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# Flows of biogenic carbon within marine pelagic food webs: roles of microbial competition switches

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**ABSTRACT:** Using a previous model based on the microbial hub (HUB; consists of heterotrophic bacteria and microzooplankton, the latter being heterotrophic protists), we investigated the effects of competition for inorganic and organic resources in planktonic food webs by proposing and developing the concept of 'competition switches'. A competition switch controls the flow of carbon toward either the HUB or other food web compartments. The 3 switches are PB: competition for inorganic nutrients between bacteria and phytoplankton; MB: competition for detritus between bacteria and mesozooplankton; and M<sub>μ</sub>: competition for large-sized phytoplankton production between microzooplankton and mesozooplankton. Here, we explored the novel hypothesis that competition for resources between the HUB and other food web compartments plays a crucial role in controlling the flows of biogenic carbon in the euphotic zone. We ran a numerical model to determine the potential effects of the 3 competition switches and found that the most important switch is MB, followed by PB and M<sub>μ</sub>. Comparison of our model results with field data indicated that the strong effects of HUB competition for resources with phytoplankton and mesozooplankton exist both in our model as well as in the world ocean. Finally, comparison of our model results with carbon flows estimated by the linear inverse approach showed that the competition switches can determine large changes in the flows of carbon in marine pelagic food webs. The focus of our study was the propagation of competition effects that occur at the core of the food web.

**KEY WORDS:** Planktonic food webs · Competition switches · Carbon flow · Microbial hub · Phytoplankton · Bacteria · Microzooplankton · Mesozooplankton

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## INTRODUCTION

In the aquatic sciences, 'microbe' has been used to mean a variety of single-celled organisms. In this paper, which focuses on pelagic microbes, we use the definitions of Legendre & Rivkin (2008), where the generic term 'microbe' includes all unicellular planktonic organisms and viruses, and combined *Archaea* and *Bacteria* under the functional category of 'heterotrophic bacteria' (BACT).

The understanding of the roles of heterotrophic microbes in the structure and functioning of pelagic

food webs, including the mediation of biogenic carbon fluxes into, within and out of the euphotic zone of the world ocean, has evolved considerably during the last decades. Empirical studies have progressively recognised the key roles of heterotrophic microbes, and this in turn has influenced the evolution of conceptual and numerical models that described, included and quantified the carbon fluxes that were mediated by food webs. This evolution has been described in some classic and recent review papers, e.g. Steele (1974), Sieburth et al. (1978), Ducklow (1983), Legendre & Rivkin (2008), Sherr & Sherr

(2008) and Sakka Hlaili et al. (2014). The concepts of microbial loop, food web nodes and microbial HUB (HUB, i.e. heterotrophic bacteria and microzooplankton, the latter being heterotrophic protists) were part of this evolution. Below, we briefly present key aspects of these concepts that led to the development of the proposed 'competition switches' hypothesised here. Although marine biogenic carbon includes marine organic matter, respiratory  $\text{CO}_2$  and  $\text{CaCO}_3$ , the present paper considers only the first 2 forms.

The general understanding of food web flows within the euphotic zone prior to the early 1970s was that carbon was transferred from large phytoplankton (PHYTO) to mesozooplankton (MZOO) and eventually to larger animals, including fish and marine mammals (called the 'traditional food chain' by Cushing 1989). In the early 1970s, the roles of marine autotrophic and heterotrophic microbes in water column production and respiration were largely ignored. The insights of researchers that include Hobbie et al. (1972), Vinogradov et al. (1972) and Pomeroy (1974) led to the emergence of the concept of the 'microbial loop' (Azam et al. 1983, Gray et al. 1984), which recognised heterotrophic microbes as being important in the flow of organic carbon toward larger organisms.

Legendre & Rivkin (2002) combined and integrated food web and biogeochemical approaches with the objective of identifying the roles of major food web compartments in controlling the main fluxes of biogenic carbon in the upper ocean. They identified 5 main fluxes, i.e. (1) photosynthetic fixation of carbon in organic matter, (2) respiration, (3) transfer to large organisms and (4,5) downward export of particulate and dissolved organic carbon (POC and DOC, respectively). They showed that the 5 fluxes were largely controlled by 3 food web nodes, i.e. PHYTO, heterotrophic planktonic microbes and large zooplankton. This was a change from the previous approaches that modelled food webs as conduits of carbon or energy toward larger organisms.

Further to the study of Legendre & Rivkin (2002), Legendre & Rivkin (2008) analysed the relationships between autotrophic microbes (i.e. PHYTO) and grouped their heterotrophic counterparts into 1 food web compartment (i.e. the HUB) and the larger organisms into the metazoan compartment (METAZ). The HUB consists of BACT and microzooplankton ( $\mu\text{ZOO}$ ), and the METAZ includes heterotrophic flagellates, ciliates and heterotrophic dinoflagellates. They showed that heterotrophic respiration ( $R$ ) is the only heterotrophic additive property of the ecosystem because unlike the other food web heterotrophic properties (e.g. heterotrophic community production,

carbon assimilation or carbon demand), heterotrophic community respiration ( $R_C$ ) cannot, during steady state or large spatial scales, exceed primary production ( $PP$ , net of autotrophic respiration). Because of the additive nature of  $R$ , the fraction of  $PP$  respired by a given heterotrophic compartment (i.e.  $R_x/PP$ ) or the fraction of total heterotrophic respiration accounted for by that compartment (i.e.  $R_x/R_C$ ) is an optimal metric for assessing trophic conditions or comparing food web compartments. In their study, Legendre & Rivkin (2008) developed an approach to compute the flows of respiratory carbon among PHYTO, HUB and METAZ.

In a subsequent review, Legendre & Rivkin (2009) examined the resources that are available to the food web (i.e. dissolved inorganic and organic matter and organic particles), which are external (i.e. from deep waters and continents) or internal (i.e. organic compounds produced by autotrophs and heterotrophs). They analysed the relationships among 3 food web properties: the sizes of the resource (i.e. dissolved matter and small and large organic particles), the sources of the resource that are internal to the food web and the use of resources by the HUB versus METAZ. The sources of internal resources include PHYTO, at the base of the food web, and METAZ, at the top of the food web, with the HUB occupying an intermediate position between PHYTO and METAZ. That unique position provides heterotrophic microbes in the HUB with access to resources from both the base and the top of the food web. As a result, the HUB uses almost all of the dissolved organic and part of the dissolved inorganic resources, it consumes a large fraction of the particulate resources and it monopolises (or dominates the use of) external and internal resources. In other words, the authors proposed that the HUB not only utilises most of the resources but also prevents METAZ from accessing them.

