CHAPTER 4

Do *Phaeocystis* colony blooms affect zooplankton in the Belgian Coastal Zone?

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4.1 Introduction

The ability of herbivorous zooplankton to control phytoplankton blooms, and to efficiently transfer primary production towards higher trophic levels such as invertebrates, fish larvae and planktivorous fish, is considered as a sign of equilibrium in marine ecosystems. This is not the case in the Southern Bight of the North Sea where massive *Phaeocystis* colony spring blooms sustained by anthropogenic nitrates, are suggested to be the consequence of a high resistance to losses, in particular grazing (Lancelot *et al.*, 1994; 2002).

To which extent *Phaeocystis* colony blooms are negatively impacting zooplankton dynamic is investigated in this chapter, based on available information on zooplankton in the Belgian coastal zone (BCZ).

4.2 Seasonal distribution of zooplankton in the BCZ

Major zooplankton groups in the BCZ were defined based on their trophic position. They include microzooplankton, herbivorous copepods and gelatinous zooplankton such as *Noctiluca scintillans*. Figure 4.1b compares their seasonal occurrence with respect to phytoplankton, *i.e. Phaeocystis* colonies and diatoms (Fig. 4.1a). Small neritic copepods represent the dominant metazoan plankton from May to September. Moderate in early spring when diatoms prevail on *Phaeocystis* colonies, copepods become abundant after the *Phaeocystis* bloom showing two distinct peaks of biomass in spring-summer (Fig. 4.1b). The summer biomass minimum is also observed for diatoms which are dominated at that time by large species such as *Guinardia delicatula*, *G. striata*, and *Rhizosolenia shrubsolei.* Both diatom and copepod summer minima are concomitant with a massive development of *N. scintillans* which starts blooming at the decline of *Phaeocystis* colonies (Fig. 4.1). Microzooplankton is particularly abundant from April to May (Fig. 4.1b). Beside these three zooplankton groups, reports exist on the occurrence of the tunicate *Oikopleura dioica* and meroplanktonic larvae (Cirripedia, Polychaetes, Bryozoa) but their biomass is not significant on a yearly basis (not shown). Predators such as cladocerans and Chaetognatha (*Sagitta elegans*) have also been observed in summer.

Based on the seasonal distribution of copepods, *N. scintillans* and microzooplankton with respect to *Phaeocystis*, a focus is given in the next sections on their respective feeding behaviour and trophic significance.

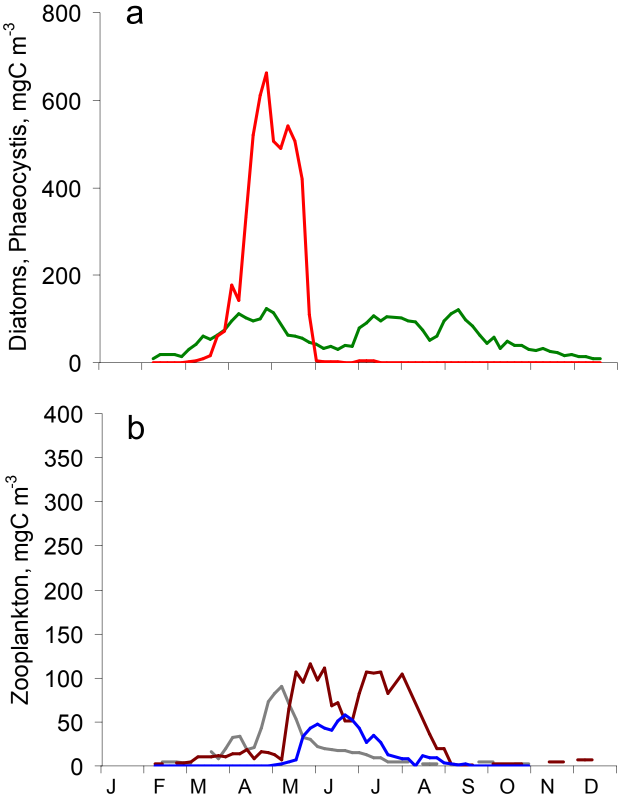

Figure 4.1. Seasonal distribution of phytoplankton (a): *Phaeocystis* colonies (red) and diatoms (green) and dominant zooplankton groups (b): microprotozooplankton (grey), copepods (brown) and *Noctiluca scintillans* (blue) at station 330 (N 51°26.0; E 2°48.5) in the central BCZ. All phyto- and zoo-plankton data available for the period 1988-2004 were 5-days averaged.

