New models for the exploration of biological processes at fronts

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The use of models in the exploration of biological processes at fronts has been limited by the poor representation of boundary-layer processes. The strongly sloping pycnocline of frontal regions forces very different buoyancy and momentum fluxes on either side of the front. This cross-frontal contrast in the vertical mixing of heat or momentum by wind or bottom stress couples to the horizontal velocities, creating non-linear cross-frontal flows. These vertical and horizontal motions have immediate impacts on the spatial and temporal patchiness of biological properties at fronts. New model architectures now couple more accurate representations of turbulent mixing in boundary layers with traditional primitive-equation models. Recently, these coupled primitive-equation/mixed-layer models have been integrated with simple ecosystem models to explore the dynamics of biological processes at fronts. I describe two different architectures of these coupled models: a slab mixed-layer/primitive-equation/ ecosystem model, and a turbulence-closure mixed-layer/primitive-equation/ecosystem model. These models have been applied to a wind-forced front and a tidal front respectively. The scales of physical features and biological patchiness described by the models with mixed-layer physics are quite different, usually smaller, than the scales predicted by the primitive-equation models alone. Resolution of vertical processes is significantly enhanced by the inclusion of mixed-layer physics, contributing to a more accurate description of biological dynamics at these intermediate scales.

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Introduction

The relatively low recruitment rate of many marine invertebrate and vertebrate species suggests that only a minute fraction of the spawned larvae find sufficient food, avoid predation, and are retained in hospitable locales. Often the mean level of prey is insufficient to sustain the measured larval growth rates, suggesting that the surviving larvae are finding and exploiting patches of food (e.g. Mullin, 1993), or that encounter rates are enhanced by turbulence (e.g. Rothschild and Osborn, 1988). How food patches form, and how their dynamics relate to the physical environment has been the subject of much study. Unfortunately, technological limitations have made field observations of the patch dynamics difficult. An alternate approach, the formulation of coupled physical–biological models, has been fruitful. However, such models usually trade-off between vertical and horizontal resolution, precluding accurate

simulation of many important physical and biological dynamics.

As computers become more powerful and cost less, numerical models of oceanographic processes are becoming more detailed. While models used in coupled biological–physical problems usually lag those used in purely physical studies by several years, there are some new model architectures that add a significant level of detail to existing physical–biological models. In particular, several types of model now include separate equations for the mixed-layer dynamics. These mixed-layer models have been used for decades, coupled to one-dimensional (vertical) biological models. However, two- and three-dimensional physical–biological models have not included mixed-layer formulations. As will be demonstrated below, the inclusion of mixed-layer dynamics in a fully coupled physical–biological model significantly improves our ability to simulate and understand intermediate-scale biological patchiness and its relation to the physical environment.

Mixed-layer models

Oceanographers are usually familiar with the concept of a surface mixed layer, often defined as the depth from the surface over which the density shows little variation (e.g. <0.1 kg m^{-3}). The surface mixed layer is a particular example of a more general class of features called boundary layers. These boundary layers include bottom, atmospheric and planetary boundary layers; the physical dynamics of boundary layers are distinct from those of the interior fluid and are governed by their own mixing rules.

Several types of model have been developed to describe the physics of boundary layers. These models tend to differ in the degree of detail used to model the turbulent fluxes. A first-order model uses prognostic (time evolution) equations for the mean quantities, but parameterizes the higher-order moments (variance, etc.) in terms of the first-order variables. This means that the mean temperature, velocity, etc. of the mixed layer can change through time, and the mixed-layer thickness can evolve due to heating, cooling or surface or bottom stress. However, these properties are always homogeneous throughout the mixed layer, implying perfect mixing (infinite vertical eddy diffusivities) within the mixed layer.