The microbes that make up the HUB are generally controlled by environmental and food web processes. On the one hand, BACT can respond to changes in the availability of limiting inorganic and organic nutrients such as labile DOC (Church 2008), especially the production of recently released photosynthate (i.e. labile DOC) by PHYTO (Nagata 2008), and can be concurrently controlled by the grazing pressure of  $\mu\text{ZOO}$  (reviewed by Strom 2000, Jürgens & Massana 2008 and references therein). On the other hand,  $\mu\text{ZOO}$  respond to changes in the availability of their food, PHYTO and BACT, (Goldman & Dennett 1990, Kimmance et al. 2006), and they are concurrently controlled by the grazing of MZOO (e.g. Sheldon et al. 1986, Wiadnyana & Rassoulzadegan 1989,

Burns & Schallenberg 2001, Gismervik 2006). This could result in a trophic cascade that would influence BACT by changing the grazing pressure of  $\mu$ ZOO (e.g. Rivkin et al. 1996, McCann et al. 1998, Pace et al. 1999, Wetz et al. 2011). Additional and indirect cascading effects of  $\mu$ ZOO and MZOO on BACT include changes in the supply of growth-regulating substrates, e.g. DOC or dissolved organic and inorganic nitrogen that are released by  $\mu$ ZOO and MZOO by excretion and sloppy feeding (Church 2008, Nagata 2008). Hence, the HUB would respond to changes in inorganic nutrient availability and PHYTO production and be controlled by the grazing pressure of MZOO.

An expanded view is that HUB microbes compete for resources with both PHYTO and MZOO. These competition effects would co-occur within the above processes. There are at least 3 potential competition mechanisms, which are described in the next paragraphs.

(1) Under conditions of limiting inorganic nutrient concentrations, BACT can effectively compete with phytoplankton for inorganic nutrients such as orthophosphate, ammonium and nitrate (Kirchman 1994, 2000, Rivkin & Anderson 1997, Fouilland et al. 2007, Church 2008, Løvdal et al. 2008 and references therein). The outcome of this competition can influence the carbon cycle both by BACT indirectly out-competing PHYTO for these nutrients (and hence reducing the rates of primary production) and by PHYTO indirectly limiting the growth of BACT and thus restricting the degradation of organic material (Joint et al. 2002, Havskum et al. 2003, Davidson et al. 2007, Grossart et al. 2007, Thingstad et al. 2008). Understanding how competition, predation and other trophic interactions structure the flows of C, N, P and other elements through the microbial food web and its coupling to other parts of the planktonic food web is central to our understanding of the role and functioning of the pelagic ecosystem. Competition between PHYTO and BACT potentially influences the species composition of the phytoplankton and bacterial communities and can alter the functioning of the marine food web and biogeochemical cycles by shifting the balance between PHYTO and BACT (Bratbak & Thingstad 1985, Caron et al. 2000, Mills et al. 2008, Peura et al. 2012).

(2) There is competition between BACT and MZOO for detrital POC (DETR), which can be consumed directly by MZOO or indirectly by BACT. There are 2 main processes by which BACT can acquire the organic carbon from DETR. One is the use by BACT of the DOC that is released from zooplankton faecal

pellets sinking through the water column (e.g. up to 50% release from diffusion of DOC from  $\mu$ ZOO and MZOO and faecal pellets; Strom et al. 1997, Urban-Rich 1999). The other is the assimilation of DOC by attached and free-living bacteria that is derived from the hydrolysis of particulate organic detritus by exoenzymes (Azam & Smith 1991, Smith et al. 1992, del Giorgio & Cole 1998, Unanue et al. 1998).

(3) There is competition between  $\mu$ ZOO and MZOO for large-sized PHYTO. This refers, for example, to the ingestion by dinoflagellates and some ciliates of phytoplankton cells that may be as large as (or larger than) themselves (e.g. reviews of Sherr & Sherr 1994, 2007).

Extending the conceptual developments of Legendre & Rivkin (2009) on the use of resources by HUB, the present paper explores the novel hypothesis that the competition for resources between the HUB and both PHYTO and METAZ plays a significant role in controlling the flows of biogenic carbon within the euphotic zone.

## MATERIALS AND METHODS

### Microbial competition switches

In testing our hypothesis, we used the food web model presented in Fig. 1, which is fully described in the Supplement at [www.int-res.com/articles/suppl/m521p019\\_supp.pdf](http://www.int-res.com/articles/suppl/m521p019_supp.pdf). Part of the organic carbon synthesised in the euphotic zone and transformed there by the pelagic food web is exported downward. Our model focuses on the fate of the organic carbon that is not exported from the euphotic zone, i.e. the  $PP_T$  (where  $PP_T$  is the sum of particulate and dissolved  $PP$ :  $PP_T = PP_P + PP_D$ ) that is respired within the euphotic zone (in the model,  $R_C = PP_T$ ). Hence, the model equations do not explicitly include carbon export terms. The specific objective of our study is to assess the competition for resources among the HUB, PHYTO and METAZ by comparing the food web carbon flows involved in such competition as normalised to the fraction of  $PP_T$  that circulates within the pelagic food web (i.e. not exported downward). Indeed, specifically including carbon exported from the euphotic zone in our model would not enhance our understanding of the competition between the HUB, PHYTO and METAZ. Of course, the outcome of the competition between the HUB, PHYTO and METAZ may affect the export of carbon from the euphotic zone, but this interesting aspect is beyond the topic of the present study.