4.3 Copepods

Temora longicornis, Pseudocalanus elongatus, Centropages hamatus and Acartia clausii are the main species reported in the BCZ. *T. longicornis* is however much more dominant during spring, representing in average for the period 1988-2004 some 62% of the total copepod biomass. This small-sized copepod produces several generations during spring explaining the co-occurrence of different developmental stages (nauplii, copepodites I-V and adults), all of them susceptible to be affected by *Phaeocystis* colony blooms. The other copepod species, *i.e. Centropages*, *Pseudocalanus* and *Acartia,* are dominant later in the year (Daro, 1985; Antajan, unpublished data).

4.3.1 Diet and feeding activities of *T. longicornis*

Measurements of feeding activities of the major copepod species present during springtime in BCZ were investigated by combining several methods under shipboard and laboratory-controlled conditions. These methods, *i.e.* HPLC pigment analysis of gut content, $^{14}CO_3$ - prelabeling of phytoplankton given as a food source to copepods and the cell count method estimating clearance rates of different prey, are described in details in Gasparini *et al.* (2000) and Antajan (2004).

All together, in situ grazing experiments conclude that the late winter-early spring diatom community, dominated by small chain-forming *Thalassiosira* spp. and *Chaetoceros* spp. are efficiently grazed by copepods with mean daily ingestion rates of 1.6 µg C ind^{-1} d^{-1} (Gasparini *et al.*, 2000; Antajan, 2004). During *Phaeocystis* colony blooms, herbivorous feeding of copepod declines, being one order of magnitude lower (in average 0.26 µg C ind^{-1} d^{-1}) than during the late winter-early spring period due to the lack or insignificant grazing on *Phaeocystis* colonies (Daro, 1985; Hansen & van Boekel, 1991; Weisse *et al.*, 1994; Breton *et al.*, 1999). They also show that the large diatoms such as *Guinardia delicatula, G. striata and R. shrubsolei* prevailing during late spring and summer, were ingested at a much lower rates than during early spring (Gasparini *et al.*, 2000; Antajan, 2004). To sustain their food requirements during *Phaeocystis* blooms, copepods feed preferentially on microzooplankton, which can represent up to 50-96% of their diet at that time (Gasparini *et al.*, 2000). These studies conclude however, that daily ingestion rates on microzooplankton would not be sufficient to sustain copepod growth, amounting for only 7-21% of the adult copepod carbon weight during and after the *Phaeocystis* bloom (Gasparini *et al.*, 2000). As that time, phytodetritus can be another possible food source for copepods but this was not quantified.

The preferential grazing of *T. longicornis* on microzooplankton over large diatoms and *Phaeocystis* colonies was demonstrated by Antajan (2004) based on the Electivity index E* method (Vanderploeg & Scavia, 1979). As shown in Figure 4.2, *T. longicornis* positively selects dinoflagellates and ciliates of different sizes but responds negatively to *Phaeocystis*, nanoflagellates and large diatoms. The positive selection of microzooplankton by *T. longicornis* (Fig. 4.2) has been related to their size but also to their nutritional quality due to their low carbon to nitrogen ratio compared to algae, making them a better source of proteins and amino acids (Stoecker & Capuzzo, 1990; Hitchcock, 1982).

