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Modelling the Mediterranean Pelagic Ecosystem using the POSEIDON ecological model. 
Part II: Biological dynamics

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Abstract

A three-dimensional coupled hydrodynamic/biogeochemical numerical model, currently in operation as part of the POSEIDON forecasting system, was implemented in the Mediterranean Sea. The model was assessed regarding its efficacy in representing the main biogeochemical components and seasonal dynamics of the Mediterranean planktonic system. Model outputs were compared with available historical data in a proposed objective eco-regionalization of the Mediterranean basin, based on productivity. The simulated production (primary, bacterial) and planktonic biomass (phytoplankton, zooplankton and bacteria), as well as particulate and dissolved organic carbon, were found consistent with observational estimates in different areas of the Mediterranean Sea, following large scale productivity gradients. Although some limitations of the model were identified, the observed variability of the phytoplanktonic community structure was reasonably well-reproduced, simulating a dominant microbial food web with an intermittent development of the classical food web. The generic POSEIDON ecosystem model skill assessment provides a benchmark for future model improvement, highlighting the need to expand the range of biological variables sampled for further model calibration and validation.
Keywords: Biogeochemical model, Mediterranean, Cluster Analysis, POSEIDON, planktonic community structure

1. Introduction

The Mediterranean Sea (MS) has been characterized as a miniature ocean (Bethoux et al., 1999), with a variety of physico-chemical and biological processes. The MS is also considered oligotrophic, with a well-defined eastward decreasing trend in primary productivity (Moutin and Raimbault, 2002). The general oligotrophy is reflected in the widespread dominance of the microbial food web, consisting of small autotrophs and microheterotrophs (Thingstad and Rassoulzadegan, 1995; Turley et al., 2000; Siokou-Frangou et al., 2002). However, even though it is smaller in size in comparison to other oceans, the MS displays a variety of trophic regimes (D’Ortenzio and Ribera d’Alcalà, 2009; Ayata et al., 2017; Kalaroni et al., 2019), from the ultra-oligotrophic deep sub-basins, i.e. the Levantine sub-basin in the Eastern MS, to the eutrophic northern Adriatic Sea, which is characterized by recurrent, algal blooms. In fact, fertilization events (i.e. nutrient enrichment) from winter vertical mixing and lateral water inputs (i.e. riverine discharges, Atlantic Water - AW and Black Sea Water - BSW inflows) may enhance primary production and result in the intermittent development of the herbivorous 'classical' food web, from diatoms to mesozooplankton (Legendre and Rassoulzadegan, 1995; Siokou-Frangou et al., 2010). In general, this is mostly controlled by the type of forcing and various sources of disturbances that may interact synergistically (anthropogenic pressures, strong mixing events etc.), producing different internal dynamics in the MS.

Moreover, the Mediterranean ecosystem is sensitive not only to human pressure, resulting from higher population and development in coastal areas, but also to climate change (Macias et al., 2015), and is, thus, identified as a main hot spot (e.g. Giorgi, 2006). Recent studies suggest that global warming and increase of atmospheric CO₂ are related with changes in ocean circulation and chemistry, altering light and nutrient regimes and having a cascading effect in the size and elemental stoichiometry of phytoplanktonic communities (Finkel et al., 2010). At present, the resulting changes in phytoplanktonic community structure and the way in which these will influence primary production and carbon export, biogeochemical cycles and marine food web dynamics are still poorly understood and cannot be investigated only with in-situ sampling or mesocosm experiments. Considering the vast number of parameters and processes
dynamically interconnected in a marine ecosystem, it is rather evident that mathematical models provide an important tool in gaining a mechanistic understanding of the long-term variability in the Mediterranean productivity and community structure. In addition, modelling approaches can be used to assess the ecosystem status and support EU policies in the development of management strategies for different marine regions. However, given the complexity and variability of the marine environment, the question that arises is whether these models are reliable or not. The way to ensure the reliability of an ecosystem model in addressing management questions is to evaluate its skill in representing the observed processes and dynamics.

In this context, the skill of the generic POSEIDON ecosystem model has been evaluated with regard to its efficacy in simulating the spatial and temporal variability of the biogeochemical characteristics of the Mediterranean marine ecosystem. The presented biogeochemical model is adequately comprehensive, describing with the necessary complexity the Mediterranean planktonic food web and biogeochemical processes, and is currently in operation as part of the POSEIDON forecasting system, providing short-term predictions (www.poseidon.hcmr.gr). In a companion paper (Kalaroni et al., 2019: Part I of this issue), the model-simulated chemical components [inorganic nutrients and chlorophyll-a (Chl-a) concentrations] were presented and validated in detail. An objective regionalisation was applied using the K-means clustering algorithm (Hartigan and Wong, 1979), delimiting provinces within which productivity conditions are reasonably homogeneous (see Part I companion paper for more details). The main objective of the present work was to assess the skill of the model in simulating the biological components (primary and bacterial production, different plankton groups biomass, organic carbon etc.) of the Mediterranean ecosystem. Given the limited spatial-temporal coverage of in-situ measurements for biological variables, model outputs were evaluated against observational historical data for different areas in each eco-region (cluster) of the Mediterranean basin.

Using the model output from a long-term (1990-2009) simulation, the Mediterranean pelagic planktonic community structure and dynamics were also investigated in each eco-region (cluster) in order to characterize the major carbon fluxes and trophic pathways. In a recent study, Ciavatta et al, 2019 assessed the spatial patterns of the dominance or relevance of three phytoplanktonic groups that have a distinct function in the ecosystem (e.g. picophytoplankton, nanophytoplankton and microphytoplankton), evaluating the spatial variability of the associated vertically integrated
carbon fluxes by merging information from model simulations and ocean colour observations. However, this study was focused on the time-averaged, surface estimates of phytoplanktonic groups and, therefore, could not represent the seasonal variability of the planktonic community structure. In this context, Romagnan et al., 2015 studied the seasonal changes in phytoplankton and mesozooplankton assemblages based on a whole planktonic time series approach in the north-western Mediterranean Sea (Bay of Villefranche). Thus, the objective of the present study was to describe the main aspects and the seasonal variability of the Mediterranean planktonic community structure, from heterotrophic bacteria to mesozooplankton, on a basin scale and examine their relative contribution to carbon fluxes.

The paper is organized as follows: Section 2 describes the coupled biogeochemical-hydrodynamic model, the set-up of the model simulation and the methodology applied for skill assessment. Validation of model-simulated biological components in the Mediterranean basin is presented in Section 3, while the obtained results are discussed in Section 4. Finally, concluding remarks and future improvements are pointed out in Section 5.

2. Materials and Methods

2.1 Model Implementation in the Mediterranean Sea

For a more detailed description of the model and the simulation set-up, the reader should refer to the companion paper (Part I) of this issue (Kalaroni et al., 2019). However, since the present study deals with the simulated biological components of the Mediterranean pelagic food web, a brief description of the three-dimensional (3-D) coupled hydrodynamic-biogeochemical Mediterranean basin scale model is provided below.

