



## Tansley review

# Intraspecific chemical communication in microalgae

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## Contents

Summary	516	VI. Processes entailing intraspecific communication	523
I. Introduction	516	VII. Conclusions	526
II. What does 'intraspecific' mean in the case of microalgae?	518	Acknowledgements	526
III. Modulation of intraspecific chemical communication	518	References	526
IV. Genetic and phenotypic bases for intraspecific communication	521		
V. Possible evolutionary trajectories of intraspecific chemical communication	523		

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## Summary

The relevance of infochemicals in the relationships between organisms is emerging as a fundamental aspect of aquatic ecology. Exchanges of chemical cues are likely to occur not only between organisms of different species, but also between conspecific individuals. Especially intriguing is the investigation of chemical communication in microalgae, because of the relevance of these organisms for global primary production and their key role in trophic webs. Intraspecific communication between algae has been investigated mostly in relation to sexuality and mating. The literature also contains information on other types of intraspecific chemical communication that have not always been explicitly tagged as ways to communicate to conspecifics. However, the proposed role of certain compounds as intraspecific infochemicals appears questionable. In this article, we make use of this plethora of information to describe the various instances of intraspecific chemical communication between conspecific microalgae and to identify the common traits and ecological significance of intraspecific communication. We also discuss the evolutionary implications of intraspecific chemical communication and the mechanisms by which it can be inherited. A special focus is the genetic diversity among conspecific algae, including the possibility that genetic diversity is an absolute requirement for intraspecific chemical communication.

## I. Introduction

Any communication system is essentially made up of three components: an 'emitter', a 'receiver' and a 'field' in which the exchange of information occurs. Chemical communication among

organisms requires biological machinery, including genes, RNA, proteins and other chemical messengers; the interaction between these components allows the production, release and/or detection of chemical cues. Equally important for a successful communication are the constraints imposed by the environment in which the

infochemical (Box 1) is released (Legrand *et al.*, 2003). For instance, medium viscosity can limit the diffusion of substances, electromagnetic radiation can affect the activity of the infochemicals (Sterr & Sommaruga, 2008), and chemical agents, such as compounds identical or similar to the cue or that interact with it modifying its signaling function, can act as infochemicals and interfere with the transmission of information (Lüring & Scheffer, 2007).

Within this contribution, we recognize three main subsets of modes of chemical communication, depending on the identities of the emitter and the receiver:

**Chemical communication between different microalgal species** The most obvious example is allelopathy, which occurs when a species produces chemicals that have a detrimental effect

on a competitor for space, nutrients or light. The outcome of this type of communication can be death, paralysis (for motile cells) or inhibition of growth of the receiver (Legrand *et al.*, 2003).

**Signaling between microalgae and other organisms** Microalgae can release compounds harmful to their grazers (Ianora & Miralto, 2010; Ratti *et al.*, 2013) or to non-algal competitors for resources such as bacteria and fungi (Burkholder *et al.*, 1960; Kellam *et al.*, 1988; Hagmann & Jüttner, 1996; Issa, 1999). We cannot exclude the possibility that microalgae are involved in chemical interactions with multiple actors (i.e. 'multitrophic' interactions), for instance by producing compounds beneficial for individuals whose presence is disadvantageous for grazers, as observed for other organisms (Vet & Dicke, 1992; De Vos *et al.*,

#### Box 1 Glossary of terms

Allelochemical	Compound involved in interspecific interactions, which is produced by a donor organism and elicits a response in a receiver organism belonging to a different species (Whittaker, 1970a,b)
Allomone	Allelochemical that triggers a response in the receiver that is favorable to the donor organism only (Nordlund & Lewis, 1976)
Apoptosis	Process that leads to specific morphological and biochemical changes during the genetically controlled death of cells. These modifications include a reduction in cell volume, condensation of chromatin, fragmentation of the nucleus, little or no ultrastructural changes in cytoplasmic organelles and blebbing of the plasma membrane in the final stage (Kerr <i>et al.</i> , 1972; Kroemer <i>et al.</i> , 2009)
Colonial (organism)	Aggregation of individuals with identical genotype and phenotype (Kirk, 2000). The genera <i>Microcystis</i> , <i>Skeletonema</i> and <i>Gonium</i> include examples of colonial microalgae
Conjugation (bacterial)	Transmission of genetic material from one bacterial cell to another through direct contact between cells (Clark & Adelberg, 1962).
Diazotrophy	Metabolic ability to reduce atmospheric N <sub>2</sub> to forms that can be assimilated into the organic matter (e.g. Postgate, 1998)
Diplontic life cycle	Life cycle in which mitotic cell divisions and development occur uniquely in the diploid phase. Gametes, originating from meiosis, fuse and restore the diploid phase (Mable & Otto, 1998)
Founder effect	Mechanism by which a few individuals from a parent population give rise to a new population with reduced genetic variability, outside of the spatial range of the parent population (Mayr, 1942; Provine, 2004)
Gene flow	Movement of genes from one population to another (Slatkin, 1985)
Haplodiplontic life cycle	Life cycle in which development occurs in both a haploid vegetative phase, interposed between meiosis and sexual fusion, and a diploid vegetative phase (Mable & Otto, 1998).
Haplontic life cycle	Life cycle in which mitotic cell divisions and development occur solely in the haploid phase. Gametes fuse and form a zygote, which undergoes meiosis (Mable & Otto, 1998)
Hormone	The original definition comes from the medical field and describes hormones as chemical messengers produced by an organ in response to the 'physiological needs of the organism' and intended to reach and affect another organ (Starling, 1905). Hormones of multicellular organisms have also been found in unicellular organisms, in which they exhibit signaling function nevertheless, there is no consensus on the use of the term 'hormone' for single-celled organisms (Lenard, 1992)
Infochemical	A chemical that conveys information from an emitter to a receiver and elicits a behavioral or physiological response in the receiver (Dicke & Sabelis, 1988). Infochemicals include pheromones and allelochemicals. Infochemical nomenclature is context specific and not compound specific, e.g. a substance acting as a pheromone in one species may be used as a kairomone in the interaction with another species (Nordlund & Lewis, 1976; Dicke & Sabelis, 1988)
Kairomone	Allelochemical that triggers a response in the receiver that is favorable to the receiver organism only (Nordlund & Lewis, 1976)
Multicellular (organism)	Aggregation of individuals with identical genotype but different phenotype (i.e. functionally and/or morphologically different) (Kirk, 2000). Examples of multicellular microalgae are <i>Anabaena</i> spp. and <i>Pleodorina</i> spp.
Pheromone	Substance secreted to the outside by an individual and received by a second individual of the same species, in which it triggers a specific response (Karlson & Lüscher, 1959). This response may be adaptively favorable to the donor and/or the receiver organism (Vet & Dicke, 1992)
Random genetic drift	Process that causes a change in a population allele frequency as a result of the random sampling of genes from generation to generation (Slatkin, 1985; Masel, 2011)
Semiochemical	Chemical involved in the interaction between organisms (Nordlund & Lewis, 1976). Semiochemicals include nutrients and toxins (which are beneficial or detrimental to the interacting organisms <i>per se</i> ) and infochemicals (which are beneficial or detrimental to the organisms through the response they evoke in the receiver) (Dicke & Sabelis, 1988)
Synomone	Allelochemical that triggers a response in the receiver that is favorable to both the donor and the receiver organism (Nordlund & Lewis, 1976)

2006; Stout *et al.*, 2006; Nevitt, 2008). Certainly, microalgae can be part of multitrophic interactions in which they act as neither donors nor receivers: this was observed, for instance, in the case of waterborne cues released by seastars of the genus *Leptasterias* that deter the snail *Tegula funebris* from feeding on tide pool microalgae (Gravem & Morgan, 2016).