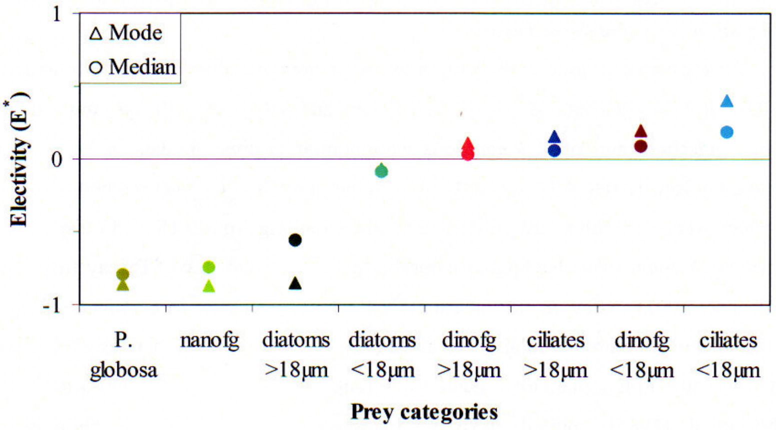

Figure 4.2. Mode and median of electivity index E* for the different prey items of *T. longicornis* calculated on basis of cell count incubations performed in the BCZ from 1999 to 2001. Redrawn from Antajan (2004).

The active predation of copepods on microzooplankton represents an important trophic pathway linking the microbial food web to the classical food chain (from diatoms to copepods). However this link could also be the basis of a trophic cascade where copepod grazing on microzooplankton could stimulate *Phaeocystis* colony blooms by releasing grazing pressure of *Phaeocystis* cells which are at the origin of colony formation (Fransz *et al.*, 1992).

The negative effect of *Phaeocystis* colonies on the feeding of the different developmental stages of *T. longicornis* was investigated, based on the measurement of day-night ingestion rates as a function of phytoplankton availability at three stages of the phytoplankton spring bloom, (in early spring when small colonial diatoms prevail, during the growing (small colonies) and stationary (large colonies) phases of *Phaeocystis* bloom; Fig. 4.3). Clearly, ingestion rates are 5 to 6 times higher during the early spring diatom bloom for all developmental stages. Feeding rates are significantly lower during the *Phaeocystis* bloom and no difference was observed for the small and large colonies.

The lack of grazing of *Phaeocystis* colonies by small copepods has been related to a prey-predator size mismatch (Weisse *et al.*, 1994), chemical deterrence by repulsive substances (Bautista *et al.*, 1992), feeding inhibition due to *Phaeocystis*-derived exopolymers (Dutz *et al.*, 2005) and/or growth stages of colonies (Long & Hay, 2006). The poor nutritional value of *Phaeocystis* colonies has also been incriminated (Claustre *et al.*, 1990; Tang *et al.*, 2001).