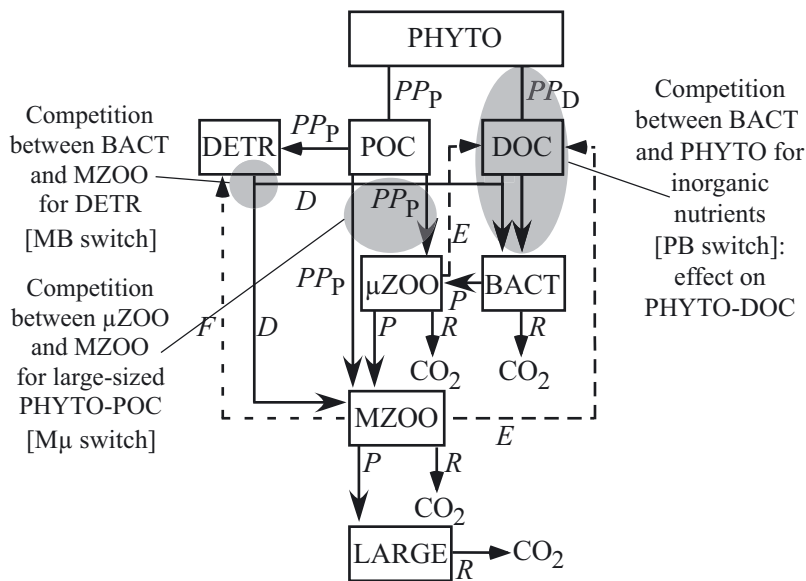


Fig. 1. Schematic representation of the food web model used to estimate the effects of HUB competition for resources in the euphotic zone (HUB = BACT +  $\mu$ ZOO). The 7 compartments of the model are (1) PHYTO-POC, the particulate organic carbon (POC) produced by phytoplankton (PHYTO); (2) dissolved organic carbon (DOC), from PHYTO and excreted by both microzooplankton ( $\mu$ ZOO) and mesozooplankton (MZOO); (3) heterotrophic bacteria (BACT), which use DOC and detrital POC (DETR); (4)  $\mu$ ZOO, which consume POC and BACT; (5) MZOO, which consume POC and DETR; (6) large animals (LARGE), which consume MZOO or food that is derived from MZOO; and (7) DETR, which comes from PHYTO and metazoans, mostly MZOO. This model is similar to that used by Legendre & Rivkin (2008) with 1 difference, i.e. the formation of phytodetritus from PHYTO-POC (in the present model, the flow from PHYTO to DETR). The arrows represent carbon flows into and out of compartments: primary production ( $PP$  particulate,  $PP_P$ ;  $PP$  dissolved,  $PP_D$ ) and heterotrophic detritus consumption ( $D$ ), excretion ( $E$ ), egestion ( $F$ ), production ( $P$ ) and respiration ( $R$ ). Solid arrows show forward flows; dashed arrows show backward flows. Shaded areas identify the locations of the 3 competition switches

The 'currency' of our model is carbon, and modelled flows are expressed as a fraction of  $R_C$ . In Fig. 1, the boxes represent food web compartments, and the arrows are flows of carbon into and out of the compartments (capital italic letters; symbols of heterotrophic flows are summarised in Table 1). The model includes 7 compartments, all of which are simplifications of complex *in situ* conditions: (1) PHYTO-POC is the particulate organic carbon produced by PHYTO (i.e.  $PP_P$ ); (2) DOC is released by phytoplankton (i.e.  $PP_D$ ) and is excreted by eukaryotic heterotrophs; (3) BACT use both DOC and DETR; (4)  $\mu$ ZOO consume both PHYTO and BACT; (5) MZOO, e.g. copepods, consume phytoplankton,  $\mu$ ZOO and DETR; (6) large heterotrophs (LARGE), e.g. large zooplankton and fish, consume MZOO or food that is derived from MZOO; and (7) DETR comes from particulate PHYTO (PHYTO-POC) and metazoans, mostly MZOO. In the model, all of the organic carbon that is not exported

from the euphotic zone is respired by heterotrophs (i.e. BACT,  $\mu$ ZOO, MZOO and LARGE). We assumed that the food web is in steady state (i.e. all of the production by one compartment is consumed by other compartments), and hence there is no net change in the biomass of any of the compartments. In the model, the fraction of  $PP_P$  channelled to  $\mu$ ZOO and MZOO is independent from the size structure of PHYTO and depends solely on the relative grazing activities of  $\mu$ ZOO and MZOO. Our model determines the partitioning of assimilated carbon between production and the sum of excretion and respiration by using temperature-dependent growth efficiencies for BACT,  $\mu$ ZOO and MZOO. The 2 model compartments MZOO and LARGE make up the overall metazoan compartment (METAZ).

Fig. 1 identifies 3 microbial 'competition switches'. We consider a competition switch in a food web to be analogous to a switch in a railroad network. In a food web, the competition switch controls the flow of carbon toward either the HUB or other food web compartments. In developing the competition-switch concept below, all competition-related food web rates are normalised to  $R_C = PP_T$ .

The literature from which the 3 competition switches were derived is summarised in the 'Introduction'. The first competition switch in Fig. 1 is between BACT and PHYTO (abbreviated PB), which compete for inorganic nutrients. Because the currency of our model is carbon, we needed to transform the competition for inorganic nutrients into an organic carbon flow. To do so, we used the observation that inorganic nutrient limitation often influences the exudation of DOC by phytoplankton (e.g. Obernosterer & Herndl 1995, Mykkestad 2000, Malej et al. 2003, Liu et al. 2012) and assumed here that an increase in the competition between BACT and PHYTO for inorganic nutrients will lead to an increase in the proportion of photosynthate being released as DOC (i.e. increased proportion of extracellular release,  $PER = PP_D/PP_T$ ). Another potential effect of the competition for inorganic nutrients could be a decrease in  $PP_T$ , but this would have no effect on the assessment of the outcome of the competition between BACT and

Table 1. Notations for variables, flows of organic carbon (parameter and modelled flows in *italics*) and subscripts used in the present study