**Intraspecific chemical communication** Despite the paucity of investigation in this field, several processes are likely to implicate the transfer of infochemicals among conspecifics. A population of algae of a given species can be genetically homogeneous or heterogeneous; the occurrence of chemical communication in these two cases has never been explicitly addressed.

In this review, we collect and discuss such information (Table 1) in order to assess how common and important is chemical communication among conspecific algae. The description of the instances available in the literature is directed at the identification of common traits and disparities between intraspecific infochemicals, and serves as a context for the discussion of the ecological and evolutionary implication of intraspecific chemical communication.

## II. What does 'intraspecific' mean in the case of microalgae?

No definition of 'species', and thus of 'intraspecific', exists that can be applied to all cases of microalgae (Hartl & Clark, 1989; Templeton, 1992; Hey, 2001). For example, the morphological species concept (i.e. conspecific individuals look the same and differ morphologically from individuals of other species) is not easily applicable to organisms with different life stages (as is common among algae) that do not share the same appearance whilst being conspecifics. Other species definitions have proved to be more inclusive. The concept of 'genetic species' (or 'biological species', *sensu* Mayr, 1963) refers to groups of natural interfertile populations that are reproductively isolated from other populations. This definition cannot be applied to asexual organisms. The 'evolutionary species' concept identifies lineages (i.e. ancestral-descendant sequences of populations) that evolved separately from other evolutionary units and 'have their own unitary evolutionary roles and tendencies' (Simpson, 1961). According to Simpson, the 'evolutionary species' concept does not exclude asexual organisms; other authors have further explained the theoretical context in which it can be used (see Wiley, 1978 for a thorough reflection on the applicability of the evolutionary species concept to asexual organisms). Furthermore, the recognition of the 'evolutionary tendency', as Simpson himself admitted, is totally arbitrary in some cases (e.g. in a fossil sample) (Mayr, 2000).

The difficulty to identify species, especially for asexual organisms, translated into the use of different approaches for the delimitation of microalgal species. Morphology has been the historically prevalent criterion for the identification of microalgal species (Hey, 2001); after the application of molecular techniques in taxonomic studies, some of these species attributions became questionable (e.g. Medlin *et al.*, 1995; Montresor *et al.*, 2003; Ellegaard *et al.*, 2008). The difficulty in the definition of species for microalgae occurs particularly in cyanobacteria, for which the application of the bacterial nomenclature has been proposed and

strain codes increasingly replace Linnaean binomial nomenclature (Castenholz, 1992; Pinevich, 2015).

In the ensuing text, we identify species in accordance with the current literature on each organism used as an example. We acknowledge that this brings in some degree of subjectivity in the definition of 'intraspecific', but the unresolved debate on this matter leaves us with no alternative. In some cases (Sections IV and VI.4), the discussion requires a further discrimination between conspecific algae that have complete genetic identity and conspecific algae that share lower degrees of genetic relatedness.

## III. Modulation of intraspecific chemical communication

The synthesis or the reception of chemicals conveying information can be either constitutive or modulated through inducible mechanisms (Agrawal & Karban, 1999; Wolfe, 2000). Induction may be controlled by either environmental factors or endogenous factors (i.e. the passing of set points, such as a certain cell size). An instance of constitutive production of a chemical that transmits information to conspecific algae is provided by the inhibition of heterocyst formation by existing heterocysts (see Section VI.1 for details). Notice that the constitutive nature of infochemical production does not necessarily correspond to a constant presence of the signal in the environment. Pheromones, for instance, are often ephemeral (Watson, 2003), so that their persistence in water depends on the persistence of the cell type from which they are constitutively produced. Various examples of inducible communication mechanisms in microalgae exist in the literature, although they are not always explicitly labeled as such (Vardi *et al.*, 2007; see Section VI.3). In the diatom *Pseudostaurosira trainorii*, the production of a pheromone (Box 1) by female cells that have achieved a certain cell size was also inferred to be 'constitutive'; this signal induces the production of male gametes, initiating a further cascade of chemical signals (Sato *et al.*, 2011; see Section VI.2 for further details). However, we believe that the 'constitutive' nature of such signaling is highly questionable, as the passing of a minimum cell size represents, in our opinion, an example of (endogenous) induction of communication.

Consistent with the topic of this review, the examples above concern intraspecific communication; however, we can also recognize instances of both constitutive and inducible communication mechanisms between organisms of different species. For instance, *Alexandrium minutum*, a bloom-forming dinoflagellate, activates a defense mechanism against copepod grazers through the production of a toxin induced by waterborne cues from the grazers themselves (Selander *et al.*, 2006). Other dinoflagellates constitutively produce chemical compounds that are toxic for potential grazers (e.g. Huntley *et al.*, 1986; Hansen *et al.*, 1992).

Inducibility is obviously linked to the management of resources; in the case of infochemicals, this means confining the production of the signaling molecules, and its energetic and other metabolic expenditure, to the time of requirement (Haukioja & Hakala, 1975). The production of infochemicals may bear consequences for basal metabolism: an example of this

**Table 1** Compounds involved in intraspecific chemical communication in microalgae (in the column 'Donor species, strain or cell type', different colors indicate organisms belonging to different algal groups (grey, cyanobacteria; green, green algae; orange, diatoms; blue, dinoflagellates; yellow, haptophytes); the numbers in parentheses refer to the references (see footnote))

