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Acquired phototrophy in aquatic protists

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ABSTRACT: Acquisition of phototrophy is widely distributed in the eukaryotic tree of life and can involve algal endosymbiosis or plastid retention from green or red origins. Species with acquired phototrophy are important components of diversity in aquatic ecosystems, but there are major differences in host and algal taxa involved and in niches of protists with acquired phototrophy in marine and freshwater ecosystems. Organisms that carry out acquired phototrophy are usually mixotrophs, but the degree to which they depend on phototrophy is variable. Evidence suggests that 'excess carbon' provided by acquired phototrophy has been important in supporting major evolutionary innovations that are crucial to the current ecological roles of these protists in aquatic ecosystems. Acquired phototrophy occurs primarily among radiolaria, foraminifera, ciliates and dinoflagellates, but is most ecologically important among the first three. Acquired phototrophy in foraminifera and radiolaria is crucial to their contributions to carbonate, silicate, strontium, and carbon flux in subtropical and tropical oceans. Planktonic ciliates with algal kleptoplastids are important in marine and fresh waters, whereas ciliates with green algal endosymbionts are mostly important in freshwaters. The phototrophic ciliate *Myrionecta rubra* can be a major primary producer in coastal ecosystems. Our knowledge of how acquired phototrophy influences trophic dynamics and biogeochemical cycles is rudimentary; we need to go beyond traditional concepts of 'plant' and 'animal' functions to progress in our understanding of aquatic microbial ecology. This is a rich area for exploration using a combination of classical and molecular techniques, laboratory and field research, and physiological and ecosystem modeling.

KEY WORDS: Mixotrophy · Radiolaria · Foraminifera · Ciliates · Dinoflagellates · Kleptoplastidy · Karyoklepty · Endosymbiosis · *Myrionecta rubra*

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INTRODUCTION

Acquisition of phototrophy through maintenance of algal endosymbionts or algal organelles is common among aquatic phagotrophic protists. Most protists with acquired phototrophy are mixotrophic; they combine heterotrophy and phototrophy. Evolutionary biologists recognize algal endosymbiosis as one of the major mechanisms of eukaryotic evolution and as a driving force partially responsible for the great diversity of protists in aquatic environments (Lane & Archibald 2008, Keeling 2009). The importance of acquired phototrophy is less recognized in aquatic microbial ecology.

Despite the information available on algal endosymbiosis (defined here as an intracellular association between a non-photosynthetic host and a potentially autonomous eukaryote alga) and organelle retention (defined here as the retention of plastids and sometimes other organelles through feeding on algal prey) in particular protist groups (Anderson 1983a, Lee & McEnery 1983, Dolan & Perez 2000, Stoecker 1999), there is little quantitative information on the occurrence and importance of acquired phototrophy across taxa in aquatic ecosystems. Thus, this review has 3 main aims: (1) to summarize information on acquired phototrophy among 4 major groups of aquatic protists — the Foram-

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inifera, Radiolaria, Ciliophora and Dinofzoa; (2) to categorize a bewildering array of relationships between protistan hosts and their algal endosymbionts or retained algal organelles so that their evolutionary significance and physiological and ecological roles can be appreciated; and (3) to summarize and synthesize information on the occurrence, abundance and biomass of protists with acquired phototrophy and their contributions to primary and secondary production and biogeochemical processes.

We hope this review will lead to increased elucidation and quantification of acquired phototrophy in aquatic protists, a greater recognition of its role in structuring trophic interactions, and a better appreciation of the contributions of mixotrophs and autotrophs with acquired phototrophy to aquatic ecology. Most ecological and biogeochemical models of aquatic ecosystems apply the traditional 'plant-animal' dichotomy which does not recognize the effects that acquired phototrophy may have on exchange between model compartments. Acquired phototrophy is a 'fact of life'

in the euphotic zone of aquatic ecosystems; understanding it is important in predicting how aquatic ecosystems respond on evolutionary and ecological time scales to changing environments.

ACQUIRED PHOTOTROPHY IN THE TREE OF LIFE

The largest research effort and scientific literature on eukaryotic acquired phototrophy concerns the antique side of the process: the obligatory endosymbioses which led to massive gene loss/transfer from the endosymbiont and its transformation into an organelle. The origin, timing, and number of secondary and tertiary endosymbiotic events in the tree of eukaryotic life (Fig. 1) is a subject of intense and often largely speculative debate (Lane & Archibald 2008, Sanchez-Puerta & Delwiche 2008). Major constraints that hinder our current understanding of the evolution of phototrophy in eukaryotes are that (1) most of the events leading to permanent plastids in eukaryotes occurred at the dawn

