. In Fig. 16b, this
initial profile is inverted, with low concentration at the surface and high at the base. Other
data as in Fig. 14.

Figure 17. Instantaneous contour plots of the horizontal $(x-y)$ distribution of a) the vertical
velocity field $w(x, t) = w^{\prime\prime}(x, t)$, since $\langle w \rangle = 0$, b) nitrate, c) phytoplankton, d)
zooplankton and at a depth of $z = 10$ m. The data was recorded 4.7 days into the intermediate
wind $(U_*, U_S) = (3.0, 3.3)$ simulation, just at the point when the primary DBM is reaching its
maximum extent (see Fig. 10b for the corresponding vertical profiles). Here the sampling
depth lies somewhat above the DBM level.

Figure 18. Instantaneous contour plots of the horizontal $(x-y)$ distribution of a) the vertical
velocity field $w(x, t)$, b) nitrate, c) phytoplankton, d) zooplankton and at a depth of $z =
20.4$ m. The data was recorded 4.7 days into the intermediate wind $(U_*, U_S) = (3.0, 3.3)$
simulation, just at the point when the primary DBM is reaching its maximum extent (see Fig.
10b for the corresponding vertical profiles). Here the sampling depth corresponds to the
centre of the DBM.

Figure 19. Key as Fig. 18, except on this occasion the data was recorded after 5.9 days. At
this time the primary DBM is coming to an end of its lifespan, as raised levels of zooplankton
predation signal its destruction.
<table>
<thead>
<tr>
<th>Parameter and Symbol</th>
<th>Numerical Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acceleration due to gravity $g$</td>
<td>$9.81 \text{ms}^{-2}$</td>
</tr>
<tr>
<td>Coriolis Frequency $f$</td>
<td>$10^{-4}\text{s}^{-1}$</td>
</tr>
<tr>
<td>Density of Water $\rho_0$</td>
<td>$1000\text{kgm}^{-3}$</td>
</tr>
<tr>
<td>Viscosity of water $\mu$</td>
<td>$1 \times 10^{-3}\text{kgm}^{-1}\text{s}^{-1}$</td>
</tr>
<tr>
<td>Reference Temperature $\theta_r$</td>
<td>$288.15\text{K}$</td>
</tr>
<tr>
<td>Wavenumber $k$</td>
<td>$0.105\text{m}^{-1}$</td>
</tr>
<tr>
<td>Stokes Drift velocity $U_S$</td>
<td>$2.2-5.6 \times 10^{-2}\text{ms}^{-1}$</td>
</tr>
<tr>
<td>Friction Velocity $U_s$</td>
<td>$1.5-5.0 \times 10^{-3}\text{ms}^{-1}$</td>
</tr>
<tr>
<td>Wave frequency $\sigma$</td>
<td>$1.015\text{s}^{-1}$</td>
</tr>
<tr>
<td>Thermal expansion coefficient $\alpha^\dagger$</td>
<td>$2 \times 10^{-4}\text{K}^{-1}$</td>
</tr>
<tr>
<td>Buoyancy flux at $z = z_{ML} \overline{w' \theta'}$</td>
<td>$-1.2 \times 10^{-6}\text{Kms}^{-1}$</td>
</tr>
<tr>
<td>Monin-Obukhov length $L_{MO}^\dagger$</td>
<td>$-3.5 \text{to} -132.7\text{m}$</td>
</tr>
</tbody>
</table>

† In the LES, the temperature field is computed directly and the density via $\rho = \rho_0 (1 - \alpha \theta)$.

‡ Here $L_{MO} = U_*^2/(kg\alpha w' \theta')$ where $k \approx 0.4$ is von Kármán’s constant.

