

Simulations of the Black Sea pelagic ecosystem by 1-D, vertically resolved, physical–biochemical models

TEMEL OGUZ,^{1,*} HUGH W. DUCKLOW,²
PAOLA MALANOTTE-RIZZOLI³ AND JAMES
W. MURRAY⁴

¹ Middle East Technical University, Institute of Marine Sciences,
Erdemli 33731, Icel, Turkey

² Virginia Institute of Marine Sciences, The College of William
and Mary, Gloucester Point, VA 23062-1346, USA

³ Massachusetts Institute of Technology, Department of Earth,
Atmospheric and Planetary Sciences, Cambridge,
MA 02139, USA

⁴ University of Washington, School of Oceanography,
Box 357940, Seattle, WA 98195–7940, USA

ABSTRACT

The present paper summarizes the results of several simulations of the central Black Sea pelagic food web using three different 1-D, physical–biochemical, water column process models. The most simplified, five-compartment version is used to explore the robust biological features of the ecosystem and the role of upper-layer physics on the evolution of the euphotic zone biological processes. The other models, introducing additional biological complexities, show how these biologically structured models become more capable of simulating intensified subsurface summer production, more dynamic plankton structure arising after the increasing role of gelatinous carnivores in the ecosystem during the 1980s, and fairly sophisticated nitrogen cycling in the water column.

Key words: Black Sea, pelagic ecosystem, physical–biochemical models

INTRODUCTION

Over the last two decades, the Black Sea has been experiencing severe environmental degradation resulting mainly from anthropogenic forcing, but also

accompanied by overfishing, and possibly climatic changes (Mee, 1992). The exceptionally high nutrient loads and contaminants entering the sea from the rivers Danube, Dniepr and Dniestr led to considerable transformation of the lower trophic levels. The most dramatic response has been drastic changes in the intensity and annual structure of primary production and nutrient cycling. Adverse effects of all these changes were also reflected at higher trophic levels that were further perturbed during the 1980s by overfishing and the population explosion of the gelatinous carnivores *Aurelia aurita* and *Mnemiopsis leidyi*. These carnivores were responsible for altering the structure of the food web, as they became the main competitors feeding on mesozooplankton as well as fish eggs and larvae, whereas they had no predators because they are at the end of the trophic chain. The most dramatic ecosystem changes have been observed in the north-western shelf and in the western coastal regions, which are heavily influenced by anthropogenic effects (Zaitsev and Mamaev, 1997).

Various research and management programmes have been developed during the 1990s (BSOFS Science Plan, 1997). A part of these efforts was the implementation of regional state-of-the-art ecosystem models which are capable of describing major characteristic features of the upper-layer biogeochemical structure of the Black Sea, its evolution in recent times, and of predicting the ecosystem variability on monthly/seasonal time scales. In the present paper, a brief review of such modelling efforts is presented with particular emphasis on GLOBEC aspects. More details on these models and comparisons of their results with observations can be found in Oguz *et al.* (1996, 1998a, 1998b).

THE MODELS

The biologically simplest version of the models is described by Oguz *et al.* (1996). It involves single phytoplankton and zooplankton groups, detritus and dissolved inorganic nitrate and ammonium. This type of five-compartment system is considered by GLOBEC to be the minimum configuration which might provide a realistic ecosystem structure. Even though the

Correspondence. Fax: +90–324–521–2327;
e-mail: oguz@pimms.metu.edu.tr

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euphotic zone is restricted to the upper 50 m of the water column in the Black Sea, the model considers a 150 m thick upper-layer water column located over the anoxic water body. The shallow summer mixed layer (around 10–15 m in depth), as well as the productive zone between the seasonal thermocline and the base of the euphotic zone, are resolved using a ≈ 3 m grid spacing. The biological processes are coupled to the upper-layer physical processes through a sophisticated upper-layer dynamics in which the vertical mixing is parametrized by the Mellor–Yamada 2.5 order turbulence parametrization. Given a knowledge of physical forcing, the model simulated fairly satisfactorily the yearly evolution of the upper-layer stratification, the annual cycle of production with the autumn and the spring blooms, the subsurface phytoplankton maximum layer in summer, as well as realistic patterns of particulate organic nitrogen. The results indicated that initiation of the spring bloom depends crucially on local mixing conditions and follows weakening of the convective overturning mechanism. This suggests timing of the bloom is governed by the year-to-year and/or local variabilities in the physical processes, in addition to the biological processes. The spring bloom may thus take place at an earlier period, say in February, during mild winters as supported by observations (Vinogradov and Shushkina, 1992).