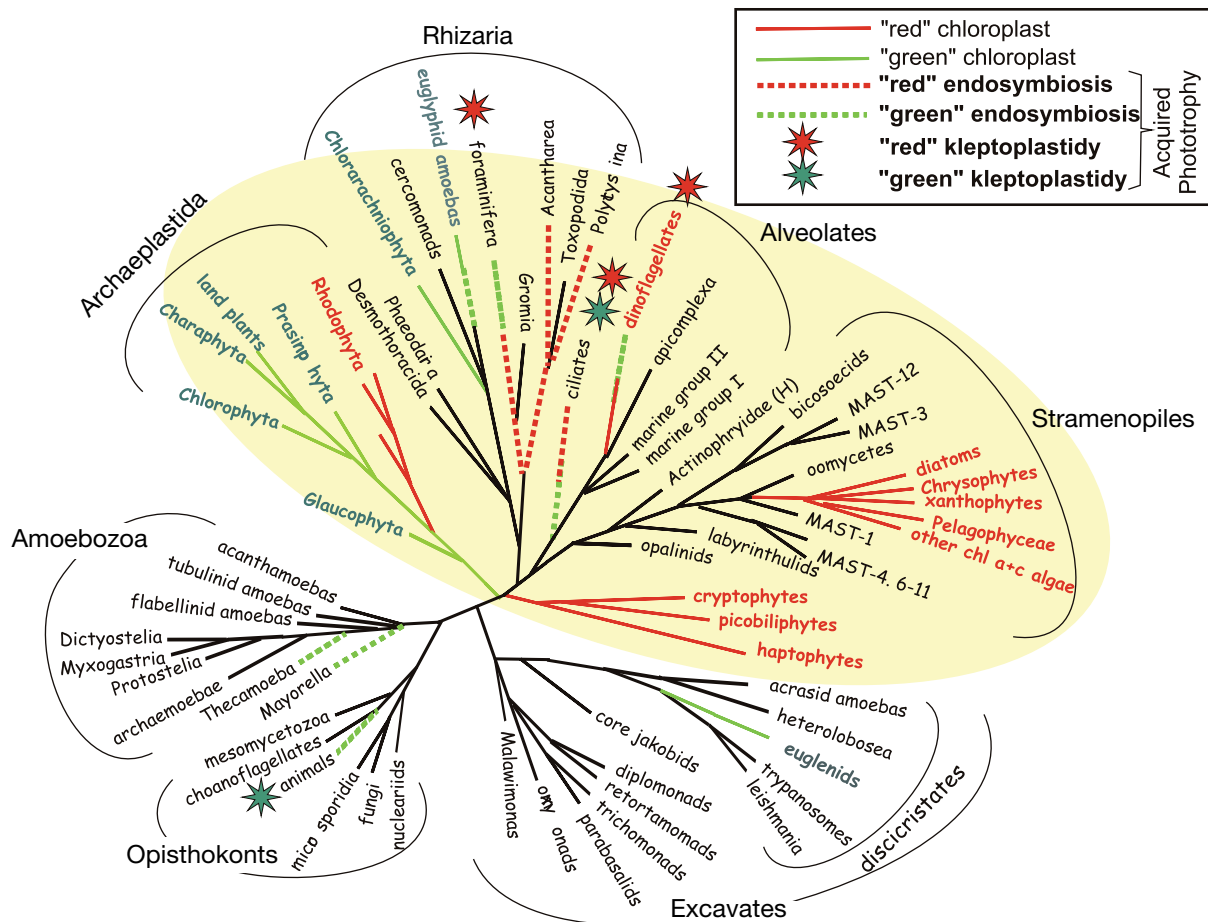


Fig. 1. Synthetic tree of eukaryotic life based on recent phylogenetic/genomic data (modified from Fehling et al. 2007). Acquired endosymbiosis and organelle retention based on both red and green plastids are concentrated in a mega-division including all permanent phototrophic protists plus pseudo-heterotrophic lineages

of their evolutionary history, many hundreds of million years ago, (2) both mixo- and heterotrophic protist lineages may have witnessed successive lateral gene transfers from their microalgal prey, adding a level of genomic complexity in addition to the classical constraints for reconstructing deep molecular phylogenies, and (3) entirely sequenced protistan genomes are still very scarce, and they typically include only 1 or 2 representatives of major lineages containing thousands or hundreds of thousands of species with various trophic status.

The tree of eukaryotic life has evolved as a function of the availability of novel genomic data. Among the recent exciting results based on multi-gene phylogenies (Hackett et al. 2003, Burki et al. 2008) is the emergence of a super-group that contains all permanent phototrophic eukaryotes (with the exception of euglenoids) resulting from primary, secondary, and tertiary endosymbioses (Burki et al. 2008) together with the 'heterotrophic' groups discussed in this review (Rhizaria, ciliates, dinoflagellates, katablepharids). Thus, the latest version of the tree of eukaryotic life divides along a primary phototrophy versus heterotrophy dichotomy, whose origin (the primary endosymbiosis between a cyanobacteria and an ancestral eukaryote) may have occurred even before the split between the 'green' (Archaeplastida) and the 'red' (Chromista + Rhizaria) protistan lineages. In such cases, the secondary endosymbiotic event(s) leading to the chlorophyll (chl) *a+c* microalgae would in fact correspond to proterozoic processes of plastid replacement. In any case, it appears that a photosynthetic capacitation impacted a major and monophyletic part of the tree of eukaryotic life very early on (yellow in Fig. 1), so that the groups of heterotrophic protists in this half of the tree would have an enhanced ability for acquired phototrophy. They may systematically come from lineages that lost their plastid early in the radiation of photosynthetic protists, and have subsequently kept a genomic memory for plastid maintenance or oxygenic photosynthesis. Interestingly, this putative ancestral capacitation left flexibility in endosymbiosis and kleptoplastidy for both 'green' and 'red' symbionts/plastids in modern rhizarian and chromistan protists (Fig. 1).

AN EVOLUTIONARY AND ECOLOGICAL SPECTRUM OF ACQUIRED PHOTOTROPHY IN PROTISTS

Jones (1994) presented mixotrophy in aquatic microbial foodwebs as a spectrum of nutritional strategies between absolute heterotrophy and autotrophy. Here we have focused on this analogy relating it to one form of mixotrophy, acquired phototrophy (endosymbiosis

and organelle retention), in an effort to categorize common trophic and evolutionary patterns among protists (Fig. 2). The simplest form of acquired phototrophy involves a transient and facultative association between host and symbiont, or prey organelles and predator. Distinguishing between transient and persistent-facultative acquired phototrophic associations is difficult in many cases, due to the lack of autecological information on most mixotrophic protists.

In protists with transient facultative acquired phototrophy, the cell will not require such an association for its survival, and in fact the association may not always be readily observed, but when present allows the host to grow faster. Transient facultative relationships in acquired phototrophy appear to be rare and are perhaps opportunistic in nature, involving the least amount of host or predator adaptation. The aplastidic dinoflagellate *Pfiesteria piscicida* is one such example, carrying out mixotrophy through organelle retention when fed cryptophyte algae (Lewitus et al. 1999). Retention time of plastids in *P. piscicida* is relatively brief in moderate light, lasting 1 to 2 d (Feinstein et al. 2002). *P. piscicida* is an extremely versatile predator, capable of ingesting diverse protistan prey under certain situations, and may even 'micro-predate' fish (Vogelbein et al. 2002).

