

Referee #1

First, we would like to thank Referee #1 for his/her careful evaluation of our manuscript. We believe that his/her comments will help to improve the manuscript. Please, find hereafter our responses to the concerns raised by Referee #1.

Specific comments

Lines 23-26: What the authors mean with the phrase “portion of the ecosystem”? Is it in terms of carbon? This needs to be rephrased appropriately. Also, the phrase “relatively high carbon biomass” could be more specific, i.e. relative to what and how much?

We agree with this comment. To clarify, we changed the phrase :

[In addition, we investigate the carbon, nitrogen and phosphorus fluxes associated with mixotrophic protists and showed that: (i) the portion of the ecosystem occupied by NCM decreases when resources (nutrient and prey concentrations) decrease, although their mixotrophy allows them to maintain a relatively high carbon biomass as photosynthesis increase as food source; (ii) the portion of the ecosystem occupied by CM increases when nutrient concentrations decrease, due to their capability to ingest prey to supplement their N and P needs.]

to:

[In addition, we investigate the carbon, nitrogen and phosphorus fluxes associated with mixotrophic protists and showed that: (i) the portion of the ecosystem in percentage of carbon biomass occupied by NCM decreases when resources (nutrient and prey concentrations) decrease, although their mixotrophy allows them to maintain a carbon biomass almost as significant as the copepods one (129.8 and 148.7 mmolC m⁻³, respectively), as photosynthesis increase as food source; (ii) the portion of the ecosystem in percentage of carbon biomass occupied by CM increases when nutrient concentrations decrease, due to their capability to ingest prey to supplement their N and P needs.].

Lines 47-48: “Studies are ... heterotrophs”. This sentence needs rephrasing. What’s the message here? That there are fewer modelling studies compared to experimental ones?

Yes, we wanted to point out that, as a lot of models still consider a food web divided into strict phototrophs and heterotrophs, there are fewer modelling studies comparing to experimental ones. We modified it to avoid confusion (l.48-54).

[Mixotrophic protists played an important role in the marine carbon cycle. Due to their adaptability, these organisms are crucial for the transfer of matter and energy to the highest trophic levels, thus impacting the structure of planktonic communities by favouring the development of larger organisms (Ptacnick et al., 2004). Moreover, by switching the biomass maximum to larger organisms, carbon export increases in presence of mixotrophs. As instance, Ward and Follows (2016) compared the results from two food web models, only one accounted for mixotrophy, and showed that carbon export to depth increased by nearly 35% when mixotrophic protists were considered. By showing the significant effect of mixotrophic protists on the food web, these studies motivated their addition to current food web models (Jost et al., 2004; Mitra and Flynn, 2010).]

Line 65: “Unlike most other models...” There are also a lot of models that use variable stoichiometry so this phrase is somewhat misleading and should be rephrased.

We modified (l.68-69) :

[Unlike most other models, Eco3m_MIX-CarbOx uses variable cellular quotas which allowed us to determine the nutritional state of the cell by comparing it to a reference quota]

to:

[Eco3m_MIX-CarbOx uses variable cellular quotas which allowed us to determine the nutritional state of the cell by comparing it to a reference quota].

Figure 2: The explanation of the abbreviation TA is missing.

Thank you for pointing this out, we added the explanation of the abbreviation TA.

In addition, it appears strange that there is no heterotrophic protists compartment in the model. Heterotrophic protists are an important component of the marine microbial food web. Thus, the authors should comment on why they chose not to include them in their model formulation.

We agree that heterotrophic protists could play an important role in the food web assemblage. We chose to not consider them because, by adding mixotrophs, we have considerably complexified the architecture of the model. To simplify the transition to 3D (coupling to a hydrodynamic model) and to limit the calculation time, we decided not to consider them. We propose to discuss it in a new section : 4.1 Mixotrophs representation assessment; as a possible improvement of the OD model in the discussion (l.501-505).

