Life cycles of HAB forming haptophytes

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The algal division Haptophyta is composed of nanoplanktonic cells characterized, at least in some stages, by two flagella and a third filiform organelle, the haptonema. Coccoid, colonial, amoeboid or filamentous stages are also observed in haptophytes (Edvardsen *et al.* 2000a). Haptophytes are widespread and may compose a significant part of the nanophytoplanktonic community. The taxonomy of the Haptophyta is based on morphometric details of cell scale coverage, flagella, haptonema and/or thread-like material (Jordan & Green 1994). This algal division and more particularly, the class Prymnesiophyceae Hibberd, includes some well known HAB forming species, either ichthyotoxic such as *Chrysochromulina* spp., *Prymnesium* spp. or high-biomass forming species such as members of the genus *Phaeocystis*. The latter includes six species: *P. globosa, P. pouchetii, P. antarctica, P. scrobiculata, P. cordata* and *P. jahnii* (Zingone *et al.* 1999), but colony forms were only reported for *P. globosa, P. pouchetii, P. antarctica* and *P. jahnii*. Haptophytes also include coccolithophorids that are generally not considered as HAB species but are seen as important species for climate regulation (e.g. *Emiliana huxleyi*). Some non-blooming coccolithophorid species (e.g. within the genera *Pleurochrysis* and *Ochrosphaera*) are suspected to be capable of producing toxins (Probert, unpublished results).

Occurrence of these haptophytes has caused serious damage to the environment. In May-June 1988, a bloom of *C. polylepis* caused the death of 900 tons of farmed fish (salmon, trout) in the Kattegat and Skagerrak area of the North Atlantic, as well as lethal effects on populations of invertebrates, macroalgae, zooplankton and bacteria due to haemolytic compounds (Rosenberg *et al.* 1988; Gjøsæter *et al.* 2000). In 1991, *C. leadbeateri* killed 600 tons of farmed salmonids in Lofoten, northern Norway (Johnsen *et al.* 1999). Toxic blooms of *P. parvum* have frequently been reported from coastal waters and brackish lakes and pounds worldwide and are often associated with fish mortalities due to haemolytic toxins, the prymnesins, acting on the permeability of biological membranes (Edvardsen & Paasche 1998). *Phaeocystis* blooms of mucilaginous colonies recur in the Barents Sea, Norwegian fjords, the Southern Ocean and the continental coastal waters of the North Sea (Lancelot *et al.* 1998). The most visible harmful effect related to these blooms, mainly those of *P. globosa* in the Southern Bight of the North Sea, is the deposition of thick layers of odorous foam on the beaches, thus affecting tourism and recreational activities. *Phaeocystis* colony blooms were also reported as responsible for clogging fishing nets, repulsing fish, and possibly for having negative impacts on benthic life. The species *P. pouchetii* was also shown to be responsible for toxin production that affected cod larvae development (Aanesen *et al.* 1998).

Current knowledge of the life cycle of haptophytes

Despite the significance of these haptophyte species, the life cycle of most species is still not completely elucidated. This is partly due to the taxonomic confusion and uncertainties about the identity of species or strains, as well as to difficulties with species identification, which requires electron microscopy. The recent implementation of new techniques, such as nucleotide sequencing and flow cytometry used for the genetic characterization and ploidy level determination, respectively, has nevertheless allowed serious progress in this field. For example, *P. parvum* and *P. patelliferum* were considered distinct species on the basis of taxonomic criteria (the organic scale morphology) until the recent demonstration that these were two stages of the same life history (Larsen & Edvardsen 1998). Investigations of life cycles also suffer from the inability to reproduce complete life cycles under laboratory conditions and to culture some stages (e.g. the microflagellates of *P. globosa*). On the other hand, interpretation of field observations is sometimes difficult due to the presence of different species or several types of cells, and ignorance of the overwintering and seeding forms.