Here we define persistent facultative relationships as cases where the host is almost always reported with acquired phototrophy, but where survival is not dependent upon symbionts or sequestered plastids. Generally, facultative associations do not involve extensive cytological or metabolic adaptation of the host or predator to accommodate foreign cells or plastids, respectively. Rather, the phenomenon enhances flexibility of nutritional sources with minimal energetic or coevolutionary investment in upkeep. This argument may be understood in terms of an organism's increased hypothetical cost in becoming a phototroph and maintaining permanent photosynthetic machinery (Raven 1997). Thus, by employing acquired phototrophy, it invests little energy while acquiring free labile carbon (Putt 1990b)

An example of a persistent facultative acquired phototrophy is the dinoflagellate *Gyrodinium gracilentum*, which is able to grow heterotrophically on cryptophyte prey in the dark (0.53 d^{-1}), but only reaches its maximum growth rate when exposed to sufficient light (1.2 d^{-1}) through kleptoplasty (Jakobsen et al. 2000). Even in this facultative relationship there appears to be some adaptation to prey selectivity and requirements for growth, as the dinoflagellate appears to only grow when fed cryptophyte algae (Jakobsen et al. 2000). An analogous example of a persistent facultative endosymbiosis may be found in tropical members of the dinoflagellate *Noctiluca scintillans* and the

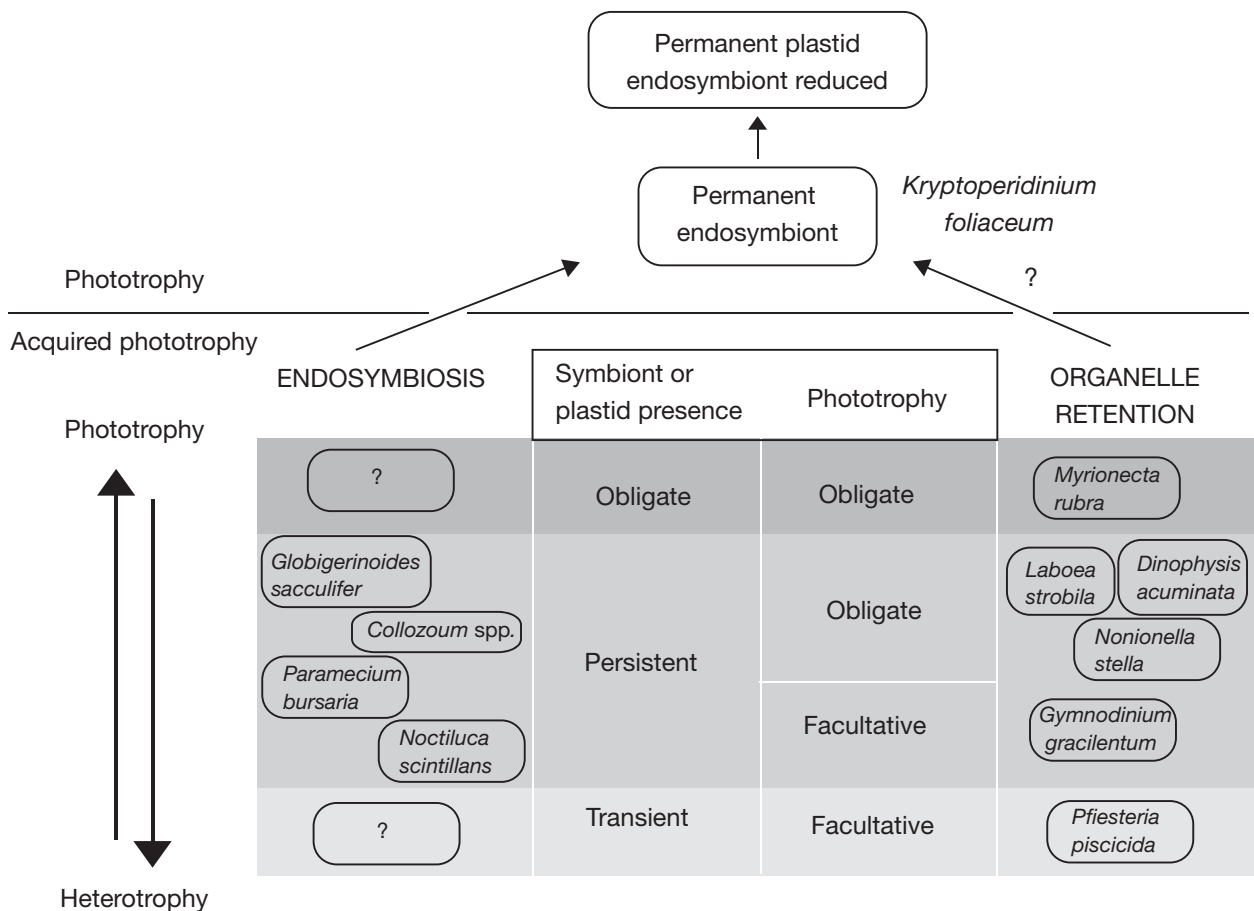


Fig. 2. An evolutionary and ecological spectrum of acquired phototrophy in protists; a conceptual gradient of acquired phototrophy between pure heterotrophy (bottom) and phototrophy (top), based on Jones' (1994) analysis of mixotrophy. The left side represents endosymbiosis in aquatic protists, while the right side represents organelle retention; the middle left column represents the degree to which a symbiont or plastid is present, while the right middle column indicates the role of acquired phototrophy in the host's metabolism. The top arrows represent a theoretical evolutionary acquisition of endosymbiont or foreign organelles, which may eventually result in a permanently integrated plastid. Examples of various protists that appear to fit into these categories are given

prasinophyte endosymbiont *Pedinomonas noctilucae* (Sweeney 1978). *N. scintillans* may possess within their large vacuolated cell thousands of free-swimming *P. noctilucae*, which provide most of the carbon requirements for their host to grow, despite its continued capacity to feed heterotrophically (Hansen et al. 2004). In the laboratory, however, *N. scintillans* loses its symbionts within 3 wk of collection, and then grows as a functional heterotroph (Hansen et al. 2004). Thus, in *N. scintillans*, mixotrophy affords nutritional flexibility, allowing cells to survive in prey-impoverished oligotrophic tropical waters. The freshwater ciliate *Paramecium bursaria* harbors numerous endosymbiotic algae (*Chlorella* spp.); however, prolonged exposure to darkness results in asymbiotic cells that are able to grow heterotrophically (Karakashian 1963). Interestingly, while selective pressure on symbiotic strains of *Chlorella* has apparently made them genetically dis-

tinct from free-living strains (Summerer et al. 2008), *Paramecium* has retained sufficient nutritional flexibility to survive as a heterotroph (Tonooka & Watanabe 2002).