[In the present model, we do not consider strict heterotrophs which belong to the nano and micro size classes. These organisms can be important competitors of ciliates, and certain species can even consume ciliates (Stoecker and Capuzzo, 1990 ; Johansson et al., 2004). The adding of these organisms could improve the representation of NCM dynamics and, accordingly, of the ecosystem and is then considered for an improved version of the model.]

Moreover, I believe that some explanation should be provided regarding the fact that there is no mortality for phytoplankton and mixotrophs but there is mortality for bacteria.

We add a point about mortality of NCM in the discussion (l.505-507). We think that adding mortality could improve the representation of NCM dynamics, and we consider it for an improved version of the model.

[Moreover, we do not consider a mortality term for NCM. Montagnes (1996) showed that mortality rates for two species of the genus *Strombidium* and two species of the genus *Strombilidium* were rapid. Accordingly, adding this term to the model could allow to represent a more realistic NCM biomass.]

For phytoplankton and CM, we performed sensitivity tests to add a mortality term when developing the model, but none were conclusive as our phytoplankton compartment and CM variable was already balanced. We believe that this is due to the fact that predators exert a strong top-down control on phytoplankton and CM populations.

Lines 112-114: To the best of my knowledge the Baklouti et al. 2006 a, b papers present the formulations only for the phytoplankton compartment. For zooplankton the authors provide the reference of Auger et al. (2011). However, some background information on the formulation of bacteria compartment is missing. I advise the authors to provide this background information and the relevant references on which they have based the formulation for bacteria.

We added the references for heterotrophic bacteria formulation (Kirchman, 2000 ; Faure et al., 2006) (l.169).

Line 130: Why copepods feed with different preference on nanophytoplankton and CM? Most of the CM belong to nanoflagellates so I don't see why copepods prefer one group more than the other.

To clarify this, we add Figure 3 which illustrate organisms' repartition in size classes and trophic interactions between them. In our model, the variable NANO aims to represent the phytoplankton

larger than 2 μm and smaller than 2000 μm (nanophytoplankton and microphytoplankton). This variable stands for diatoms, autotrophic dinoflagellates. In the northwestern Mediterranean Sea, diatoms are an important component of phytoplankton assemblage especially during the spring bloom (Margalef, 1978, Leblanc et al., 2018) and cover wide size-range, we decided to consider them as representative of the variable. To avoid confusion, we switch the name NANO to NMPHYTO (for nano+micro-phytoplankton).

We modified the lines 136 to 141:

[We considered two types of phytoplankton based on size: nanophytoplankton (NANO) and picophytoplankton (PICO). Nanophytoplankton includes autotrophic flagellates and small diatoms. We used *Minidiscus spp.* as the representative species of nanophytoplankton as the *minidiscus* genus proliferates throughout the NW Mediterranean when light and nutrients are less limiting (Leblanc et al., 2018). Picophytoplankton includes autotrophic prokaryotic organisms such as *Prochlorococcus spp.* and *Synechococcus spp.* The *Synechococcus* genus is ubiquitous in the Mediterranean (Mella-flores et al., 2011) and was therefore considered the representative genus of picophytoplankton in the model.]

to:

[We considered two types of phytoplankton based on size (Fig. 3): picophytoplankton (PICO) and nano+micro-phytoplankton (NMPHYTO). PICO includes autotrophic prokaryotic organisms such as *Prochlorococcus spp.* and *Synechococcus spp.* which are ubiquitous in the Mediterranean (Mella-flores et al., 2011). NMPHYTO aims to represent phytoplankton larger than 2 μm and smaller than 200 μm . It mainly includes diatoms and autotrophic nanoflagellates. As diatoms are an important component of Mediterranean spring blooms (Margalef, 1978, Leblanc et al., 2018) and cover wide size-range, we decided to consider them as representative of the NMPHYTO]

and the rest of the manuscript accordingly.

