Mediterranean Marine Science

Vol 15, No 4 (2014)

Vol 15, No 4 (2014) special issue

Sensitivity of the N. AEGEAN SEA ecosystem to Black Sea Water inputs

G. PETIHAKIS, K. TSIARAS, G. TRIANTAFYLLOU, S. KALARONI, A. POLLANI

doi: 10.12681/mms.955

To cite this article:

PETIHAKIS, G., TSIARAS, K., TRIANTAFYLLOU, G., KALARONI, S., & POLLANI, A. (2014). Sensitivity of the N. AEGEAN SEA ecosystem to Black Sea Water inputs. *Mediterranean Marine Science*, *15*(4), 790–804. https://doi.org/10.12681/mms.955

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.955

Sensitivity of the N. Aegean Sea ecosystem to Black Sea Water inputs

G. PETIHAKIS[1], K. TSIARAS[2], G. TRIANTAFYLLOU[2], S. KALARONI[2] and A. POLLANI[2]

[1] Hellenic Centre for Marine Research, Institute of Oceanography, P.O. Box 2214, 71003 Heraklion, Crete, Greece
[2] Hellenic Centre for Marine Research, Institute of Oceanography, PO Box 712, 19013 Anavyssos, Greece

Corresponding author: gpetihakis@hcmr.gr

Handling Editor: Ioanna Siokou

Received: 13 June 2014; Accepted: 13 November 2014; Published on line: 23 December 2014

Abstract

The effect of Black Sea Water (BSW) inputs on the productivity and food web dynamics of the N. Aegean Sea was investigated, by means of sensitivity simulations, investigating the effect of the inflowing BSW, in terms of inorganic nutrients and dissolved organic matter. Considering the importance of the microbial loop in ecosystem functioning and the role of dissolved organics, the bacteria sub-model was appropriately revised, towards a more realistic representation of the Dissolved Organic Matter (DOM) pool. The importance of the microbial loop is highlighted by the simulated carbon fluxes, where almost 50% of carbon is channelled within it. The impact of DOM (in the inflowing to the Aegean Sea BSW) appears to be stronger than the impact of dissolved inorganic nutrients, showing a more extended effect over the N. Aegean. Bacterial production and biomass is more strongly affected in the simulations by modified DOM, while phytoplankton biomass and production are more dependent on inflowing nutrients and particularly phosphorus (inorganic and dissolved organic). As regards phytoplankton composition, the dinoflagellates appear to be affected most, being favoured by higher nutrient availability at the expense of all other groups, particularly picoplankton, indicating a shift to a more classical food chain.

Keywords: N. Aegean Sea, sensitivity, Black Sea, inflow, modelling, biogeochemical, organic matter.

Introduction

The N. Aegean is a marginal sea that is characterized by relatively pronounced productivity within the oligotrophic eastern Mediterranean basin, sustaining important fish stocks (Stergiou *et al*., 1997). This increased productivity is related to the significant amount of riverine nutrient inputs (Tsiaras *et al*., 2012, 2014), as well as to the discharge of waters of Black Sea (BSW) origin through the Dardanelles strait, from the Marmara Sea that connects the Black and Mediterranean Seas (Fig. 1). BSW have low-salinity and are rich in particulate and dissolved organic matter (POM, DOM) (Polat & Tugrul, 1996; Sempéré *et al*., 2002; Zeri *et al*., 2014), triggering increased primary and secondary production especially in spring as shown in Siokou-Frangou *et al*. (2002) (Primary Production 2339±905, Bacterial Production 110±77, Copepod Production 41±31 mgC m^{-2} day^{-1}). The concentration of dissolved inorganic nutrients in the BSW reaching the Dardanelles strait, is found similar to that in the surface waters of the N. Aegean due to their consumption in the Marmara Sea (Polat & Tugrul, 1996; Lagaria *et al*., 2013; Zeri *et al*., 2014). Therefore, BSW inputs of dissolved inorganic nutrients seem to be less important compared to riverine inputs, while DOM could be a significant driver for the system. The above show that an analysis of the role of the various inputs and their impact on the Aegean Sea ecosystem is imperative.

DOM degradation through photochemical (Moran & Zepp, 1997) and microbial processes (e.g. Azam *et al*., 1993) provides an important source of inorganic nutrients that are necessary for phytoplankton growth. In the deep ocean, bacteria are considered to function as net remineralizers, decomposing organic matter and fuelling the deep nutrient pools. In surface nutrient depleted waters, depending on DOM stoichiometry and the availability of dissolved organic nitrogen (DON) and phosphorus (DOP), bacteria can also compete with phytoplankton for inorganic nutrients, in order to meet their demands for growth. This appears to be the case in the Mediterranean, with both phytoplankton and bacteria being limited by phosphorus availability (Thingstad & Rassoulzadegan, 1995). Therefore, the effect of DOM cycling on primary production is expected to change both in time and space, depending on the availability of organic and inorganic nutrient pools. Although it has been pointed out by several studies (Polat & Tugrul, 1996; Sempéré *et al*., 2002; Zeri *et al*., 2014) that the increased organic matter BSW input is an important driver, which may be associated with the increased primary and secondary production in the area, its effect on productivity and food web dynamics has not been yet fully investigated. Tsiaras *et al*. (2014) implemented a compre-

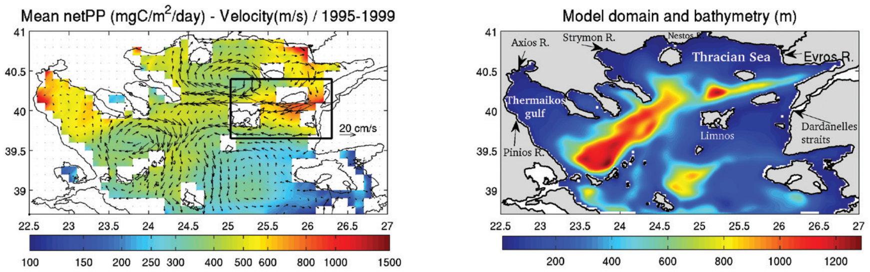

Fig. 1: N. Aegean bathymetry (right) and mean (1995-1999) simulated integrated net primary production (mg C m^{-2} day^{-1}), along with near surface velocity field. Major rivers and the Dardanelles Strait are indicated. The Dardanelles area, to which Figures 6, 10, 11 refer to is indicated by the black box.

hensive coupled hydrodynamic/ biogeochemical model to investigate the impact of river nutrient load variability on N. Aegean ecosystem functioning over the last decades. In this study, the effect of BSW inputs on N. Aegean productivity and food web dynamics is investigated, by means of sensitivity simulations, adopting different properties of the inflowing BSW, in terms of inorganic nutrients and dissolved organic matter. Our aim is to gain insight on the role of BSW inputs in N. Aegean ecosystem functioning. Moreover, the adopted scenarios of modified BSW inputs might also reflect possible changes related to climate and human activities in the neighbouring seas (Black Sea and Marmara Sea) (Ludwig *et al*., 2010).

Materials and Methods

Model Description

The coupled hydrodynamic/biogeochemical model by Tsiaras *et al*. (2014) is used in this study. The hydrodynamic model is based on the Princeton Ocean Model (Blumberg & Mellor, 1983), while the biogeochemical model is based on the European Regional Seas Ecosystem Model (ERSEM, Baretta *et al*., 1995; Petihakis *et al*., 2002). ERSEM is a comprehensive functional type model that resolves carbon, nitrogen, phosphorus and silicate dynamics, describing the marine ecosystem with different groups of primary producers (diatoms, nanoplankton, picoplankton, dinoflagellates), heterotrophic consumers (heterotrophic nanoflagellates, microzooplankton, mesozooplankton) and bacteria, based on their functioning role and size classes. The pelagic food web has been slightly modified by Petihakis *et al*. (2002) from the original ERSEM, to better represent the microbial loop that is particularly important in the Mediterranean. A schematic diagram of the trophic interactions among different groups is shown in Figure 2. Heterotrophic nanoflagellates (HNAN) feed on bacteria, picophytoplankton and nanophytoplankton. Microzooplankton that is considered to include protozoans (e.g. ciliates, heterotrophic dinoflagellates), feed on nanophytoplankton, heterotrophic nanoflagellates, diatoms and dinoflagellates, while mesozooplankton feed on diatoms, dinoflagellates and microzooplankton. The model configuration and parameter set has been adopted from Petihakis *et al*. (2002), to which the interested reader may refer for a more detailed description of the model. Changes in the parameter set of Petihakis *et al*. (2002) may be found in Tsiaras *et al*. (2014). Moreover, the bacteria sub-model that is briefly described below has been revised from the one in Petihakis *et al*. (2002), following Petihakis *et al*. (2009) and Anderson & Williams (1998), allowing for a more realistic representation of the DOM pool.

Bacteria are assumed to utilise DOM as a substrate for growth. DOM is produced by the mortality, excretion and lysis of primary and secondary producers. The change in bacterial carbon biomass is described by:

$$dB/dt = (u - m - r) * B - g \quad (1)$$

where B is the bacterial carbon biomass, u is the uptake of DOC, m is the mortality rate due to viral lysis, r is the respiration rate and g is the loss term due to grazing by heterotrophic nanoflagellates. The uptake of DOC is described by:

$$u = sumB * f(T) * f(O2) * min(min\ (Nlim, Plim), Clim) \quad (2)$$

$sumB$ is the maximum bacterial growth rate, $f(T)$ is the growth temperature dependence, $f(O2)$ the oxygen limitation, $(Nlim,\ Plim)$ is the nutrient limitation and $Clim$ the limitation on available DOC. The nutrient limitation was slightly modified, to use the intracellular nutrient limitation functions as in Petihakis *et al*. (2009), rather than the external nutrient concentrations, employed in Petihakis *et al*. (2002) and Allen *et al*. (2002):

$$Nlim=min(1,\ max\ (0,\ qnB\ /\ qnSTc\$))$$
$$Plim=min(1,\ max\ (0,\ qpB\ /\ qpSTc\$)) \quad (3)$$

where qnB, qpB are the internal nitrogen and phosphorus bacteria N/C and P/C quotas, while $qnSTc\$$, $qpSTc\$$ are similarly the maximum internal quotas.