The hydrodynamic model is the Princeton Ocean Model (POM; Blumberg and Mellor, 1987), which is a 3-D, primitive equation, free-surface and sigma-coordinate circulation model. The configuration of the model has been adopted from the POSEIDON operational Mediterranean hydrodynamical model (Korres at al., 2007). The biogeochemical model (Figure 1) is a modified version of the European Regional Seas Ecosystem Model (ERSEM; Baretta et al., 1995). ERSEM is a generic comprehensive biogeochemical model that uses a 'functional' group approach to describe the ecosystem, where the biota are grouped together according to their trophic level and subdivided according to size classes or feeding methods. The phytoplankton functional groups are diatoms, dinoflagellates, nanophytoplankton and picophytoplankton, while
the heterotrophic ones are heterotrophic nanoflagellates, microzooplankton, mesozooplankton, and heterotrophic bacteria. The biological functional group dynamics are described by the primary physiological (ingestion, respiration, excretion and egestion) and population (growth and mortality) processes as fluxes of carbon and nutrients. Benthic processes are described by a simple, first-order benthic returns module that includes the settling of organic detritus into the benthos and diffusional nutrients fluxes out of the sediment.

The model domain extends from 7° W to 36° E and 30.25° N to 45.75° N (Figure 2) with a resolution of 1/10°x1/10° (~10 x 10 Km) in the horizontal axis and 24 sigma-levels in the vertical axis, following a logarithmic distribution approaching the surface and bottom layers. After a 5-year model spin-up, a long-term simulation with the 3-D on-line coupled model was performed over the 1990-2009 period, during which in-situ data were mostly available.

2.2. Methodology

A K-means cluster analysis (Hartigan and Wong, 1979) was carried out to determine an objective MS ‘biogeography’ in different eco-regions (clusters), where the model skill was assessed in reproducing the seasonal variability of the main chemical and biological components of the pelagic ecosystem. A detailed description of the cluster analysis is presented in the companion paper Part I of this issue (Kalaroni et al., 2019).

The cluster analysis identified 4 eco-regions (Figure 3) on the basis of the seasonality of the model-simulated surface Chl-a, phosphate and temperature. Regions receiving lateral water inputs (i.e. AW/BSW inflows and river runoff areas) were associated with the most productive eco-region (cluster #1) of relatively low temperature, high nutrient and Chl-a concentrations. Cluster #2, including most of the western Mediterranean (WMED) basin, was identified as the second most productive eco-region, characterized by an intense winter-spring bloom and relatively low temperatures, subjected to the nutrient enrichment from AW inflow and deep vertical mixing in the Liguro-Provencal cyclonic gyre. The same cluster also included some areas not in the immediate vicinity, however these were influenced by river and BSW nutrient loads (i.e. North Adriatic and North Aegean Seas). Regions with oligotrophic conditions were identified as clusters #3 (Tyrrhenian, South Adriatic, Ionian and South Aegean Seas) and #4 (South-Eastern Mediterranean basin), with the latter one characterized by ultra-oligotrophic
conditions, showing the lowest values of Chl-a concentrations due to the particularly low
phosphate concentration and relatively high temperatures.

Given the limited spatio-temporal coverage of in-situ measurements for biological state
variables, such as primary and bacterial production, plankton biomass and organic carbon, model
outputs were compared against averaged observational data found in different areas of each eco-
region of the MS.

3. Results

3.1. Primary Production and biomass

A clear west-to-east decreasing gradient is evident in the climatological map (1990-2009
period) of the model-simulated net primary production (NPP) and biomass (Figures 4a and 4d).
As mentioned above, the most productive regions of the Mediterranean pelagic system were
identified in areas characterized by lateral nutrient inputs or strong vertical mixing (Table S1 in
Supplementary Material, eco-regions #1, #2) in contrast to the oligotrophic nutrient-depleted
eco-regions #3 and #4.

Model results are in good agreement with field measurements of the surface NPP along the
west-east sampling transect of the TransMediterranean Cruise (Table S2 in Supplementary
Material, Ignadiades et al., 2009) during June of 1999. Regardless of a few discrepancies, the
model-simulated NPP rates and phytoplanktonic biomass are also in line with previous studies in
different Mediterranean sub-basins (Table 1). In particular, Moutin and Raimbault (2002)
reported higher mean integrated in-situ NPP measurements compared to the model output (Table
1) in the north-western basin (eco-region #2). Moreover, satellite-based estimates of NPP rate
from Bosc et al., 2004 were found slightly higher that the modelled one. The simulated NPP and
phytoplankton biomass are also lower than the mean observed values of Turley et al. (2000),
although field measurements exhibit significant variability and, thus, have a high degree of
uncertainty when averaged. In the eastern basin (i.e. Ionian and Levantine Seas), the modelled
NPP are in fair agreement with the observed rates, while the model shows a tendency to
overestimate phytoplanktonic biomass in the Cretan (eco-region #3) and the North Aegean Seas
(eco-region #2). The largest difference between simulated and observed primary production
occurs in the North Aegean Sea (Table 1), where the modelled NPP rate is much lower, as
compared to measurements reported by Siokou et al. (2002) during March 1997, which can
probably be attributed to some specific event, triggering an increased primary production. We should note that productivity in this sampling area is significantly influenced by the BSW inflow (Petihakis et al., 2014), which presents an important inter-annual variability. However, this is not taken into account in the model, as BSW nutrient inputs are based on mean climatologic data.

In order to give a synthetic view of the Mediterranean phytoplanktonic community structure, the contribution of each phytoplanktonic group to the total phytoplanktonic biomass, integrated to 100m, is shown in Figure 5. According to the model results, and in agreement with previous in-situ studies (Marty & Chiaverini, 2002; Ignatiades et al., 2009; Siokou-Frangou et al., 2010), ocean colour observations (Uitz et al., 2012; Navarro et al., 2014; Sammartino et al., 2015) and other modelling studies (Ciavatta et al., 2019), the spatial distribution of each phytoplanktonic group varies by region, as it is influenced by various factors, such as hydrodynamic conditions and nutrients. Overall, small cells (picophytoplankton MS:~54%, followed by nanophytoplankton MS:~32%) dominated mainly in open-sea, oligotrophic areas (eco-regions #3 and #4, Table S1), while both diatoms (MS: 9.9%) and dinoflagellates (MS: 3.7%) were found in productive nutrient-rich areas (eco-region #1 and #2). Dinoflagellates generally contributed a very small percentage to the total phytoplanktonic biomass (~2-10%) and were mainly found in the more productive coastal areas, influenced by river loads (eco-region #1, e.g. North Adriatic and North Aegean Seas). An exception is observed in the Gulf of Gabes, where the modelled dinoflagellates showed a relatively higher contribution (~7%) than diatoms (~4). Given that the two groups have the same predators (i.e. microzooplankton and mesozooplankton), this is mostly related to the low silicate concentration in this shallow coastal area (not shown) and the resulting limitation on diatoms growth, giving an advantage to the growth of dinoflagellates. The contribution of diatoms was generally higher than dinoflagellates, showing a significant contribution in regions receiving lateral nutrient inputs (eco-region #1, Table S1) or strong vertical mixing (eco-region #2), with values almost twice (~27%) on average, as compared to oligotrophic open sea waters (~15%).