In persistent obligatory acquired phototrophy, an endosymbiont or plastid is nearly always present and the host does not grow without it. This is the most common type of acquired phototrophy in marine protists. The marine oligotrich ciliate *Laboea strobila* is one such example, requiring light and algal prey for growth and surviving longer during starvation in light than in darkness (Stoecker et al. 1988). Certain benthic foraminifera (Lopez 1979) may also fall into this category, although few laboratory studies are available to determine the precise role of sequestered plastids in their physiology. In the planktonic foraminifera *Globigerinoides sacculifer*, loss of dinoflagellate endosymbionts reduces survival time, induces gametogenesis,

and results in smaller shell size compared to cells with symbionts (Bé et al. 1982, Caron et al. 1982). Persistent obligatory endosymbiotic relationships between freshwater or marine ciliates and *Chlorella* spp. or *Symbiodinium*, respectively, may also occur; however, few laboratory data are available to support these conclusions.

The most evolutionarily advanced form of acquired phototrophy involves obligate–obligate relationships, where the symbiont or sequestered organelles are always present, more or less stable (the host has some regulatory control), and removal of these symbionts or organelles from the host, results in its rapid death. While no eukaryotic-endosymbiont containing protists fit this classification (an example of a non-protist host could be certain cnidarians), several organelle-retaining protists appear to satisfy these hypothetical requirements. The marine ciliate *Myrionecta rubra* (= *Mesodinium rubrum*) has been reported to both possess a permanent endosymbiont (Hansen & Fenchel 2006) and to have the capacity to sequester nuclei from its cryptophyte prey (a process known as karyoklepty), in order to maintain and divide its ‘symbiotic’ organelles (Johnson et al. 2007). It’s likely that *M. rubra* represents a ‘species complex’, and that certain members have a permanently integrated ‘endosymbiont’ of cryptophyte origin, while others still require acquisition of cryptophyte nucleus. Other taxa that may also fit into this category include an unidentified marine dinoflagellate isolated from Antarctica (RS-Dino) (Gast et al. 2007) and the katablepharid flagellate *Hatena* sp. (Okamoto & Inouye 2006).

OVERALL DIVERSITY OF ACQUIRED PHOTOTROPHY FROM ENDOSYMBIONTS AND SEQUESTERED PLASTIDS

The diversity of modern eukaryotic phytoplankton in today’s oceans is dominated by algae with red plastids (major pigment chlorophyll *c*), including the dinoflagellates, diatoms, and coccolithophores, while freshwater and terrestrial environments continue to be dominated by green algae (major pigment chlorophyll *b*) (Falkowski et al. 2004). One major reason for this difference in evolutionary selection between environments is believed to be the dramatic rise in oxidation state of the surface ocean during the end of the Phanerozoic eon, making biologically available iron and manganese scarce in surface oceans, both of which are more abundant in cells of the green plastid lineage (Quigg et al. 2003). As expected, these patterns of plastid selection between fresh and marine habitats hold true for diversity of endosymbionts and sequestered plastids in acquired phototrophy. In all

cases where the endosymbiont is identified in freshwater protists it belongs to the chlorophyte lineage (mostly *Chlorella* spp.), whereas only 12.5% of known marine endosymbiotic associations include a green lineage endosymbiont (Fig. 3A,B). While the amount of described diversity of red lineage sequestered plastids in freshwater protists is about twice that of the green, in about 66% of all cases the kleptoplast is undefined (Fig. 3D). The diversity and functional role of organelle retention in freshwater habitats appears to be one of the largest gaps in our knowledge of acquired phototrophy. In marine environments, where organelle retention has been studied in greater detail, half of all known examples of organelle retention involve a prey cell of red plastid origin, while only 11% are green (Fig. 3C). The red dominated disparity for marine endosymbiotic associations is even greater, with nearly 70% of all known symbiont-associated protists having a symbiont with red-lineage plastids (Fig. 3A). Most of these described marine endosymbionts are dinoflagellates. Pelagic foraminifera are known to house a diverse assemblage of dinoflagellate endosymbionts related to the *Symbiodinium* complex, better known for its associations with cnidarians (Pochon et al. 2006, Shaked & de Vargas 2006), whereas endosymbionts of Radiolaria are associated with the dinoflagellate genus *Scrippsiella*. In comparison to the corals, a higher diversity of symbiotic dinoflagellates are observed in pelagic rhizaria, this may be a result of their complex alternation of generations life history, which requires their pelagic endosymbionts to maintain a partially free-living existence (Shaked & de Vargas 2006).

Taxon diversity of sequestered plastids in marine environments appears to vary somewhat with host specificity and diversity. Planktonic oligotrich ciliates are perhaps the most generalist of all organelle sequestering protists, retaining plastids from nearly all of the chlorophyll *c* containing algal groups, and a few chlorophyll *b* containing algae, such as prasinophytes (Laval-Peuto & Febvre 1986). In contrast, nearly all (~76%) organelle-retaining dinoflagellates sequester plastids from cryptomonad algae. The reason for this is unclear; however, some have speculated that the persistence of the nucleomorph (NM: a vestigial eukaryotic nucleus from a red-algal ancestor) and the periplastidal membrane (PM), which surrounds cryptomonad plastids and the NM, may aid in maintaining some plastid autonomy (Lewitus et al. 1999). However, an exception to this rule is the kleptoplastidic dinoflagellate *Dinophysis*, which sequesters its plastids from the photosynthetic ciliate *Myrionecta rubra* (Park et al. 2006). In *D. fortii*, the dinoflagellate siphons cellular contents from *M. rubra* by myzocytotic feeding, and reduces cryptophyte plastids to