A carbon limitation was also introduced, following Anderson & Williams (1998):

$$Clim= DOC/(DOC+K_{DOC}) \quad (4)$$

DOC represents both labile and semi-labile DOC. K_{DOC} is a half-saturation constant for DOC uptake that was calculated (~2500 mgC m^{-3}) from the average of the constants used in Anderson and Williams (1998) for labile and semi-labile uptake. In the old formulation (Allen *et al*., 2002; Petihakis *et al*., 2002), there was no carbon limitation applied in the DOC uptake; this was calculated taking the minimum of potential uptake (u, eq.2

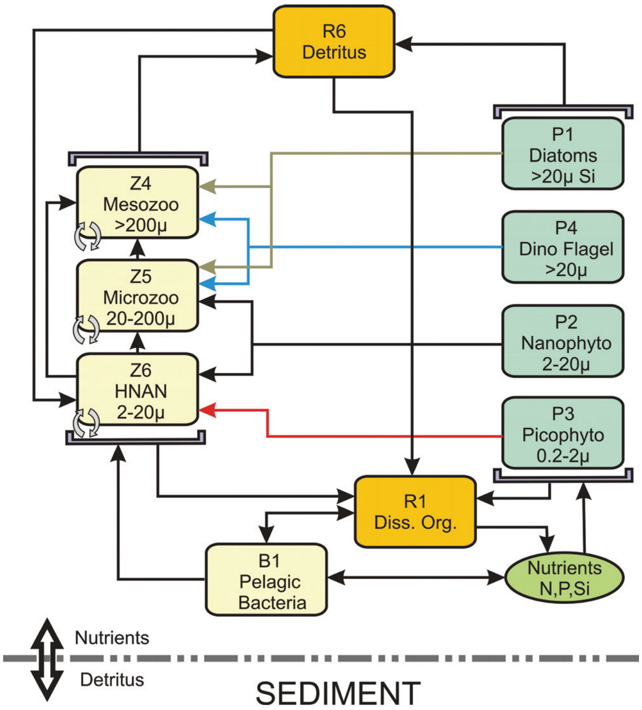

Fig. 2: Schematic diagram of the biogeochemical model (ERSEM). Arrows indicate fluxes among different model compartments.

with *Clim*=1) and the available DOC pool; resulting in a slight underestimation of the simulated DOC pool. This was not a significant problem in the previous model application in the Cretan Sea (Petihakis *et al.*, 2002), since in open sea areas, the primary source of DOC is the excretion and lysis of plankton biomass. In this case (Cretan Sea), the DOC pool was adjusted to a (lower) level, where the carbon limitation and the resulting bacterial production would be similar to those with the present formulation. In the N. Aegean however, where there are significant lateral inputs of DOM from river and BSW discharge, the simulated DOM pool has to be consistent with these inputs and bacterial production would be significantly overestimated if the old formulation was used.

Bacterial ectoenzymatic hydrolysis is an important process, mediating the breakdown of POM and polymeric DOM into labile forms that are readily available as a substrate for bacteria (Azam *et al*., 1993; Thingstad & Rassoulzadegan, 1995; Karl & Bjorkman, 2002). This process is implicitly represented in the model, since only one DOM (labile and semi-labile) pool is considered, with a constant breakdown rate (0.05 day^{-1}) from POM to DOM, following Anderson & Williams (1998). However, it must be taken into account that there is a preferential remineralisation of organic phosphorus over nitrogen and over carbon (Smith *et al*., 1992; Loh & Bauer, 2000), while hydrolysis products such as phosphate are not directly taken up by bacteria but are also available to phytoplankton (loose coupling) (Azam *et al*., 1993, Karl & Bjorkman, 2002). Moreover, there is photochemical hydrolysis (Moran & Zepp, 1997) that is not described in the model. To account for the above, an additional first order remineralisation ($Rdom$) of dissolved organic nitrogen (DON) and phosphorus (DOP) into ammonia (0.02 day^{-1}) and phosphate (0.03 day^{-1}) respectively, was adopted. Depending on the quality of available DOM, bacteria may act as remineralizers producing ammonium and/or phosphate, when the available DON/DOP exceeds their needs to assimilate the available DOC. Following Anderson & Williams (1998), nutrient release (of PO4, in this example) may be expressed as follows:

$$Rpo4 = u * DOMqp - qpB * (u - r - m) = u * (DOMqp - qpB * BGE), \quad (5)$$

where u is the DOC uptake (gross bacterial production), $DOMqp$ is the DOP:DOC, qpB is the bacterial internal P:C ratio and BGE is bacterial growth efficiency that can be calculated as the ratio of bacterial production over total carbon utilization:

$$BGE = (u - r - m) / u,$$

with mortality m depending on temperature ($m = sdST\$ * etB$) and respiration r consisting of an activity and a temperature dependent maintenance part:

$$r = (1 - puST\$ * eO2 - puSTo\$ * (1 - eO2)) * u + srsB * etB, \quad (6)$$

where $puST\$$ is the bacterial assimilation efficiency, $eO2$ is the relative oxygen saturation, etB is a Q10 temperature dependence and $srsST\$$ the rest.

The PO4 release occurs when $DOMqp > qpB * BGE$. Bacteria may also release or uptake phosphate and/or ammonium based on their internal stoichiometry, in order to cover their needs in nitrogen and phosphorus:

$$Rbac = (qpB - p\_qpc) * B, \quad qpB > qpSTc\$$$
$$-qur\_p * po4 * B, \quad qpB < qpSTc\$ \quad (7)$$

B is bacterial biomass, qpB and $qpSTc\$$ are the bacterial actual and maximum internal P:C ratios respectively, while qur_p is the bacterial nutrient affinity. The parameter values are given in an Appendix.

Model setup

The coupled hydrodynamic/biogeochemical model described above was employed to perform sensitivity 5-year (1995-1999) simulations, adopting different properties of the inflowing Black Sea Water (BSW) in terms of inorganic nutrients and dissolved organic matter.

The atmospheric forcing was based on the ECMWF ERA40 reanalysis dataset, downscaled to 0.5 degree resolution (Herrmann & Somot, 2008). The Dardanelles water exchange was parameterized by employing a two-layer (inflow of surface BSW and outflow of subsurface Aegean water) open boundary condition with prescribed water transport and salinity (Nittis *et al*., 2006). A uniform velocity is calculated for the two layers based on the prescribed transports, obtained from Tugrul *et al.* (2002). In the reference simulation, seasonal mean concentrations were used for dissolved inorganic nutrients (phosphate, nitrate) based on long-term data (Tugrul *et al.*, 2002) and annual mean concentrations (Polat & Tugrul, 1996) for ammonia, particulate (POC=20 mmol m^{-3}, PON=1.95 mmol m^{-3}, POP=0.21 mmol m^{-3}) and dissolved (DOC=166 mmol m^{-3}, DON=13 mmol m^{-3}, DOP=0.14 mmol m^{-3}) organic matter. We should note that since only the labile/semi-labile DOM pool is represented in the model, constant background concentrations for DOC ~45mmol m^{-3}, DON ~2.85 mmol m^{-3} and DOP ~0.03 mmol m^{-3} (Aminot & Kerouel, 2004) that represent the refractory pool are subtracted by the BSW and river DOC/DON/DOP concentrations. An input of phytoplankton biomass was also imposed at the Dardanelles mouth, based on a monthly climatology of available (1998-2001) SeaWiFS (Sea-viewing Wide Field-of view Sensor) Chlorophyll (Chl-a) data that were obtained using the Ocean Chlorophyll 4 - version 4 (OC4-v4) algorithm [O'Reilly *et al.*, 1998] from the global Level-3 monthly composite products (9×9 km^2 resolution).

River nutrient loads were set to average values for the 1995-1999 period adopted from Skoulikidis (2009). Along the model southern open boundary, both the hydrodynamic and biogeochemical properties were obtained from a basin scale Mediterranean coupled hydrodynamic/biogeochemical model (Korres *et al.*, 2007; Tsiaras *et al.*, 2008) simulation over the same period. This model is currently operational within the POSEIDON forecast system (www.poseidon.hcmr.gr). The initial fields for dissolved inorganic nutrients were obtained from the Medatlas 2002 climatology (http://www.ifremer.fr/medar/). The N. Aegean coupled model was initialized in 1995, using the output from the long-term simulation (1980-1999) in Tsiaras *et al.* (2014).