In Table 2, the model-simulated phytoplanktonic community structure is compared against field data obtained from Uitz et al., 2012 (in terms of Chl-a composition), showing a fairly good overall agreement. The model tends to underestimate the contribution of the microphytoplankton in the western basin (i.e. Algerian, Ligurian and Balearic Seas, eco-region #2), but simulated values in most cases fall within the observed value range. Comparing mean simulated values
with the observed ones, a model underestimation (~27%) of the nanophytoplankton’s contribution was found in the Alboran Sea (eco-region #1) during spring (May). An underestimation (~30%) of the largest phytoplanktonic groups’ contribution (i.e. nanophytoplankton, diatoms and dinoflagellates) was also found in the Balearic Sea (eco-region #2) in winter (February), and a similar underestimation of picophytoplankton in the Tyrrenian Sea (eco-region #3) during late-autumn (December). Nonetheless, some model deviations from the observed composition of the phytoplanktonic community are expected, given that field measurements obtained from Uitz et al. (2012) are expressed as the percent contribution of each size class to the total Chl-a. Carbon to Chl-a ratio (C:Chl-a) is known to exhibit a wide variability in living organisms, depending on the trophic status (Wang et al., 2009 and references therein), which is not considered in the model, adopting a constant C:Chl-a ratio.

### 3.2. Heterotrophic Bacterial Production and Biomass

Spatial distributions of model-derived heterotrophic bacterial biomass (BB) and production (BP), averaged over the 1990-2009 period (Figures 4b and 4c), follow a west-to-east decreasing gradient, which is consistent with previous field studies (Dolan et al., 1999; Christaki et al., 2001, 2011; Pitta et al., 2001; Van Wambeke et al., 2002). The lower BB and BP were simulated in the most oligotrophic eco-regions #3 and #4 (Table S1, Levantine, Cretan and Ionian Seas), while higher values were found in areas enriched with nutrients and organic carbon, such as regions influenced by river loads (North Adriatic and North Aegean Seas, eco-region #2) and the AW/BSW inflows (North-East Aegean and Alboran Seas).

In Tables 3 and 4, the model-simulated BP and BB are compared against historical in-situ data, covering selected areas in the MS. In the oligotrophic eastern basin (eco-regions #3 and #4), the agreement between model and in-situ measurements is generally good. The main discrepancy was found in the most productive areas, such as the north-western basin (eco-region #2). In fact, this is related to the model’s underestimation of primary production in these areas, leading to an underestimated dissolved organic carbon (DOC) production that is excreted by phytoplankton and is the main substrate for heterotrophic bacterial growth (Ducklow and Carlson, 1992; Van Wambeke et al., 2004).

### 3.3. Organic Carbon
The model-simulated spatial distribution of DOC and POC (particulate organic carbon) concentrations (Figures 4e and 4f) shows an eastward decreasing gradient, similar to that of the primary and heterotrophic production. In off-shore areas, DOC ranged from 63 to 110 mmol m\(^{-3}\) and POC from 0.5 to 4 mmol m\(^{-3}\), whilst in coastal areas concentrations may exceed 170 and 4 mmolC m\(^{-3}\) respectively. The spatial variability of organic carbon is mostly attributed to the biogeochemical processes that produce (excretion, lysis and mortality of primary and secondary producers) or consume (uptake by bacteria) organic matter in the model. Hence, increased POC and DOC concentrations were modelled in eco-regions #1 and #2 (Table S1) related to the high primary production (i.e. the Algerian and Liguro-Provençal basins, the Alboran and North Aegean Seas), as well as to the organic carbon enrichment, resulting from river loads and the BSW inflow in the North-East Aegean Sea.

The comparison of observed and model-simulated DOC concentrations (Table 5) shows quite good agreement, although some model discrepancies were found in areas receiving external inputs of organic matter (e.g. North Adriatic and North Aegean Seas). Given that a mean value is adopted for riverine and BSW DOC, the model cannot capture the seasonal variability of organic carbon external inputs. In contrast to DOC, model-simulated POC concentrations were found underestimated, compared to field measurements (Table S3 in Supplementary Material). This is partly due to the fact that in-situ data include living organisms in the measurements, while the simulated particulate organic carbon represents only the non-living organic matter.

3.4. Primary and Bacterial production dynamics

Figure 6 shows the mean climatological monthly evolution of model-simulated primary and bacterial productions and biomasses, as well as DOC and POC concentrations in each eco-region (integrated in the 0-100m layer). The primary production (NPP) and phytoplanktonic biomass cycles (Figures 6b and 6d) are very similar to that of Chl-a (see Part I companion paper). In eco-regions #2 - #4 these showed a late winter maxima (March), due to the nutrient enrichment of the euphotic zone by vertical mixing, and minima during the nutrient-depleted summer period. A less pronounced temporal variability was simulated in the most productive eco-region #1, showing an extended peak of primary production and phytoplanktonic biomass during the spring period, attributed to the seasonal variability of the nutrient supply by river loads and AW/BSW inflows. As the water stratification begins to establish (April-May), preventing nutrient supply
from deeper layers, the phytoplanktonic production and biomass were decreased, being sustained only in subsurface layers. The DOC concentration seasonal variability (Figure 6f) is largely controlled by the phytoplanktonic extracellular release (not shown) that is higher in nutrient-depleted conditions. Thus, DOC follows the phytoplanktonic cycle, peaking one month after maximum DOC phytoplanktonic excretion rate (April in eco-regions #2, #3 and #4; May in eco-region #1 - not shown), showing relatively higher values at surface (Figure S1a in Supplementary Material). Its gradual summer-autumn decrease is linked to its consumption by heterotrophic bacteria in the model (Petihakis et al, 2014). Bacterial biomass and production were low in winter (Figures 6a and 6c), while higher values were simulated in June - August. Similarly, POC follows the phytoplankton’s variability, as a proportion of the phytoplanktonic biomass is transformed to detritus, i.e. POC through mortality, sloppy feeding and egestion processes (maximum POC concentrations April - May Figure 6e). A gradual reduction of the upper layer POC concentration is observed in late spring-summer, through sinking and gradual degradation by heterotrophic bacteria. It is worth noticing that during summer, the highest POC concentrations were simulated at the DCM depth (Figure S1b), i.e. where the maximum of the biological activity takes place in that period.

3.5. Zooplankton

The model-simulated biomass of all zooplanktonic (mesozooplankton, microzooplankton, heterotrophic nanoflagellates - HNAN) groups (not shown) follows the spatial distribution of the prey availability, showing a declining eastward gradient, in agreement with previous field studies (e.g. Mazzocchi et al., 1997; Dolan et al., 1999, 2002; Pitta et al., 2001; Christaki et al., 2011;Siokou et al., 2004; Santinelli et al., 2012). The highest biomass concentrations were simulated in the Gulf of Lion and the Alboran, Adriatic and North Aegean Seas (eco-regions #1 and #2, Table S1). During summer, the maximum HNAN biomass (Figure S2a in Supplementary Material) was simulated close to the thermocline, following the vertical distribution of bacteria (not shown) i.e. their most abundant prey during that period. The vertical distribution of the simulated microzooplankton and mesozooplankton biomass (Figures S2b and S2c in Supplementary Material) shows a similar pattern with HNAN, with the maximum summer biomass located close to the DCM level (microzooplankton: 50-75m, mesozooplankton: 40-80m).
As mentioned above, the horizontal variability of the contribution of different zooplanktonic groups in the total zooplanktonic biomass is determined by the variability of their preys (see prey preferences in Table S4, Supplementary Material of Part I companion paper). Model-simulated HNAN was the dominant zooplanktonic group in the MS (~52%, Figure 7a) with a relatively higher contribution in the oligotrophic eco-regions #3 and #4 (Table S1), following a similar pattern to their favorable prey, i.e. picophytoplankton. On the contrary, larger zooplanktonic groups (microzooplankton MS: ~21%, mesozooplankton MS: ~28%, Figures 7b and 7c) showed a higher contribution in the most productive eco-regions #1 and #2 (Table S1). In particular, mesozooplankton's higher contribution was simulated in areas with a considerable abundance of diatoms and dinoflagellates - their main preys - i.e. eco-regions #1 and #2, showing an increasing gradient toward coastal areas that receive lateral nutrient inputs. Microzooplankton presented a more uniform distribution, with a slightly higher abundance in eco-region #1, due to the wide distribution of its preferable preys, HNAN and nanophytoplankton.