Alternation of different morphological stages (e.g. free-living cells, colonies, amoebae, presence of various scale coverings) and motility capability seem to be characteristic of the life cycle of haptophytes (Hibberd 1980; Billard 1994). Both *C. polylepis* and *P. parvum* exist as two types of flagellates characterized by different organic scales and one non-motile cell stage (amoeboid, cyst) in culture (Edvardsen this issue). Coccolithophorids also alternate between holococcolithophorids and heterococcolithophorids (Thomsen *et al.* 1991) or coccolithophorids and scale-bearing cells (Billard 1994; Green *et al.* 1996). Some *Phaeocystis* species exhibit an alternation between several types of free-living cells (motile and non-motile of various size) and gelatinous colonies (Rousseau *et al.* 1994; Peperzak *et al.* 2000). This has been clearly demonstrated for *P. globosa*, which is referred to in most field and culture investigations (Fig. 2). The function of the various cell types within the life cycle of *P. globosa* life cycle, and in particular their involvement in colony formation, is not yet fully understood. Colonies are composed of cells that are deprived of flagella, haptonema, and organic scales, and are embedded in a mucilaginous matrix secreted by the cells themselves. Their size varies considerably from 10 µm for a 2-cell colony to several mm with several thousands of cells (Rousseau *et al.* 1990). The termination of the *P. globosa* colonial stage is characterized by colonial lysis (Brussaard *et al.* 1995; Rousseau *et al.* 2000), aggregate formation, or by cell motility development and subsequent emigration from the colonies, leaving behind ghost colonies (Peperzak *et al.* 2000).

Haplo-diplontic life cycles have been demonstrated in some haptophytes, e.g. in *Emiliana huxleyi* (Green *et al.* 1996; Medlin *et al.* 1996), *Chrysochromulina* spp. (Edvardsen & Vaulot 1996; Edvardsen, this issue) and *Prymnesium parvum* (Larsen & Edvardsen 1998). The existence of two ploidy levels and haploid microzoospores released from colonies gives some support to the existence of a haplo-diplontic life cycle in *P. globosa* as well (Rousseau *et al.* 1994; Vaulot *et al.* 1994). Observation of syngamy and meiosis is, however, restricted to a few genera such as the coccolithophorid *Pleurochrysis*.

The nature of the benthic stages is also still unclear for most of the haptophytes. Non-motile amoeboid or walled cells of *Chrysochromulina* spp. and cysts of *Prymnesium* spp. could possibly function as a resting stage. However, only limited information is available on the abundance, role in bloom formation, and survival conditions in nature of the benthic stages. The role of sediment as a seeding reservoir for the water column also deserves more attention.