Infochemical name and chemical nature	Biosynthetic precursor	Donor species, strain or cell type	Molecular mass (kDa)	Role as infochemical	Active concentration	Conditions for activity	Effect on other algae
HetR (protein)	–	<i>Anabaena</i> sp. (1)	–	Control of heterocyst development (1)	HetR in heterocysts is 20-fold more than in other cells of the filament (2)	Transcription of <i>hetR</i> gene is stimulated by low external combined nitrogen (2)	–
PatS (peptide) (Unsaturated fatty acids)	–	<i>Anabaena</i> sp. (3) Lysed cells of <i>Phormidium tenue</i> (4)	–	Inhibition of heterocyst development (3) Autotoxin (4)	–	–	–
L-Glutamic acid (amino acid)	–	<i>Volvox capensis</i> K27 strain (5)	0.15	Induction of development of sexual spheroids (5)	$< 7 \times 10^{-8}$ M (5)	Developing spheroids must be exposed not later than at 64-cell stage (5) 6 h of exposure to trigger the activity (7)	No sexual induction in <i>V. carteri</i> (5)
(Glycoprotein)	–	Male spheroids of <i>Volvox carteri</i> f. <i>nagariensis</i> (6)	30 (7)	Induction of development of sexual spheroids (8, 9)	$6 \times 10^{-17}$ M (7) probable signal amplification (9)	–	–
(Glycoprotein)	–	<i>Volvox carteri</i> f. <i>weismannia</i> strain 65–30 (10)	27 (10)	Induction of development of sexual spheroids (8)	$10^{-12}$ M (10)	–	Sexual induction in <i>V. carteri</i> f. <i>nagariensis</i> at $10^5$ -fold higher concentration (10)
(Glycoprotein)	–	<i>Volvox carteri</i> f. <i>weismannia</i> strain 1b (10)	28.5 (10)	Induction of development of sexual spheroids (10)	$10^{-13}$ M (10)	–	Sexual induction in <i>V. carteri</i> f. <i>nagariensis</i> at $10^5$ -fold higher concentration (10)
Sexual cell division inducing pheromone SCD-IP (glycoprotein)	–	mt– cells of <i>Closterium ehrenbergii</i> (11)	18–20 (11)	Induction of sexual cell division of mt+ vegetative cells (11)	–	Light-dependent release	–
Lurline (pentosylated hydroquinone)	Plastoquinone-4 (12) Plastoquinone-6 (13)	Female gametes of <i>Chlamydomonas allensworthii</i> (13, 14)	532 <sup>a</sup> (13)	Attraction of the motile ale gamete (13)	$< 10^{-12}$ M (14) Synthetic analog: $10^{-13}$ M (12)	–	–
Di- <i>n</i> -propyl diketopiperazine ('diproline')	–	mt– cells of <i>Seminavis robusta</i> (15)	0.11	Attraction of mt+ cells (15)	–	Production is light-dependent (15) and induced by SIP+ (16)	–
2- <i>trans</i> , 4- <i>trans</i> -decadienal (polyunsaturated aldehyde)	–	<i>Thalassiosira weissflogii</i> (17)	0.15	Triggering of degenerative processes that culminate in the death of cells (17)	–	–	–

Table 1 (Continued)

Infochemical name and chemical nature	Biosynthetic precursor	Donor species, strain or cell type	Molecular mass (kDa)	Role as infochemical	Active concentration	Conditions for activity	Effect on other algae
Ph-1 (unknown)	–	Female vegetative cells of <i>Pseudostaurastrum trainorii</i> in the sexual size range (18)	–	Sexualization of male cells (18)	–	–	–
Ph-2 (unknown)	–	Male vegetative cells of <i>Pseudostaurastrum trainorii</i> in the sexual size range (18)	–	Sexualization of female cells (18)	–	–	–
Sex Inducing Pheromone SIP+	–	mt+ cells of <i>Seminavis robusta</i> (16)	–	Induction of cell cycle arrest in G1 and synthesis and secretion of dipropine in mt– cells (16)	Sip+ is secreted at much lower concentration than dipropine (16)	–	–
15-Hydroxyeicosa-pentaenoic acid	–	Dying and dead cells of <i>Skeletonema costatum</i> (19)	0.32	Autotoxin (19, 20)	–	–	Also toxic for other diatoms, but not for two tested dinoflagellates (19)
(Protease)	–	Senescing cells of <i>Peridinium gatunense</i> (21)	–	Sensitizes younger cells to oxidative stress (21)	–	–	–
(Unknown)	–	Cells of <i>Alexandrium ostenfeldii</i> that were infected by the flagellate <i>Panvilucifera infectans</i> (22)	–	Stimulates motile cells of <i>A. ostenfeldii</i> to form temporary cysts (22)	–	–	–
1-[Hydroxyl-diethyl malonate]-isopropyl dodecanoic acid (Unknown)	–	<i>Isochrysis galbana</i> (23)	414 <sup>a</sup> (23)	Autotoxin (23)	–	–	Also toxic for eight other species of microalgae (23)
	–	<i>Diacronema lutheri</i> (24)	–	Autotoxin (24)	–	–	–

<sup>a</sup>m/z.

References: (1) Buikema & Haselkorn (1991); (2) Zhou *et al.* (1998); (3) Yoon & Golden (1998); (4) Yamada *et al.* (1994); (5) Starr *et al.* (1980); (6) Starr & Jaenicke (1974); (7) Gilles *et al.* (1984); (8) Starr (1970); (9) Sumper *et al.* (1993); (10) Al-Hasani & Jaenicke (1992); (11) Fukumoto *et al.* (2002); (12) Mori & Takanashi (1996); (13) Jaenicke & Marnett (1995); (14) Starr *et al.* (1995); (15) Gillard *et al.* (2013); (16) Moeyss *et al.* (2016); (17) Casotti *et al.* (2005); (18) Sato *et al.* (2011); (19) Imada *et al.* (1991); (20) Imada *et al.* (1992); (21) Vardi *et al.* (2007); (22) Toth *et al.* (2004); (23) Yingying *et al.* (2008); (24) Yamasaki *et al.* (2015).



is provided by Pohnert (2000, 2005), who suggested that the polyunsaturated aldehydes (PUAs) of diatoms have their precursors in fatty acids, such as the C20 eicosapentenoic acid. The impact of infochemical production on metabolism in terms of the diversion of resources (energy, chemicals) may also be of relevance, although no study, to the best of our knowledge, has yet addressed this aspect directly.

In some cases (e.g. in genetically identical organisms), the differential expression of the systems devoted to the production and reception of infochemicals may be necessary to prevent self-communication (i.e. the same cell both produces and receives the signal) that may occur after induction. In the bacterial pheromone-induced conjugation (Box 1), cells potentially capable of both emitting and receiving the signal activate only one of the two abilities, preventing self-communication (Dunny *et al.*, 1995). The inducibility of the production and reception mechanisms is not necessarily mutually exclusive and self-signaling may occur. For instance, it has been proposed that the wound-induced production of PUAs in diatoms not only affects other algae, bacteria and microinvertebrates (see Ianora & Miralto, 2010 for a review on the effect of PUAs on various organisms, and Dutz *et al.*, 2008 for contrasting results), but also the emitters themselves, although, allegedly, the intoxication of neighboring diatoms is minimized by the fact that grazers ingest most of the PUAs (Casotti *et al.*, 2005; Wichard *et al.*, 2007). If PUAs are passively released from dead cells, rather than being actively produced by wounded cells, this questions the existence of chemical communication (as discussed in Section VI.3).