Results and Discussion

The present model has been extensively validated in Tsiaras *et al.* (2014), against available remote sensing and *in situ* data. The main features of the simulated plankton food web in the N. Aegean have also been discussed in Tsiaras *et al.* (2014) and are briefly summarized below. The simulated phytoplankton biomass (see Figure 11 in Tsiaras *et al.*, 2014 and Figure 3 here in) is dominated by smaller cells, particularly picoplankton that comprises 44% of total biomass, in agreement with *in situ* data (Ignatiades *et al.*, 2002; Siokou-Frangou *et al.*, 2002), despite an overestimation of large phytoplankton biomass (diatoms+dinoflagellates), simulated in the spring period. Furthermore, a size-based horizontal variability in phytoplankton composition was found, with diatoms and dinoflagellates being relatively more abundant in coastal productive areas and smaller phytoplankton dominating the open sea areas. This was attributed to size-based resource competition, with smaller cells being favoured in less productive areas and reduced grazing pressure favouring larger phytoplankton in coastal productive waters (Tsiaras *et al.*, 2014). A similar horizontal variability was also found for heterotroph groups, following the variability of their preys, with HNAN being relatively more abundant in open sea waters and mesozooplankton that feed mainly on diatoms and dinoflagellates being more numerous in coastal more productive waters. The interannual variability in river nutrient loads, as well as sensitivity simulations performed in Tsiaras *et al.* (2014), revealed that dinoflagellates were mainly favoured by increased river nutrient inputs, resulting in a stronger silicate limitation on diatom growth. Another interesting finding of Tsiaras *et al.* (2014), was the significant response of productivity

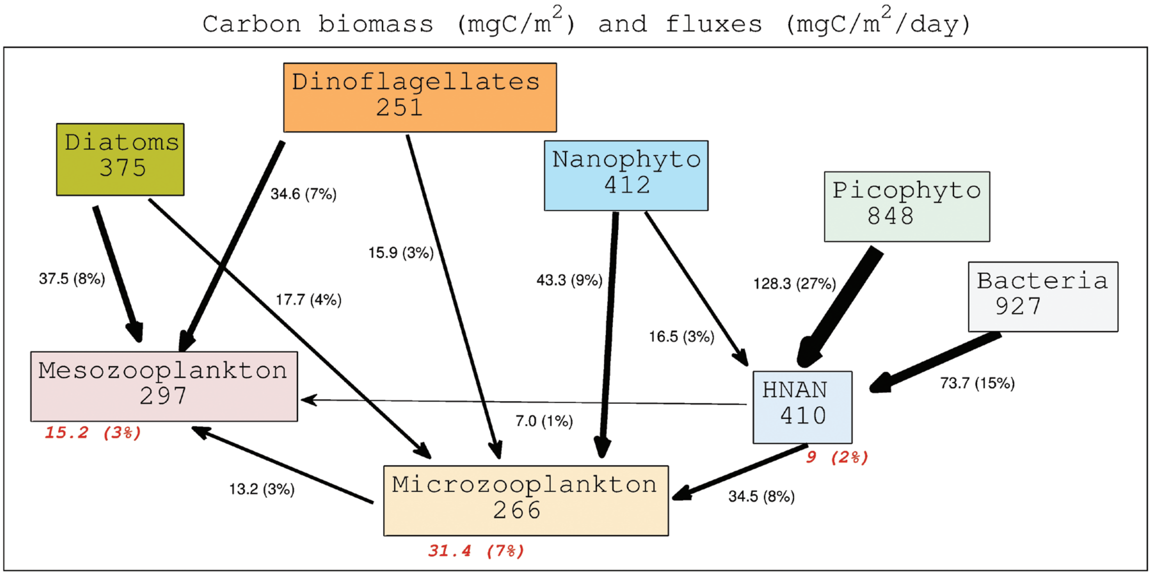

Fig. 3: Average integrated carbon biomass (mg C m^{-2}, inside the boxes) and fluxes (mg C m^{-2} day^{-1}, next to the arrows) among different plankton groups. The percentage of the total carbon flux is indicated in brackets, while for mesozooplankton, microzooplankton and HNAN the flux within the same group is indicated in red/italics.

in the Dardanelles area, related to the river input interannual variability that was attributed to the advection of nutrient-rich waters from the northern coastal areas and the semi-permanent anticyclonic circulation in the north eastern Aegean (Fig. 1). This finding suggests that interannual variability in the Dardanelles plume area may also be related to river inputs and not necessarily to the interannual variability of BSW inputs.

In an attempt to identify the major carbon pathways within the simulated web, the average depth integrated carbon fluxes and biomass were computed (Fig. 3). The flux within the microbial loop (picophytoplankton, bacteria, heterotrophic nanoflagellates (HNAN)) represents almost 59% of the total as expected, given the dominance of smaller cells among both autotrophic and heterotrophic groups mentioned above (see also Figure 11 in Tsiaras *et al.*, 2014). This highlights the important role of the microbial loop within the N. Aegean ecosystem. Smaller - compared to the microbial loop - but still significant fluxes in terms of magnitude, are those from nanophytoplankton to microzooplankton, diatoms and dinoflagellates to mesozooplankton and from HNAN to microzooplankton. Finally, relatively small fluxes are simulated from diatoms and dinoflagellates to microzooplankton and from nanophytoplankton to HNAN. It is interesting to note that relatively little carbon is channelled from microzooplankton and HNAN to mesozooplankton; however, Zervoudaki *et al.* (2007) estimated a higher consumption of copepods on ciliates than on phytoplankton. In a review paper by Calbet (2008) on the trophic role of microzooplankton, it is shown that microzooplankton are relevant contributors to the diet of copepods and the relative importance of ciliate consumption by copepods depends on the trophic state of the system. Thus, in oligotrophic ecosystems (most of the world's oceans), the ciliate-associated carbon supply for copepods equals that of phytoplankton, and this value declines in more productive environments, where ciliates account for ca. 25% of the diet. Furthermore, heterotrophic dinoflagellates are also a significant food source for mesozooplankton, which are, at times, cleared at higher rates than ciliates. Therefore, the combined contribution of heterotrophic ciliates and dinoflagellates (as well as other microzooplankters) to the mesozooplankton diet may surpass that of phytoplankton in certain systems. The quite high microzooplankton internal flux simulated by the model indicates carbon exchange between ciliates and heterotrophic dinoflagellates. Some heterotrophic dinoflagellates are predators of and simultaneously prey for other dinoflagellates, while some ciliate species were found feeding on heterotrophic dinoflagellates (Jeong, 1999). Finally, one also ηας to take into account that the above picture is an average picture of the system in space and time, while coastal areas are closer to a typical web in contrast with the open sea areas.

A more dynamic picture of the simulated fluxes is shown in Figure 4. The biomass variability of small-sized phytoplankton is tightly coupled with the flux towards their predator (HNAN) and only when the picophytoplankton population drops and bacteria become abundant (summer period) does HNAN begin to take up almost equal quantities of both. The internal flux within the microzooplankton group (from ciliates and heterotrophic dinoflagellates to small nauplii) is rather strong all year round and it even gets equally significant to the flux from HNAN during summer. Mesozooplankton takes advantage of the presence of large phytoplankton, switching between diatoms and dinoflagellates, according to which one is more abundant. On the contrary, there is a rather constant flux rate from microzooplankton to mesozooplankton, similar to the internal mesozooplankton flux.

As mentioned above, the BSW is mostly enriched in terms of dissolved organics, particularly DOC and DON (Polat & Tugrul, 1996; Sempéré *et al.*, 2002; Zeri *et al.*, 2014). BSW contributes significantly more DOC, compared to the main rivers (Fig. 5a), (Table 1) enriching the whole northern area, while increased DOC may be also tracked along the BSW pathway to the southwest, showing a similar pattern with net primary production (Fig. 1). The model simulated DOC (Fig. 5) is in good agreement with measurements by Zeri *et al.* (2014) that show a similar gradient from 65 mmol m^{-3} in the open sea (~25.2E, 39.3N) to 107 mmol m^{-3} near the Dardanelles strait. Vertically, the model DOC (not shown) also follows a similar pattern with the data, extending as deep as 100m, where it reduces to its background value. We should note that since only the labile/semi-labile DOC pool is represented in the model, a constant background DOC ~45mmol m^{-3} (a range of 40-50 mmol m^{-3} is reported over the world ocean, Aminot & Kerouel, 2004) that represents the refractory pool is added in order to obtain total DOC. The simulated DON (not shown) exhibits the same pattern with DOC, presenting a similar gradient (1.5-5.56 mmol m^{-3}) with the data (3.08-5.69 mmol m^{-3}, Zeri *et al.*, 2014) with, however, lower concentrations in the open sea area. Nevertheless, it should be noted that both DON and DOP are considered to be labile/semi-labile in the model, not including a refractory constant pool. Therefore, some underestimation is expected in oligotrophic areas. If a constant refractory DON (2.85 mmol m^{-3}, Aminot & Kerouel*,* 2004) were to

Table 1. Dissolved organic carbon (DOC), nitrogen (DON) and phosphorus (DOP) total input from Rivers and BSW. River DOC is based on Skoulikidis et al. (1993), while river DON and DOP inputs are assumed to be 12% of total nitrogen and 15% of total phosphorus respectively (Ludwig et al., 2009). BSW inputs are based on Polat and Tugrul (1996) concentrations and water discharge from Tugrul et al. (2002).