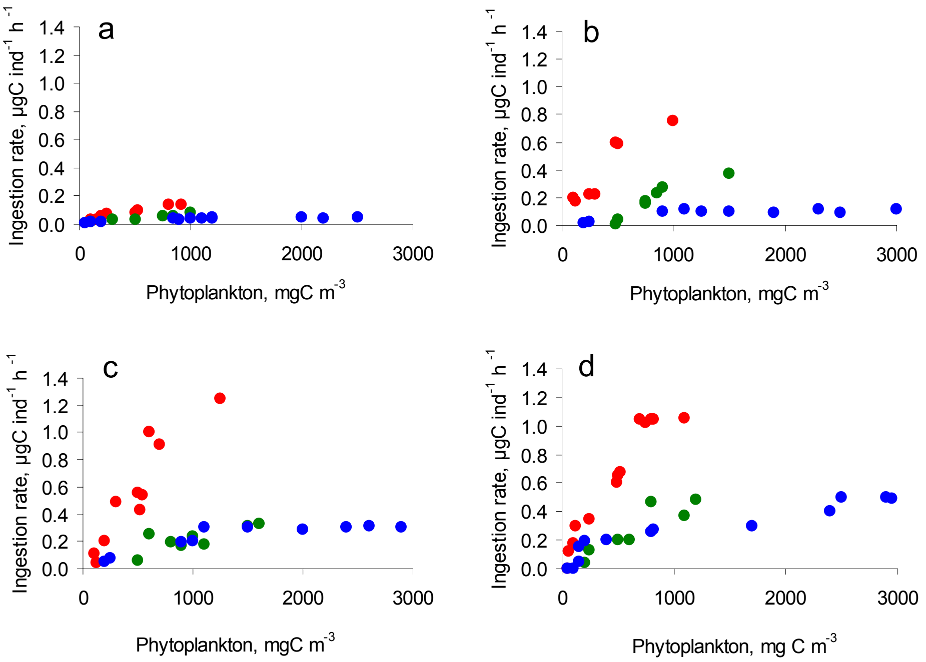

Figure 4.3. Day-night averaged ingestion rates of *T. longicornis* copepodites I & II (a); III & IV (b); V (c) and adults (d) at three different periods of the spring bloom, *i.e.* in March during the early spring diatoms (red); in mid April during the exponential (green) and in early May during the stationary (blue) growing phases of *Phaeocystis* colony bloom in the BCZ. Ingestion rates were calculated according to Daro & Baars (1986).

4.3.2 Effect of *Phaeocystis* colony bloom on *T. longicornis* reproduction

Grazing experiments suggest that adult copepods are in food shortage during *Phaeocystis* blooms (section 4.3.1), which could impact negatively egg production and therefore the next copepod generation (*e.g.* Peterson & Dam, 1996). Egg production and herbivorous feeding by freshly caught *T. longicornis* females were measured along a seasonal cycle in 2001 at 3 stations in the BCZ (Fig. 4.4; Antajan, 2004).

Clearly egg production at the time of *Phaeocystis* bloom (7-20 eggs female^{-1} d^{-1}; Fig. 4.4a) is far below the maximal rate of egg production reported for this copepod (40-65 eggs female^{-1} d^{-1}; Peterson & Dam, 1996). Such optimal values are however observed in end-March during the early-spring diatom bloom (30-60 eggs female^{-1} d^{-1}; Fig.4.4a). The contribution of herbivorous feeding to *T. longicornis* egg production (Fig. 4.4b) is very low in late spring, suggesting that ingestion of phytoplankton during *Phaeocystis* bloom is not sufficient to cover the needs for *T. longicornis* egg production (Antajan, 2004).

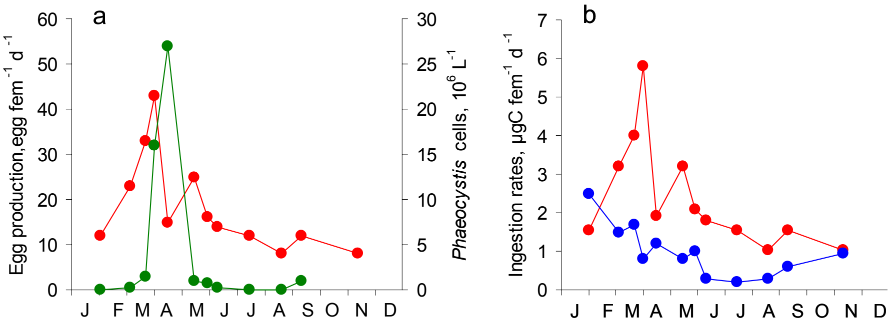

Figure 4.4. Seasonal evolution in 2001 of copepod eggs production (red) and *Phaeocystis* colonies (green) (a) and copepod ingestion rates estimated from egg production (red) and gut content (blue) (b). Redrawn from Antajan (2004).

The impact of *Phaeocystis* bloom development on *T. longicoris* reproduction was assessed by comparing the ingestion (Fig. 4.5a) and egg production (Fig. 4.5b) rates of three successive generations hatching respectively on 1st, 25 April and 25 May, i.e. at three distinct periods of the spring bloom. Daily ingestion rates were calculated considering the prevailing phytoplankton taxa (diatoms, *Phaeocystis*), size and concentrations and the copepod stages using the feeding functions represented on Figure 4.3. These results show that only the first generation of *T. longicornis* feeds properly, and produces eggs at a high rate. The second generation grazes properly up to the age of 15 days (dominance of young copepodites) when individual ingestion rates decrease up to the adult stage, lowering egg production rates. The third generation suffers much more from the very young stages with a strong impact on egg production which stops after 12 days. In the field, the production of dormant eggs by the first spring generations could well explain the summer occurrence of *T. longicornis*. The impact of *Phaeocystis* colony blooms on the other copepod species such as *Pseudocalanus* prevailing about one month later than *Temora* is less significant (Daro, 1985).