Accordingly, we assumed that copepods feed on strictly smaller sized preys with the strongest preference for the largest organism: NCM. NCM are considered to be ciliates, copepods preferential ingestion of ciliates in environments where diatoms and dinoflagellate are present has been demonstrated by Verity (1996). They also represent a preferential food source for the reproduction of some copepod species (Dutz & Peters, 2008). Next, we decided to apply a strongest preference on diatoms as they cover a largest size range with possibly bigger organisms than CM.

Line 145: Why only PICO can consume DON and DOP but not PHYTO. As far as I know most phytoplankton species can consume DON and DOP. Therefore, the authors should provide some justification on this assumption. Moreover, dissolved organic phosphorus and nitrogen should be stoichiometrically coupled with dissolved organic carbon, accounting of course for variable stoichiometry of dissolved organic matter. That is PICO as well as heterotrophic bacteria and mixotrophs will consume a mol of dissolved organic matter containing x mols of DON and y mols of DOP, i.e. by definition DON and DOP is coupled to organic carbon. The way that the consumption of dissolved organic matter is formulated in the current model does not account for the uptake of dissolved organic carbon along with DON and DOP.

Thank you for this interesting comment. We decided to consider osmotrophy only for the smaller organisms (PICO and CM, Duhamel et al. (2018) ; Glibert and Legrand, (2006)). However, we agree that recent studies show that some diatoms (which are representative of NMPHYTO in our model) are able to perform dissolved organic compounds uptake (Villanova and Spetea, 2021). Then, we will consider it as possible improvement for next versions of the model.

We agree with the fact that DON, DOP and DOC are coupled, as an example we consider the three uptakes for heterotrophic bacteria. In fact, we decided to add only DON and DOP uptake for CM and PICO because we assumed that, as a type of mixotrophy, these uptakes are done to supplement N and P needs when NO_3^- , NH_4^+ and PO_4^{3-} are limiting the growth. We represent it by limiting these uptakes

by nutrients concentration (by considering the internal content of the cell in N and P). When N (P) content of the cell is high the uptake is close to 0 and vice versa. In the model, carbon is entirely provided by photosynthesis and organisms are rarely limited by this element which explain that we do not consider DOC uptake.

Line 185: Why the NCM as well as the CM have different preferences for the different types of prey. This is somewhat arbitrary and some support for this assumption should be provided.

For NCM: We made the choice to prioritize the ingestion of smaller organisms by considering bacteria and picophytoplankton as the preys with the highest preference as it is the case for small ciliates (Rassoulzadegan et al. 1988, Price & Turner, 1992, Christaki et al., 1999). We then prioritize nanophytoplankton which has been shown to be a great food source for ciliates in the Gulf of Lion (Christaki et al., 2009). We apply the lowest preference to NMPHYTO as they cover a wide range of size (they can be as large as NCM) and species including diatoms which are associated with smaller ciliates grazing rates (Epstein et al., 1992).

For CM: We assumed that CM consume strictly smaller sized preys. They are known to consume bacteria and picophytoplankton (Christaki et al., 2002 ; Zubkhov & Tarron, 2008, Millette et al., 2017, Livanou et al., 2019).

We provided references in the text (l.204 and l.260), the caption of the new figure 3:

[From most to least preferred prey, NCM feed on heterotrophic bacteria, picophytoplankton, CM and nano+micro-phytoplankton (Verity, 1991 ; Price & Turner, 1992 ; Christaki, 1999).]

[CM feed on heterotrophic bacteria (preferred) and picophytoplankton (less preferred, Christaki et al., 2002 ; Zubkhov & Tarron, 2008, Millette et al., 2017 ; Livanou et al., 2019) and the same grazing formulation as for zooplankton and NCM is used except that CM grazing is limited by DIN (DIP) concentration and light (Stoecker, 1997, 1998; Eq. 9).]