mol/s	DOP	DON	DOC
River	3.6	29.4	134.5
BSW inflow	4.5	416	5312

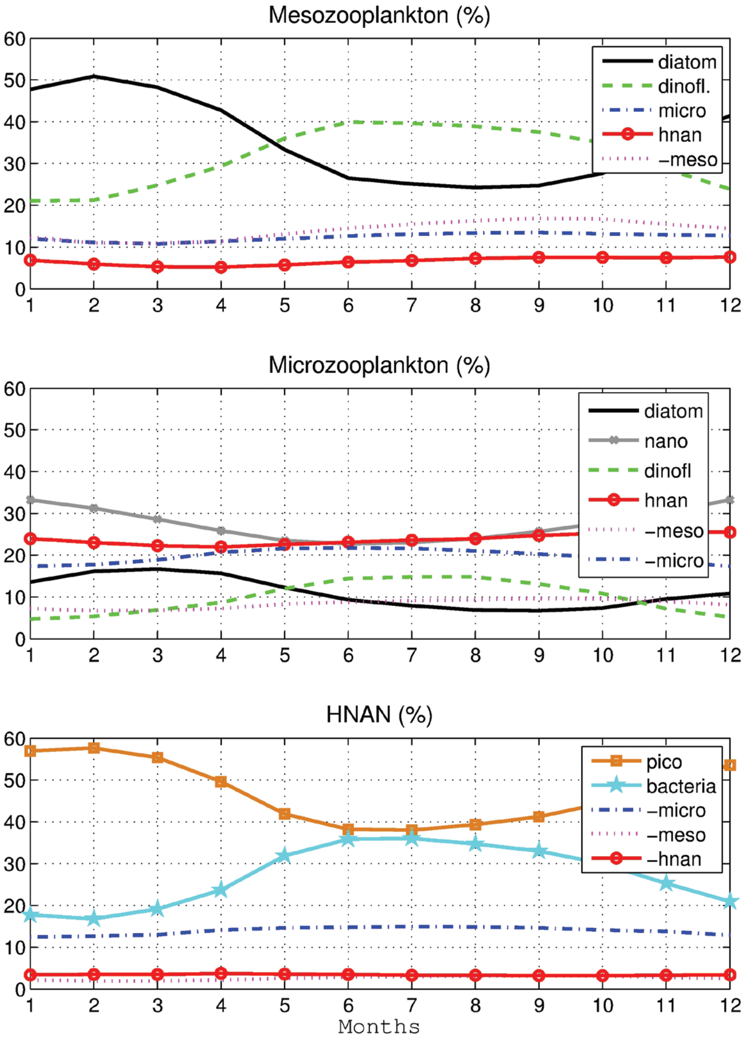

Fig. 4: Percentage carbon fluxes to/from mesozooplankton (top) from/to diatoms (black line), dinoflagellates (green line), microzooplankton (blue line), HNAN (red line) and mesozooplankton (magenta line), to/from microzooplankton (middle) from/to diatoms (black line), nanoplankton (grey line), dinoflagellates (green line), HNAN (red line), microzooplankton (blue line), mesozooplankton (magenta line), and to/from heterotrophic nanoflagellates (HNAN, bottom), from/to picoplankton (orange line), bacteria (cyan line), HNAN (red line), microzooplankton (blue line), and mesozooplankton (magenta line). Negative signs indicate an outward flux.

be added, model DON would be slightly higher (3.5-7.5 mmol m^{-3}) as compared to 3.08-5.69 mmol m^{-3}; reported by Zeri *et al*. (2014). Unfortunately, there are no available data for DOP to compare with in the area. However, the simulated range for DOP (0.05-0.1mmol m^{-3}) is similar with measurements in the North-western Mediterranean (0.08mmol m^{-3}, Aminot & Kerouel, 2004; 0.06-0.1 mmol m^{-3}, Raimbault *et al*., 1999).

An important characteristic is the stoichiometry of the organic inputs (Fig. 5) as it directly affects the dynamics of the DOM cycling by bacteria. The DON/DOP ratio indicates that much higher quantities of organic nitrogen are entering the system, which effectively contributes towards phosphorus limitation. Thermaikos gulf is an exception, with DON/DOP being particularly low, as is the case with inorganic nutrients (Tsiaras *et al*., 2014), indicating nitrogen deficiency. While DOP inputs from rivers and BSW are comparable (Table 1), the DON in BSW input is more than ten times higher (DON:DOP~92), which is demonstrated by the particularly high DON:DOP ratio in the Dardanelles plume area.

Considering the importance of the microbial loop in ecosystem functioning and the role of dissolved organics as a suitable substrate for bacteria, a model analysis on the low-trophic level dynamics focusing in the area of Dardanelles was carried out (Fig. 6). This area is of particular interest, as the ecosystem dynamics are largely forced by the BSW inputs and thus can depart from the standard East Mediterranean production pattern. As indicated by the model simulation, a spring maximum in production and biomass is associated with the primary producers and not with the bacteria that remain at low levels. Looking at the concentration of the near surface DOC and that excreted by phytoplankton, as well as the biomass of the bacteria predators (HNAN), the emanating picture is that bacteria are both top down and bottom

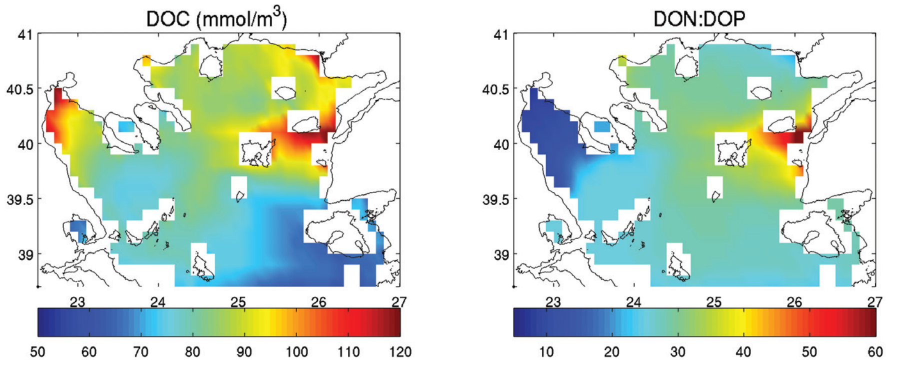

Fig. 5: Mean model simulated dissolved organic carbon (DOC, mmol m^{-3}) and dissolved organic nitrogen over phosphorus ratio (DON:DOP).

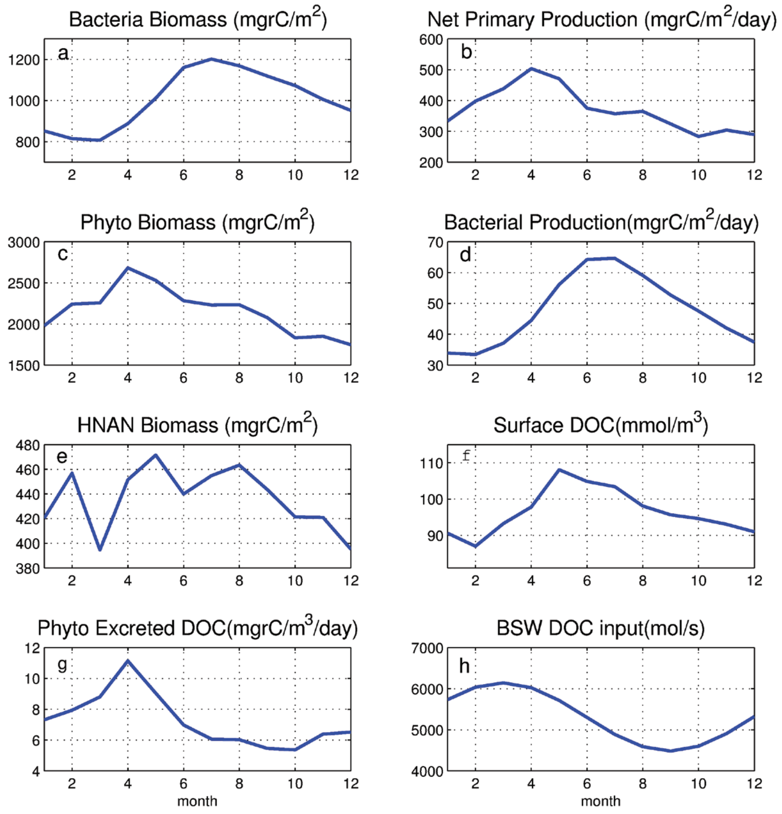

***Fig. 6**:* Seasonal variability of a) bacterial biomass (mg C m^{-2}), b) net primary production (mg C m^{-2} day^{-1}), c) total phytoplankton biomass (mg C m^{-2}), d) bacterial production (mg C m^{-2} day^{-1}), e) heterotrophic nanoflagellates (HNAN) biomass (mg C m^{-2}), f) surface DOC (mmol m^{-3}), g) rate of excreted surface DOC (see Varela *et al*., 1995) from phytoplankton (mg C m^{-2} day^{-1}), averaged over the Dardanelles area (indicated in Figure 1) and h) DOC BSW input (mol s^{-1}).

up controlled during spring. Bacterial production and biomass are higher in summer, following the increase of DOM in April-May that is related to DOM input from BSW and to phytoplankton excretion.

Sensitivity experiments on BSW properties

In order to investigate the effect of the BSW on the productivity and food web dynamics of the N. Aegean Sea ecosystem, a series of sensitivity simulations were performed. The simulation chosen covers the 1995-1999 period, which is considered as being representative of present-day conditions. Dissolved inorganic nutrient (PO4, NO3, NH4) and organic matter (DOC, DON, DOP) concentrations of the inflowing BSW were modified by a factor of 0.5 (half the reference) or 2 (twice the reference). Two additional simulations were performed adopting 5 times higher dissolved inorganic nutrients (PO4, NO3, NH4), as an extreme scenario of a potential increase of nutrients in the Marmara Sea due to local effluents (i.e. sewage effluents from Istanbul and other cities, mucilage events etc.), and another with only DOP increased in order to test the effect of DOM quality on marine productivity. The simulated results for PO4, net primary production and bacterial production are shown in Figures 7, 8 and 9. respectively.