Following the spring bloom, the model predicts a weaker and shorter phytoplankton growth event within April as the water column begins to stratify and the seasonal thermocline begins to form in the near-surface levels. The formation of this bloom is caused by the recycled nitrogen generated as a by-product of the spring bloom, and trapped in the mixed layer. A period of very low primary productivity prevails throughout the summer as a consequence of severe nitrogen limitation in the surface mixed layer. However, some phytoplankton production occurs beneath the seasonal thermocline as long as this zone has sufficient light to support phytoplankton growth. Towards the end of autumn, rapid de-stratification of the water column and subsequent intensification of the vertical mixing enhances the nutrient flux to the surface waters, and causes a phytoplankton bloom development for 2–3 weeks during the October / November / December period, depending on local conditions.

Contrary to the formation of two distinct blooms during the late autumn and the early spring, one long-term bloom event may occur during the December to March period if the grazing pressure is too weak to be able to control the phytoplankton growth. Then, once the late-autumn bloom is initiated, it persists for the

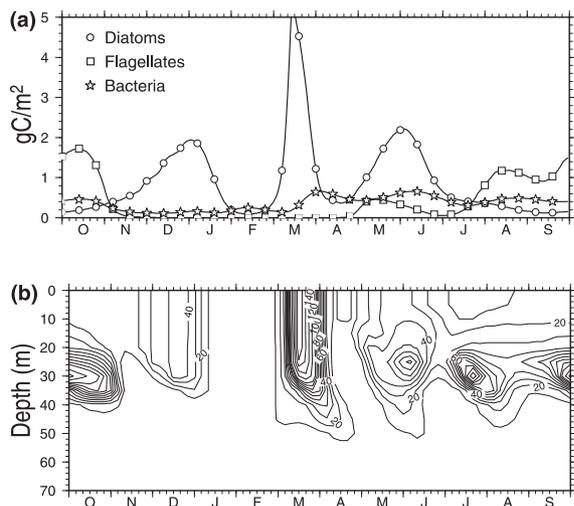
entire winter, because sufficient nutrient is always entrained into the surface layer to maintain production during this period. Such modifications on the standard case of the two-bloom phytoplankton structure may also be traced in the data as a part of the year-to-year variabilities of the biological system.

One drawback of this five-compartment ecosystem model was underestimation of summer production. To alleviate the limitations imposed by such a simplified approach, Oguz *et al.* (1998a) introduced a multiple prey–multiple predator system characterized by two phytoplankton species groups, typifying diatoms and flagellates, and two zooplankton groups (microzooplankton and mesozooplankton). Both of these groups feed on two types of prey with different prey-capture efficiencies. Microzooplankton are considered to be more efficient at capturing flagellates, whereas diatoms are consumed predominantly by mesozooplankton. All other features of the model were similar to those given by Oguz *et al.* (1996).

Such a simple fractionation of the biogenic community structure was shown to yield increased primary production and development of a more pronounced subsurface chlorophyll maximum layer during the summer period. A diatom-based early spring (March) bloom is followed by summer and autumn blooms of flagellates. In the presence of two phytoplankton and two zooplankton groups, diatoms are responsible for the March bloom, and support increased mesozooplankton activity later in the spring and summer months. Because mesozooplankton exert predatory control on the microzooplankton, flagellates do not experience any grazing pressure from the microzooplankton group, and may therefore provide a stronger subsurface production during the summer. This result implies that the choice of a five-compartment model may not be entirely adequate for representation of all seasonal bloom events in the Black Sea.