Notation	Variable, model parameter, model flow
BACT	Heterotrophic bacteria
<i>D</i>	Detritus consumption in the euphotic zone
DETR	Detritus (POC)
DOC	Dissolved organic carbon
<i>E</i>	Excretion in the euphotic zone
<i>F</i>	Egestion in the euphotic zone
HFW	Herbivorous food web
HUB	Microbial hub, i.e. BACT + $\mu$ ZOO
L	Less (competition)
LARGE	Large heterotrophs
M	More (competition)
MB	MZOO-BACT competition switch
METAZ	Metazoan heterotrophs
MFW	Microbial food web
MZOO	Mesozooplankton
$M\mu$	MZOO- $\mu$ ZOO competition switch
PB	PHYTO-BACT competition switch
PER	Proportion of extracellular release
PHYTO	Phytoplankton
PHYTO-POC	Particulate organic carbon produced by PHYTO
POC	Particulate organic carbon
<i>PP</i>	Primary production <sup>a</sup>
<i>R</i>	Respiration in the euphotic zone
$\mu$ ZOO	Microzooplankton
Subscript	Meaning
b	Bacteria (heterotrophic)
hub	Microbial hub
lg	Large heterotrophs
mz	Mesozooplankton
met	Metazoa
$\mu$ z	Microzooplankton
x	Heterotrophic food web compartment
C	Heterotrophic community
D	Dissolved ( <i>PP</i> )
P	Particulate ( <i>PP</i> )
Pd	Phytodetritus from <i>PP<sub>p</sub></i>
PL $\mu$ Z	Large-sized <i>PP<sub>p</sub></i> consumed by $\mu$ ZOO
<i>PP<sub>PL</sub></i>	Large-sized <i>PP<sub>p</sub></i>
<i>PP<sub>PmZ</sub></i>	<i>PP<sub>p</sub></i> consumed by MZOO
Pnd	Non-detrital <i>PP<sub>p</sub></i>
P $\mu$ Z	<i>PP<sub>p</sub></i> consumed by $\mu$ ZOO
T	Total ( <i>PP</i> ) = D + P

<sup>a</sup>In our model, *PP* is primary production that is respired in the euphotic zone, i.e. not exported

PHYTO because all competition-related food web rates are normalised below in the text to  $PP_T$ .

The second competition switch in Fig. 1 is between BACT and MZOO (abbreviated MB), which compete for DETR. An increase in the competition between BACT and MZOO will lead to an increased use of DETR by BACT (i.e. increased  $D_b/D$ ).

The third competition switch in Fig. 1 is between  $\mu$ ZOO and MZOO (abbreviated  $M\mu$ ), which compete for large-sized particulate PHYTO production ( $PP_{PL}$ ). An increase in the competition between  $\mu$ ZOO and MZOO will lead to an increased fraction of  $PP_{PL}$  being ingested by  $\mu$ ZOO, i.e. increased  $PP_{PL\mu Z}/PP_{Pnd}$ , where  $PP_{Pnd}$  is the non-detrital  $PP_p$ , and  $PP_{PL\mu Z}$  is the fraction of  $PP_{Pnd}$  ingested by  $\mu$ ZOO.

When testing our hypothesis, we assumed that competition which leads to a loss from one group causes a gain in another group. We estimated the competitive losses (or gains) by the HUB and METAZ on the assumption that food web compartments can be compared on the basis of their respective contributions to  $R_C$  (see the 'Introduction'). The fraction of  $R_C$  accounted for by the HUB is the sum of respiration by bacteria and microzooplankton ( $R_{hub} = R_b + R_{\mu z}$ ), and the fraction accounted for by the METAZ is the sum of respiration by mesozooplankton and large heterotrophic  $R$  ( $R_{met} = R_{mz} + R_{lg}$ ). We considered that a decrease in the fraction of  $R_C$  accounted for by either the HUB or METAZ, i.e.  $R_{hub}/R_C$  or  $R_{met}/R_C$ , was a measure of competitive loss by this compartment and that an increase in the fraction of  $R_C$  is a measure of competitive gain. In other words,  $R_x/R_C$  reflected the fractional share of heterotrophic compartment  $x$  in the processing of biogenic carbon by the whole heterotrophic community. Although significant differences in gross growth efficiency (GGE) may compromise this assumption, both mean and median GGE appears to vary very little among protistan and metazoan heterotrophic compartments (Straile 1997) and in bacteria (del Giorgio & Cole 1998).

## Model runs

To test our hypothesis, we used the model structure shown in Fig. 1 to investigate 7 competition scenarios: 3 that examined single switches (i.e. PB, MB and  $M\mu$ ), 3 that examined paired switches (i.e. PB + MB, PB +  $M\mu$  and MB +  $M\mu$ ) and 1 that combined the 3 switches (i.e. PB + MB +  $M\mu$ ). Details on model structure and model runs are provided in the Supplement. The resulting outputs of the runs were the proportions of  $R_C$  accounted for by the HUB and METAZ compartments (i.e.  $R_{hub}/R_C$  and  $R_{met}/R_C$ ; it was stated above that in the model,  $R_C = PP_T = R_{hub} + R_{met}$ ). We computed  $R_{hub}/R_C$  and  $R_{met}/R_C$  for 3 temperatures (i.e. 5, 15 and 25°C) and 2 pelagic food web types (i.e. the microbial and herbivorous food webs, MFW and HFW, respectively). The food webs differed only in the fraction of particulate *PP* consumed by  $\mu$ ZOO (i.e.

$PP_{\mu Z}/PP_P$ ), and we used the same model parameters as in Legendre & Rivkin (2008), where  $PP_{\mu Z}/PP_P = 0.90$  and  $0.25$  for the MFW and HFW, respectively. Although Legendre & Rivkin (2008) did not include the production of phytodetritus from  $PP_P$  ( $PP_{Pd}$ , i.e.  $PP_{Pd}/PP_P = 0$ ), in the present study, we included the formation of phytodetritus and considered for the reference runs of the model that  $PP_{Pd}/PP_P = 0.2$ ; hence,  $PP_{\mu Z}/PP_P = (0.90 \times 0.8) = 0.72$  and  $(0.25 \times 0.8) = 0.20$  for MFW and HFW, respectively. We used these values and the parameter values of Legendre & Rivkin (2008) (third column of present Table 2) in our model to calculate the reference  $R_{hub}/R_C$  and  $R_{met}/R_C$  values.