#### IV. Genetic and phenotypic bases for intraspecific communication

We see no theoretical impediment to the possibility that intraspecific communication occurs both between genetically identical and genetically distinct individuals. The information in the literature suggests that within-species variability is fertile ground for the development of communication, because it allows intraspecific diversification in the mechanism and extent of signal emission and reception (Wood & Leatham, 1992; Eigemann *et al.*, 2013). However, signals can also be exchanged within a genetically uniform population, providing a feedforward mechanism that allows the response to external stimuli to propagate across the population. Clearly, interacting clonal cells are capable of acting as both emitter and receiver; the same is not necessarily true when the communicating cells are not genetically identical.

##### 1. Origin of genetic diversity in microalgal species

The generation of within-population genetic variability is mainly a result of sexual reproduction. The probability of generation of variability among different populations, in the case of microalgae, is often considered to be low, because these organisms often reproduce asexually and have a high dispersal capacity (De Meester *et al.*, 2002). However, large genetic differences have been detected within algal populations. This is not only true for algal populations that are spatially distant, but also occurs within the same

population; substantial genetic variability was even observed in phytoplankton blooms (Evans *et al.*, 2005; Rynearson & Armbrust, 2005; Rynearson *et al.*, 2006; Shilova *et al.*, 2016).

Over time, microalgae have adapted to changes in environmental conditions, so that the gene complement of an extant algal species is likely to be different from that of the same species in the past. This may have led to speciation, or genetic heterogeneity, within the same species. Obviously, organisms that do not coexist in time, whether conspecific or not, are unable to exchange chemical information. This may not be true for conspecific populations that differentiate *across space* because of adaptive responses to local selective forces and/or stochastic events, such as founder effects and genetic drift (Box 1; Hartl & Clark, 1989; for a recent review on phytoplankton biogeography, see Padisák *et al.*, 2016). In this review, we therefore focus on the case of spatial differentiation.

The occurrence of genetically distinct populations of microalgae may result from the interruption of gene flow (Box 1) because of the development of geographical barriers (Kim *et al.*, 2004; but also see Koester *et al.*, 2012 and Scholin *et al.*, 1994 for cases in which genetic distance and geographical separation do not seem to be correlated). However, the absence of geographical barriers does not prevent the development of distinct populations of the same species (metapopulations *sensu* Levins, 1969). The dispersal of individuals over a large region may be followed by recombination, genetic drift and/or genotype selection based on local conditions that lead to a differentiation from the original population(s) (Vanormelingen *et al.*, 2009). This may be similar to that observed by Koester *et al.* (2012), who reported positive selection of several genes in different strains of *Thalassiosira pseudomana* living in connected habitats in which different selective forces prevailed (e.g. temperature and UV radiation). Furthermore, biological interactions, such as predation, competition and allelopathy, can operate as 'environmental filters' that may impede or favor the successful establishment of a population in a new environment, and selectively act upon the genotypes it contains (Naselli-Flores & Padisák, 2016).

##### 2. Communication between genetically distinct conspecific individuals: premises and paradigms

The generation of genetic diversity becomes relevant with respect to intraspecific communication when individuals coexist. Coexistence is a condition that can either precede the generation of genetic diversity (e.g. via sexual reproduction within a single algal population) or follow it. The latter case can occur by the breakdown of a geographical barrier that allows the populations from the two sides to converge into a single population, or in the case of chemical or physical barriers that constitute a boundary with intermediate properties. The actual occurrence of the breakdown of geographical barriers is questioned by those who deny the existence of such barriers for phytoplankton (see Hedlund & Staley, 2004 for a review on this debate). According to these authors, the geographical isolation of algal populations is hampered by the fact that these organisms are numerous, small-sized, have a great dispersal ability and most can produce resting stages (Finlay, 2002; Cermeño & Falkowski, 2009). This calls to mind the famous assertion of the Dutch microbiologist Martinus Wilhelm

Beijerinck (1851–1931): ‘everything is everywhere, the environment selects’ (reported by Baas-Becking, 1934). This paradigm, however, has been challenged, for instance, by Kim *et al.* (2004), who reported evidence for geographically isolated populations of the dinoflagellate *Peridinium limbatum* that diverged genetically because of a limited gene flow. A restriction of the gene flow between distant populations of the diatom *Pseudo-nitzschia pungens* has also been reported (Casteleyn *et al.*, 2010).

The existence of boundary zones between different marine habitats (e.g. benthic vs planktonic; deep chlorophyll maximum vs surface mixed zone; areas separated by well-defined thermoclines or chemoclines, etc.) that are not separated by geographical barriers is more widely accepted (see, for instance, Ribalet *et al.*, 2010).

### 3. Communication between genetically identical conspecific individuals

Environmental variations may trigger differential gene expression in genetically identical individuals (Choi & Kim, 2007; Roberfroid *et al.*, 2016). Such differential expression may result in the activation of intercellular communication, i.e. inducible communication between identical cells can be based on the generation of a phenotypic difference. If the environmental variation affects only a portion of the area occupied by the population, the activation of communication may concern a fraction of the population, which may then propagate the signal to the cells that have not yet encountered the environmental perturbation (Fig. 1). In nature, this is only possible in specific conditions, implying short diffusional distances among cells that share information. This network of communication can be beneficial or not for the receiver (e.g. leading to population control processes). From an evolutionary point of view, the case of an altruistic network is more easily comprehended for a clonal population (kin selection; see Section VI.4). The case just described is based on a cause–effect process determined by environmental inducers (nutrients, toxic agents,