These models are easily adapted to finite-difference models, and are computationally efficient. They specify the evolution of the mixed-layer depth, usually based on the turbulent kinetic energy budget of the mixed layer, including wind and mean shear forcings. Many of these models have sharp gradients in properties at the base of the mixed layer (e.g. Denman, 1973), although some use local Richardson number dependencies to smooth out unrealistic jumps (e.g. Garwood, 1977; Price *et al.*, 1986). Such models are often called ''slab'', or ''bulk'' mixed-layer models because they assume the mixed layer to be homogeneous in all properties. One example that will be used in the analyses below was presented in Garwood (1977).

A second-order mixed-layer model uses prognostic equations for both the mean and variance (second-order moments) of properties, including the turbulent fluxes. This means that temporal and spatial changes in both the mean properties, and the variability of those properties can be modelled. The mixed layer in these models is not completely homogeneous, unlike the slab models, and can maintain a degree of patchiness not possible with slab models.

An example of this type of model is given by the Mellor and Yamada (1982) level 2.5 turbulence-closure scheme, which uses a diagnostic (no time dependence) equation for temperature variance, but a prognostic equation for the variance of turbulent kinetic energy. The second-order turbulence-closure models are particularly useful for biological applications in specifying a time- and space-varying vertical profile of the vertical eddy diffusivity within the boundary layer. Because of the greater number of prognostic equations that need to be solved, however, these higher-order turbulence-closure models are more computationally intensive, and more difficult to integrate with higher-dimensional primitive-equation models.

There are several reviews comparing different mixed-layer model structures to observations from several locations. Martin (1985) compares both slab and turbulence-closure models to the OWS November and Papa data sets, looking at the replication of annual cycles. More recently, Large *et al.* (1994) compare several extant mixed-layer models, and present a new type of model with a nonlocal parameterization of the mixing. These models are also compared to data, using several data sets of annual and diurnal cycles to select the most appropriate model architecture. It was found in both these studies that the Mellor-Yamada Level 2.5 and the Garwood models can give quite accurate simulations of the mixed-layer dynamics.

Coupled models

The mixed-layer models are typically one-dimensional, describing the evolution of properties in a vertical column of fluid. To obtain realistic descriptions of two- and three-dimensional processes, these vertical models must be coupled to higher-dimensional models describing the vertical and horizontal distribution and evolution of the fluid's properties. These models often solve the fully non-linear equations of motion, and are known as primitive-equation models. The method of solving these equations varies, but must be done numerically. The coupling of the models involves specification of how the mixed-layer depth relates to the underlying model grid, how boundary forcings are distributed within the mixed-layer and primitive-equation portions of the model, and how the underlying primitive-equation dynamics influence the vertical turbulent kinetic energy budget (e.g. Adamec *et al.*, 1981). Examples of issues to be considered are: does the mixed-layer depth have to correspond to a model grid point, or can the mixed layer vary continuously? How does vertical shear driven by the primitive-equation model couple to the mixed-layer model and vice-versa?

Examples

Two examples of coupled mixed-layer/primitive-equation models will be presented below. These two physical models have been coupled to the simple phytoplankton–zooplankton–nutrient ecosystem model of Franks *et al.* (1986). The first example uses the Garwood (1977) slab mixed-layer model in a study of

the effects of wind forcing on phytoplankton production at an oceanic front (Franks and Walstad, 1997). In the second example, the level 2.5 turbulence-closure model of Mellor and Yamada (1982) is used in the study of the effects of tidal forcing on the planktonic ecosystem of Georges Bank (Franks and Chen, 1996). In both examples, a comparison is made between identical model runs with the mixed-layer models active and inactive. The examples with inactive mixed-layer models are similar to most two- and three-dimensional coupled physical–biological models in the literature to date.

The biological models were initialized at a steady state representative of summer conditions. In the slab mixed-layer model, a nutrient gradient was specified across the front, whereas there was no horizontal dependence to the initial condition for the turbulence-closure model. The phytoplankton sank at 1 m d^{-1} in both models.