For each of the 7 competition scenarios, we ran the model with the same parameter values as in Legendre & Rivkin (2008) except for PER,  $D_b/D$  and  $PP_{\mu Z}/PP_P$ , for which we used the parameter values reported in the last two columns of Table 2. In successive runs, we either decreased or increased by 50%, relative to their values in the reference runs, the values of these parameters for each switch or combination of switches.

## RESULTS AND DISCUSSION

### Effects of competition intensity in various scenarios

The main components of the HUB are bacteria and heterotrophic protists, and although the influence of PHYTO and MZOO on the HUB components is explicit in many studies, the feedbacks of HUB components on both PHYTO and MZOO are generally not considered. Within the framework of our hypothesis, we assess the possible effects of competition feedbacks between the HUB and both PHYTO and MZOO on food-web-mediated carbon fluxes.

Using our model, we computed  $R_{hub}/R_C$  and  $R_{met}/R_C$  first with the parameter values corresponding to the reference model (Table 2) and then for the parameters either increased or decreased by 50% for the 7 competition scenarios (Fig. 2). The model runs were repeated for MFW and HFW, with the values of the 3 temperature-dependent parameters calculated for 15°C. A decrease in the competitiveness of HUB (i.e. 50% less competition, L) decreased the  $R_{hub}/R_C$ ; conversely, an increase in the competitiveness of HUB (i.e. 50% more competition, M) increased the  $R_{hub}/R_C$ . For both MFW and HFW, the effect of competition was greatest when the 3 switches were included,  $PB + MB + M\mu$ , followed by scenarios that included 2 switches,  $(PB + MB) > (MB + M\mu) > (PB + M\mu)$ , and then single switches,  $MB > PB > M\mu$ . The general pattern of responses was the same for the MFW and HFW, although the  $R_{hub}/R_C$  was significantly greater (i.e. Wilcoxon signed rank test for paired samples) for the MFW than for the HFW for scenarios with both 50% less competition ( $Z = -2.388$ ,  $n = 14$ ,  $p = 0.017$ ) and 50% more competition ( $Z = -2.375$ ,  $n = 14$ ,  $p = 0.018$ ). The reported probabilities are only indicative because the different pairs of values (i.e. MFW and HFW) were not chosen randomly and independently. We repeated the model runs at 5 and 25°C, respectively, and found that the rank ordering of the competition scenarios were the same at 5, 15 and 25°C (not illustrated).

The effect on  $R_{hub}/R_C$  of decreasing or increasing by 50% the values of the competition switches (L and M, respectively) was different among the competition scenarios. This effect was quantified as the difference between the value of  $R_{hub}/R_C$  in each competition scenario and the value in the corresponding reference run and was expressed as a percentage, i.e.  $[(\text{Scenario} - \text{Reference})/\text{Reference}] \times 100$  (see Tables 3 & 4).

Table 2. Values of parameters used for the model runs to assess the effects of competition switches. For successive runs, competition was decreased and increased by 50% relative to parameter values in the reference model (see 'Materials and methods: Model runs' and columns 4, 5 and 2, respectively). For the reference model (column 3), the values of PER and  $D_b/D$  are from Legendre & Rivkin (2008), and the sources of the other values are explained in 'Model runs'. MFW and HFW refer to the microbial and herbivorous food webs, respectively. PHYTO-POC was partitioned among DETR ( $PP_{Pd}/PP_P = 0.20$ ),  $\mu ZOO$  ( $PP_{\mu Z}/PP_P$  in this table) and MZOO ( $PP_{mZ}/PP_P = 0.80 - PP_{\mu Z}/PP_P$ );  $PP_{\mu Z} + PP_{mZ} = PP_{Pnd}$  (nd: non-detrital).  $PP_{PL\mu Z}/PP_{Pnd}$  is the fraction of non-detrital PHYTO-POC consumed by  $\mu ZOO$  (e.g. dinoflagellates) as large-sized cells. See Table 1 for notation definitions

Competition switch	Corresponding parameter	Value in the reference model	Competition decreased by 50%	Competition increased by 50%
PB	PER	0.2	0.1	0.3
MB	$D_b/D$	0.6	0.3	0.9
$M\mu$	$PP_{PL\mu Z}/PP_{Pnd}$	0.20	0.10	0.30
$M\mu$ (MFW)	$PP_{\mu Z}/PP_P$	0.72	0.64	0.80
$M\mu$ (HFW)	$PP_{\mu Z}/PP_P$	0.20	0.12	0.28