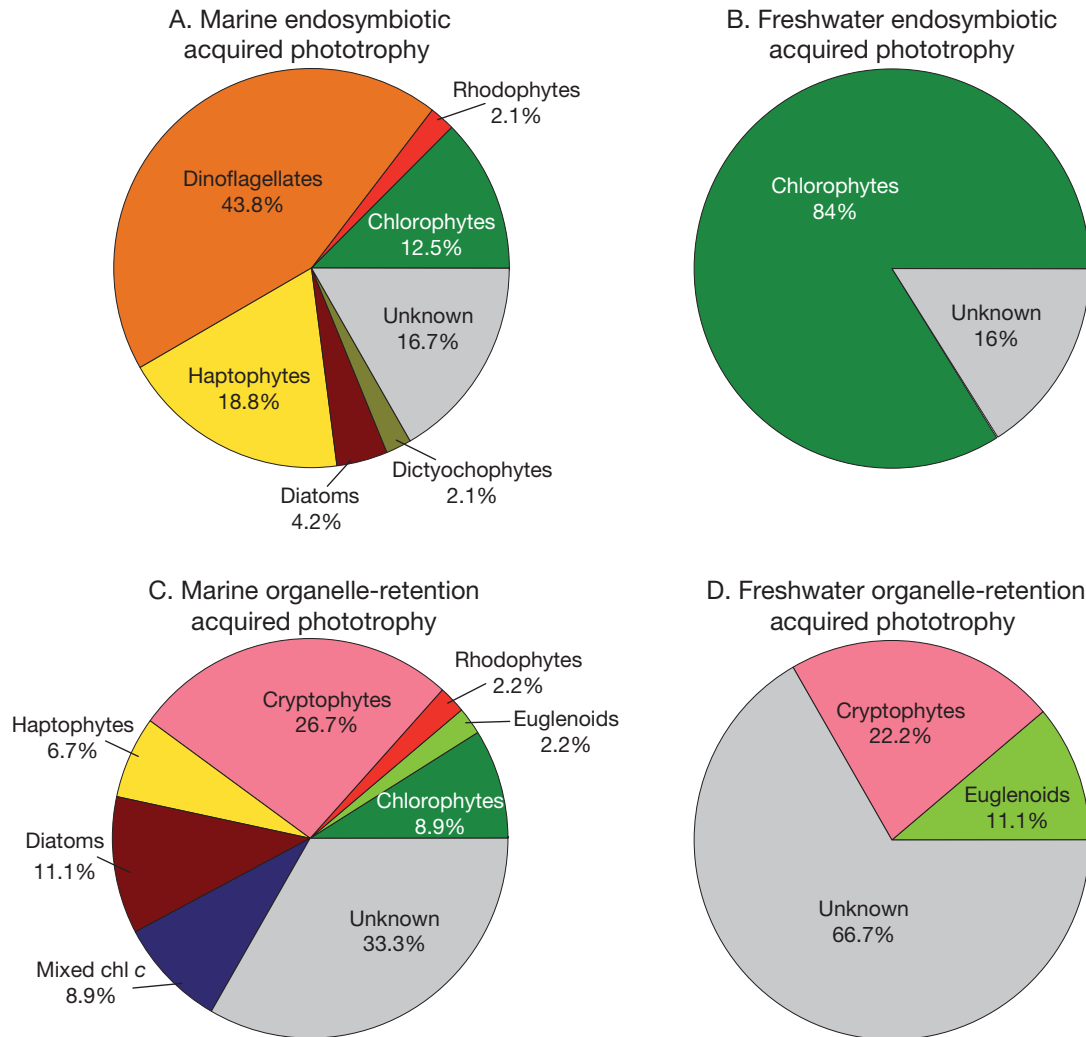


Fig. 3. Diversity of acquired phototrophy endosymbionts and sequestered plastids in marine and freshwater ecosystems. (A) Marine endosymbiotic acquired phototrophy; (B) freshwater endosymbiotic acquired phototrophy; (C) marine organelle-retention acquired phototrophy; (D) freshwater organelle-retention acquired phototrophy. Numbers in each pie represent percentage of total acquired phototrophy interactions for the rhizaria (foraminifera, radiolaria), ciliates, and dinoflagellates combined

their double membranes, digesting away the PM and NM (Nagai et al. 2008). Thus far, nearly all sequestered cryptophyte plastids in marine protists have been shown to be from the *Teleaulax/Geminigera* clade of cryptophytes (Takishita et al. 2002, Hackett et al. 2003, Johnson et al. 2006, Minnhagen & Janson 2006, Park et al. 2006, 2008, Koike & Takishita 2008), while most freshwater cryptophyte kleptoplasts are usually *Chroomonas* spp. (Wilcox & Wedemayer 1985, Fields & Rhodes 1991). The dinoflagellates *D. mitra* (Koike et al. 2005) and an unidentified Ross Sea dinoflagellate (RS-Dino) (Gast et al. 2007) are exceptions to this trend of plastid selection, as they sequester organelles from prymnesiophyte algae rather than cryptomonads.

Previous studies have made linkages between plastid genome size and its evolutionary 'portability' in symbiotic associations (Grzebyk et al. 2003). However, with the exception of dinoflagellate minicircle genomes, differences in plastid genome content in red and green lineages pale in comparison to the thousands of nuclear-encoded, plastid-targeted genes that reside in all algal genomes (Martin & Herrmann 1998). Thus, it is unclear as to how much plastid genome size influences the stability and function of kleptoplasts. Selection of kleptoplasts or symbionts by predators or hosts, respectively, may be driven in many cases by adaptation and selection of predator-prey dynamics, rather than optimal kleptoplast or symbiont performance per se.

OCCURRENCE AND FUNCTION OF ACQUIRED PHOTOTROPHY IN AQUATIC PROTISTS

Rhizaria

Among the planktonic foraminifera, an estimated 25% of the 40 to 50 extant species are known to harbour algal symbionts (Hemleben et al. 1989). Caron et al. (1995) estimated that roughly half of foraminiferan species in surface waters of oceanic gyres possess symbiotic algae at some point of their life history. In the Equatorial Pacific (140°W equator) Stoecker et al. (1996) observed that over 80% of foraminifera were plastidic and contributed ~70% of foraminifera biomass.