Slab mixed layer

In this model, a simple exponential front in a geostrophic balance was specified for the hydrographic initial condition. The front was forced with a transient wind stress of 0.2 N m^{-2}, with a duration of 1.5 d. The wind excited inertial oscillations of the front, leading to strong vertical and horizontal pumping at the front (Fig. 1). Without a mixed-layer model, the wind stress was trapped in a relatively thin surface layer, leading to a pronounced cross-frontal surface jet and weak vertical velocities. The inclusion of the mixed-layer physics allowed much deeper penetration of the surface wind stress, leading to a deep mixed layer and a weaker surface jet. Differences in the mixed-layer depth across the front enhanced the cross-frontal density gradient, leading to strong ageostrophic circulations, including oscillating vertical velocities with amplitudes reaching 100 m d^{-1}.

Over the course of the simulation, the phytoplankton developed a subsurface patch at the front, sustained by cross-frontal nutrient fluxes into the euphotic zone. Because of the weak penetration of the wind stress in the case with no mixed-layer physics, the subsurface patch was shallow and elongate, stretching for about 85 km in the cross-frontal direction. The modification of the distribution of turbulent kinetic energy in the case with mixed-layer physics led to the formation of a deeper, more distinct phytoplankton patch. This patch was closely associated with the front, and had a cross-frontal scale of about 40 km. The dynamics underlying the formation of such phytoplankton patches at fronts have been explored by Franks (1992); the dynamics simulated by the case with mixed-layer physics are more consistent with our understanding of the mechanisms underlying such frontal patchiness than the case without mixed-layer physics.

Turbulence-closure mixed layer

The turbulence-closure mixed-layer model was configured for a cross-bank transect of Georges Bank, and forced with an M$_2$ tide at the southern open boundary (right-hand side of Fig. 2). A linear vertical temperature gradient was used for the initial density distribution, with no horizontal dependence. The tidal forcing was gradually ramped up over five tidal cycles; the results of the 25th tidal-averaged fields are shown in Figure 2. Without the turbulence-closure physics, a thermally well-mixed region develops over the shallow portion of the bank, although the surface waters are also homogenized by the high level of vertical diffusion necessary to satisfy the numerical stability criteria (0.001 m^2 s^{-1}). While the model forms tidal fronts, their structure bears little resemblance to those measured on Georges Bank: the horizontal stratification is too weak, and the vertical structure is incorrect (compare to Loder *et al.*, 1982; and see Chen *et al.*, 1995). The phytoplankton develop some horizontal structure, with high values in the surface waters off the bank, and abrupt horizontal gradients in the northern tidal front. The phytoplankton are not vertically homogenized on the bank, contrary to observations, and the spatial patterns are not a good representation of those seen on Georges Bank (e.g. Horne *et al.*, 1989).