Model-simulated mesozooplankton biomass presents a rather good agreement with the field measurements, as shown in Table 6, except for some deviations found in the Alboran Sea. In this area, the model simulated a significantly lower mesozooplankton biomass, as compared to the observed one in winter 1997 (eco-region #1, Youssara and Gaudy (2001), Table 6), whilst a model overestimation was found, as compared to the SESAME EU project field data (Mazzocchi et al. (2014), Table S4 in Supplementary Material) in spring and autumn of 2008. Moreover, the model could not capture the strong variability of the field measurements, which was revealed in some areas of the eco-region #2 western sub-basin, such as the Balearic, Catalan and Ligurian Seas. This is related to the increased hydrodynamic variability, influencing nutrient availability and thus mesozooplankton’s prey (i.e. phytoplankton) availability in these areas (Siokou-Frangou et al. (2010) and references therein). In the North Aegean Sea, modelled and observed mesozooplankton biomasses were almost equal to the field studies during the ANREC project (Table 6), unlike the measured values during the SESAME field experiment in spring and autumn of 2008 (Table S4). This model deviation is related to the variability of the river loads and BSW inflow that affect productivity in the North Aegean Sea, as it was shown in the sensitivity simulations of Petihakis et al. (2014) and Tsiaras et al. (2014), and is not fully represented in the model. However, it must be noted that a model mismatch on mesozooplankton biomass could also arise from the under-representation of important mesozooplankton's size
fraction, when samples are taken with the use of a single vertical plankton net with a mesh size of 200 µm (Saiz et al., 2014). A recent study by Frangoulis et al. (2016) showed that a combination of data obtained from three nets with different mesh sizes (45, 200 and 500 µm) can give a better estimation of the mesozooplankton standing stock in a Mediterranean area, and of its size fractions and functional groups.

The model simulated HNAN biomass in the Aegean Sea is in satisfactory agreement with field measurements during two contrasting seasons, March and September (Table 7), notwithstanding the rather poor performance of the model in the oligotrophic South Aegean Sea during September. In the more productive Ligurian Sea (eco-region #2) the model-simulated HNAN biomass is within the observed value range (Table 7). Given the scarcity of observations, only a few observational records were found for the smaller zooplanktonic groups in terms of biomass.

3.6. Food web dynamics

A more dynamic picture of the simulated contribution of each planktonic group in each eco-region is presented in Figure 8, illustrating the complex food web dynamics, emerging from top-down control and resource competition. The seasonal variability of HNAN and nanophytoplankton contribution is characterized by a decrease during late winter/early spring period and an increase during summer/autumn, which appears closely linked with microzooplankton variability, i.e. their main predator (i.e. increase during spring and decrease during summer/autumn). The nanphytoplankton's contribution increase during summer/autumn (35 - 42%) is also favored from the reduction of picophytoplankton, its main competitor for nutrients, which is mainly related to the HNAN increase (main picophytoplankton's predator). The decrease in microzooplankton during summer suggests a top-down effect of the increase in mesozooplankton. The latter shows a more abrupt short-time increase in oligotrophic eco-regions #3 and #4, where food availability is sufficient only during spring bloom period, in contrast to its much weaker variability in productive areas, particularly eco-region #1, since the relatively constant planktonic biomass is sustained throughout the year by river inputs. Looking at the seasonal succession of the different phytoplanktonic groups, the time-period of the lowest picophytoplankton contribution (i.e. April-May) in the productive eco-regions #1 and #2, coincide with the maximum microphytoplankton contribution, particularly diatoms, that co-
compete for nutrients. Although both diatoms and dinoflagellates constitute a food resource (with similar preference) for microzooplankton and mesozooplankton, they exhibit a different seasonal variability. Diatoms show an early peak during spring period, given their slightly higher growth rate (maximum growth: 2.5 day\(^{-1}\)), as compared to dinoflagellates (maximum growth: 1.5 day\(^{-1}\)) that peak during summer stratified period, when low silicate concentrations are limiting diatoms growth (Marty et al., 2002; Ignatiades et al., 2009; Siokou-Frangou et al., 2010). These results give a more comprehensive understanding on the succession of marine plankton at the scale of the whole Mediterranean Sea.

The model's adequate description of the planktonic food web allows for further examination of the system dynamics, describing the major carbon pathways among autotrophic and heterotrophic groups and their differentiation in different MS eco-regions. In Figure 9, food web carbon fluxes in different eco-regions have been normalized, dividing with the total flux in each eco-region, identifying the dominant fluxes. The major carbon flux was found from picophytoplankton and heterotrophic bacteria to HNAN, given the overall dominance of smaller cells. This is less pronounced in the more productive eco-region #1, where larger autotrophic and heterotrophic groups co-exist with the smaller ones. The second most significant fluxes in terms of magnitude were simulated from nanophytoplankton and HNAN to microzooplankton in all eco-regions. Important fluxes were also channeled from diatoms to mesozooplankton in eco-region #1; these were less pronounced in the other eco-regions. Relatively small fluxes of carbon were also directed from nanophytoplankton to HNAN, from microzooplankton and HNAN to mesozooplankton, and in eco-region #1 from diatoms to microzooplankton. Finally, the smallest fluxes were those directed from dinoflagellates to microzooplankton and mesozooplankton (all eco-regions) and from diatoms to microzooplankton in the less productive eco-regions #2 - #4.

The differentiation of dominant carbon pathways among different eco-regions are closely related to the charges in the diet of zooplanktonic groups. These are mainly controlled by changes in the availability of different preys, modulated by the different prey preferences (see Table S2 in Supplementary material of Part I companion paper, Kalaroni et al, 2019). Thus, the carbon flux increases from diatoms to microzooplankton and particularly mesozooplankton in the most productive eco-region #1 (Figure 9) is consistent to diatoms increasing availability in more productive areas that results in their increase in the diet of their predators (Figure 10). The relatively small carbon flux from diatoms to microzooplankton is however explained by the low
preference as compared to other preys, such as nanophytoplankton and HNAN. We should note
that although dinoflagellates are an equally favorable prey with diatoms in mesozooplankton’s
diet, their normalized carbon fluxes are very low due to their limited biomass availability (Figure
10). The increased availability of bacteria in oligotrophic eco-regions (#3 and #4) results in their
increasing contribution to HNAN diet, at the expense of picophytoplankton. On the other hand,
the microzooplankton diet shows an increased contribution of nanophytoplankton and HNAN in
more oligotrophic eco-regions, given their higher availability as compared to other preys
diatoms, dinoflagellates, microzooplankton). The same holds for mesozooplankton’s diet,
showing an increase of HNAN contribution and a decrease of diatoms and mesozooplankton. In
all cases, cannibalism appears to decrease with oligotrophy, which can be explained by the
relative decrease of the predators:prey biomass. Despite the increased importance of bacteria in
oligotrophic regions, picophytoplankton remains the HNAN main prey, resulting in the most
important carbon pathway.