Algal symbionts of planktonic foraminifera belong to dinoflagellates and prymnesiophytes (see Table S1 available as supplementary material at www.int-res.com/articles/suppl/a057p279_app.pdf). Recent molecular investigations resulted in more accurate identification of foraminiferan algal endosymbionts. For instance, *Globigerinella siphonifera* symbionts were first described as chrysophytes based on ultrastructure images, but molecular evidence suggests that they actually belong to the prymnesiophytes and are closely related to the *Prymnesium* genus (Table S1) (Gast et al. 2000, Gast & Caron 2001). Dinoflagellate symbionts of foraminifera are regarded as relatives to *Symbiodinium* of corals but form a separate and consistent clade close to the described species *Gymnodinium beii* (Shaked & de Vargas 2006). Neither diatoms or green algal symbionts, nor plastid retention phenomena, have been reported in planktonic foraminifera.

It is currently assumed that all marine benthic larger foraminifera harbour algal symbionts or retain plastids and each host cell can bear hundreds of algal endosymbionts (Lee 1998, Lee 2006). Benthic foraminifera exhibit a great variety of symbionts, members of various families (Peneroplidae, Archaiasidae, Sortidae, Alveolinidae) are hosts of red, chlorophyte, dinoflagellate, and diatom endosymbionts, respectively (Pawlowski et al. 2001a, Lee 2006). Small pennate diatoms are the most common algal symbionts found in benthic foraminifera. In Caribbean waters 75% of the algal endosymbionts were identified as diatoms, with the genus *Nitzschia* isolated from more than 55% of the hosts (Lee et al. 1995). In addition to several *Nitzschia* species, diatoms from the genera *Fragilaria* and *Navicula* have also been regularly found as symbionts in benthic foraminifera (Lee 2006). Occasionally, more than one diatom species can be isolated from the same host (Lee & McEnery 1983, Lee 2006). Dinoflagellate symbionts of benthic foraminifera belong to the *Symbiodinium* species complex (Pawlowski et al. 2001b). They appear to be more closely related to the

symbionts of benthic invertebrates than to the symbionts of the planktonic Foraminifera (*Gymnodinium*) (Gast & Caron 1996). According to molecular investigations, the green symbionts of 5 genera in the Archaiasidae family all belong to distinct species within the *Chlamydomonas* genus. The species *C. noctigama* is thought to be the ancestor for this group of symbionts (Pawlowski et al. 2001a). The red alga *Porphyridium purpureum* has been isolated from the foraminiferan genus *Peneroplis* (Lee 1990, 2006) and the prymnesiophyte *Pleurochrysis scherffellii* has been reported as a symbiont in the species *Marginopora vertebralis* (Lee et al. 1997). Kleptoplastids of benthic foraminifera are all from diatoms (Table S1). Species of *Elphidium* have been shown to retain $\sim 3.7 \times 10^4$ plastids per cell. The plastids have half-lives of up to 9 wk in starved hosts incubated in the dark (Correia & Lee 2002). Plastids from diatoms are also retained in benthic bathyal foraminifera inhabiting extreme environments, such as cold seeps or anoxic waters, where no light is present. None of the freshwater foraminifera are reported to have algal endosymbionts or plastids (Holzmann et al. 2003).

Radiolaria (Acantharea and Polycystinea) are exclusively marine planktonic protists. No kleptoplastidy has been reported in these groups. It is assumed that nearly all Acantharea, except primitive forms in the Holacanthida (Tregouboff 1953, C. Febvre-Chevalier pers. comm.) bear algal endosymbionts at some point of their life history. However, because Acantharea lose their symbiotic algae before reproduction, large individuals can be aposymbiotic (Caron et al. 1995). Field studies in the Equatorial Pacific and in the Gulf of Mexico observed that ~40% of Acantharea had plastids and contributed to ~80% of Acantharea biomass (Stoecker et al. 1996) and that 70% of Acantharea in the upper 50 m of the water column north of Puerto Rico had algal symbionts (Taylor 1982).

All Acantharea algal endosymbionts described so far have been identified as belonging to the prymnesiophytes (Febvre & Febvre-Chevalier 1979, Gast et al. 2000) (Table S1). The average number of algal symbionts per cell is 15 (range 11 to 23) (Michaels 1988, 1991). The presence of dinoflagellate-related symbionts can not be ruled out in the Chaunacanthida group, but this has to be confirmed by molecular techniques (C. Febvre-Chevalier pers. comm.). Conclusions about endosymbiont specificity in many of the Acantharea are essentially based on electron microscopy images and require further investigation using culturing methods associated with molecular tools. Despite their relative abundance in surface waters of tropical seas and their significant contribution to biomass, very little information is available regarding the algal endosymbiont diversity of Acan-

tharea. Moreover, because their strontium sulphate skeleton dissolves rapidly, there is no fossil record for Acantharea (Kunimoto et al. 2006) and this group has received much less attention than Polycystinea.

Polycystinea is a group composed of both colonial and solitary organisms. Colonial radiolarians occur predominantly in oligotrophic open oceans but can be found to a lesser extent in more coastal settings (Swanberg 1983). All possess photosynthetic symbionts and all endosymbionts that have been described so far are dinoflagellates related to the *Scrippsiella* genus (Table S1) (Swanberg 1983, Zettler et al. 1998). Among the solitary Spumellarida and Nassellarida, many species inhabiting photic layers of the oceans have endosymbiotic algae in contrast to deep dwellers which usually do not possess endosymbionts (Anderson 1983a). Caron and co-authors (1995) estimated that roughly half of the radiolarian species in surface waters of oceanic gyres possess symbiotic algae. In the Equatorial Pacific (140°W equator), up to 50 % of solitary Radiolaria had algal endosymbionts (Stoecker et al. 1996).

Three kinds of algal endosymbionts, dinoflagellates, prymnesiophytes and prasinophytes, have been reported so far in solitary Radiolaria (Table S1). The most common symbionts are dinoflagellates related to the *Scrippsiella* genus, which are closely related to the symbiont type found in the medusa *Vellela vellela* (Gast & Caron 1996) and, therefore, are distinct from the foraminiferan dinoflagellate symbionts identified as relatives to the *Gymnodinium* genus (Gast & Caron 2001, Shaked & de Vargas 2006). The second most common symbionts are prymnesiophytes (Anderson et al. 1983, Anderson & Matsuoka 1992). Their molecular taxonomy remains to be elucidated, but ultrastructural observations suggest that prymnesiophyte symbionts of Radiolaria and Acantharea are closely related (Anderson et al. 1983). Finally, green algae belonging to the prasinophytes were found in some species, such as *Spongodymus* sp. and *Thalassolampe margarodes* (Table S1). It is noteworthy that some genera can bear different types of photobionts. For instance, *Spongodymus* sp. has been observed in symbiosis with dinoflagellates, prymnesiophytes and prasinophytes (Table S1), but in contrast to benthic foraminifera only one kind of algal symbiont can be found in individual specimens. These observations raise questions about symbiont/host specificities in particular groups of Radiolaria and Foraminifera, but also certainly point out the requirement for improved taxonomic identification of both hosts and symbionts.