With the turbulence-closure physics included, much more realistic tidal fronts form on the northern and southern flanks of the bank. The thermal gradients closely match those measured on Georges Bank during the summer months, as do the currents associated with the tidal forcing. Since there is no wind forcing or surface heat flux, all the turbulence is generated by the friction of the tidal currents over the bottom. This upward mixing led to a well-mixed region on top of the bank separated from the offshore waters by surface-to-bottom tidal fronts. Tidally rectified flows led to strong cross-frontal circulation cells within the fronts. The phytoplankton patterns were very different from the simulation without the mixed-layer physics, and agreed both qualitatively and quantitatively with patterns observed on Georges Bank. A subsurface chlorophyll maximum in the offshore waters was separated from the well-mixed region on the top of the bank by regions of enhanced biomass, particularly on the northern flank. The distinct patch within the northern front was supported by nutrients advected and diffused from below. This mixing was very isolated in time and space; the bulk of the mixing occurred during a 2 h period near the flood-to-ebb transition, in a region only 5 km wide. The shape of the phytoplankton patch changed radically over a tidal cycle, as it was advected downward in the cross-frontal circulation cell during the flood tide.
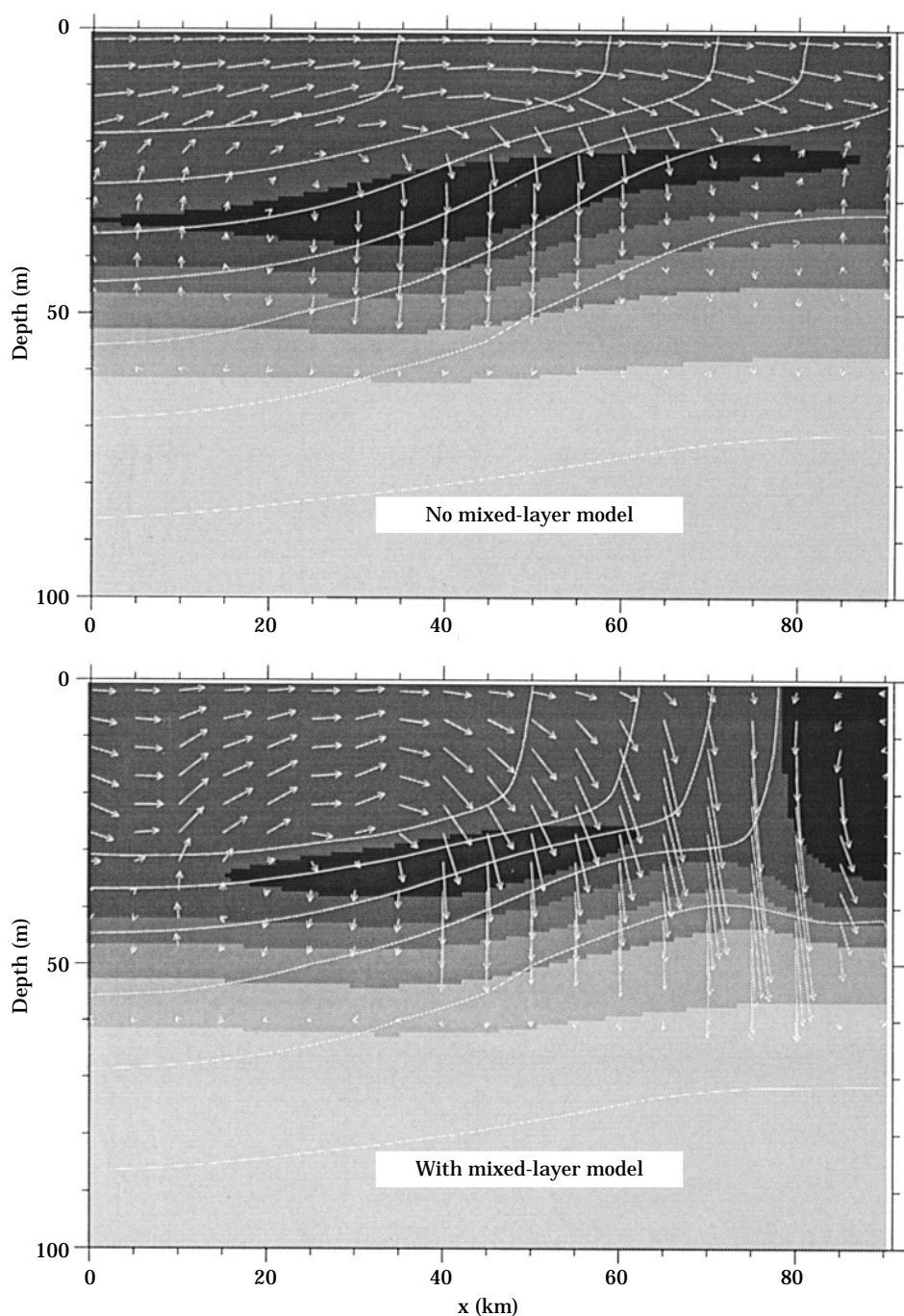
Figure 1. Cross-frontal structure of temperature (solid lines, °C), phytoplankton biomass (grey scale, black: maximum, white: minimum) and cross-frontal velocities (arrows) one day after the cessation of a wind event at a front. *Top panel*: no mixed-layer dynamics. *Bottom panel*: using a slab mixed-layer model.