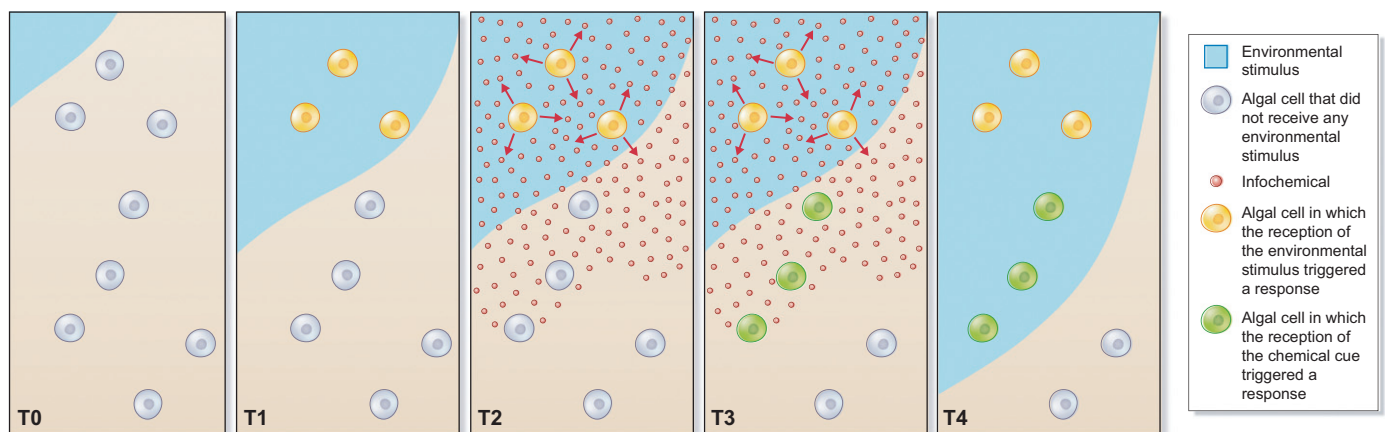
presence of grazers, etc.). Other scenarios may be represented by the activation of communication pathways in randomly selected individuals, because of stochastic gene expression (Roberfroid *et al.*, 2016). Another possibility is that interacting conspecific cells represent different stages in the life cycle of a non-synchronous population, which have been proven to exhibit, in some cases, very different phenotypes originating from drastic differentiation in gene expression (e.g. diploid and haploid phases in *Emiliana huxleyi*; Frada *et al.*, 2008; von Dassow *et al.*, 2009).

Other examples of communication between genetically identical cells are provided by the exchange of information between cells in filaments resulting from mitotic division from a single progenitor. These cases are discussed in detail in Section VI.1.

### 4. Phenotypic differences that are relevant for communication between conspecific organisms

Among the phenotypic differences that have been observed between conspecific individuals, the ability to produce toxins (Carrillo *et al.*, 2003), the vulnerability to toxic compounds (e.g. Behra *et al.*, 1999; Lopez-Rodas *et al.*, 2001) and the sensitivity to allelochemicals (Box 1; Eigemann *et al.*, 2013) are of special relevance to this review.

When the individuals of a population are distributed along a physical and/or chemical gradient, they can perceive the same stimulus with different sensitivity (Maan *et al.*, 2006; Yewers *et al.*, 2015). This different sensitivity often results from the presence of distinct types or numbers of receptors (Schoonhoven, 1982) or from differences in other cell components involved in signal processing (e.g. enzymes involved in the modification of the chemical that is sensed; Van Straalen, 1994). Differences in the sensitivity to chemicals between conspecific algae have been reported (Fisher, 1977; Murphy & Belastock, 1980). For instance, estuarine clones of *Thalassiosira pseudonana* and *Skeletonema costatum* are less susceptible to chemicals from industrial waste



**Fig. 1** Gradual interaction of a clonal algal population with an environmental perturbation. T0, the perturbation has not reached the populations. T1, the front of the perturbation reaches the cells at the borders of the population, triggering a phenotypic response. T2, the cells that responded to the perturbation in T1 produce and release a chemical cue, which conveys information on the environmental change. T3, cells that were not directly affected by the perturbation receive the cue and enact the phenotypic response to the perturbation. T4, the perturbation front moves forward and reaches the cells in the population that had been alerted by the cue; these cells are ready to respond to the perturbation. The cells represented in this model are close enough to ensure that the diffusion of the chemical cue towards unaffected cells is faster than the propagation of the environmental perturbation. Arrows in panels T2 and T3 represent the release of the chemical cue.

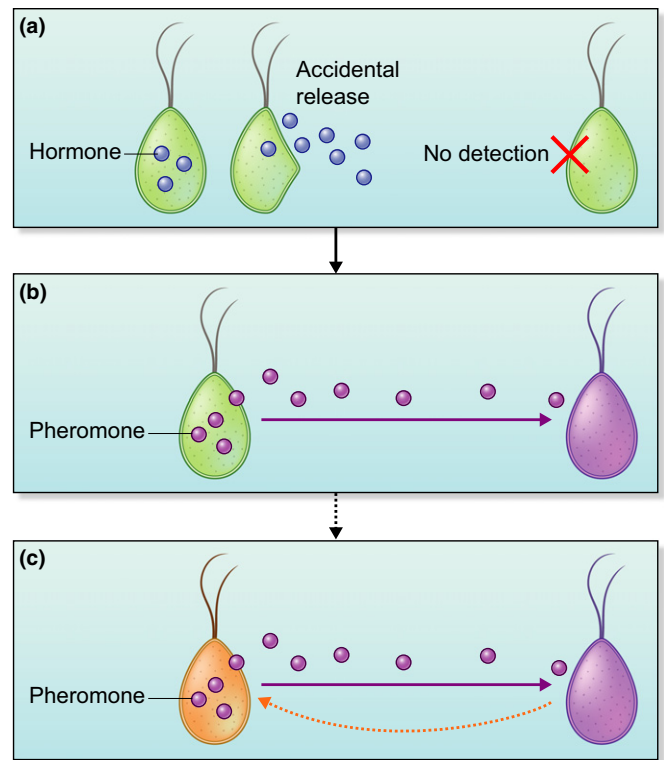
than are conspecific strains that originated in other environments (Murphy & Belostock, 1980). Different strains of *Scenedesmus obliquus* exhibited different responses to chemical substances released by *Daphnia*: cells of three strains responded by forming four- and eight-celled coenobia; cells of another strain responded by the irregular aggregation into colonies having more than eight cells; cells of a fifth strain did not show obvious responses (Lüring, 1999).

In animals, sensory abilities are an important component of the reproductive behavior and can result in reproductive isolation and speciation, through natural selection based on sensory performance ('sensory drive hypothesis'; Schluter & Price, 1993; Seehausen *et al.*, 2008). In the light of the obvious role of signal sensing in mating, it is likely that, also in microalgae, sensory capabilities of individuals drive behavioral and genetic differentiation (i.e. changes to the nucleotide sequence in the genome) through the selection of distinct signaling modalities.

### V. Possible evolutionary trajectories of intraspecific chemical communication

Infochemicals probably derive from chemicals that had different original functions or from products released by the cells as waste (Wyatt, 2003). More specifically, it can be hypothesized that intraspecific chemical communication derives from the conversion of a molecule capable of conveying signals within a cell into an infochemical that operates on different cells of the same species (Fig. 2). In other words, a hormone-like (Box 1) molecule capable of modulating metabolic processes within a cell may be able to interact with cells that share similar metabolic pathways and intracellular signaling cascades. The more the metabolic pathways and intracellular signaling cascades between the cell of origin and the target cells are similar, the more likely is the acquisition of an infochemical function for a hormone-like molecule.