The vertically resolved model of Oguz *et al.* (1998a) was further modified by adding a gelatinous, carnivorous macrozooplankton group (representing essentially the medusa, *Aurelia aurita*), as well as bacterioplankton and dissolved organic nitrogen compartments (Oguz *et al.*, 1998b). The dissolved oxygen was also incorporated as a prognostic variable in order to model the remineralization and nitrification processes more realistically and to study the suboxic zone dynamics and the related redox processes across the anoxic interface zone. The simulations indicated that peaks of phytoplankton (diatoms and flagellates) and zooplankton (mesozooplankton and macrozooplankton) biomass follow sequentially one after the other as a result of their prey–predator interactions (Figs 1 and 2). Three

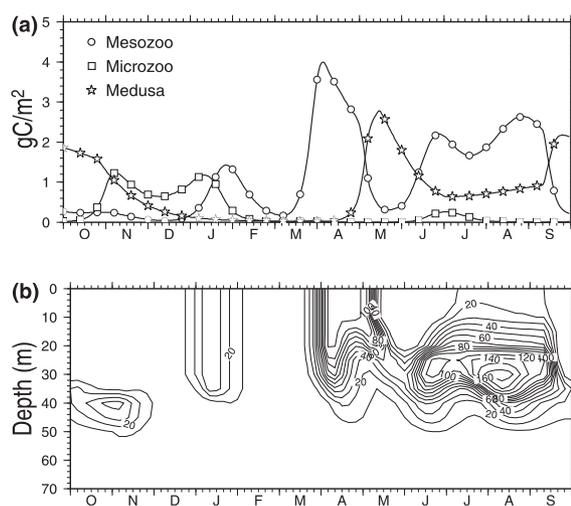
Figure 1. Modelled annual distributions of (a) the euphotic zone integrated diatom, flagellate and bacterioplankton biomass and (b) total phytoplankton biomass within the upper-layer water column (contours at intervals of 10 mgC m^{-3} up to 100 mgC m^{-3} , and at 20 mgC m^{-3} thereafter). In both plots, the time axis starts at 1 October and ends at 30 September.



diatom blooms occur, these being in March (with maximum biomass of $\approx 5 \text{ gC m}^{-2}$), in late May/early June and in December/early January ($\sim 1.5 \text{ gC m}^{-2}$), whereas flagellates dominate the system later in the summer and autumn ($\sim 1\text{--}2 \text{ gC m}^{-2}$; Fig. 1a). This phytoplankton structure possesses more pronounced bloom characteristics during the summer months compared with the previous model described in Oguz *et al.* (1998a), and may highlight the role of gelatinous carnivores starting to dominate the ecosystem during the 1980s. This domination is due to a new 'top-down' control mechanism in the food web structure, in which increasing the gelatinous carnivore population puts a stronger control on the mesozooplankton community, which subsequently weakens their grazing pressure on the phytoplankton. The most pronounced signature of this effect is observed towards the end of May and September, which coincide with the periods of major increase in the medusa population (Fig. 2a).

It may be inferred from the vertical structure of the total phytoplankton distribution (Fig. 1b) that the March and December blooms are surface-intensified events. They extend to a depth of 40–50 m, coinciding approximately with the depth of winter convective overturning and the 1% light level. Their formation is the result of entrainment of subsurface nitrates by the convective overturning and therefore is related to the new production. The late-spring diatom bloom and

Figure 2. Modelled annual distributions of (a) the euphotic zone integrated microzooplankton, mesozooplankton and medusa biomass and (b) total mesozooplankton biomass within the upper-layer water column (contours at intervals of 10 mgC m^{-3} up to 100 mgC m^{-3} , and at 20 mgC m^{-3} thereafter). In both plots, the time axis starts at 1 October and ends at 30 September.



the subsequent summer flagellate blooms, on the other hand, are formed between the seasonal thermocline and the base of the euphotic zone and are essentially originated by recycled nitrogen.

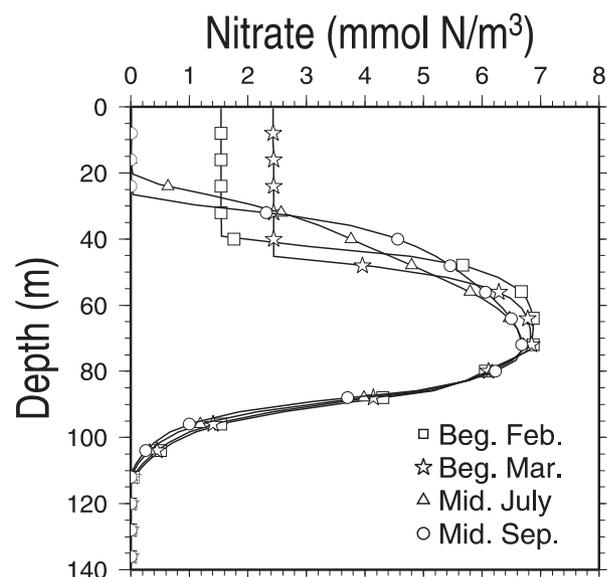
In contrast to diatoms and flagellates, bacterioplankton biomass exhibits a somewhat weaker distribution within the euphotic zone (Fig. 1a). The stock is typically less than 0.5 gC m^{-2} in the late autumn and winter months. It almost doubles after the March diatom bloom until the end of summer. The summer bacterioplankton population is located mainly below the seasonal thermocline at the same levels as the flagellates.