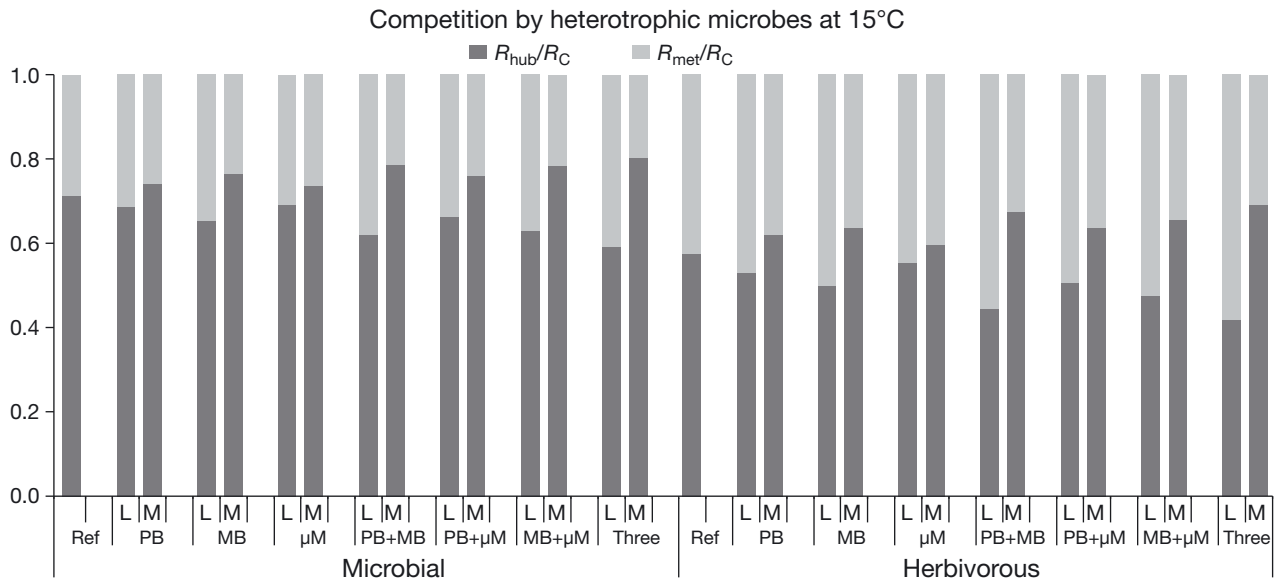


Fig. 2. Modelled  $R_{hub}/R_C$  and  $R_{met}/R_C$  for the reference run (Ref) and the 7 competition scenarios for 2 food webs (MFW and HFW) at 15°C. For the 2 food webs and 2 competition intensities (i.e. 50% less and more competition, L and M, respectively), the effect of competition (i.e. decrease of  $R_{hub}/R_C$  for L or increase for M) was highest for the scenario that involved the 3 switches, PB + MB +  $M\mu$ , followed by the scenarios that involved 2 switches, (PB + MB) > (MB +  $M\mu$ ) > (PB +  $M\mu$ ), and then by the scenarios with single switches, MB > PB >  $M\mu$ . The rankings of scenarios were the same at 5 and 25°C (not illustrated). See Table 1 for notation definitions

Table 3 (columns 2 to 5) shows the percent difference, relative to the reference run, in  $R_{hub}/R_C$  at 15°C for the 7 competition scenarios, the 2 pelagic food web types (MFW and HFW) and the 2 intensities of competition (L or M) between the HUB and other food web compartments. Table 3 (columns 6 and 7) also shows the corresponding values for alternate temperatures (i.e. 5 and 25°C) and for 50% more competition (M) for the HFW. Table 4 summarises the percent differences in the responses of  $R_{hub}/R_C$  for all modelled conditions, including those presented in Table 3.

At 15°C, the largest effects in the percent difference in the response of  $R_{hub}/R_C$  were with concur-

rent changes in the 3 competition switches (up to an absolute change of 27%), PB + MB +  $M\mu$ , followed by concurrent changes in 2 competition switches (up to an absolute value of 22%), rank-ordered PB + MB > MB +  $M\mu$  > PB +  $M\mu$ , and changes in single competition switches (up to an absolute change of 13%), rank-ordered MB > PB >  $M\mu$ . Changes in temperature (i.e. 5, 15 and 25°C) had only small effects on the percent differences in the modelled responses of  $R_{hub}/R_C$  (Table 3 columns 6 and 7 versus Table 3 columns 2 to 5).

The values presented in Fig. 2 and Tables 3 & 4 show that decreasing or increasing the values of model

Table 3. Percent difference of  $R_{hub}/R_C$  between each competition scenario and the corresponding reference run: [(Scenario – Reference)/Reference] × 100. Results are shown for the 2 modelled food webs (MFW and HFW) and competition intensities (L and M) at 15°C and for only 1 food web (HFW) and competition intensity (M) at 5 and 25°C. The  $R_{hub}/R_C$  values computed at 15°C are shown in Fig. 2. See Table 1 for notation definitions

Scenario	15°C MFW		15°C HFW		5°C HFW	25°C HFW
	50% less	50% more	50% less	50% more	50% more	50% more
PB	-4	4	-8	8	8	7
MB	-9	7	-13	11	12	10
$M\mu$	-3	3	-4	4	3	4
PB + MB	-13	10	-22	17	19	16
PB + $M\mu$	-7	6	-12	11	11	11
MB + $M\mu$	-12	10	-17	14	15	14
PB + MB + $M\mu$	-17	13	-27	20	22	19



Table 4. Effects of competition, expressed as the range of absolute percentage change of  $R_{\text{hub}}/R_C$  for all competition switch combinations; i.e. PB + MB + M $\mu$ ; PB + MB, MB + M $\mu$ , PB + M $\mu$ ; or PB, MB, M $\mu$ . The parameter values were either decreased or increased by 50% relative to parameter values in the reference model (see Table 2). Column 1 gives the rank ordering of the effects of competition on  $R_{\text{hub}}/R_C$ , and columns 2 to 4 provide the range of percent differences for  $R_{\text{hub}}/R_C$  in the competition scenario with the largest responses (positive and negative) and the corresponding reference run. The rankings in column 1 are the same at 5, 15 and 25°C. Taking the single competition switches as an example (last row of the table), the competition scenario with the largest responses (positive and negative) is MB, and the range at 15°C is 7 to 13 because the corresponding  $R_{\text{hub}}/R_C$  values for 15°C in Table 3 are -9 and 7 (MFW) and -13 and 11 (HFW). See Table 1 for notation definitions

Rank ordering of competition scenarios	Range of % changes for the highest ranked scenario		
	5°C	15°C	25°C
PB + MB + M $\mu$	15–28	13–27	11–26
PB + MB > MB + M $\mu$ > PB + M $\mu$	13–25	10–22	6–21
MB > PB > M $\mu$	9–15	7–13	6–12

parameters corresponding to HUB competition switches resulted in substantial changes in the partitioning of respiration flows between the HUB and METAZ. With the model configuration used here (Fig. 1), the most important switch was the competition between BACT and MZOO for detritus, followed by the competition between BACT and PHYTO for inorganic nutrients and between  $\mu$ ZOO and MZOO for large-sized PHYTO. The rank ordering of competition switches was independent of temperature (between 5 and 25°C), composition of the food web (i.e. MFW or HFW) or intensity of the competition (i.e. L or M). Because of the strong and consistent responses of respiration flows to changes in competition switches, we cannot reject our hypothesis that the competition for resources between the HUB and the other food web compartments plays a crucial role in controlling the flows of biogenic carbon in the euphotic zone.