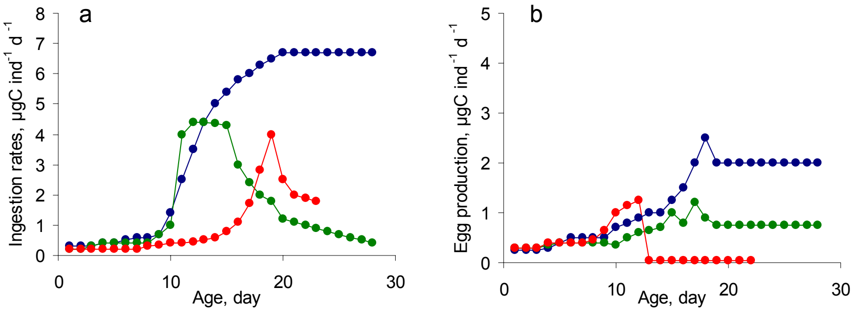

Figure 4.5. Daily ingestion (a) and egg production (b) rates of *T. longicornis* as a function of their age for 3 successive generations hatching on 1st April (blue), 25 April (green) and 25 May (red), at three stages of the phytoplankton spring bloom.

4.4 *Noctiluca scintillans*

The other main zooplankton playing a key trophic role in BCZ is the intriguing *N. scintillans*. This large-sized (in average 600 µm) heterotrophic red tide dinoflagellate is considered as ichtyotoxic due to the release of high concentrations of ammonium as catabolic by-product. Being largely un-preyed, *N. scintillans* is, like other gelatinous organisms, considered as dead end in food web. *N. scintillans* biomass culminates in June-July (Fig. 4.1b) but the maximum cell density reached varies significantly from year to year, being as high as 16 000 cells m^{-3}; Breton, unpublished data).
The diet of *N. scintillans as* determined on basis of vacuole content analysis, consists in diatoms, *Phaeocystis* aggregates, copepod eggs and moults, faecal pellets and various protists (dinoflagellates, ciliates and suctorians). The feeding strategy of *N. scintillans* is qualified as generalist based on the analysis of Costello (1990). This methodology compares the prey relative abundance (%A) and frequency of occurrence (%F) in the diet (Fig. 4.6). In this analysis, equivalence between %A and %F indicates a generalist feeding behaviour with the most important prey characterized by high %A and %F (Fig. 4.6). On the contrary, prey ingested at low occurrence but high abundance indicates a specialized feeding behaviour of the predator.

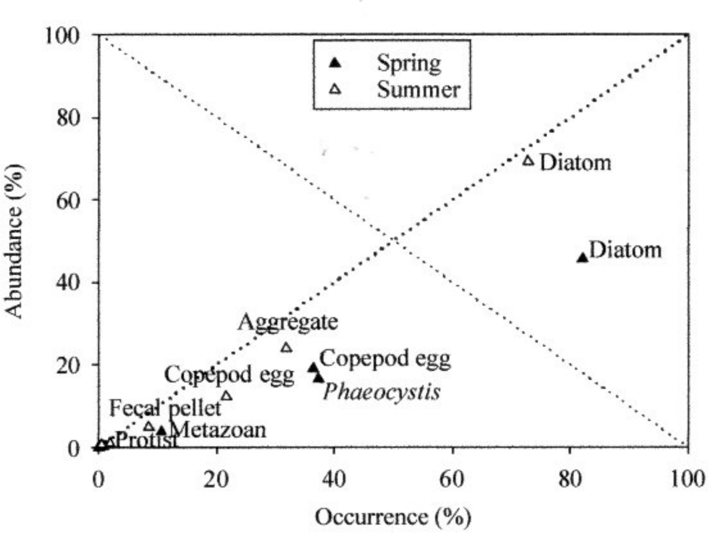

Figure 4.6. Feeding strategy of *N. scintillans* in the BCZ based on the Costello (1990) analysis which relates prey relative abundance (A in %) and its frequency of occurrence (F in %).