Comparing the different simulations, we notice that the impact of DOM (in the inflowing to the Aegean Sea, BSW) appears to be stronger than the impact of dissolved inorganic nutrients, showing a more extended effect over the N. Aegean (Fig. 7). As expected, bacterial production presents the stronger response to the modified BSW DOM input (Fig. 9), being directly linked to the availability of DOM, since it is the primary resource of bacterial growth. It is interesting to note that net primary production (Fig. 8) also exhibits a significant response to modified DOM, which is stronger than the one to modified inorganic nutrients. This stronger effect of DOM is attributed to the importance of DOM remineralization to inorganic nutrients, given the much smaller quantity of inorganic, as compared to organic matter input through BSW (see Table 1 in Tsiaras *et al.,* 2012). Furthermore, the BSW input of DOP (4.1 ktons P year^{-1}) is, for example, 2.4 times higher than the input of PO4 (1.7 ktons P year^{-1}). Therefore, when the DOP input is doubled (e.g. 8.2 ktons P year^{-1}), an additional amount of phosphorus is added (8.2-2*1.7=4.8 ktons P year^{-1}) to the system, as compared to the case where phosphate is doubled. Since DOP is not directly available to phytoplankton, but has to be remineralized to phosphate, its effect will extend over a much wider area, as compared to the case where BSW inorganic nutrients were increased. When only DOP is increased, remineralization to PO4 is further enhanced, causing increased PO4 (Fig. 7e, 7f) and triggering net PP (Fig. 8e, 8f) but with a smaller bacterial production (Fig. 9e, 9f). Since in this scenario, DOC is not increased, the bacteria, cannot efficiently respond to increased PO4 concentrations in contrast with phytoplankton, which responds with increased production. Finally, the modified BSW DOM appears to have a stronger effect in the Thermaikos gulf, particularly in terms of primary production and phosphate, which is related to the nitrogen deficiency characterizing this area (Tsiaras *et al*., 2014). Given the increased DON/DOP ratio (~92) of the BSW DOM, when the latter is increased, relatively more DON is added to the system and remineralized to inorganic nitrogen. This results in a strong increase of primary production (Fig. 8) and a strong decrease of phosphates (Fig. 7) in the nitrogen deficient Thermaikos Gulf.

The overall effect of different scenarios in the Darda-

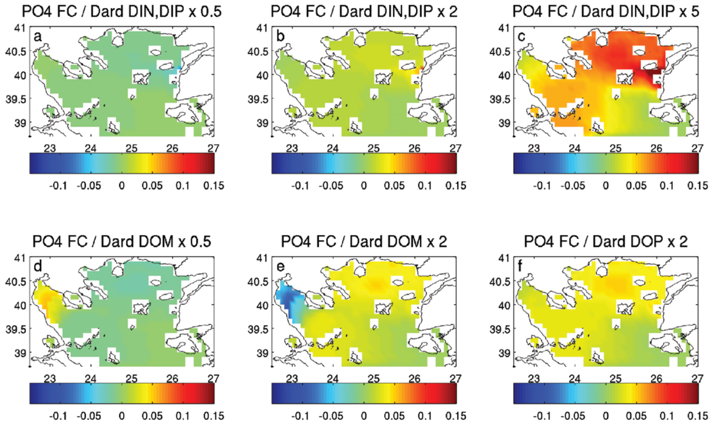

Fig. *7:* Model simulated PO4 fractional change (scenario/reference-1) of the simulation adopting BSW a) (PO4, NO3, NH4) x 0.5, b) (PO4, NO3, NH4) x 2, c) (PO4, NO3, NH4) x 5, d) (DOC, DON, DOP) x 0.5, e) (DOC, DON, DOP) x 2, f) DOP x 2.

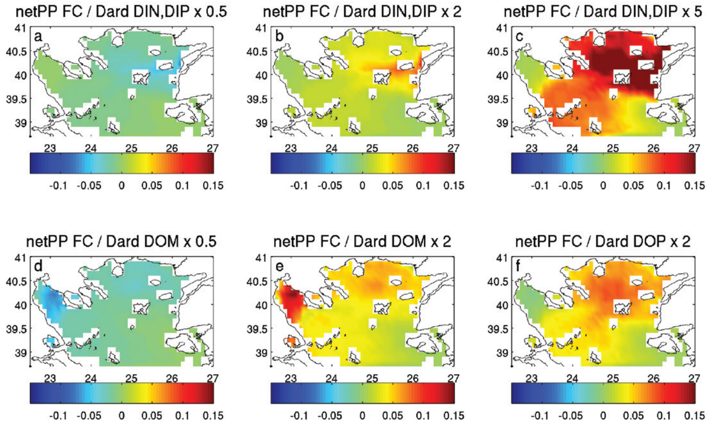

Fig. 8: Model simulated integrated net primary production fractional change (scenario/reference-1) of the simulation adopting BSW a) (PO4, NO3, NH4) x 0.5, b) (PO4, NO3, NH4) x 2, c) (PO4, NO3, NH4) x 5, d) (DOC, DON, DOP) x 0.5, e) (DOC, DON, DOP) x 2, f) DOP x 2.

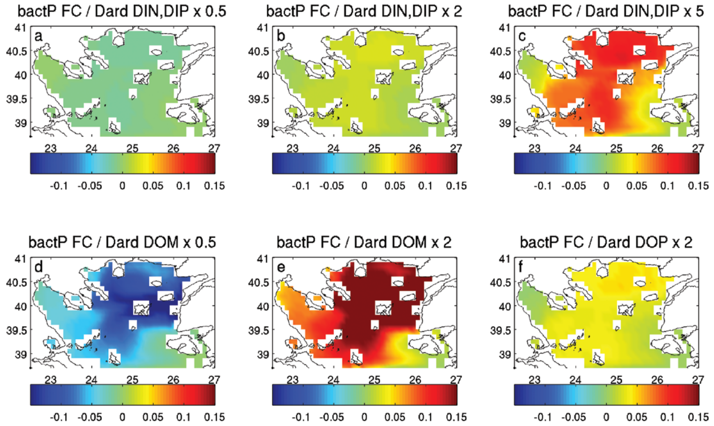

Fig. 9: Model simulated bacterial production fractional change (scenario/reference-1) of the simulation adopting BSW a) (PO4, NO3, NH4) x 0.5, b) (PO4, NO3, NH4) x 2, c) (PO4, NO3, NH4) x 5, d) (DOC, DON, DOP) x 0.5, e) (DOC, DON, DOP) x 2, f) DOP x 2.

nelles area is shown in Figure 10, in the form of fractional change for net PP, plankton (autotrophs and heterotrophs) biomass and phytoplankton composition. As mentioned above, bacterial production and biomass are more strongly affected in the simulations by modified DOM, unlike phytoplankton biomass and production, which are more dependent on inflowing nutrients and particularly phosphorus (inorganic and dissolved organic). In the phytoplankton composition, dinoflagellates appear to be mostly affected, being favoured by higher nutrient availability at the expense of all other groups, particularly picoplankton, indicating a shift to a more classical food chain. Considering that increased inputs are void of silicate, dinoflagellates gain a competitive advantage over diatoms, thus increasing the risk of HAB's. As expected, the scenario with smaller inputs and in particular smaller DOM ones produces a small but noticeable increase in picoplankton, which outcompetes bacteria and larger phytoplankton cells. In the wider model domain (NAEG), the fractional change (Fig. 10) confirms that the impact of DOM is

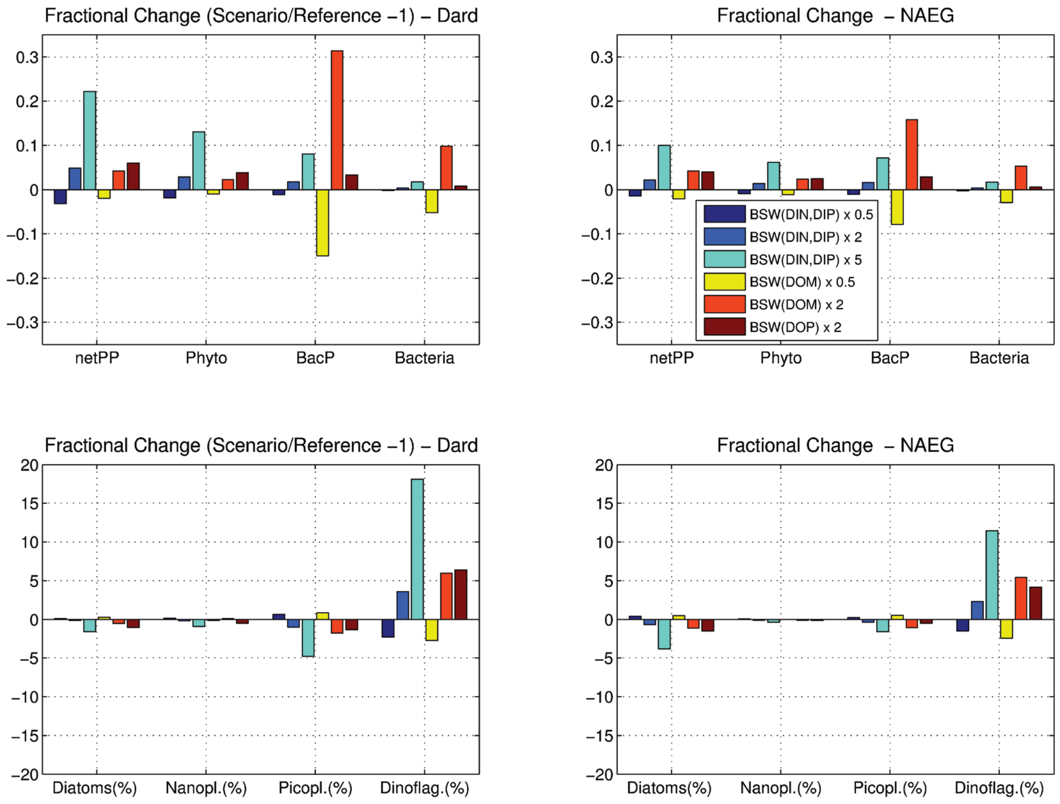

***Fig. 10**:* Fractional change (Scenario/Reference-1) of scenario simulations with different dissolved inorganic (NO3, NH4, PO4 x 0.5, x 2, 5) or organic matter (DOM x 0.5, x 2, DOP x 2) BSW inputs over the reference simulation, for net primary and bacterial production, plankton biomass and phytoplankton composition, averaged over the Dardanelles area (left, indicated in Figure 1) and the entire N. Aegean (right).

stronger than that of dissolved inorganic nutrients.