4. Discussion

The quantitative comparison of the numerical simulation with the ecological POSEIDON
model against various types of field data shows a fairly good agreement between the field-
measured biomasses and rates and the model-simulated state variables. The model performance
was adequate in representing phytoplanktonic biomasses and production. Some model deviations
from observations were identified mainly in areas receiving lateral nutrient inputs (rivers, BSW)
due to the uncertainty of the adopted inputs, pointing out the need for more detailed data and
systematic monitoring. The model also revealed some limitations in capturing the intensity of
winter mixing (see also Kalaroni et al., 2019 part I, this issue), underestimating (e.g. north-
western basin) or overestimating (e.g. Cretan Sea) the entrainment of deep-water nutrients and
phytoplanktonic biomasses and/or production in these areas, which illustrates the importance of
hydrodynamics in driving the pelagic ecosystem. The impact of assimilating satellite data (sea
surface temperature and sea surface height) in the hydrodynamic coupled model, on the skill of
the biogeochemical model is currently under investigation. The simulated bacterial production
and biomass was generally in agreement with observations, with main discrepancies found in the
most productive areas, such as the north-western basin (eco-region #2). However, it should be
noted that bacterial production is one of the most sensitive model variables, particularly affected
by the bacterial assimilation efficiency parameter (Table S3 in Supplement Material of Part I companion paper, see also Tsiaras et al., 2017). This is directly linked with the bacterial growth efficiency that is known to vary according to the trophic richness of the ecosystem (e.g. Del Giorgio and Cole, 1998). Given the lack of sufficient data for the parameterization of a varying bacterial assimilation efficiency in the model code, the constant parameter adopted in the present model-configuration could therefore account for such model deviations from bacterial production observations. The comparison of the model-simulated zooplankton with field measurements is less satisfactory, which is partly due to the observational undersampling of zooplanktonic data, and the difficulty in converting it to the modelled-state variables. On the other hand, zooplanktonic data exhibits strong variability that is not captured by the model. Overall, model results are generally in line with the field-measured biological rates, suggesting that the model provides a good description of the Mediterranean Sea ecosystem. After the validation of key ecosystem components, the model simulation of physical-biogeochemical dynamics can provide analytical information on processes which are extremely difficult or impossible to measure, and address outstanding scientific questions exploring the ecosystem dynamics that underlie in particular in-situ observations.

An important piece of information that can be retrieved from the model output is the planktonic community structure and seasonal succession. The model-simulated planktonic functional groups have shown a well-marked variability due to the complex physical and biogeochemical environment. Small planktonic cells are dominant in large parts of the oligotrophic MS (i.e. eco-regions #3 and #4, and #2 during the stratification period). The modelled contribution of microphytoplankton and their predators was significant in nutrient-rich areas in response to deep-water convection phenomena (eco-region #2) and important river discharges, particularly during winter. Model results are thus comparable to the whole-planktonic time series approach of Romagnan et al. (2015) which is based on the verbal Plankton Ecology Group (PEG) model (Sommer et al, 2012), indicating that the planktonic succession is not only controlled by the bottom-up effect due to the establishment of favorable abiotic conditions, i.e. nutrient enrichment by vertical mixing and river loads, but also by the relaxation of the top-down control. Model simulations reveal the highest abundance of smaller phytoplanktonic cells in the oligotrophic MS, which is mainly attributed to their advantage over larger cells in nutrient-limited conditions, given their higher nutrient affinity due to the high
surface-to-volume ratio (Legendre and Rassoulzadegan, 1995). This is reflected by their increased growth rates in the model (picophytoplankton: $3.3 \text{ day}^{-1}$, nanophytoplankton: $2.9 \text{ day}^{-1}$, diatoms: $2.5 \text{ day}^{-1}$, dinoflagellates: $1.5 \text{ day}^{-1}$ in model). As mentioned above, another important factor that contributes to the size-based spatial variability in the phytoplanktonic community structure is grazing control (e.g. Thingstad, 1998), which is reflected by the size-based decrease of zooplankton maximum growth rate (HNAN: $4 \text{ day}^{-1}$, microzooplankton: $1.2 \text{ day}^{-1}$, mesozooplankton: $0.7 \text{ day}^{-1}$; see Table S4 in Supplementary Material of Part I companion paper). The top-down control is thus stronger for picophytoplankton, serving as prey to the faster growing HNAN and weaker for microphytoplankton (prey for micro- and mesozooplankton), allowing the relatively increased abundance of the latter in more productive areas. Overall, larger size-classes of phytoplankton coexist with smaller cells in regions of higher total planktonic biomass (i.e. ecoregion #1, #2), since the intense grazing pressure prevents the dominance of the latter. These results are consistent with other modelling studies (Ward et al., 2014) suggesting that two key processes dominate the community structure. Although small phytoplanktonic groups are the best competitors for nutrients, the top-down control (i.e. grazing pressure) prevent them from exhausting the nutrients supply, giving the potential to the larger groups (i.e. microphytoplankton) to outcompete for limiting nutrients. Despite this top-down control of phytoplanktonic composition, the simulated contribution of microphytoplankton was slightly underestimated in the most productive areas, suggesting that the phytoplankton parameter set should be further optimized, in order to better describe the phytoplanktonic community structure variability. The recently released datasets of ocean colour phytoplankton functional type distributions (Di Cicco et al., 2017) will provide sufficient data in order to obtain a better phytoplankton parameterization and improve the model-simulated phytoplanktonic community structure.

An increasing relative dominance of heterotrophic bacteria over phytoplankton was also simulated with the productivity decrease in different clusters (Bacterial:Phytoplankton Biomass ratio $>65\%$ in eco-regions #3 and #4, Figure S3 in Supplementary Material). Multiple studies have shown the bacterial dependence on the DOC extracellular release by phytoplankton, revealing higher rates under sub-optimal growth conditions (e.g. P-limitation, Thingstad & Rassoulzadegan, 1995 and references therein). Additionally, the model-simulated Bacterial:Primary Production (BP:NPP) ratio (Figure S4 in Supplementary Material) increases
eastward as available nutrients decrease, with values reaching over 55%, close to the reported ones (Robarts et al., 1996; Turley et al., 2000; Van Wambeke et al., 2000, Table S3 in Supplementary Material). The relatively higher simulated ratio in the eastern Mediterranean basin supports the hypothesis of the increased dependence of heterotrophic bacterial production on the DOC excreted by primary producers, suggesting that a higher percentage of primary production (in terms of DOC) circulates through the microbial loop in the eastern basin (Turley et al., 2000).