A similar evolutionary process has been proposed for metazoans by Sorensen & Stacey (1999). These authors proposed that fish pheromones evolved in three steps. In the first phase, some individuals of a species produce a hormone which (by definition; Starling, 1905) functions as an internal chemical messenger (in the context of unicellular organisms, this would be equivalent to intracrine or autocrine signaling; Csaba, 1996). In the second phase, some other individuals evolve the ability to detect, and respond to, the hormone accidentally released by conspecifics, for instance after algal cell breakage; these receiver organisms obtain a benefit from this acquired ability (notice that, at this stage, only the receiver develops a new ability). Finally, in the third phase, which does not necessarily occur, the receiver responds to the signal. If this response, which does not inevitably involve the generation of chemical cues and may consist, for instance, in the sexualization of the receivers, elicits a positive response in the producers, the establishment of a two-way communication can occur (Sorensen & Stacey, 1999). Although similar models have been mostly proposed for Metazoa, the underlying mechanisms do not seem to belong to any group in particular, and are likely to have occurred in all organisms with intraspecific chemical communication.



**Fig. 2** Evolution of pheromones from pre-existing hormones. (a) A hormone is accidentally released into the medium and conspecifics are unable to detect it. (b) The receiver specializes to detect the hormone and to respond to it. (c) The response of the receiver exerts a selective pressure for the specialization of the producers. Changes in the color of the cells (receiver in b; receiver and donor in c) indicate specialization. The dashed line indicates that the last step may or may not occur. Inspired by Sorensen & Stacey (1999).

### VI. Processes entailing intraspecific communication

#### 1. Cell–cell communication in colonial and multicellular microalgae

Intraspecific communication, in most cases, serves the scope of coordinating functions among individual unicellular microalgae in a population. It is not known whether this coordination is an evolutionary precursor to the tighter interaction among individuals in colonial (no intercellular differentiation) and multicellular (with intercellular differentiation) organisms (Beardall *et al.*, 2009; Box 1). Nevertheless, it has been pointed out that several features that were considered to be a hallmark of multicellular organization (for example, programmed cell death (PCD), cell–cell adhesion and communication) probably evolved in ancestral unicellular organisms (Ameisen, 2002; Grosberg & Strathmann, 2007).

The signaling machinery of multicellular organisms was inherited, in several cases, from their unicellular ancestors (Kawabe *et al.*, 2015 for amoebae; also see König & Nedelcu, 2016 for a discussion on the evolution of multicellularity in volvoclean algae). It is also worthwhile noting that cell differentiation in multicellular organisms is commonly recognized as one of the main selective factors in favor of the evolution of this habit (Stanley, 1973). Multicellularity is attained from sequential divisions of a single cell



without separation of the progeny (Bell & Mooers, 1997). As cells share the same genetic profile and no major differential effect can be exerted on them by the environment, so the production of distinct cell types presumably results from communication between the descendants of the first cell. Another possible scenario is the production of different cell types (somatic vs reproductive) in *Volvox*, which is determined through a series of asymmetric divisions, in a size related process (Kirk, 2000): the smaller cells produce a transcriptional repressor of reproduction-related genes (thus they become the somatic cells).

It is interesting to note that the transition from single cells to colonies has been shown to respond to chemical cues from herbivores or epiphytes (Lüring, 2003; Leflaive *et al.*, 2008; Verschoor *et al.*, 2009). The link between the formation of colonies and communication with other species certainly endorses the idea that coordination among cells can result from the exchange of infochemicals.

In filamentous cyanobacteria, cell–cell communication allows genetically identical cells within the same filament, originating from mitotic division, to carry out distinct tasks and thus become multicellular (Beardall *et al.*, 2009). Diazotrophy (Box 1) in *Anabaena*, for instance, requires the differentiation of specialized cells, the heterocysts, in which nitrogen fixation occurs and oxygen diffusion is hampered (Wolk *et al.*, 1994). Such differentiation takes place in approximately one in every 10 cells (Wolk *et al.*, 1994) and is controlled by a set of genes that are expressed in a precise sequence (Golden & Yoon, 2003). According to the ‘activator–inhibitor model’ (Gierer & Meinhardt, 1972; Meinhardt & Gierer, 1974), the development of heterocysts and the maintenance of their spacing depend on the presence of a protein activator (HetR) acting over a short spatial range and of an inhibitor (the peptide PatS) acting over a longer spatial distance. The transcription of the *hetR* gene is triggered by low external combined nitrogen; when nitrogen is abundant, the gene *hetR* is transcribed at basal levels in all cells. The process is self-promoting because HetR stimulates its own synthesis. Increased levels of HetR also stimulate the transcription of *patS*, whose product (PatS) is responsible for the inhibition of *hetR* transcription and thus heterocyst formation (Black & Wolk, 1994; Gerdtzen *et al.*, 2009). The inhibition only operates in the cells surrounding the heterocyst, which itself is insensitive to PatS (Haselkorn, 1998; Yoon & Golden, 1998). This mechanism bears similarities to the plasmid-mediated system that prevents bacterial emitter cells from self-signaling during pheromone-induced conjugation (Dunny *et al.*, 1995).

## 2. Role of infochemicals in mating and sexual differentiation

Sexual reproduction requires that two sexually competent cells meet and recognize reciprocally. These cells can originate from meiosis of diploid cells or by activation of haploid cells in algae with diplontic, or diplohaplontic and haplontic, life cycles, respectively (Box 1; Frenkel *et al.*, 2014). Sex reshuffles the deck of genes in the population, but can also be seen as a strategy to overcome hostile environmental conditions, for instance through the production of resistant zygotes. Environmental stressors, such as high temperature or limited nutrient supply, have been shown to trigger sexuality

(Starr *et al.*, 1995; Chepurnov *et al.*, 2004). Nedelcu *et al.* (2004) proposed that sex and death are the outcomes of different extents of environmental stress. Pheromones, which can be involved in different phases of sexual reproduction, and whose synthesis and activity are often subject to environmental influence, may play a pivotal role in the signaling pathway linking sex to the environment (Fukumoto *et al.*, 1998; Gillard *et al.*, 2013).

In many diatoms, mostly centric, asexual cell division causes a gradual decrease in cell size; the original cell size is restored by vegetative enlargement or, more commonly, by sexual reproduction (Round *et al.*, 1990). The latter does not occur in cells whose size is above the ‘sexual size threshold’ (SST; Drebes, 1977). Below this limit, external factors, such as light, photoperiod and temperature, can trigger sexualization in some of the cells in a population (Werner, 1971; Furnas, 1985; Armbrust *et al.*, 1990); sexualized cells can then initiate the sexualization of other cells mediated by chemical signals.