Discussion

The two examples presented above clearly demonstrate the utility of coupled mixed-layer/primitive-equation/ ecosystem models in simulating the formation of biological patchiness in response to physical forcings. Without the mixed-layer physics, the models did a poor job of describing the physical and biological patchiness:
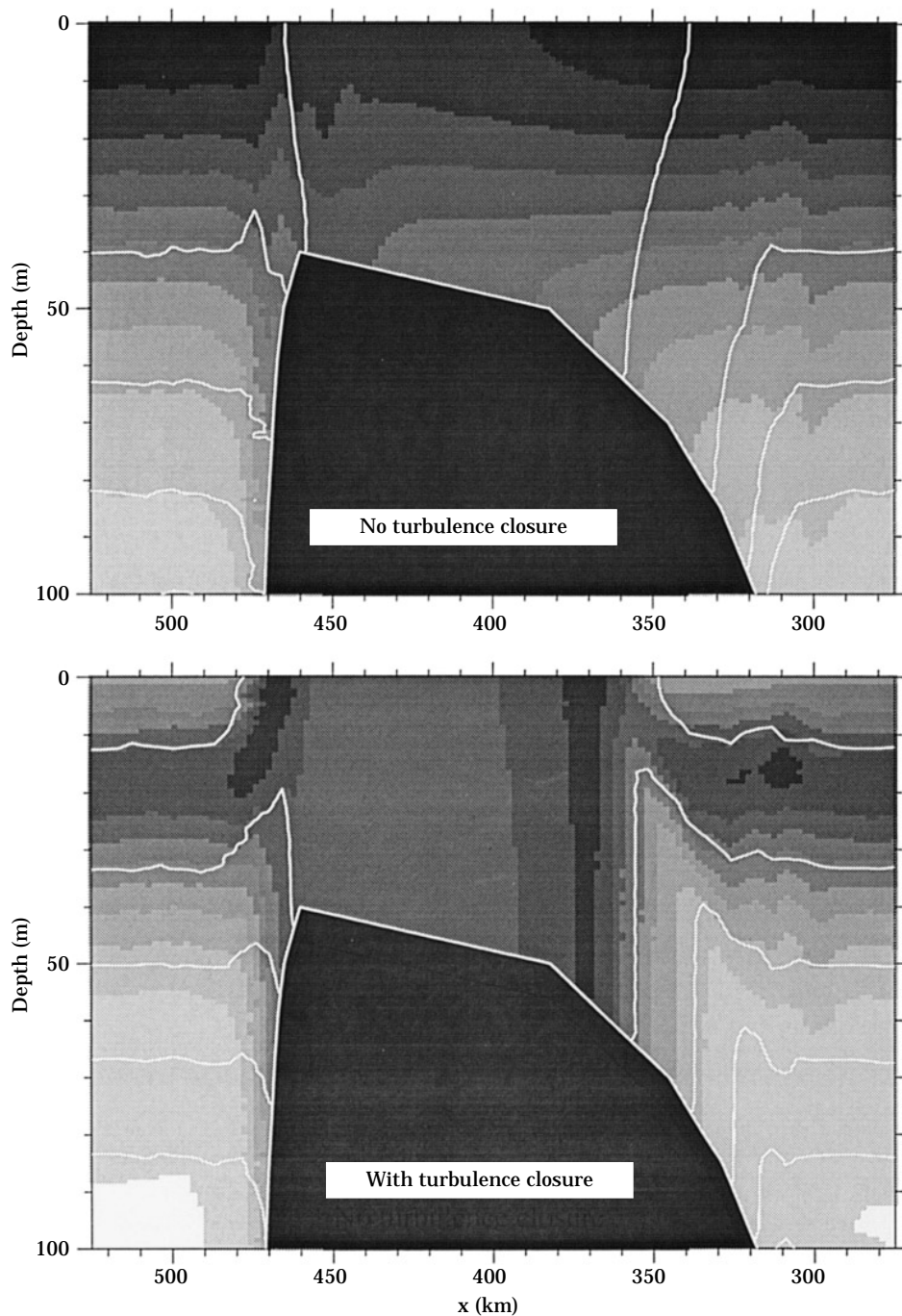
Figure 2. Tidally-forced fronts on Georges Bank. Tidal-average fields of temperature (solid lines, °C) and phytoplankton (grey scale, black: maximum, white: minimum) after 24 tidal cycles. Black area is bottom contour of the bank. *Top panel*: no turbulence-closure mixed-layer dynamics. *Bottom panel*: including turbulence-closure mixed-layer dynamics.