The analysis of the dominant planktonic groups and carbon pathways among them indicates that the model reproduces the two trophic pathways of the Mediterranean food web, depending on the season and the region: the classical food web and the microbial loop, in agreement with previous findings (Cushing, 1989; Legendre and Rassoulzadegan, 1995). Large phytoplanktonic groups (diatoms, dinoflagellates) and mesozooplankton form the classical food chain, which describes the energy transfer from the microphytoplankton through mesozooplankton to higher trophic levels (Turley et al., 2000). The overall trend of total normalized carbon fluxes to each zooplanktonic group shows that the amount of prey biomasses ingested by consumers increase according with the trophic state of the ecosystem and, thus, the biomass availability of planktonic groups. In particular, eutrophic and mesotrophic eco-regions, #1 and #2 respectively, are characterized by higher carbon fluxes from large planktonic preys to microzooplankton and mesozooplankton, where the largest phytoplanktonic groups seem to benefit from nutrient-rich areas. The dominant carbon pathway in the most oligotrophic eco-regions (#3 and #4) and in eco-region #2 during the nutrient depleted seasons, is the microbial loop, which is composed by the smallest fractions of plankton (i.e. microzooplankton, HNAN, picophytoplankton, nanophytoplankton, bacteria, Figure S5 in Supplementary Material). The carbon flux increases from bacteria to HNAN in large parts of the oligotrophic MS, resulting to a decrease in the amount of carbon transferred to the upper trophic levels of the pelagic food web. These results are coherent with the findings of Thingstad and Rassoulzadegan (1995), Christaki et al. (1996), Turley et al. (2000) and Siokou-Frangou et al. (2002, 2010) among others, that the oligotrophic MS is characterized in large parts by a microbial dominated food web.

5. Conclusions

The present study is a further step towards the skill assessment of the 3-D coupled
POSEIDON ecological model that is currently in operation as part of the POSEIDON forecasting system (www.poseidon.hcmr.gr). A previous work presented the Part I of the companion paper in this issue focused on the model skill assessment of the main model chemical components (i.e. chlorophyll and nutrients) through an extensive comparison of a 20-year (1990-2009) simulation outputs with available data. The current work focused on the verification of the model’s ability to represent the biological (plankton) dynamics of the Mediterranean ecosystem.

The main model-simulated biological components (i.e. primary and bacterial production and biomass, zooplankton, organic carbon) were validated with available data from the published literature in different areas of the specified eco-regions proposed in Part I of the companion paper. Validation results indicate that the presented model is a good descriptor of the observed Mediterranean marine ecosystem. The quantitative validation with in-situ observations in the identified patterns of productivity (eco-regions) has demonstrated the capability of the model to represent the full scale of the MS ecosystem, ranging from oligotrophic open ocean (such as eco-regions #3 and #4), to mesotrophic and/or eutrophic conditions in productive coastal areas with elevated nutrient concentrations and increased production rates (such as eco-regions #1 and #2 during the spring bloom period). The simulated planktonic food-web dynamics are in agreement with observations, representing the spatial shifts and seasonal succession of the planktonic trophic web in relation to nutrient and organic matter availability. Model results indicate the dominant microbial food web (small planktonic groups) in the open sea and the occurrence of the herbivorous 'classical' pathway (large planktonic groups) in more productive areas. The major carbon fluxes were simulated within the microbial food web (bacteria – HNAN - picophytoplankton), highlighting the important role of the microbial loop in the oligotrophic regions of the Mediterranean marine ecosystem.

We acknowledge the limits of our simulation and thus some future modifications of the model code are necessary. The use of three different state variables for dissolved organic carbon (labile, semi-labile, and refractory) and the introduction of a functional group for virus would further improve the representation of heterotrophic bacteria and the microbial food web. Additionally, the diel vertical migration of mesozooplankton is also missing from the model, while this seems to have a countable contribution to the organic carbon flux (Potiris et al., 2018). In addition, the introduction of mixotrophic functional groups could improve the representation of the planktonic food web, since mixotrophs can profoundly influence the cycling of carbon and trophic dynamics.
among bacteria, primary and secondary producers, both in oligotrophic waters (Stoecker, et al, 2017) and waters characterized by harmful algal bloom events (Mitra and Flynn, 2010). However, limited information is available on the mixotrophs ecophysiology, particularly those inhabiting the open ocean oligotrophic environments such as the MS, due to the large diversity of mixotrophic types. Thus, the inclusion of mixotrophy in biogeochemical/ecological models is quite challenging, also taking into account the scarcity of data sets suitable for the parameterization of the diverse mixotrophic physiological processes. This study emphasizes the need for a more systematic ecosystem monitoring across multiple scales, processes, and trophic levels. In particular, it highlights the need for in-situ data of more biochemical variables and processes, such as zooplanktonic (i.e. microzooplankton, HNAN) biomass data and bacterial production, along with long-term monitoring data of phytoplanktonic cell size and elemental stoichiometry. This will help towards better calibration of the model and a further examination of the microbial food web that is the dominant carbon pathway in the oligotrophic MS. The use of more detailed data on lateral nutrients inputs in the Mediterranean basin (riverine discharges, BSW/AW inflow) could also give a better representation of nutrients variability and hence of productivity (primary and heterotrophic). With this in mind, the acknowledgement of the importance of biological observations both at European and global scales is very promising. The significant funds within H2020 program, the G7 science and the directions of the Minister of Technology together with technological advancements indicate that the amount of biological in-situ data will increase in the future, while new biological variables will be added to the existing ones. Models are expected to play an important role in this process, not only benefiting from the increased information but also as tools towards operational observation-planning and informed decision-making.

Even with some limitations, the presented model provides a better understanding of biogeochemical processes linked to the plankton ecology of the Mediterranean basin. This work illustrates that the generic POSEIDON ecosystem model can achieve a realistic skill that is enough to provide valuable information for the implementation of the European Union’s Marine Strategy Framework Directive (MSFD), which seeks to achieve, for all European seas, “Good Environmental Status” (GES), by 2020. Simulation results point to the specific needs for further refinement of the model that will make it more useful and reliable as a management tool to predict and understand the consequences of anthropogenic and climate-driven changes in the
natural environment.

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**Tables**

**Table 1.** Model simulated and observed net primary production and phytoplanktonic biomass (integrated over the 0-100m layer) in selected Mediterranean regions. Observations from years previous to 1990 were compared with climatological mean simulated values. (Maguzzu & Decembrini, 1995: calculated from hourly primary production rates assuming a 12-h day and model euphotic zone).