The multicellular alga *Volvox carteri*, for instance, which lives in temporary ponds that dry out in the summer, reproduces asexually most of the time (Hallmann *et al.*, 1998); when the temperature is critical, this alga switches to sexual reproduction and forms dormant zygotes that survive the drought (Sumper & Hallmann, 1998). Heat shock, specifically, induces somatic cells to produce a glycoprotein infochemical that triggers gametogenesis in the gonidia (Starr & Jaenicke, 1974; Kirk & Kirk, 1986; Sumper *et al.*, 1993). The same signal, later on, is released at lower concentrations by the male gametes to induce differentiation and agglutination in the surrounding cells (Gilles *et al.*, 1984; Hallmann *et al.*, 1998; Sumper & Hallmann, 1998).

In the pennate diatom *Pseudostaurosira trainorii*, some vegetative cells in the ‘sexual size range’ (hereafter named ‘A’) produce a signal of unspecified chemical nature (ph-1); this signal induces meiosis in other vegetative cells (‘B’) which subsequently release two motile (amoeboid) male gametes (it is worth mentioning that amoeboid motion can only occur on a solid surface, so the ‘A’ and ‘B’ cells must be close to each other). The ‘B’ cells and/or the ‘male’ gametes themselves release another chemical message (ph-2; also of unknown identity); ph-2 triggers sexualization of the ‘A’ cells which undergo meiosis and produce female gametes. Then, the ‘A’ cells are thought to produce a third pheromone (ph-3), which stimulates the amoeboid movement of the ‘male’ gametes towards the ‘female’ gametes (Sato *et al.*, 2011). In *Seminavis robusta*, a heterothallic pennate diatom, meiosis occurs only after the pheromone-mediated interaction between two types of compatible cells (mating types) has taken place (Gillard *et al.*, 2013).

The contact between sexually competent motile cells can happen by chance, as observed in *Chlamydomonas reinhardtii* and *Volvox* (Starr *et al.*, 1995; Coleman, 2012), or can be guided by pheromone-induced chemotaxis (Tsubo, 1961; Ichimura, 1971; Hill *et al.*, 1989; Al-Hasani & Jaenicke, 1992; Maier, 1993; Starr *et al.*, 1995; Mori & Takanashi, 1996). The greater the resource investment for the synthesis of attracting signals, the greater the benefits obtained by the alga in terms of increased encounter rates of gametes (Frenkel *et al.*, 2014). The trade-offs associated with the cost of producing the attracting signals, however, are not known. This is not the only aspect of chemically regulated sexuality in algae

that still needs to be clarified. Whether or not sexual determination in heterothallic species is only genetically predetermined, as recently observed for the diatom *Seminavis robusta* (Vanstechelma *et al.*, 2013), or environmental factors can concur with the modulation of such phenomena, as happens in macroalgae, such as *Laminaria religiosa*, *Lessonia nigrescens* and *Lessonia variegata* (Funano, 1983; Nelson, 2005; Oppliger *et al.*, 2011), is also not clear. It is interesting that some of the compounds operating in brown algae were also found in diatoms, although their infochemical role in microalgae has not been demonstrated (Pohnert & Boland, 1996). Sex determination may also be determined epigenetically by the interaction with conspecifics, possibly through the mediation of chemical cues (Godwin *et al.*, 2003).

### 3. Role of infochemicals as inducers of the death of conspecific individuals

Senescent or dead cells in microalgal populations have been shown to release chemical compounds that determine the death of cells of the same species (Imada *et al.*, 1991, 1992; Yingying *et al.*, 2008; Yamasaki *et al.*, 2015). The signaling nature of these so-called autotoxins or autoinhibitors is, however, not always clear. If they are passively released and interact with the receiver cell only after the death of the producer cell, this eliminates one of the elements characterizing cell–cell communication: the existence of an emitter (Dicke & Sabelis, 1988). The existence of cells with a reduced viability, in which photosynthesis still occurs but membranes are compromised, and thus allow the efflux of metabolites (Veldhuis *et al.*, 2001), makes the recognition of an actual donor even more complicated.

It should also be noted that most of the work on autotoxins has been conducted on laboratory cultures. Yamada *et al.* (1994) showed that a mixture of fatty acids from lysed cells of *Phormidium tenue* exerted an autotoxic activity on axenic cultures of the same species. The algal population was completely annihilated in the absence of non-photosynthetic bacteria, whereas it continued to grow when bacteria of the genera *Flavobacterium* and *Micrococcus* were present in the culture: according to these authors, bacteria, which are typically present in algal blooms in large numbers (Mayali & Azam, 2004), were capable of degrading the toxins (Yamada *et al.*, 1994).

Programmed cell death (PCD) is defined as the genetically regulated self-destruction of a cell. It requires a highly coordinated interaction among receptors, nuclear factors, signal kinases and other cellular components (Leist & Nicotera, 1997; Aravind *et al.*, 1999). PCD is essential for development and tissue turnover in multicellular organisms (Fukuda, 1997; Leist & Nicotera, 1997; Pennell & Lamb, 1997). In several filamentous cyanobacteria, the PCD of 'sacrificial' cells, known as necridia, is involved in the separation of hormogonia (i.e. short motile filaments that act as dispersal units) from a trichome (Lamont, 1969; Reichenbach & Golecki, 1975). PCD has also been described in non-photosynthetic bacteria (Yarmolinsky, 1995; Lewis, 2000), yeasts (Fröhlich & Madeo, 2000), protozoa (Lee *et al.*, 2002) and algae (Berges & Falkowski, 1998; Vardi *et al.*, 1999; Veldhuis *et al.*, 2001; Ning *et al.*, 2002; Segovia *et al.*, 2003; Berman-Frank *et al.*, 2004; Casotti

*et al.*, 2005), although, for these organisms, the molecular hallmarks of the cell death machinery are not unequivocal and some are still controversial (Franklin *et al.*, 2006; Deponte, 2008; Jiménez *et al.*, 2009). Several rationalizations have been proposed for PCD in unicellular microalgae (e.g. removal of mutated/damaged cells, limitation of viral infection), which have been critically reviewed by Nedelcu *et al.* (2010), together with the possibility that PCD is the side-effect of the mechanistic basis of an adaptive trait (Nedelcu *et al.*, 2010). Environmental changes, such as nutrient and light limitation (Berges & Falkowski, 1998), high doses of UV (Moharikar *et al.*, 2006), increase in salinity (Ning *et al.*, 2002) or oxidative stress (Vardi *et al.*, 1999), are alleged determinants of PCD in microalgae. In the case of oxidative stress, Nedelcu *et al.* (2004) proposed that the effect is dose dependent, with low levels of oxidative stress inducing sexuality and high levels triggering PCD.