Both in spring and summer, large diatoms such as *Guinardia delicatula*, *G. striata* and *Rhizosolenia shrubsolei* are by far the most important food item found in *N. scintillans* vacuoles (Fig. 4.6). Copepod eggs and aggregates represent a significant part of the *N. scintillans* diet in spring and summer while fecal pellets and protists are only minor components. Such a diet composed of a high variety of large items and few small-sized organisms was already observed in other areas (Enomoto, 1956; Prasad, 1958; Kimor, 1979). A predator - prey size ratio of 5:1 together with a linear functional feeding response to food concentration indicates that *N. scintillans* is characterized by a voracious feeding behaviour (Breton, unpublished data).

The preferential grazing of *N. scintillans* on large-sized prey is well illustrated on Figure 4.7 which indicates that the occurrence of prey in the *N. scintillans* diet corresponds to an unimodal function of the prey biovolume in both spring and summer. In spring the optimal volume corresponds to that of copepod eggs. By contrast, *Phaeocystis* healthy colonies or free-living cells are respectively at the lower and upper limits of the size range suggesting a trophic size mismatch (Fig. 4.7). During the bloom, size of un-preyed *Phaeocystis* colonies is indeed 5 times larger than those observed in *N. scintillans* food vacuoles. By contrast, the aggregates found in *N. scintillans* vacuoles at the end of the bloom have a smaller size and can represent suitable prey. These observations suggest that trophic interaction between *Phaeocystis* colonies and *N. scintillans* might be significant during the collapse of the bloom. In summer, the optimum biovolume is corresponding to that of the diatom *G. delicatula* (Fig. 4.7).

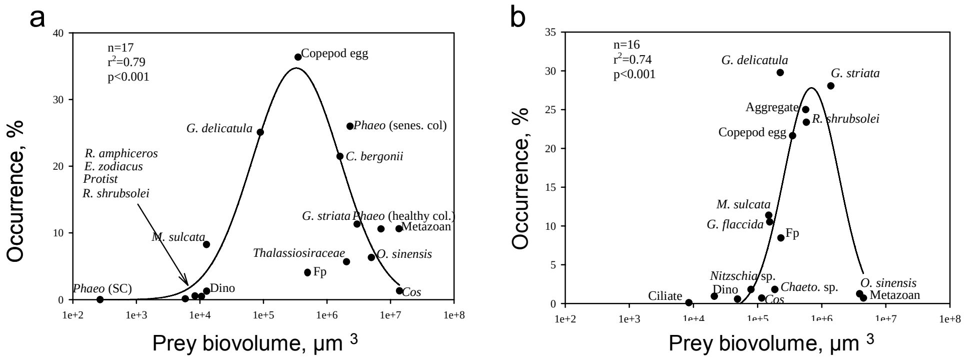

Figure 4.7. Gaussian relationship between the biovolume of prey and their occurrence (in %) in the diet of *N. scintillans* during spring (a) and summer (b).

N. scintillans ingestion rates, estimated from vacuole content during shipboard digestion experiments, are in average of 0.27 µg C cell^{-1} d^{-1} in spring and 0.14 µg C cell^{-1} d^{-1} in summer, corresponding to 118% and 59% of *N. scintillans* body carbon weight, respectively. From this, daily grazing pressure by the *N. scintillans* population can be calculated and expressed as the part (in %) of diatom, *Phaeocystis* and copepod eggs standing stocks. In spring, *N. scintillans* daily grazing pressure on *Phaeocystis* was estimated to 0.06, 2 and 60% per day for colonies, aggregates and small sized (< 300 µm) aggregates respectively. Daily grazing pressure on spring diatoms and copepod eggs amounts for 3% and 52% respectively. In summer, *N. scintillans* were shown to graze some 15% and 31% of large diatoms and copepod eggs respectively. This indicates that *N. scintillans* has probably a minor role in controlling *Phaeocystis* colony blooms. On the contrary, our estimations suggest that *N. scintillans* has a strong impact on the large late spring and summer diatoms and copepod eggs.