| Cluster | Area                  | Net Primary Production (mgC m\(^{-2}\) d\(^{-1}\)) | Phytoplankton Biomass (mgC m\(^{-2}\)) | Period          | Reference                  |
|---------|-----------------------|-----------------------------------------------|----------------------------------------|-----------------|----------------------------|
| #1      | Alboran Sea            | 330-660                                       | 720-1480                               | 1159            | May 1986                   |
|         |                       | **462**                                       | **720-1480**                           |                 | Lohrenz et al., 1988       |
| #2      | North-West Mediterranean Sea | 502.7±342.2                                | 1168±778                               | 920.5           | November 1994, April & November 1995 |
|         |                       | **406.5**                                    | **1168±778**                           |                 | Turley et al., 2000        |
Table 2. Model simulated phytoplanktonic class-specific Chl-a biomass against field measurements of corresponding size-fractionated parameters, expressed as percent contribution of each size class to the total Chl-a biomass as reported to Uitz et al., 2012. Phytoplanktonic groups are indicated as: Micro- refers to dinoflagellates and diatoms, Nano- refers to nanophytoplankton and Pico- refers to picophytoplankton.
| Cluster | Area | Period | Size | In-situ Chl-a% | Model Chl-a% | Reference |
|---------|------|--------|------|---------------|--------------|-----------|
| #1&2    | Adriatic Sea | August 1986-1988 | Micro- >20 µm | 10-23 | 10-20 | Revelante & Gilmartin, 1995 |
|         |       | July 1987 |       |       |       |           |
| #2      | Ligurian Sea | May - June 1995 | Nano- 3-10 µm | 22 | 25 | Vidussi et al., 2000 |
|         |       |         | Diatoms | 29 | 22 |           |
| #4      | Levantine Sea | March 1992 | Pico- <2 µm | 54.3-64.2 | 55-63 | Zohary et al., 1998 |
| #2      | Algerian Sea | October 1996 | Pico- <2 µm | 42-62 | 55-60 | Moran et al, 2001 |
|         |       |         |       |       |       |           |
| #1      | Alboran Sea | May 1998 | Pico- <2 µm | 26-51 | 35-53 | Arin et al., 2002 |
|         |       |         | Nano- 2-20 µm | 36-47 | 25-35 | Arin et al., 2002 |
|         |       |         | Micro- >20 µm | 6-35 | 15-35 | Arin et al, 2002 |
| #2      | Balearic Sea | February 1997 | Pico- <2 µm | 26-47 | 35-55 | Arin et al, 2005 |
|         |       |         | Nano- + Micro- >2 µm | 53-74 | 40-48 | Arin et al, 2005 |
|         |       |         |       |       |       |           |
| #2&3    | Aegean Sea | May 1997 (NA, SA) | Pico- 0.2-3 µm | 181, 257 | 155, 257 | Siokou - Frangou et al., 2002 |
|         |       | September 1997 (NA, SA) | Pico- 0.2-3 µm | 181, 272 | 155, 258 | Siokou - Frangou et al., 2002 |
|         |       | May 1997 (NA, SA) | Nano- >3 µm | 119, 243 | 132, 230 | Siokou - Frangou et al., 2002 |
|         |       | September 1997 (NA, SA) | Nano- >3 µm | 119, 228 | 130, 230 | Siokou - Frangou et al., 2002 |
| #3      | South Tyrrhenian Sea | July 2005 | Pico- <2 µm | 44-81 | 53-58 | Decembrini et al., 2009 |
|         |       | December 2005 | Pico- <2 µm | 76-90 | 55-60 | Decembrini et al., 2009 |

Table 3. Model simulated mean bacterial biomass and production (integrated in the 0-120m layer) against available historical data covering selected areas in the Mediterranean Sea [*(g C m⁻² Yr⁻¹), **(integrated 0-100m)].
Table 4. Model simulated bacterial production (integrated over the 0-150m layer) against in-situ data from Propose Cruise (September – October 1999, Van Wambeke et al., 2002).

| #  | Region                  | Range | Mean | Standard Deviation | Year | Reference                  |
|----|-------------------------|-------|------|--------------------|------|----------------------------|
| #2 | North-West Mediterranean Sea | 90±54.2 | 50   | 1372±274           | 1995 | Turley et al., 2000       |
| #2 | Gulf of Lions           | 75.9  | 31.15| -                  | November 1994 | Yoro et al., 1997       |
| #2 | Algerian Sea            | 33-384| 80-110| -                  | October 1996 | Moran et al., 2001      |
| #1 | Alboran Sea             | 124-199| 90-120| -                  | May 1991 | Fernández et al.,          |
| #2 | Ligurian Sea            | -     | -    | 1026±314           | 1995  | Turley et al., 2000       |
| #4 | North Levantine Sea     | 8.2-43.4 | 42.5-48.5 | 400-800 | 703 | October & November 1991 | Robarts et al., 1996 |
| #3 | Cretan Sea              | 48.5±39.2 | 57   | 1372±274           | 1994-1995 | Turley et al., 2000     |
| #2 | DYFAMED                 | -     | -    | 720±111.6          | September-October 2004 | Mével et al., 2008 |
|     |                         | -     | -    | 2757.6 ± 81.6      | 867 | March 2003                 |
|     |                         | -     | -    | 472.8±211.2        | 1829 | June 2003                  |
|     |                         |       |      | 60-468             | 22-102 | 1999 | Lemée et al., 2002       |
| #3 | POSEIDON-E1-M3A         |       |      | 732               | 983  | 2012-2015 | HCMR POSEIDON system team |
|     |                         |       |      | 13.14†             | 14.7† | -              | Van Wambeke et al, 2001  |
|     |                         |       |      | 48 ± 31            | 67   | -              | Siokou - Frangou et al., 2002 |
| #2 | North Aegean Sea**      | 48 ± 31 | 67   | -                  | March 1997 | Siokou - Frangou et al., 2002 |
|     |                         | 48 ± 31 | 111  | -                  | September 1997 | Siokou - Frangou et al., 2002 |

**Table 4. Model simulated bacterial production (integrated over the 0-150m layer) against in-situ data from Propose Cruise (September – October 1999, Van Wambeke et al., 2002).
Table 5. Model simulated DOC concentrations (averaged in the upper 100m layer) against available historical data covering selected areas in the MS.

| Cluster | Region | Date | DOC (mmol m$^{-3}$) | Bacterial Production (mgC m$^{-2}$ d$^{-1}$) | Reference |
|---------|--------|------|---------------------|-----------------------------------------------|-----------|
| #1      | Strait of Gibraltar | September – October 1999 | 349 | 95.7 | Santinelli et al. 2002 |
| #1      | Alboran Sea | May 2003 (0-100m) | 36.05N 5.11W | 68 ± 10 (50–100) | 75-78 |
| #2      | East Algerian Sea | March 2008 (0-100m) | 36.28N 13.19E | 60 ± 9 (48–95) | 78 |
| #2      | Strait of Sicily | April 1999 (0-100m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
| #2      | South Ionian Sea | November 1997 (0m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
| #2      | South-West Levantine Sea | June 1995 (0-100m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
| #3      | West Algerian Sea | November 2006 (0-100m) | 37.95N 8.31E | 62 ± 9 (48–95) | 78 |
| #3      | Ionian Sea | April 2002 (0-100m) | 39.06N 14.42E | 62 ± 9 (48–95) | 78 |
| #3      | North Tyrrhenian Sea | March 2008 (0-100m) | 41.53N 10.26E | 62 ± 9 (48–95) | 78 |
| #2      | Ligurian Sea | May 2003 (0-100m) | 36.05N 5.11W | 68 ± 10 (50–100) | 75-78 |
| #2      | Gulf of Lion | May 2003 (0-100m) | 36.24N 0.51W | 68 ± 10 (50–100) | 75-78 |
| #2      | Algerian Sea | May 2003 (0-100m) | 37.95N 8.31E | 62 ± 9 (48–95) | 78 |
| #2      | South-West Levantine Sea | May 2003 (0-100m) | 37.95N 8.31E | 62 ± 9 (48–95) | 78 |
| #2      | Ionian Sea | May 2003 (0-100m) | 39.06N 14.42E | 62 ± 9 (48–95) | 78 |
| #2      | North Tyrrhenian Sea | May 2003 (0-100m) | 41.53N 10.26E | 62 ± 9 (48–95) | 78 |
| #3      | Strait of Sicily/North-East Ionian Sea | November 2006 (0-100m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
| #3      | South Tyrrhenian Sea | May 2003 (0-100m) | 37.95N 8.31E | 62 ± 9 (48–95) | 78 |
| #3      | North Tyrrhenian Sea | May 2003 (0-100m) | 39.06N 14.42E | 62 ± 9 (48–95) | 78 |
| #3      | South Ionian Sea | May 2003 (0-100m) | 41.53N 10.26E | 62 ± 9 (48–95) | 78 |
| #3      | Adriatic Sea | May 2003 (0-100m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
| #2      | North Adriatic Sea | May 2003 (0-100m) | 36.24N 0.51W | 68 ± 10 (50–100) | 75-78 |
| #2      | South-West Levantine Sea | May 2003 (0-100m) | 37.95N 8.31E | 62 ± 9 (48–95) | 78 |
| #2      | Ionian Sea | May 2003 (0-100m) | 39.06N 14.42E | 62 ± 9 (48–95) | 78 |
| #2      | North Tyrrhenian Sea | May 2003 (0-100m) | 41.53N 10.26E | 62 ± 9 (48–95) | 78 |
| #3      | East Mediterranean Sea | May 2003 (0-100m) | 37.23N 15.36E | 62 ± 9 (48–95) | 78 |
Table 6. Model simulated mesozooplankton biomass against field studies in selected Mediterranean regions derived from Siokou-Frangou et al. (2010) and the ANREC project (Isari et al., 2006, 2007).