Some chemical compounds have been reported to induce PCD in microalgae. Casotti *et al.* (2005) showed that the application of synthetic PUAs to diatom cultures leads to degenerative processes that culminate in apoptosis-like death of the cells (Box 1; Casotti *et al.*, 2005). Similarly, Vardi *et al.* (2006) demonstrated that the application of the PUA (2*E*,4*E*/*Z*)-decadienal to *Thalassiosira weissflogii* and *Phaeodactylum tricornutum* cultures triggers a cascade of events which culminates in the death of diatom cells (Vardi *et al.*, 2006). These PUAs or other chemical compounds produced by microalgae may play a role as PCD inducers in conspecifics (Casotti *et al.*, 2005; Vardi *et al.*, 2006; Vidoudez & Pohnert, 2008), although conclusive proof of this is still to be produced.

A proteolytic activity present in the spent medium from ageing cultures of the dinoflagellate *Peridinium gatunense* increases the sensitivity of younger conspecific cultures to oxidative stress, which, in turn, triggers PCD (Vardi *et al.*, 2007). In this case, the viability of donor cells has been confirmed and the observations are suggestive of an active secretion of the active compound (Vardi *et al.*, 2007).

In bacteria, the compounds that cause intraspecific induction of death have been proposed to derive from substances that kill other species (Ameisen, 2002). This is also a plausible scenario for microalgae. The final phase of an algal bloom is often characterized by increasing levels of cell death as a result of viral (Bratbak *et al.*, 1993; Jacquet *et al.*, 2002; Frada *et al.*, 2008) and bacterial (Mayali & Azam, 2004) attack, nutrient limitation (Van Boekel *et al.*, 1992) or the interaction between these factors (Pal *et al.*, 2007). Franklin *et al.* (2006) suggested that PCD may explain why dinoflagellate blooms can vanish in times that are too short to be justified by sedimentation or grazing (Franklin *et al.*, 2006; also see Raven & Waite, 2004 for non-PCD means of removal of infected cells from the population). The triggering of PCD by intraspecific communication appears to be especially suited for the control of population density in an unfavorable environment (Vardi *et al.*, 2007), similar to what happens in bacterial biofilms in which PCD is propagated via quorum sensing (Oleskin *et al.*, 2000).

### 4. Chemical communication in processes that benefit conspecifics

Chemical signaling may be beneficial to conspecifics that receive the signal in many ways; for instance, the infochemicals can warn of

the presence of predators and/or induce defensive behavioral responses. Toth *et al.* (2004) showed that temporary cysts of the dinoflagellate *Alexandrium ostenfeldii* are more resistant to the parasitic flagellate *Parvilucifera infectans* than motile cells; when *A. ostenfeldii* motile cells were exposed to cell-free spent medium from a culture of conspecifics that were infected by the parasite, they formed temporary cysts (Toth *et al.*, 2004). These authors proposed that this is a response to either a chemical that leaks from infected cells or an unknown infochemical actively released by infected cells, forewarning other members of the population of the presence of the parasite (Toth *et al.*, 2004). In organisms with a biphasic life cycle, changes in ploidy have also been related to different degrees of sensitivity to infections (e.g. shift from diploid to haploid phase, the latter being more resistant to viral infection, in *Emiliana huxleyi*; Frada *et al.*, 2008). Whether these changes in ploidy are mediated by communication among conspecifics, however, is not known.

Some authors have shown that the death of unicellular algae can generate an immediate benefit to the neighboring cells through the mediation of chemicals (but, see above, for the actual infochemical role of substances released by dead cells). Durand *et al.* (2011) reported that *Chlamydomonas reinhardtii* cells that undergo PCD release unidentified compounds that stimulate the growth of conspecific cells, whereas chemicals coming from cells that die from causes different from PCD inhibit growth in cells of the same strain (Durand *et al.*, 2011). The effect determined by compounds deriving from cells that die by PCD stimulates growth only in *C. reinhardtii*, but inhibits growth of *C. moewusii* and *C. debaryana* (Durand *et al.*, 2014).

Vardi *et al.* (1999), in the above-mentioned work on PCD in *P. gatunense*, proposed that, under unfavorable environmental conditions, part of the population sacrifices itself via PCD, so that other cells can encyst and re-establish the population when favorable environmental conditions resume. Whether a cell is destined to die or to encyst is determined through processes that involve cysteine protease(s), as the application of a commercial cysteine protease inhibitor (E-64) prevents PCD and also stimulates cyst formation; the link between these two pathways has been proposed as the result of high selective pressure for the formation of cysts from non-stressed cells only, whereas the other cells are purged from the population (Vardi *et al.*, 1999). It is not clear whether the 'other cells' are genotypically distinct from those that encyst and, in this case, how their genotype is preserved so that the same mechanism can occur again.

The existence of an 'altruistic' chemical signal that favors conspecific individuals raises many doubts. Group selection, i.e. the selectability of the group (Wynne-Edwards, 1986; Wilson, 1997), as a counterpart for the generally accepted selection of genes (Dawkins, 1989) and individuals, is much more difficult to maintain through natural selection. Furthermore, a 'cheating' strategy (i.e. the ability of cells to take advantage of shared resources without giving any contribution in return) could rapidly spread through a non-clonal population by virtue of the higher fitness it confers (Thornton, 2002). Kin selection, involving the sacrifice of individuals in permitting the survival of the same genotype in other members of a clonal population (Hamilton, 1963, 1964), has

much more support (Nedelcu *et al.*, 2010; Durand *et al.*, 2011, 2014; Pepper *et al.*, 2013).

As pointed out by Franklin *et al.* (2006), if 'altruism' is restricted to clonal populations, blooms may not provide suitable conditions for kin selection to occur (Thornton, 2002), as they seem to be more genetically heterogeneous than previously believed (Medlin *et al.*, 2000; Rynearson & Armbrust, 2005). However, this would depend on the degree of relatedness of the cells in the bloom.

## VII. Conclusions

1. The latest findings on chemical communication in algae suggest that the exchange of signals between conspecifics is more common than generally believed. Intraspecific chemical communication appears to be present in all major algal groups (Table 1) and is involved in several processes, such as sexual reproduction, cell differentiation in algal colonies, induction of death and protection of conspecifics from grazers, viruses and parasites.

2. Intraspecific communication operates on both clonal and non-clonal populations. In the former case, the potential of each cell to act as both a producer and a receiver of the signal can be modulated, resulting in either a producer or a receiver phenotype (e.g. through differential gene expression); this appears to be particularly useful for the rapid propagation of a response to an environmental stimulus through the whole population, because it allows the cells that first come into contact with the stimulus to 'inform' other cells of the population of the external change. In the case of interacting, genetically different cells, the diversification of communication mechanisms can also have genetic bases. Such diversification allows communication whenever the cells come into contact; this does not exclude cells that owe their genetic distinctness to a temporary geographical segregation.

3. The evolution of intraspecific communication was presumably based on the recruitment of pre-existing mechanisms and compounds that operated within the cell with other functions. It can be envisaged that communication between similar cells originated via the perception of hormone-like molecules occasionally released by related neighbors.

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