The rank order of the 3 competition switches is competition between BACT and MZOO for detritus (MB) > BACT and PHYTO for inorganic nutrients (PB) >  $\mu$ ZOO and MZOO for large-sized PHYTO (M $\mu$ ). This suggests that MB may be important in determining the carbon flows in the ocean. Bacteria readily hydrolyze and use detrital carbon as a substrate for

growth (Van Wambeke et al. 2001, Sala & Güde 2004, Azam & Malfatti 2007). Moreover, the ingestion of detritus (i.e. non-living POC) has been experimentally determined for copepods (Roman 1984, Paffenhöfer & Van Sant 1985), and results from modelling studies have suggested that the ingestion of phytoplankton is significantly decreased when detritus is also present and ingested (Fasham 1993, Edwards 2001). The competition between BACT and MZOO for detritus has not been quantified experimentally, nor has this interaction been explicitly examined in predictive models (although see Miki 2012). Both BACT and MZOO have important roles in the mediation of vertical carbon fluxes within and below the euphotic zone of the world ocean (Steinberg et al. 2008, Giering et al. 2014). The competition between BACT and MZOO for detritus may control the proportion of the detritus that is remineralised to CO<sub>2</sub> (via BACT) and, thus, potentially returned to the atmosphere; versus detritus that is repackaged and transported to the deep ocean (via MZOO) and, thus, potentially sequestered. The results of our competition switch model provide an important insight into a heretofore poorly studied trophic relationship.

### HUB competition for resources in the world ocean

For each modelled temperature (5, 15 and 25°C), the lowest  $R_{\text{hub}}/R_C$  values corresponded to the model runs for the HFW with less competition (L), and the highest  $R_{\text{hub}}/R_C$  values corresponded to model runs for the MFW with more competition (M), with various combinations of food webs and competition intensities in between, including the reference run

Table 5. Values of  $R_{\text{hub}}/R_C$  from our model runs for the 7 competition scenarios and the reference run (Ref) at 5, 15 and 25°C and (last row) average values estimated for 3 zones of the world ocean by Legendre & Rivkin (2008, their Table 3). Values given in each cell of rows L and M (i.e. less and more competition, respectively) are based on 7  $R_{\text{hub}}/R_C$  values (i.e. 7 scenarios), and those in each cell of the intermediate row (L, M, or Ref) are based on 16 values, which gives a total of 30  $R_{\text{hub}}/R_C$  values for each temperature, i.e. (7 scenarios  $\times$  2 food webs  $\times$  2 competition intensities) + 2 reference runs (one for each of the 2 food webs). See Table 1 for notation definitions

Competition intensity	Food web	$R_{\text{hub}}/R_C$		
		5°C	15°C	25°C
L	HFW	<0.50	<0.56	<0.60
L, M, or Ref	HFW or MFW	0.49–0.62	0.57–0.72	0.61–0.80
M	MFW	$\geq$ 0.63	$\geq$ 0.73	$\geq$ 0.81
	World ocean	Polar (2°C)	Temperate (15°C)	Tropical (25°C)
		0.67	0.67	0.96

(Table 5). These results indicate that high  $R_{\text{hub}}/R_C$  values are associated with strong HUB competition for resources, whereas low  $R_{\text{hub}}/R_C$  values correspond to weak HUB competition and dominance of food web processes by herbivorous grazers.

The model we used as reference in the present study produced results that were consistent with values of  $R_{\text{hub}}/R_C$  that had been estimated from large field data sets for polar ( $>56^\circ$  S to  $>56^\circ$  N), temperate ( $22\text{--}55^\circ$  S to  $22\text{--}55^\circ$  N) and tropical ( $22^\circ$  S to  $22^\circ$  N) regions of the world ocean (data synthesis from Anderson & Ducklow 2001,  $R_{\text{hub}}/R_C$  from Legendre & Rivkin 2008). The  $R_{\text{hub}}/R_C$  values for these 3 regions were similar to or greater than the values we obtained for the 7 competition scenarios at 5, 15 and  $25^\circ\text{C}$  (Table 5), including the model values corresponding to strong HUB competition. This suggests that in these ocean regions, there is strong HUB competition for resources with PHYTO and MZOO.

Food web models where carbon flows among compartments have been estimated by the linear inverse approach (e.g. Vézina & Platt 1988) may provide insights for assessing the roles of our proposed competition switches in carbon flows in pelagic food webs. Based on such carbon flows at 32 stations of the world ocean, Sakka Hlaili et al. (2014) identified 4 types of planktonic food webs, i.e. herbivorous (diet of MZOO dominated by PHYTO), multivorous (diet of MZOO equally made up of PHYTO and  $\mu\text{ZOO}$ ), phytomicrobial ( $\mu\text{ZOO}$  mostly graze on PHYTO) and polymicrobial ( $\mu\text{ZOO}$  graze almost equally on all food resources), which are illustrated in Fig. 3 of Sakka Hlaili et al. (2014). Using published carbon flows representative of these 4 planktonic food web types (references in Table 6), we estimated the

potential effects of the 3 competition switches on carbon flows (calculations explained in the footnotes of Table 6). The resulting estimates of the strength of the 3 competition switches in Table 6 show that according to the planktonic food web type, the production of DOC was 7 to 52 % of phytoplankton gross production (PB switch), the fraction of organic detritus consumed by  $\mu\text{ZOO}$  relative to their consumption by  $\mu\text{ZOO} + \text{MZOO}$  was 0 to 58 % (MB switch) and the fraction of microphytoplankton ( $>20\ \mu\text{m}$ ) consumed by  $\mu\text{ZOO}$  was 57 to 92 % of that consumed by  $\mu\text{ZOO} + \text{MZOO}$  ( $\text{M}\mu$  switch). Hence, the switches that control the competition between the HUB (BACT and  $\mu\text{ZOO}$ ) and both PHYTO and MZOO can potentially cause large changes in the flows of carbon in marine pelagic food webs in the world ocean.