the inaccurate description of the transport of momentum from the boundaries led to over-estimation of the phytoplanktonic patch scales, and an inaccurate simulation of their relationship to the physical dynamics. Inclusion of the mixed-layer models tended to increase the amount of biological patchiness, and to

decrease the scale of the patchiness. Strong temporal and spatial variability of the patchiness became evident, and the relationship of the patches to the underlying physics could be studied.

There are two types of biological patchiness that need to be considered in these higher-dimensional models, and in the field. The first is biological patchiness created by physical patchiness. An example of this is advection of biological properties in eddies as they are formed across fronts, or the seaward advection of properties in squirts and jets of the California Current. In these examples, to first order, the biological patchiness is directly correlated with the physical patchiness, as seen in comparisons of remotely sensed temperature and pigment fields (Smith *et al.*, 1988; Abbott and Barksdale, 1991). The second type of biological patchiness is formed as a biological response to physical dynamics. These patches may not be strongly correlated with any particular physical property, but rather a suite of dynamics. The subsurface chlorophyll patches found at fronts (e.g. Franks, 1992), and banding of planktonic organisms in internal wave trains (e.g. Jillett and Zeldis, 1985) are examples of this. Biological growth and swimming behaviours lead to patchiness of organisms in certain physical regimes. The difference between the two types of patchiness is that one results from advection of existing gradients, the other from a local biological response to physical dynamics.

The inclusion of mixed-layer models in coupled physical–biological models is essential for accurate simulation and understanding of both types of biological patchiness. Accurate simulation of the mixed layer is necessary for reasonable descriptions of wind-driven upwelling fronts, for example (Allen *et al.*, 1995). Without a mixed-layer model, the heat flux and surface wind stress are not correctly distributed within the surface layers of the ocean, leading to inaccurate estimation of hydrographic (and consequently biological) spatial scales. Similarly, models of river plume fronts under wind and topographic forcing give more accurate simulations when mixed-layer models are included (R. Signell, pers. com.). Both these systems are known to have a high correlation of physical and biological patchiness, so an accurate simulation of the physical patchiness is essential to an understanding of the biological fields.

Accurate simulation of the mixed-layer dynamics is also necessary to accurately predict the biological response to the physical dynamics. Predator–prey interactions can be strongly affected by ambient turbulence (e.g. Rothschild and Osborn, 1988); the second-order turbulence-closure mixed-layer models supply vertical profiles of vertical eddy diffusivity and dissipation of turbulent kinetic energy. These properties are essential to an accurate prediction of predator–prey encounter rates. Phytoplankton growth at fronts is strongly depen-

dent on cross-frontal nutrient fluxes. As shown above, these nutrient fluxes can change rapidly over a wind event or a tidal cycle. However, accurate modelling of these temporally and spatially variable processes can only be achieved using some type of mixed-layer model. Thus, mixed-layer models are necessary not only for accurate simulation of physical patchiness and consequent biological patchiness, but also for accurate simulation of the nonlinear interactions of biological fields and responses to the physical dynamics.

The studies presented above have examined only the two-dimensional behaviour of coupled mixed-layer/primitive-equation models. The inclusion of along-front variability will add a further degree of patchiness, created by frontal meanders and instabilities. These patches will have strong local influences on the mixed-layer dynamics and vertical distribution of turbulent kinetic energy. To understand the relationship of biological and physical dynamics in these regions, we must accurately describe the boundary-layer physics and their coupling to the larger-scale flows. Such studies should help us understand the influences of biological and physical patchiness on fish feeding and aggregation in the world's oceans.

Acknowledgements

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