[Figure 3: Repartition of modelled organisms (COP: copepods, PICO: picophytoplankton, NMPHYTO: nano+micro-phytoplankton, and BACT: heterotrophic bacteria) in size classes and trophic interactions between them. Preference values are indicated in grey for copepods (Verity and Paffenhofer, 1996) and NCM (Epstein, 1992; Price & Turner, 1992 ; Christaki, 2009) and CM (Christaki et al., 2002 ; Zubkhov & Tarron, 2008, Millette et al., 2017 ; Livanou et al., 2019).]

and added a reference column to the Table E2.

Line 210: It is not clear to me why the photosynthetic flux is weighted by the prey preference. Shouldn't it be analogous to the grazing rate to each of the different prey since prey should be first consumed and then it can be used for photosynthesis by the mixotroph?

In the present formulation we do not directly consider the ingested chlorophyll for each prey. It is another possibility to represent this process. We chose the present formulation as it was less complex and more adapted to our model. However, we would like to point out that the present formulation considers the benefits of grazing through the calculation of a quota function ($f_{Q,NCM}^G$). Prey dependence is then added through photosynthesis calculation parameters (i.e., we used prey parameters to calculate temperature (f^T) and light limitation (liml) functions and based the calculation of the maximum photosynthetic rate on the C-specific photosynthetic rate of the prey at a reference temperature ($P_{REF,PREY}^C$) and the portion of each photosynthetic prey through their associated preference value.

Lines 252-253: Authors should provide further information regarding this statement. To what evidence is this assumption based on?

It is not a formulation choice but a result from the CM grazing representation. When DIN (DIP) concentration is limiting CM will ingest prey in addition to the uptake of nutrient. As their internal content in N (P) is particularly low, exudation of DON (DOP) is not allowed (equal to 0). When DIN (DIP) concentration is high, CM only perform nutrient uptake (no grazing as it only supplements N and P needs in limiting conditions). Then, all the N (P) from uptake is exuded as the cell is already loaded in N (P) and as no grazing is performed, no N (P) from grazing is exuded in these conditions.

We changed (l.277):

[The formulations for DON and DOP exudation are similar except neither N nor P obtained from grazing are released, only N and P obtained from nutrient uptake if the cell's N and P content is high are released. Respiration uses the same formulation as for phytoplankton i.e., a constant fraction of photosynthesis and nutrient uptake is respired (Section 2.2.2 and Appendix C).]

to:

[The formulations for DON and DOP exudation are similar. Exudation only occurs on the N and P obtained from nutrient uptake. In other words, neither N or P obtained from grazing are released through exudation. When DIN (DIP) concentration is limiting CM will ingest prey in addition to the uptake of nutrient. As their internal content in N (P) is particularly low, exudation of DON (DOP) is not allowed (equal to 0). When DIN (DIP) concentration is high, CM only perform nutrient uptake (no grazing as it only supplements N and P needs in limiting conditions). Then, all the N (P) from uptake is exuded as the cell is already loaded in N (P) and as no grazing is performed, no N (P) from grazing is exuded in these conditions.]

Lines 431-433: Mixotrophic organisms must invest in the synthesis and maintenance of both a phototrophic and a phagotrophic apparatus, which can lead to an increased metabolic cost. Trade-offs of mixotrophy are not taken into account in the current model, however the authors should comment on the potential effect of trade-offs of mixotrophy on the competitive advantage of mixotrophs.