Table 1. Key physical parameters used to prescribe the LES turbulent boundary layers.
<table>
<thead>
<tr>
<th>Parameter and Symbol</th>
<th>Numerical Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Background Z Concentration $Z_0$</td>
<td>$2 \times 10^4 \ (1 \times 10^2)$ cells m$^{-3}$</td>
</tr>
<tr>
<td>Background $P$ Concentration $P_0$</td>
<td>$5 \times 10^6$ cells m$^{-3}$</td>
</tr>
<tr>
<td>Background $N$ Concentration $N_0$</td>
<td>$2.8 \times 10^{-5}$ kg m$^{-3}$</td>
</tr>
<tr>
<td>$Z$ cell radius $r_Z$</td>
<td>$5 \times 10^{-5} (3 \times 10^{-4})$ m</td>
</tr>
<tr>
<td>$P$ cell radius $r_p$</td>
<td>$1 \times 10^{-5} m \equiv V_p = 4.2 \times 10^{-15} m^3$</td>
</tr>
<tr>
<td>$P$ cell density $\rho_p$</td>
<td>$1.002 \rho_0$</td>
</tr>
<tr>
<td>$Z$ cell density $\rho_Z$</td>
<td>$1.02 \rho_0$</td>
</tr>
<tr>
<td>$b^b P$ maximum growth rate $\mu_p^{\max}$</td>
<td>$5 \times 10^{-5} s^{-1}$</td>
</tr>
<tr>
<td>$b^b Z$ maximum growth rate $\mu_Z^{\max}$</td>
<td>$1.0 \times 10^{-5} \ (2.9 \times 10^{-6}) s^{-1}$</td>
</tr>
<tr>
<td>$Z$ death rate $\mu_Z^{death}$</td>
<td>$\sim 2.4 \times 10^{-5} V_Z^{-0.21}$</td>
</tr>
<tr>
<td>$Z$ swimming or pursuit speed $\sigma_Z$</td>
<td>$4 \times 10^{-6} \ (1.2 \times 10^{-6}) s^{-1}$</td>
</tr>
<tr>
<td>Contact radius $R$</td>
<td>$2 \times 10^{-3} \ (1.2 \times 10^{-2}) m \uparrow$</td>
</tr>
<tr>
<td>$Z$ reaction time $T_R$</td>
<td>$1 \ or \ 5 \ s$</td>
</tr>
<tr>
<td>Predation rate integral $I(R, T_R, \sigma_Z)$</td>
<td>$7 \times 10^{-10} m^3 s^{-1}$</td>
</tr>
<tr>
<td>Yield $Y$</td>
<td>$0.003 \ (1.2 \times 10^{-5}) \sim 0.33 V_p/V_Z$</td>
</tr>
<tr>
<td>$P$ growth efficiency $\beta_G$</td>
<td>0.75</td>
</tr>
<tr>
<td>Light attenuation coefficient $\alpha$</td>
<td>$0.04 m^{-1}$</td>
</tr>
<tr>
<td>$U_{sink} = 2 gr_Z/p (\rho_Z/p - \rho_0)/9\mu$</td>
<td>$2.2 \times 10^{-3} (1.3 \times 10^{-2}) \ &amp; 4.4 \times 10^{-5} ms^{-1}$</td>
</tr>
<tr>
<td>Proportion of dead $P$ cells $\phi_{p, dead}$</td>
<td>$10^{-3}$</td>
</tr>
<tr>
<td>Proportion of dead $Z$ cells $\phi_{Z, dead}$</td>
<td>$10^{-5}$</td>
</tr>
<tr>
<td>Nitrate stoichiometry coefficient $s_N$</td>
<td>$2.7 \times 10^{-14} kg cell^{-1} \sim 1.38 \times 10^3 V_p/3$</td>
</tr>
</tbody>
</table>

$\uparrow$ Default value unless stated otherwise in text or figures.

$\downarrow$ For the simple NPZ model of (20-21) only. For the full LES-NPZ model this is derived as a function of depth from the appropriate $\varepsilon, R$ and $T_R$ values, e.g. the profiles shown in Figs. 5, 7 & 11.

Table 2. Key biological parameters used to prescribe the NPZ plankton model. The zooplankton values are for the small predator, the corresponding values in parentheses are for the large predator.

Figure 1
Figure 2
Figure 3
Figure 5

(a) [Graph showing depth vs. predation rate with different line styles for various conditions.]

(b) [Graph showing depth vs. predation rate with different line styles for various conditions.]

Legend:
- Blue line with style: \((U_r, U_\phi) = (2.0, 2.2)\)
- Red dotted line with style: \((U_r, U_\phi) = (3.5, 3.9)\)
- Orange dashed line with style: \((U_r, U_\phi) = (5.0, 5.6)\)
Figure 6
Figure 7
Figure 8
Figure 9
Figure 10
Figure 15
Figure 16
Figure 19