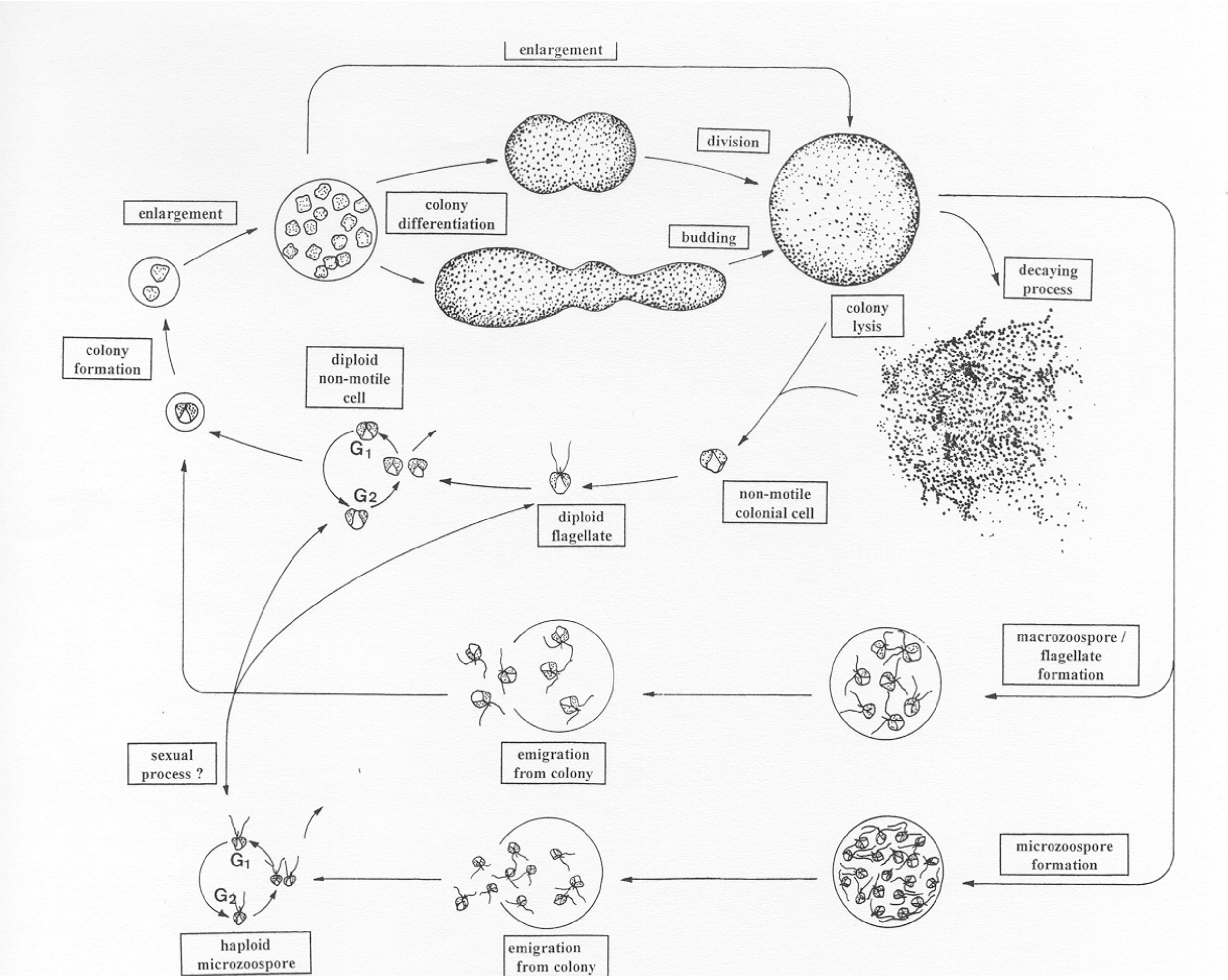

Fig. 2. The life cycle of *Phaeocystis globosa*, as compiled from culture and field observations, illustrates the complexity of haptophyte life cycle events. Based on microscopic observations and flow cytometric DNA analysis, 3 different types of free-living cells were shown to alternate with mucilaginous colonies composed of non-motile cells deprived of flagella, haptonema and scale coverage (from Rousseau *et al.* 1994).

The transition between the life stages in haptophytes is presumably controlled by the interplay of endogenous and environmental factors, but the role and the relative importance of these factors are poorly known. Such information is, however, essential for understanding how and why blooms form and species survive during non-bloom periods. The lack of knowledge is at least partly due to difficulties in distinguishing between factors affecting the transition between the different life stages and those affecting growth of a particular stage. This is clearly illustrated in the case of *P. globosa*, for which several factors have been suggested to play a role in triggering the passage to the colonial stage from a free-living cell. Among them, the requirement of a solid substrate for cell attachment has been suggested from the observation of small colonies attached to the setae of *Chaetoceros* spp. at the early stage of the bloom (Boalch 1987; Rousseau *et al.* 1994). Phosphate concentration has also been suspected to be important for colony formation (Veldhuis *et al.* 1986; Veldhuis & Admiraal 1987; Cariou *et al.* 1994), but it is still unclear if phosphate deficiency triggers the colonial form, or if this form outcompetes free-living cells due to its higher ability to use organically bound phosphate (Veldhuis & Admiraal 1987). Chemical substances derived from the vernal diatom bloom have also been suspected to be important for colony formation (Weisse *et al.* 1986; Rousseau *et al.* 1994), but have never been demonstrated. Flagellate formation into colonies at the end of a *P. globosa* bloom is presumably linked to unfavourable conditions for colony survival, e.g. nutrient stress and light limitation, subsequent to vertical transport (Peperzak *et al.* 2000).

The ecological importance of life cycle events for haptophytes

Some features of the life cycle of haptophytes appear to be important for the dynamics of these species. The difference in autecology, with various light and temperature tolerances, of the authentic and alternate cells of *C. polylepis* would allow this species to occupy different ecological niches (Edvardsen, this volume). The occurrence of a cyst in some *Prymnesium* species would represent a seeding stage for blooms (Edvardsen, this volume). The alternation of *Phaeocystis* life forms, i.e. free-living nanoplanktonic cells and large gelatinous colonies, have different implications for planktonic and benthic ecosystem structure and function. The success of *Phaeocystis* and its impacts on the marine ecosystem have been linked to their capacity to form large gelatinous colonies (Lancelot *et al.*, this volume). The colony matrix structure does indeed provide a competitive advantage to this alga for a limiting resource, but it also protects *Phaeocystis* from grazing and viral and/or bacterial infection (Lancelot *et al.*, this volume). Possibly, the suspected common occurrence of sexuality in haptophytes, resulting in high genetic plasticity, could well be an explanation for their widespread distribution.