We thank the referee for this interesting comment. We reorganised the last point of our discussion to included it (l.635-647):

[In the present work, we provided a relatively simple model (reduced number of compartments, 0D reasoning) to represent mixotrophy in the BoM. Even though we showed that we reproduced well the two types of mixotrophs modelled (all properties from Stoecker, 1998 were verified), Eco3M_MIX-CarbOx could still be improved. When developing Eco3M_MIX-CarbOx, we considered a simplify food web with a reduced number of compartments, consequently we made the choice to not consider strict heterotrophs which belong to the nano and micro size classes. This choice can affect the representation of NCM biomass as these organisms are known to compete with ciliates for resources. Some species can even ingest ciliates (Stoecker and Capuzzo, 1990 ; Johansson et al., 2004). Moreover, in the current version of the model, we do not take into account the possible increasing metabolic cost associated with mixotrophy (i.e., maintenance of both autotrophic and heterotrophic apparatus). Raven (1997) shown that the cost of maintaining phagotrophic apparatus for a primarily phototrophic organism remains low, but the cost of maintaining a phototrophic apparatus for a primarily phagotrophic organism can be significant and often resulting in lower growth rates than strict heterotrophs. It might be interesting to consider it as it could improve the representation of the NCM biomass.]

Lines 454-455: “Although CM biomass... not co-limiting”: These findings should be further explained. i.e. What are the model assumptions and formulations that give rise to these results?

These results are explained by the high nutrient concentration applied to this simulation and the parameters used to calculate light limitation for each organism. By lifting the nutrient limitation, NMPHYTO which is particularly sensitive to nutrient concentration, can grow more easily. In addition,

NMPHYTO include mainly diatoms which are known to be advantaged in low light environment (Fisher and Halsey, 2016) we then chose the parameters for light limitation calculation accordingly. Due to the chosen parameters, CM are more affected by low light, in addition they do not perform grazing in these conditions as nutrient concentration is high.

We modified:

[Although CM biomass remains high in low light, its share of the pie decreases in favour of NANO which seem to gain a slight edge. While the share of NANO increases slightly under low light PICO appears to be unaffected which is in agreement with observations by Timmermans et al. (2005) for when nutrients are not co-limiting (Fig. 9a, b).]

to (I.545):

[Although CM biomass remains high in low light, its share of the pie decreases in favour of NANO which seem to gain a slight edge. While the share of NANO increases slightly under low light PICO appears to be unaffected (Fig. 10a, b). In this simulation nutrient levels were kept artificially high to prevent nutrient limitation. By lifting the nutrient limitation NMPHYTO which is particularly sensitive to nutrients concentration, can grow more easily. In addition, NMPHYTO includes mainly diatoms which are known to be advantaged in low light environment (Fisher and Halsey, 2016). CM are more affected by low light and are not able to use mixotrophy in these conditions (nutrient concentration is high). The low effect of light on PICO agrees with observations by Timmermans et al. (2005) who showed that when nutrients are not co-limiting picophytoplankton still developed well.]

Technical corrections:

Thank you for this, we took into account all these corrections.

Figures :