As soon as the March diatom bloom degrades, the mesozooplankton biomass starts increasing as they assimilate the diatoms (Fig. 2a). Their biomass tends to decline during May, which coincides with the period of medusa growth up to a maximum value of $\approx 2.8 \text{ gC m}^{-2}$. The summer mesozooplankton growth is principally caused by the reduction in the medusa population to a minimum level of $\sim 1.0 \text{ gC m}^{-2}$, with additional contributions by the degradation of the phytoplankton blooms towards the end of June. A similar interaction between mesozooplankton and medusa, taking place in May, repeats itself once again during September. A secondary increase on the mesozooplankton stock of up to $\sim 1.5 \text{ gC m}^{-2}$ follows the December diatom bloom. The medusa population

decays during the winter months, until a new cycle of growth and reproduction begins in April. The winter (January) and late March/April mesozooplankton growth takes place in the upper 40 m of the water column, whereas the summer growth is confined below the seasonal thermocline (Fig. 2b). Following the vertical structure of the mesozooplankton community, the first medusa growth event is distributed uniformly within the upper 40 m of the water column, whereas the second event is confined below the seasonal thermocline. The microzooplankton biomass, on the other hand, remains negligibly small throughout the year (Fig. 2a), because of its almost complete predation by the mesozooplankton community.

Another major feature of the latter model is its ability to reproduce a fairly realistic nutrient-recycling mechanism. Dead cells and faecal matter sinking from the euphotic zone are continually remineralized to ammonium, which is subsequently oxidized to nitrate. These conversion processes are accompanied at the same time by upward transport of both nitrate and ammonium to resupply them to the surface waters. The nitrogen cycling, which supports the plankton productivity within the interior Black Sea, seems to occur within the uppermost 75 m of the water column. During the winter months, prior to the March diatom bloom, intense vertical convective mixing gives rise to enhanced nitrate concentrations of more than 2 mmol m^{-3} within the upper 50 m of the water column (Fig. 3). The summer mixed layer, on the other

Figure 3. The model simulated nitrate profiles during the winter (at the beginning of February and March) and during the summer (at mid-July and mid-September).



hand, is characterized by depleted nitrate, because of the lack of sufficient supply from the subsurface levels across the strong seasonal pycnocline. In the region below the seasonal thermocline, nitrate concentrations increase linearly and support the summer subsurface production near the base of the euphotic zone. Further below this depth, the nitrate profiles possess a distinct maximum of about 7 mmol m^{-3} near 70 m depth, which coincides approximately with the 15.4 sigma-t level, as suggested by available observations (Tugrul *et al.*, 1992; Basturk *et al.*, 1994; Murray *et al.*, 1995). The nitrate concentrations, on the other hand, do not possess any seasonal variability below the depth of their peak values. As a result of excessive nitrate consumption during anaerobic organic-matter decomposition, they tend to decrease uniformly to their trace-level values around the 16.0 sigma-t level, corresponding to 100 m depth in the present simulation. This is located roughly 30 m below the depth of the nitrate maximum, and identified as the lower limit of the suboxic zone and upper boundary of the deep anoxic pool.

CONCLUSIONS

The process model studies described briefly here, constitute a part of our ongoing efforts to understand the functioning and structure of the Black Sea ecosystem through a combination of observations, retrospective analyses and modelling. We plan to introduce gradually more sophisticated models which will have more emphasis on the herbivores, primary and gelatinous carnivores, and will eventually be linked to the dynamics of higher trophic levels. From the GLOBEC standpoint, the Black Sea offers a unique opportunity to study and synthesize the effects of various kinds of forcing (e.g. climatic variability, pollution and the result of other human activities) on the evolution of the ecosystem.

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