A potential application of our competition-switch approach is to examine the changes in the processing of carbon by marine pelagic ecosystems because of global climate change. Two predictions of global change models are warming of the surface ocean (Kirtman et al. 2013) and overall increase in the importance of the MFW, although with large differences among regions (Bopp et al. 2005). These predicted changes have already been reported in the North Atlantic (e.g. Beaugrand et al. 2010). Two predictions of our model are that  $R_{\text{hub}}/R_C$  will increase as the euphotic zone warms up and that  $R_{\text{hub}}/R_C$  could potentially be very high in areas dominated by the MFW, i.e. up to 0.88 in the case of high HUB competition (Table 7a). Even if the percent difference of  $R_{\text{hub}}/R_C$  between competition intensity (L or M) and the corresponding reference run is not temperature dependent (Tables 3 & 7b), the absolute values of  $R_{\text{hub}}/R_C$  increase by 1 to 2 % per degree Celsius (Table 7c). This

Table 6. Strength of the 3 competition switches for the 4 planktonic food web types identified by Sakka Hlaili et al. (2014) based on carbon flows estimated from field observations using the linear inverse approach. For each food web, Sakka Hlaili et al. (2014) identified a representative site where all carbon flows between trophic compartments had been determined. The strength of each competition switch reported in this table was calculated as defined in the footnotes using carbon flows provided in the relevant publications. The values in the last 3 columns of the table are ratios of carbon flows and thus dimensionless. See Table 1 for notation definitions

Planktonic food web	Representative station	Reference	Strength of each switch		
			PB <sup>a</sup>	MB <sup>b</sup>	M $\mu$ <sup>c</sup>
Herbivorous	Bizerte Lagoon (MJ, autumn)	Grami et al. (2008), Grami (2009)	0.1	–	0.6
Multivorous	Bay of Biscay (Biomet 3S)	Marquis et al. (2007)	0.2	0.0	0.9
Phytomicrobial	Equatorial Pacific (TS2, late October)	Richardson et al. (2004)	0.5	0.3	0.9
Polymicrobial	Arabian Sea (N7, NE monsoon)	Richardson et al. (2006)	0.3	0.6	0.8

<sup>a</sup>Strength of PB = (production of DOC by phytoplankton)/(gross primary production)  
<sup>b</sup>Strength of MB = (consumption of organic detritus by  $\mu\text{ZOO}$ )/(consumption of organic detritus by  $\mu\text{ZOO} + \text{MZOO}$ ); in the herbivorous food web, detritus is not consumed by  $\mu\text{ZOO}$  or MZOO  
<sup>c</sup>Strength of M $\mu$  = [consumption of microphytoplankton ( $>20\ \mu\text{m}$ ) by  $\mu\text{ZOO}$ ]/(consumption of microphytoplankton by  $\mu\text{ZOO} + \text{MZOO}$ )

means that the progressive increase in surface ocean temperature will potentially be accompanied by a proportional channelling of the biogenic carbon processed by the food web toward the HUB and enhanced competitiveness of the HUB for resources.

Based on models, comparative analyses and mesocosm studies (e.g. Vázquez-Domínguez et al. 2007, Wohlers et al. 2009, Sarmiento et al. 2010), a future ocean with higher temperature leads to increased activity of heterotrophic microbes and higher rates of respiration. Since an increase in ocean temperature also favours competition by the HUB, there could be in the future warmer ocean magnification of the HUB-mediated carbon flows toward remineralisation in the upper ocean, with CO<sub>2</sub> being ventilated back to the atmosphere.

The approaches to marine ecosystem modelling have evolved from simple representations of bottom-up driven food chains that linearly transferred carbon and energy toward large metazoans to more complex food webs in which microbes played important roles. Some models focussed on the bottom-up channelling of organic carbon by microbes toward larger organisms. Legendre & Rivkin (2008) proposed an approach to quantify the proportions of carbon originating from

several food web sources that are channelled into the HUB and METAZ, respired by the 2 compartments and redirected from there toward other food web compartments. In a further step, the approach described here characterised the potential competition for resources by the HUB with both PHYTO and METAZ. Unlike several usual bottom-up and top-down modelling approaches that are centred on the propagation of effects that take place at the bottom or at the top of the food web (e.g. Cury & Shannon 2004), we focused here on the propagation of competition effects that occur at the core of the food web, and we showed that the HUB competition likely dominates carbon flows within pelagic food webs both in our models as well as in the world ocean.

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Table 7. Three estimates of the effect of temperature (5, 15 and 25°C) on  $R_{\text{hub}}/R_{\text{C}}$  for the combined 3-competition-switch scenario (i.e. PB + MB + M $\mu$ ) and the 2 modelled food webs (MFW and HFW) and competition intensities (L and M). (a) Modelled  $R_{\text{hub}}/R_{\text{C}}$ , as in Fig. 2, where the values at 15°C are also presented. (b) Percent difference of  $R_{\text{hub}}/R_{\text{C}}$  between competition intensity (L or M) and the corresponding reference run, as in Table 3, where the values for all scenarios at 15°C and selected values at 5 and 15°C are provided. (c) Percent increase in  $R_{\text{hub}}/R_{\text{C}}$  corresponding to an increase of 10°C:  $\{[(R_{\text{hub}}/R_{\text{C}})_{(T+10^\circ\text{C})} - (R_{\text{hub}}/R_{\text{C}})_T] / [(R_{\text{hub}}/R_{\text{C}})_T]\} \times 100$ . See Table 1 for notation definitions

	MFW			HFW		
	5°C	15°C	25°C	5°C	15°C	25°C
(a) $R_{\text{hub}}/R_{\text{C}}$						
Reference	0.62	0.71	0.80	0.51	0.57	0.62
L	0.50	0.59	0.68	0.37	0.42	0.46
M	0.71	0.80	0.88	0.63	0.69	0.74
(b) $\{[(\text{Competition intensity} - \text{Reference}) / \text{Reference}]\} \times 100$						
L	-20	-17	-15	-28	-27	-26
M	15	13	11	22	20	19
(c) $\{[(R_{\text{hub}}/R_{\text{C}})_{(T+10^\circ\text{C})} - (R_{\text{hub}}/R_{\text{C}})_T] / [(R_{\text{hub}}/R_{\text{C}})_T]\} \times 100$						
Reference		16 <sup>a</sup>	12 <sup>b</sup>		11 <sup>a</sup>	8 <sup>b</sup>
L		20 <sup>a</sup>	13 <sup>b</sup>		14 <sup>a</sup>	9 <sup>b</sup>
M		13 <sup>a</sup>	10 <sup>b</sup>		9 <sup>a</sup>	7 <sup>b</sup>
<sup>a</sup> Increase from 5 to 15°C						
<sup>b</sup> Increase from 15 to 25°C						

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