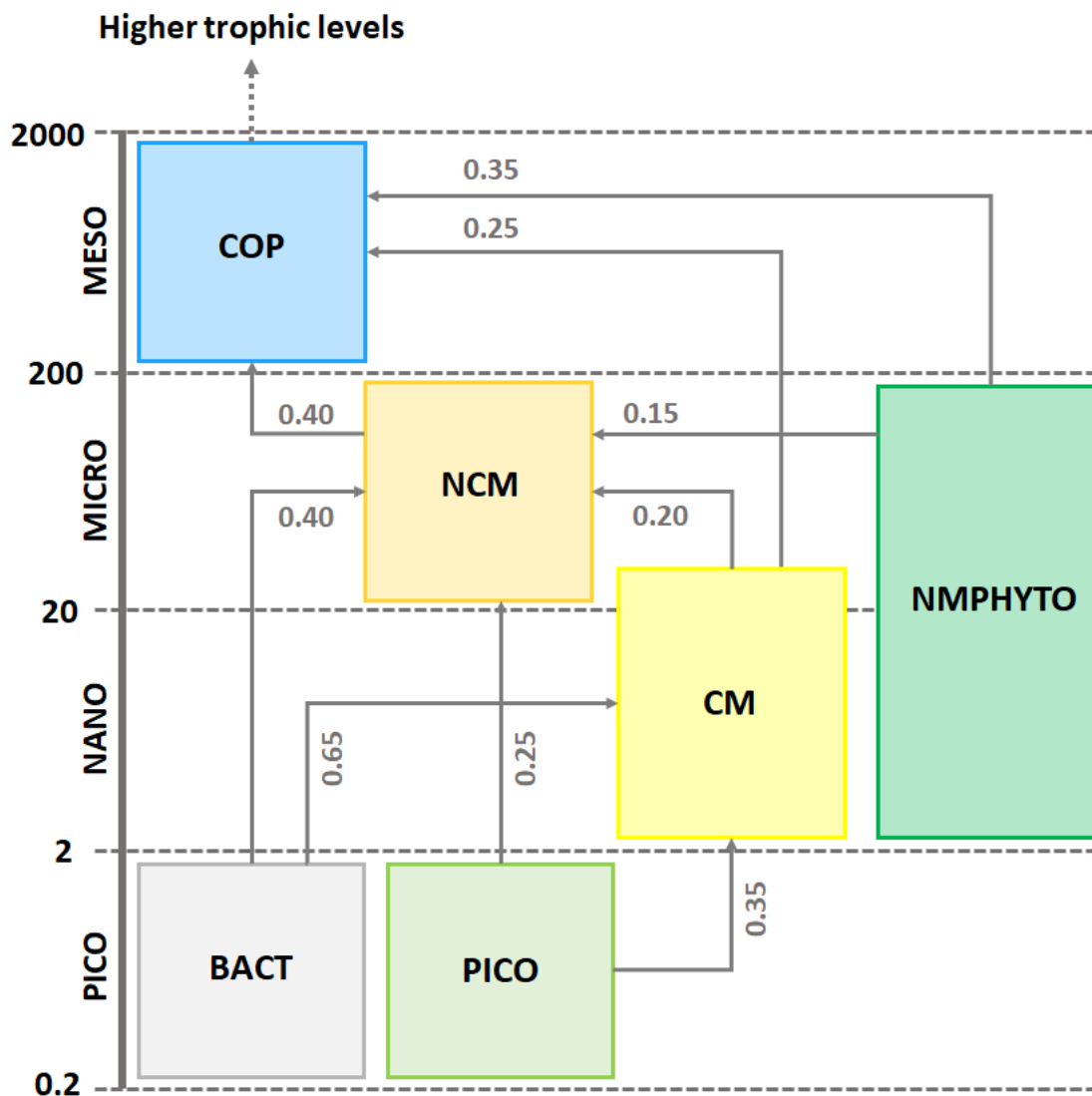


Figure 3: Repartition of modelled organisms (COP: copepods, PICO: picophytoplankton, NMPHYTO: nano+micro-phytoplankton and BACT: heterotrophic bacteria) in size classes and trophic interactions between them. Preference values are indicated in grey for copepods (Verity, 1996) and NCM (Epstein, 1992; Price & Turner, 1992; Christaki, 2009) and CM (Christaki et al., 2002; Zubkhov & Tarron, 2008; Millet et al., 2017; Livanou et al., 2019). **[added to the manuscript]**

Tables:

Table E2: Predator preference for their preys (COP: copepods, NMPHYTO: nano+micro-phytoplankton, PICO: picophytoplankton and BACT: heterotrophic bacteria). (20) Verity and Paffenhofer (1996), (21) Price & Turner, 1992, (22) Christaki et al., 2009, (23) Epstein et al., 1992, (24) : Christaki et al., 2002, (25) Zubkhov & Tarron, 2008, (26) Millette et al., 2017, (27) Livanou et al., 2019, (*) Calibrated.

		PREYS					References
		NCM	CM	NMPHYTO	PICO	BACT	
PRED	COP	0.4	0.25	0.35			20, *
	NCM		0.20	0.15	0.25	0.40	21, 22, 23, *
	CM				0.35	0.65	24, 25, 26, 27 *

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