The stronger response of dinoflagellates to changing nutrient availability is also reflected in the fractional change of carbon fluxes among different groups (Fig. 11). Fluxes from dinoflagellates to mesozooplankton and particularly microzooplankton present the largest change with varying BSW input, confirming the shift to a classical food web and the increase of energy transfer to higher levels, either with inorganic or organic nutrient increase. As said above, bacteria are sensitive to DOM, while phytoplankton is sensitive to nutrient inputs. However, under all the different scenarios, the highest proportion (~50%) of the total carbon flux is concentrated in the microbial loop, circulating between bacteria and heterotrophic nanoflagellates, as well as between picoplankton and heterotrophic nanoflagellates.

Heterotrophic bacteria perform two major functions in the transformation of organic matter: They produce new bacterial biomass (bacterial production), and they respire, converting organic carbon to inorganic carbon (bacterial respiration). Bacterial Growth Efficiency (BGE) is the amount of new bacterial biomass produced per unit of organic C substrate assimilated. The modelled BGE is calculated from the ratio of Bacterial Production (BP) (carbon fixed) to Bacterial Carbon Demand (BCD) (carbon fixed + carbon respired) and is depicted in Figure 12, reaching 0.14 in DOC rich areas and ~0.1 in oligotrophic off shore waters. *In situ* measurements in August 2008 at Lemnos Plateau have estimated BGE at 0.19 (Zeri *et al.*, 2014), which is higher than the simulated one. The lower the growth efficiency, the higher is the flux of carbon that is respired and not assimilated

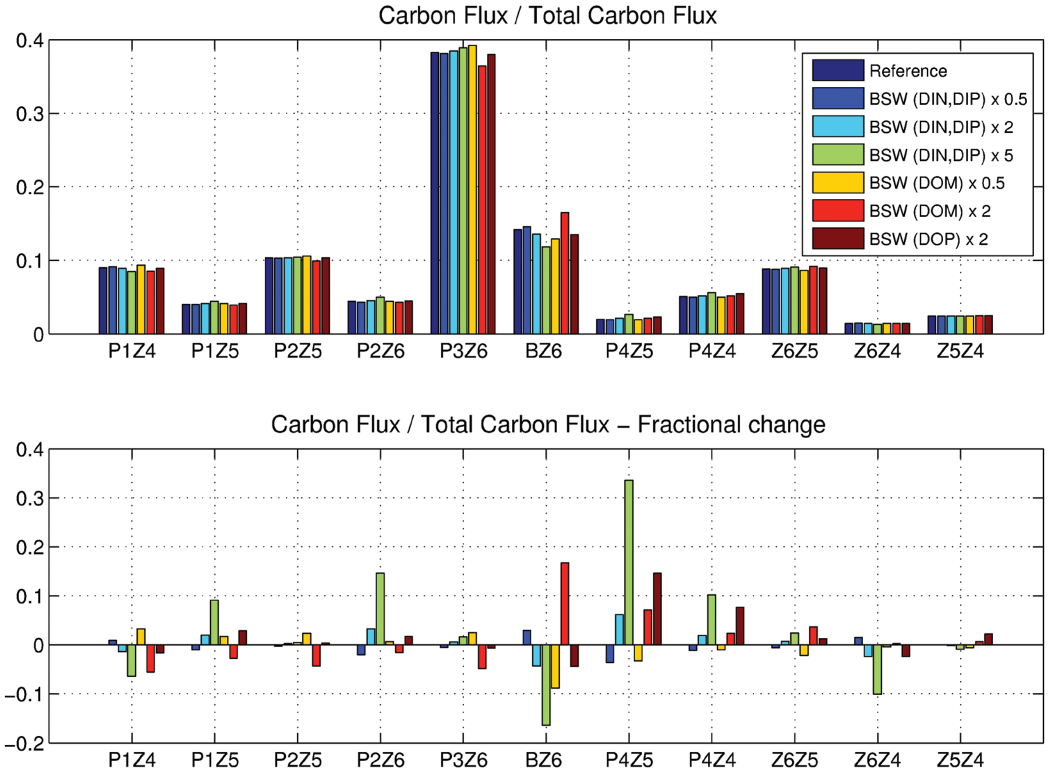

Fig. 11: Model simulated a) carbon fluxes among different plankton groups for the different sensitivity simulations (see Table 2), normalized by the total carbon flux and b) fractional change of scenario simulations over the reference, averaged over the Dardanelles area (indicated in Figure 1). P1=diatoms, P2=nanophyto, P3=picophyto, P4=dinoflagellates, Z4=mesozooplankton, Z5=microzooplankton, Z6=HNAN, B=bacteria.

Table 2. Sensitivity simulations with different BSW properties

Reference run inputs	**PO4, NO3, NH4, DOC, DON, DOP**
Reduced inorganic inputs	0.5 x (PO4, NO3, NH4)
Mild increased inorganic inputs	2.0 x (PO4, NO3, NH4)
Extreme increased inorganic inputs	5.0 x (PO4, NO3, NH4)
Reduced organic inputs	0.5 x (DOC, DON, DOP)
Mild increased organic inputs	2.0 x (DOC, DON, DOP)
Qualitative increase	2.0 x (DOP)

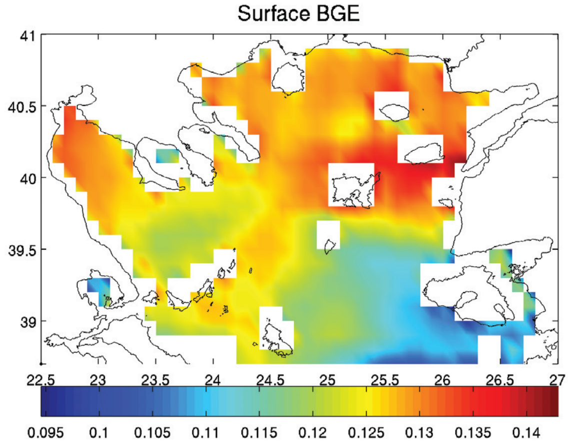

Fig. 12: Mean surface bacterial growth efficiency (BGE).

into biomass. Estimates of BGE for natural planktonic bacteria range from <0.05 to as high as 0.6, but little is known about what might regulate this enormous range (del Giorgio & Cole, 1998). Factors known to affect BGE are temperature (inverse relation), primary production (BGE increase along a productivity gradient from oligotrophic to eutrophic environments), DOM composition (DOC exudates from actively growing cells appears to support higher BGE) and bacterial growth rates (growth rate is maximized at the expense of BGE). Estimations of BGE in the eastern Mediterranean, using field data, range from 17 to 29% with a geometric mean of 22% (Turley *et al.*, 2000), while field studies in the oligotrophic Sargasso Sea found BGE of around 8 – 20% (Carlson *et al.*, 1994). BGE varies systematically with BP and the trophic richness of the ecosystem (del Giorgio & Cole, 1998). In the most dilute, oligotrophic systems, BGE is as low as 0.01; in the most eutrophic systems, it plateaus near 0.5. Planktonic bacteria appear to maximize carbon utilization rather than BGE. A consequence of this strategy is that maintenance energy costs (and therefore maintenance respiration) seems to be highest in oligotrophic systems. In this study, the BGE appears to follow the DOC/DOM distribution (both in surface and in depth) (Fig. 5 and 12) that mainly controls bacterial production.

The cycling of Carbon (C), nitrogen (N), and phosphorus (P) proceeds at different rates such that the ratio of C:N:P can vary widely between particulate, dissolved, organic, and inorganic pools. Respiratory activities of heterotrophic bacteria also return nutrients to mineral form, thus completing the cycle from inorganic to organic and back to inorganic. consequently, the final turn of this cycle is termed remineralization. Field estimates of the amount of primary production passing through bacterioplankton is 10 – 60% with about half of that being fixed into bacterial cells (Ducklow *et al.*, 1986). Experiments in mesocosms (Coffin *et al.*, 1993) indicate that bacteria are closely coupled to substrate from phytoplankton and thus, when growth conditions are adequate, bacteria may cycle a significant amount of carbon and nutrients to bacterial predators, while when conditions are limited, bacteria may mineralise a greater proportion of the material that they assimilate.

The role of bacteria in nutrient regeneration from DOM depends on the balance between substrate and biomass stoichiometry, as well as on bacterial growth efficiency (Equation 5). Modelled nitrogen remineralisation from bacteria (Fig. 13) generally follows the DOM distribution (Fig. 5) with the exception of the wider Thermaikos Gulf area, where relatively higher DOP inputs push the system towards high phosphorus remineralization, indicated also by the decreased DON:DOP in this area (Fig. 5). High levels of phosphorus remineralization are also simulated around river Evros (low DON/DOP inputs). Thus, with the exception of these two areas (Thermaikos and Evros) bacteria actively remineralize DON releasing inorganic nitrogen, while they uptake inorganic phosphorus due to the shortage of DOP. This is more evident in the Dardanelles plume area that is characterized by relatively high DON:DOC ($>qnB$*BGE) and low DOP:DOC ($<qp$*BGE) (Fig. 5). Generally, assuming a BGE of ~15%, a net positive remineralization is expected to occur when DOC:DON<27 for nitrogen and DOC:DOP<370 for phosphorus. This is illustrated in Figure 13 c,d, where DOC:DON and DOC:DOP are shown, considering only the labile/semi-labile pools. Indeed, DOC:DON is below 20 in all areas except the Thermaikos gulf, indicating a positive remineralization for nitrogen, while DOC:DOP is above 400, except in the Thermaikos and Evros areas, indicating a negative remineralization (phosphate uptake). In deeper layers, bacteria function as net remineralizers (positive remineralization rate) of both DON and DOP (not shown). This is mostly due to the decrease of BGE with depth, as maintenance respiration becomes an increasing fraction of total carbon utilization (equation 6), following the decreasing DOC availability. As a result, bacteria need increasingly more DOC, remineralizing the excess DON and DOP. The decreasing BGE may explain the increasing DOC:DON and DOC:DOP ratios with depth (not shown) that are well documented in the global ocean (Loh and Bauer, 2000). However, it is interesting to note that without the additional first order remineralization (*Rdom*) of DON/DOP, described in the *Model Description* section, the deviation of bacterial stoichiometry (bacterial internal N:P~10) from Redfield would result in a preferential remineralization of DON. Therefore, an additional remineralization rate that is higher for DOP is necessary in to obtain the increasing DON:DOP with depth that is observed in the global ocean (Loh and Bauer, 2000). This additional remineralization is important particularly in the surface layer, where DON/DOP increases.