| Cluster | Region               | Date                | Depth     | Mesozooplankton Biomass (mgC m$^{-3}$) | Reference                      |
|---------|----------------------|---------------------|-----------|---------------------------------------|---------------------------------|
| #1      | Alboran Sea          | Winter 1997         | 0-200m    | 14.4 (5.5-25)                         | Youssara & Gaudy, 2001         |
| #2      | Catalan Sea          | Autumn 1992         | 0-200m    | 2.9 (2.2-3.4)                         | Calbet et al., 1996            |
|         |                      | June 1993           | 0-200m    | 5.8 (4.8-8)                           | Calbet et al., 1996            |
|         |                      | Annual mean         | 0-200m    | 8                                     | Alcaraz et al., 2007            |
| #2      | North Balearic Sea   | March 2003          | 0-200m    | 8.4 (0.4-17.8)                        | Siokou-Frangou et al., 2010     |
|         |                      | April 2003          | 0-200m    | 5.9 (2.0-13.2)                        | Siokou-Frangou et al., 2010     |
| #2      | Gulf of Lion         | Spring 1998         | 0-200m    | 8.7 (3-13.5)                          | Gaudy et al., 2003              |
| #2      | East Ligurian Sea    | December 1990       | 0-200m    | 2.5 (0.8-4.2)                         | Licandro & Icardi, 2009         |
| #2      | Central Ligurian Sea | September-October 2004 | 0-200m    | 9.9 (0.8-19)                          | Raybaud et al., 2008            |
| #3      | South Aegean Sea     | Spring 1999         | 0-100m    | 7.9 (4.4-13.4)                        | Mazzocchi et al., 2003          |
| #2      | North Aegean Sea     | July 2003           | 0-200m    | 3.07±1.3                              | Isari et al., 2007, 2006 (ANREC project) |
|         |                      | September 2003      | 0-200m    | 1.8±0.95                              | Isari et al., 2007, 2006 (ANREC project) |
|         |                      | July 2004           | 0-200m    | 4.45±2.61                             | Isari et al., 2007, 2006 (ANREC project) |

Table 7. Model simulated heterotrophic nanoflagellates biomass against field measurements.

Heterotrophic Nanoflagellates biomass
| Cluster | Region                        | Period            | Unit     | In-Situ | Mo del | Reference                        |
|--------|-------------------------------|-------------------|----------|---------|--------|----------------------------------|
| #2     | North Aegean Sea              | September 1997    | mgC m⁻²  | 418±90  | 483    | Siokou-Frangou et al., 2002      |
| #3     | South Aegean Sea              | March 1997        | mgC m⁻²  | 192±54  | 291    | Siokou-Frangou et al., 2002      |
|        |                               | September 1997    | mgC m⁻²  | 812±376 | 266    | Siokou-Frangou et al., 2002      |
| #2     | Ligurian Sea (DYFAMED)        | May 1999 -        | mgC m⁻³  | 0.03-6.4| 3.8    | Tanaka & Rassoulzadeh, 2002      |
|        |                               | March 2000        |          |         |        |                                  |

**Figure Captions**

**Figure 1.** Model food web.

**Figure 2.** Mediterranean model domain and bathymetry (m). Major rivers are indicated. Abbreviations: LPC for Liguro-Provencal and Catalan sub-basin.

**Figure 3.** Spatial distribution of the clusters (eco-regions) obtained from the K-means analysis.

**Figure 4.** Model simulated mean (1990-2009) spatial distribution of 0-100m average a) net primary production (mgC/m³/d), b) bacterial biomass (mgC/m³), c) bacterial production (mgC/m³/d), d) phytoplanktonic biomass (mgC/m³), e) DOC (mmol/m³) and f) POC (mmol/m³).

**Figure 5.** Model simulated mean (1990-2009) spatial distribution of 0-100m average contribution (%) of different phytoplanktonic groups [a) diatoms, b) dinoflagellates, c) nanophytoplankton d) picophytoplankton] on the total phytoplanktonic biomass.

**Figure 6.** Model simulated mean (1990-2009) monthly variability (integrated over the 0-100m layer) of a) bacterial biomass (mgC/m³), b) phytoplanktonic biomass (mgC/m³), c) bacterial production (mgC/m³/d), d) net primary production (mgC/m³/d), e) POC (mmol/m³) and f) DOC (mmol/m³) in each eco-region (cluster). Abbreviations: CL #1 for cluster #1, CL #2 for cluster #2, CL #3 for cluster #3 and CL #4 for cluster #4.

**Figure 7.** Model simulated mean (1990-2009) spatial distribution of 0-100m average contribution (%) of different zooplanktonic groups [a) heterotrophic nanoflagellates (HNAN), b) microzooplankton, c) mesozooplankton] on the total zooplanktonic biomass.

**Figure 8.** Model simulated mean (1990-2009) monthly variability of 0-100m integrated phytoplanktonic [a) diatoms, b) nanophytoplankton, c) picophytoplankton, d) dinoflagellates] and zooplanktonic [e) heterotrophic nanoflagellates (HNAN), f) microzooplankton, g) mesozooplankton] community composition (%) in each eco-region (cluster). Abbreviations: CL #1 for cluster #1, CL #2 for cluster #2, CL #3 for cluster #3 and CL #4 for cluster #4.

**Figure 9.** Percentage of the integrated (0-100m) mean (1990-2009) total carbon flux among different planktonic groups. The integrated carbon biomass (mgC/m²) is indicated inside the boxes. Abbreviations: HNAN for heterotrophic nanoflagellates.

**Figure 10.** Food availability (%) for heterotrophic nanoflagellates (HNAN), microzooplankton and mesozooplankton in each cluster.
Conflicts of Interest Statement

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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