Algal symbionts provide their rhizarian hosts with energy from photosynthesis necessary for survival and growth in oligotrophic environments. Such symbiotic associations short-cut the traditional microbial food web and allow large protistan grazers to inhabit otherwise hostile environments (Norris 1996). Assimilation

of symbiont-derived photosynthates has been demonstrated for several Radiolaria and Foraminifera species (Anderson 1983a, Lee 2006). Algal endosymbiosis, although transient, is required for normal growth and reproduction of many Rhizarian species and thus is obligate. In Foraminifera, the role of endosymbionts in growth and calcification has been clearly demonstrated (Erez 1978, Lee & McEnery 1983, Lee 2006). In Radiolaria, there is evidence that some dinoflagellate symbionts produce sterols which may be secreted into the environment and which could render the host less vulnerable to predators or diseases (Anderson 1983b). A tight control by the hosts over the symbiont populations has been observed and influences symbiont distribution (e.g. day versus night to optimize photosynthesis) and abundances (e.g. partial digestion for energy purposes such as gametogenesis) (Anderson & Bé 1976, Anderson 1983a).

In benthic foraminifera within the photic zone, plastid retention also appears to be obligate and may play a role in providing oxygen in low oxygen habitats as well as in providing photosynthate (Bernhard & Bowser 1999). The role of plastids in benthic foraminifera living below the euphotic zone is a matter of speculation, although providing nitrate reductase activity has been suggested (Grzyski et al. 2002, Bernhard 2003).

Ciliates

Foissner et al. (1999) estimate that about 23 % of the planktonic ciliate species (combined freshwater and marine) carry out acquired phototrophy. Acquired phototrophy occurs in at least 8 major ciliate taxa (Heterotrichea, Hypotrichia, Oligotrichida, Stichotrichia, Litostomatea, Prostomatea, Peniculia, Peritrichia) and is reported, but with less evidence, in a 9th, the Choreotrichia (see Table S2 available as supplementary material at www.int-res.com/articles/suppl/a057p279_app.pdf). In 7 of the 8 major ciliate taxa, phototrophy is usually acquired by algal endosymbiosis, but in the Oligotrichida it is usually by plastid retention (Table S2). Interestingly, most of the ciliates with algal endosymbionts are from freshwater ponds and lakes and in most cases the algal endosymbiont is a Chlorophyte, often *Chlorella* sp (Table S2) (Dolan 1992, Reisser 1986). The estuarine and marine examples of algal endosymbiosis in ciliates are rare but involve a variety of algal taxa (Table S2). The coral reef ciliates *Maristentor dinoferus* and *Euplotes uncinatus* have a dinoflagellate endosymbiont (Lobban et al. 2002, 2005). Small prasinophyte endosymbionts have been observed in estuarine Oligotrichida (Jonsson 1987, Stoecker et al. 1988–1989). Populations of the marine

photoautotrophic ciliate *Myrionecta rubra* (in the Litostomatea) retain organelles from cryptophytes (Johnson et al. 2007) or have a permanent cryptophyte endosymbiont (Hansen & Fenchel 2006).

Plastid retention is very common among marine and freshwater oligotrichous ciliates, but a greater number and diversity of plastid-containing oligotrichs have been reported among the marine than freshwater species (Table S2). In marine ciliates, plastid retention occurs in some or all members of the genera *Cyrtostrombidium*, *Laboea*, *Strombidium* and *Tontonia*. *L. strobila* with plastids is ubiquitous in marine and estuarine waters. Among the marine oligotrichs, retention of cryptophyte, prymnesiophyte, and prasinophyte plastids has been well documented (Table S2). In early reports of 'green' oligotrichous ciliates in freshwater, it was usually assumed that the 'green' color was due to algal endosymbionts. However, it is now evident that plastid retention occurs in some very common freshwater oligotrichous ciliates including *Limnostrombidium viride* (formerly *Strombidium viride*) and *Pelagostrombidium* spp.; however, the source of the plastids has not been documented (Rogerson et al. 1989, Foissner et al. 1999). The freshwater ciliates *Rimostrombidium velox*, *Halteria bifurcata* and *Pelagohalteria viridis* have green algal endosymbionts (Foissner et al. 1999).

Ciliates with acquired phototrophy are common in aquatic ecosystems world wide, ranging in trophic status from eutrophic to oligotrophic (Tables 1 & 2, see also Table S2). Acquired phototrophy in ciliates can have several functions. Below we describe 4 common ecological types of ciliates with acquired phototrophy and the niches which they inhabit.

(1) Large colonial and sessile ciliates with algal endosymbionts are most common in oligotrophic, relatively high light, stable freshwater environments. Examples are photosynthetic ciliates in the Heterotrichea and Peritrichia (Table S2). These are the K-selected ciliates of the microbial food web. They are suspension feeders on small prey, such as bacteria. They have persistent algal endosymbionts although number and activity of endosymbionts may be regulated and change seasonally. Asymbiotic strains have not been observed in nature; thus, these species are considered obligate mixotrophs. Photosynthesis may cover all or part of their respiratory demands for carbon and, thus, they are probably relatively resistant to starvation. They appear to use 'excess' carbon (Hessen & Anderson 2008) from photosynthesis in building support and protective structures such as gelatinous colonies (e.g. *Ophrydium versatile*), contractile stalks (e.g. *Vorticella chlorellata*) and some produce anti-predation compounds and/or myco-sporine-like compounds to prevent UV damage (e.g. *Maristentor*

dinoferus and *O. naumanni*) (Lobban et al. 2002, Modenutti et al. 2005, Sommaruga et al. 2006).