In order to examine the role of the first order additional remineralization rate (*Rdom*) discussed above, a series of sensitivity simulations were performed (Table 3), adopting a different rate. These indicate that as the rate increases more phosphate is passed from the dissolved organic pool

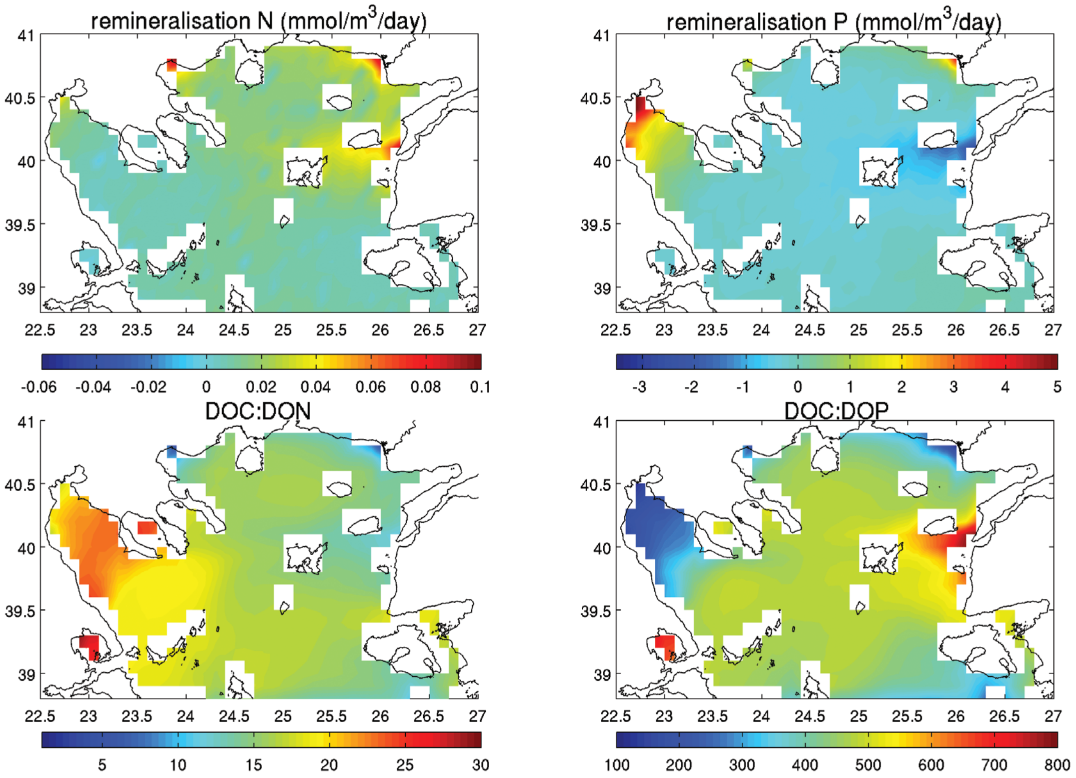

Fig. 13: Mean simulated (top) bacterial phosphorus (right) and nitrogen (left) remineralisation rates (mmol m^{-3} day^{-1}) and (bottom) labile/semi-labile DOC:DON (left) and DOC:DOP (right) elemental ratios.

Table 3. Average DOP (mmol/m^3), bacterial production (BP, mgC/m^2/day), net primary production (netPP, mgC/m^2/day), and their ratio (BP/netPP), simulated with sensitivity experiments, adopting a different first order remineralisation rate (*Rdom*). In the reference *Rdom* was 0.02 day^{-1} and 0.03 day^{-1} for DON and DOP respectively. Percentage fractional change with regard to the reference is indicated in parentheses.

	Refeference	Rdom x 2	Rdom x 0.5	Rdom = 0
DOP (mmol/m^3)	0.07	0.056 (-20%)	0.084 (+20%)	0.1 (+43%)
BP (mgC/m^{2}day)	43.6	46.6 (+7%)	41.1 (-6%)	37.0 (-15%)
netPP(mgC/m^{2}day)	286.3	317.4 (+11%)	260.4 (-9%)	219.5 (-23%)
BP/netPP	0.15	0.147	0.157	0.1685

to bacteria and phytoplankton production (higher rates) without a significant differentiation in the respective ratio (bacterial production/phytoplankton production). As remineralization decreases and eventually becomes zero the phosphate balance is moved towards the dissolved organic pool and production rates slow down.

Conclusions

The N. Aegean Sea is an ecologically important area sustaining the largest fish stocks in Greece and at the same time exhibits particular characteristics due to the combined effects of several riverine systems and the connection with the Black Sea and the Sea of Marmara through the Dardanelles. The above contribute to a unique system, the analysis of which requires a partial analysis of the driving mechanisms. Tsiaras *et al.* (2012) investigated the impact of thermohaline circulation changes on N. Aegean productivity with an emphasis on open-sea processes and discussed the relative importance of the riverine and BSW inputs in the modulation of the nutrient budget directly linked to the increased plankton productivity in the N. Aegean. As a next step, the role of the circulation patterns and the importance of the riverine systems in the production and channelling of organic carbon between the various trophic groups were analyzed (Tsiaras *et al.*, 2014). The analysis showed a significant coupling between the river input inter-annual variability and the productivity in the Dardanelles area, as nutrient-rich waters are advected towards the south, suggesting that inter-annual variability in the Dardanelles plume area may also be related to river inputs and not necessarily to the inter-annual variability of the BSW inputs.

The above prompt for the next rational step, which is the analysis of the role of BSW. Since a prominent characteristic of those inputs is the elevated concentrations of organic matter triggering the microbial loop, the original bacteria sub-model employed by Petihakis *et al*. (2002) was upgraded to a more realistic representation both for bacteria and DOM.

Simulation results show that most of the carbon flows within the microbial loop, indicating the importance of smaller cells (both autotrophic and heterotrophic). Carbon flux estimation indicates a tight coupling of small-sized phytoplankton with their predators (HNAN), while a balanced uptake between small phytoplankton and bacteria is established in summer when the picophytoplankton population decreases and bacteria become abundant. Also, there seems to be a strong and rather constant internal flux within the microzooplankton group, while mesozooplankton appears to equally exploit diatoms and dinoflagellates, according to the respective availabilities. Bacteria are effectively controlled during spring (both top down and bottom up) but as DOM inputs from BSW increase in the period from April to May, there is a time lag response, with maximum bacterial production and biomass during summer. It must be noted that the excretion of phytoplankton also contributes to this effect.

Taking advantage of the analytical capabilities offered by a model, a series of sensitivity experiments were performed, providing helpful insight into the mechanisms and processes governing the system. The different simulations show that the impact of the inflowing BSW DOM is stronger compared to that of the dissolved inorganic nutrients, and that it affects a wider area of the N. Aegean. Bacteria show a stronger response to changing DOM, while phytoplankton biomass and production are more dependent on inflowing nutrients and phosphorus In particular. Not all phytoplankton groups respond equally to BSW inputs, with dinoflagellates being favoured by higher nutrient availability, unlike picoplankton, which is reduced. This indicates a shift to a more classical food chain and since diatoms are limited by silicate availability, there is an increased associated risk for HABs. It is interesting to note that under all the different scenarios the highest proportion (~50%) of the total carbon flux is concentrated in the microbial loop, directed from picoplankton and bacteria to heterotrophic nanoflagellates.

Considering the importance of the N. Aegean Sea ecosystem as the major fishing ground in Greece and the particular characteristics in terms of its trophic status, the comprehensive coupled biogeochemical model proves to be a valuable tool. Through a step up approach (Tsiaras *et al.,* 2012, 2014 and this work) a holistic representation of the system was achieved, while a thorough analysis of the underlying dynamics through a series of sensitivity experiments was performed. In the absence of quantitative in situ information, a probably crude assumption was made regarding the percentage of refractory DOM in the lateral river and BSW inputs. Acknowledging the significant response of the lower trophic levels to the DOM inputs, it is important to stress the need for in situ measurements of DOM bioavailability.

Acknowledgements

This work constitutes part of a *MarinERA* project "Inter-basin exchange in the changing Mediterranean Sea: Impact on the ecosystems in the vicinity of the Straits connecting the Mediterranean Sea with the adjacent Basins - MedEX", which was funded by the General Secretariat of Research and Technology (Greece) under contract 201ΣE01380001. Also some parts of the work took place in the framework of Seasera project "Spatially resolved Ecosystem models and their Application to Marine MANagement - SEAMAN", funded by the General Secreteriat of Research Technology (Greece). Satellite Chl-a data were kindly provided by Dionysios Raitsos from Plymouth Marine Lab. We thank Samuel Somot from METEOFRANCE for kindly providing the downscaled ERA40 dataset.

References

Allen, J.I., Somerfield, P.J., Siddorn, J., 2002. Primary and bacterial production in the Mediterranean Sea: A modelling study. *Journal of Marine Systems*, 33-34, 473-495.

Aminot, A., Kerouel, R., 2004. Dissolved organic carbon, nitrogen and phosphorus in the N-E Atlantic and the N-W Mediterranean with particular reference to non-refractory fractions and degradation. *Deep-Sea Research I*, 51, 1975-1999.