4.5 Microzooplankton

Microzooplankton is a functional group which is not taxonomically homogeneous. This group is largely dominated by microprotozooplankton composed of heterotrophic protists such as dinoflagellates and ciliates but also includes young metazoan stages such as nauplii, copepodites I - II and pluteus larvae. Microzooplankton diet is composed of both nanophyto- (autotrophic flagellates) and nanoprotozoo- plankton (bacterivorous nanoflagellates). In the BCZ, microzooplankton is particularly abundant from the end of winter to April-May at the time of *Phaeocystis* blooms (Fig.4.1). At that time, it actively grazes on nanoplanktonic *Phaeocystis* free-living cells (Weisse & Scheffel-Möser, 1990) and heterotrophic nanoflagellates (Rousseau *et al.*, 2000). These latter feed on bacteria which degrade the dissolved organic matter supplied by *Phaeocystis* cell lysis and matrix dissolution (Rousseau *et al.*, 2000). Microzooplankton constitutes an alternative food item for copepods during *Phaeocystis* colony blooms, when copepod herbivorous feeding declines (section 4.3.1). Because it feeds on nanoplankton but is grazed by mesozooplankton, microzooplankton occupies a key trophic position in the BCZ ecosystem transferring part of the un-preyed *Phaeocystis* production (free-living cells and dissolved organic matter available to bacteria) to higher trophic levels (mesozooplankton).

4.6 Trophic efficiency of the *Phaeocystis*-dominated planktonic food-web in the BCZ

As shown in previous sections, phytoplankton groups that succeed along the spring bloom in the BCZ are feeding different zooplankton groups with different trophic efficiency, *i.e.* the ratio between zooplankton grazing and phytoplankton production). Early spring diatoms feed copepods, late spring-summer large diatoms are ingested by *N. scintillans* and *Phaeocystis* colonies resist grazing by both zooplankton groups. During *Phaeocystis* decline however, ungrazed colonies are releasing in the ambient dissolved organic matter available to bacteria and colony cells which are grazed by microzooplankton.

The carbon budget and trophic efficiency of the *Phaeocystis*-related food web was calculated, based on field measurements (Rousseau *et al.*, 2000) and model simulation (Lancelot *et al.*, 2005) of carbon biomass and activities associated to the different plankton groups. Both conclude that *Phaeocystis* colonies represent 70-75% of the spring phytoplankton biomass production. The produced biomass escapes grazing by copepods but feeds the microbial network formed of microzooplankton and bacteria throughout the release of *Phaeocystis* cells and organic matter. The trophic efficiency of this pathway is estimated to 1.5%. One third of the diatom production fuels directly the mesozooplankton corresponding to a trophic efficiency of 34%. However, this figure is lowered to 5.6% if the total available phytoplankton production is considered.

Altogether these estimations conclude that most of the *Phaeocystis*-derived production is remineralised in the water column.

4.7 Conclusions

Anthropogenic loads of nutrients to the BCZ have stimulated the phytoplankton production without enhancing the overall yield of biological resources. In this area the unbalanced nutrient sources, over-enriched in nitrates with respect to phosphate and silicic acid have stimulate the development of *Phaeocystis* colonies resistant to grazing. As a consequence, the trophic interactions in the eutrophied BCZ show a prevalence of the remineralisation processes over the transfer of matter and energy towards higher trophic levels. This contrasts with the less eutrophied Northern and Central North Sea, where the phytoplankton development is submitted to a top-down control by copepods (Daro, 1980). Using qualitative structural network analysis of a generic food web, Vasas *et al.* (2007) demonstrate that HAB-forming species (as *Phaeocystis* colonies) and *N. scintillans* blooms are resulting from anthropogenic nutrient enrichment. These undesirable species reduce the abundance of the principal bottom-up controllers with far-reaching effects throughout the food-web. Stimulating the microbial network but inhibiting the higher trophic levels seems to be intrinsic properties of temperate pelagic ecosytems strongly affected by human activities. This effect is exacerbated by overfishing (Vasas *et al.*, 2007).

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