Anderson, T.R., Williams, P.J. le B., 1998. Modelling the seasonal cycle of dissolved organic carbon at Station E1 in the English Channel. *Estuarine, Coastal and Shelf Science*, 46, 93-109.

Azam, F., Smith, D.C., Steward, G.F., Hagstrom, A., 1993. Bacteria-organic matter coupling and its significance for oceanic carbon cycling, *Microbial Ecology,* 28, 167-179.

Baretta, J.W., Ebenhoh, W., Ruardij, P., 1995. The European regional seas ecosystem model, a complex marine ecosystem model. *Netherlands Journal of Sea Research,* 33, 233-246.

Blumberg, A.F., Mellor, G.L., 1983. Diagnostic and prognostic numerical circulation studies of the South Atlantic Bight. *Journalof Geophysical Research,* 88(C8), 4579-4592.

Calbet, A., 2008. The trophic roles of microzooplankton in marine systems, *ICES Journal of Marine Science,* 65, 325-331.

Carlson, C.A., Ducklow, H.W., Michaels, A.F., 1994. Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature,* 371, 405-408.

Coffin, R.B., Connolly, J.P., Harris, P.S., 1993. Availability of dissolved organic carbon to bacterioplankton examined by oxygen utilization. *Marine Ecology Progress Series,* 101, 9-22.

Del Giorgio, P.A., Cole, J., 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics,* 28, 503-541.

Ducklow, H.W., Purdie, D.A., Williams, P.J.L., Davies, J.H., 1986. Bacterioplankton: A sink for carbon in a coastal marine plankton community. *Science*, 232, 865-867.

Herrmann, M.J., Somot, S., 2008. Relevance of ERA40 dynamical downscaling for modeling deep convection in the Mediterranean Sea. *Geophysical Research Letters*, 35, L04607.

Ignatiades, L., Psarra, S., Zervakis, V., Pagou, K., Souvermezoglou, E. *et al*., 2002. Phytoplankton size-based dynamics in the Aegean Sea (Eastern Mediterranean). *Journal of Marine Systems*, 36, 11-28.

Jeong, H.J., 1999. The ecological roles of heterotrophic dinoflagellates in marine planktonic community. *Journal of Eukaryotic Microbiology*, 46, 390-396.

Karl, D.M., Bjorkman, K.M., 2002. Dynamics of DOP, p. 249–366. In: *Biogeochemistry of Marine Dissolved Organic Matter*. Hansell, D.A., Carlson, C.A. (Eds). Academic Press, Amsterdam, Boston.

Korres, G., Hoteit, I., Triantafyllou, G., 2007. Data assimilation into a Princeton Ocean Model of the Mediterranean Sea using advanced Kalman filters. *Journal of Marine Systems,* 65(1-4), 84-104.

Lagaria, A., Psarra, S., Gogou, A., Tugrul, S., Christaki, U., 2013. Particulate and dissolved primary production along a pronounced hydrographic and trophic gradient (Turkish Straits System- NE Aegean Sea). *Journal of Marine Systems*, 119-120, 1-10.

Loh, A.N., Bauer, J.E., 2000. Distribution, partitioning and fluxes of dissolved and particulate organic C, N and P in the eastern North Pacific and Southern Oceans. *Deep-Sea Research Part II,* 47, 2287-2316.

Ludwig, W, Dumont, E., Meybeck, M., Heussner, S., 2009. River discharges of water and nutrients to the Mediterranean and Black Sea: Major drivers for ecosystem changes during past and future decades? *Progress in Oceanography*, 80, 199-217.

Ludwig, W., Bouwman, A.F., Dumont, E., Lespinas, F., 2010. Water and nutrient fluxes from major Mediterranean and Black Sea rivers: Past and future trends and their implications for the basin-scale budgets. *Global Biogeochemical Cycles*. doi: 10.1029/2009GB003594.

Moran, M.A., Zepp, R.G., 1997. Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. *Limnology and Oceanography*, 42, 1307-1316.

Nittis, K., Perivoliotis, L., Korres, G., Tziavos, C., Thanos, I., 2006. Operational monitoring and forecasting for marine environmental applications in the Aegean Sea. *Environmental Modelling and Software*, 21, 243-257.

O'Reilly, J.E., Maritorena, S., Mitchell, B.G., Siegel, D.A., Carder, K.L. *et al*., 1998. Ocean color chlorophyll algorithms for SeaWiFS. *Journal of Geophysical Research*, 103, 24937-24953.

Petihakis, G., Triantafyllou, G., Allen, I.J., Hoteit, I., Dounas, C., 2002. Modelling the spatial and temporal variability of the Cretan Sea ecosystem. *Journal of Marine Systems,* 36 (3-4), 173-196.

Petihakis, G., Triantafyllou, G., Tsiaras, K., Korres, G., Pollani, A. *et al.,* 2009. Eastern Mediterranean biogeochemical flux model – Simulations of the pelagic ecosystem. *Ocean Science*, 5, 29-46.

Polat, C., Tugrul, S., 1996. Chemical exchange between the Mediterranean and Black Sea via the Turkish straits. *CIESM Science Series No.2, Bulletin. De l'Institut Oceanographique*, 17, 167-186.

Raimbault, P., Pouvesle, W., Diaz, F., Garcia, N., Sempéré, R., 1999. Wet-oxidation and automated colorimetry for simultaneous determination of organic carbon, nitrogen and phosphorus dissolved in seawater. *Marine Chemistry*, 66 (3-4), 161–169.

Sempéré, R., Panagiotopoulos, C., Lafont, R., Marroni, B., Van Wambeke, F., 2002. Total organic carbon dynamics in the Aegean Sea. *Journal of Marine Systems*, 33-34, 355-364.

Siokou-Frangou, I., Bianchi, M., Christaki, U., Christou, E.D., Giannakourou, A. *et al.,* 2002. Carbon flow in the planktonic food web along a gradient of oligotrophy in the Aegean Sea (Mediterranean Sea). *Journal of Marine Systems*, 33-34, 335-353.

Skoulikidis, N.Th., 1993. Significance evaluation of factors controlling river water composition. *Environmental Geology*, 22, 178-185.

Skoulikidis, N.Th., 2009. The environmental state of rivers in the Balkans-A review within the DPSIR framework. *Science of the Total Environment,* 407, 2501-2516.

Smith, D. C., Simon, M., Alldredge, A.L., Azam, F., 1992. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature,* 359, 139-142.

Stergiou, K.I., Christou, E.D., Georgopoulos, D., Zenetos, A., Souvermezoglou, C., 1997. The Hellenic seas: physics, chemistry, biology and fisheries. *Ocean and Marine Biology an Annual Review*, 35, 415-538.

Thingstad, T.F., Rassoulzadegan, F., 1995. Nutrient limitations, microbial food webs, and 'biological C pumps': suggested interactions in a P limited Mediterranean. *Marine Ecology Progress Series*, 117, 299-306.

Tsiaras, K., Korres, G., Petihakis, G., Nittis, K., Raitsos, D. *et al.,* 2008. The Poseidon ecosystem model: The Mediterranean case. p. 191-198. In: *5th International Conference of EuroGOOS, Sopot, Poland, 4–6 October 2011*. EuroGOOS publication n. 28, Norrköping Sweden.

Tsiaras, K., Kourafalou, V.H., Raitsos, D., Triantafyllou, G., Petihakis G. *et al.,* 2012. Inter-annual productivity variability in the North Aegean Sea: influence of thermohaline circulation during the Eastern Mediterranean Transient. *Journal of Marine Systems*, 96-97, 72-81.

Tsiaras, K., Petihakis G., Kourafalou, V., Triantafyllou G., 2014. Impact of the river nutrient load variability on the N. Aegean ecosystem functioning over the last decades. *Journal of Sea Research*, 86, 97-109.

Tugrul, S., Besiktepe, S.T., Salihoglou, I., 2002. Nutrient exchange fluxes between the Aegean and Black Seas through the Marmara Sea. *Mediterranean Marine Science,* 3 (1), 33-42.

Turley, C.M., Bianchi, M., Christaki, U., Conan, P., Harris, J.R.W. *et al*., 2000. Relationships between primary producers and bacteria in an oligotrophic sea- the Mediterranean and biogeochemical implications. *Marine Ecology Progress Series*, 193, 11-18.

Zeri, C., Besiktepe, S., Giannakourou, A., Krasakopoulou, E., Tsortziou, M. *et al.,* 2014. Chemical properties and fluorescence of DOM in relation to biodegradation in the interconnected Marmara-North Aegean Seas during August 2008. *Journal of Marine Systems*, 135, 124-136.

Zervoudaki, S., Christou, E.D., Nielsen, T.G., Siokou-Frangou, I., Assimakopoulou, G. *et al*., 2007. The importance of small-sized copepods in a frontal area of the Aegean Sea. *Journal of Plankton Research,* 29 (4), 317-338.

Varela, R.A., Cruzado, A., Gabaldon, J.E., 1995. Modelling primary production in the North Sea using the European Regional Seas Ecosystem Model. *Netherlands Journal of Sea Research,* 33, 337-361.

APPENDIX. Table 1. Bacterial model parameter set.

Parameter	Symbol	Value
Maximum growth rate at 10 °C	*sumB*	5 (day^{-1})
Half-saturation for DOC uptake	*Kdoc*	2500 (mg C m^{-3})
Characteristic Q10	*Q10*	2 (day^{-1})
Half Oxygen saturation	*chrSTO$*	0.3125 (mmol m^{-3})
Assimilation efficiency	*puST$*	0.15
Assimilation efficiency at low temperature	*puSTo$*	0.1
Rest respiration at 10 °C	*srsST$*	0.01
Mortality rate	*sdST$*	0.001
Maximum internal N/C ratio	*qnSTc$*	0.02 (mmol N mg C^{-1})
Maximum internal P/C ratio	*qpSTc$*	0.0015 (mmol P mg C^{-1})