Stentor spp. and *Ophrydium* spp. with algal endosymbionts can dominate the annual ciliate biomass and make an important contribution to total photosynthetic biomass in some oligotrophic lakes (Beaver & Crisman 1989a, Bienert et al. 1991, Woelfl & Geller 2002) (Table 1). *Maristentor dinoferus* is conspicuous on coral reefs in Guam (Lobban et al. 2002). However, large cell-size, sessile photosynthetic ciliates are generally rare in marine environments (Table S2), perhaps because of the lack of suitable substrates in most oligotrophic, marine planktonic ecosystems and also perhaps due to greater predation pressure on large cell-size ciliates in the marine than in the freshwater ecosystems they inhabit.

(2) Oxyclyne photosynthetic ciliates are common in freshwater lakes with a euphotic zone that penetrates into hypoxic or anoxic waters during stratification (Table S2). Acquired phototrophy is used by these ciliates as a source of oxygen as well as carbon.

Oxyclyne photosynthetic ciliates usually have green algal endosymbionts and include ciliate genera from several lineages including the Hypotrichia, Oligotrichida, Litostomatea, Prostomatea, and Peniculia (Table S2). They include large 'benthic' species, such as *Euplotes daidaleos* and *Frontonia*, that migrate into the water column from anoxic sediments during summer stratification in temperate lakes, as well as planktonic species, such as *Acaryophyra* and *Disemastoma butschlii* (Berninger et al. 1986, Beaver & Crisman 1989b). In some cases, the algal endosymbiosis is persistent, but in many cases it is transient, with asymbiotic ciliates found in the benthos or water column during mixing (Berninger et al. 1986, Beaver & Crisman 1989b). Thus, many of these species are facultative rather than obligate mixotrophs (Fig. 2). Although most oxyclyne photosynthetic ciliates have algal endosymbionts, there is an interesting example, *Perispira ovum*, which retains organelles from ingested *Euglena*. It was found at the oxic-anoxic boundary in a fjord-like estuary (Johnson et al. 1995).

Photosynthetic ciliates can reach very high population densities in thin layers within or just below the oxyclyne in some lakes (Berninger et al. 1986, Finlay et al. 1996, Macek et al. 2008). Finlay et al. (1996) observed ciliate populations of over $3 \times 10^3 \text{ ml}^{-1}$, 96% of which had algal endosymbionts, in thin layers within anoxic water of a pond (Finlay et al. 1996). They calculated that algal endosymbionts can evolve enough oxygen to meet about one-half of the respiratory demands of the ciliate hosts. Residence, for whole or part of the day, in hypoxic or anoxic waters can have many advantages for an aerobic ciliate able to obtain oxygen, including high food density and refuge from predators.

Table 1. Location and importance of ciliates that carry out acquired phototrophy in freshwater plankton assemblages

Location	Contribution/comments	Source
Eurasia		
Lake Baikal, Russia	Contribute up to 6 % of the under ice and 80–90 % of the summer ciliate assemblage, augment autotrophic biomass by 30–40 %.	Obolkina (2006)
Small lakes, southern Estonia	<i>Strombidium viride</i> common in epilimnion, high densities of <i>Coleps hirtus</i> and <i>C. spetai</i> in metalimnion.	Zingel & Ott (2000)
Oligotrophic lakes, North Europe	Ciliate biomass in lakes above timberline dominated by large photosynthetic oligotrichs.	Macek et al. (2006)
Alpine Lake Traunsee, Austria	Ciliates with endosymbionts up to 25 % of total ciliate abundance in surface waters.	Sonntag et al. (2006)
Piburger See (oligo-mesotrophic lake), Austria	Mixotrophic ciliates present under ice and in surface waters during summer.	Sommaruga & Psenner (1995), Macek et al. (1996)
Řimov Reservoir (eutrophic), Czech Republic	Autotrophy covers ~43 % of <i>Pelagohalteria viridis</i> carbon requirements.	Šimek et al. (1996)
Lake Constance, Germany	<i>Pelagohalteria viridis</i> abundant at onset clear-water phase.	Müller et al. (1991)
Gravel Pit Lake (meso-eutrophic), Germany	<i>Coleps hirtus viridis</i> dominant planktonic ciliate, averages 68 % of ciliate biomass.	Auer et al. (2004)
Priests Pot (eutrophic pond), England	Ciliates with endosymbionts abundant in oxic-anoxic boundary during summer stratification; up to 3466 ciliates ml ⁻¹ of which 96 % contain algal endosymbionts.	Berninger et al. (1986), Rogerson et al. (1989), Finlay et al. (1996)
Lake Carter (pond), England	In July, <i>Strombidium viride</i> contributed ~0.5 % of primary production; its abundance was 12 000 cells l ⁻¹ , its chlorophyll content was 160 pg chl cell ⁻¹ , and its photosynthetic rate was 18–54 pg C fixed cell ⁻¹ h ⁻¹ .	Perriss et al. (1994)
Lake Windermere, England	<i>Strombidium viride</i> one of the dominant ciliates, especially in oligotrophic section, densities of 2.5–3.0 cells l ⁻¹ .	Laybourn-Parry & Rogerson (1993)
Lake Pavin (oligomesotrophic), France	Mixotrophic oligotrichs abundant in euphotic zone, 2–53 % ciliate abundance and 5–91 % of ciliate biomass; <i>S. viride</i> dominant mixotrophic ciliate.	Carrias et al. (1998)
Reservoir, France	<i>Pelagohalteria viridis</i> dominant ciliate.	Thouvenot et al. (1999)
Oligomesotrophic Lake, France	Mixotrophic ciliates >50 % of the ciliate biomass during spring.	Amblard et al. (1993)
Bog Lake, Germany	Mixotrophic oligotrichs dominated ciliate biomass during ice melt.	Macek et al. (2001)
Africa		
Lake Tanganyika, Africa	<i>Strombidium viride</i> biomass is equal to or more than that of phytoplankton during stable stratification, but lower during mixis. Contributes most of the ciliate biomass.	Hecky & Kling (1981), Pirlot et al. (2005)
North America		
Small oligotrophic lake, Pennsylvania, USA	Mixotrophic ciliates 58 % of abundance and 88 % of ciliate biovolume during summer and fall; after winter mixis, mixotrophic ciliates 5 % of abundance and 58 % of ciliate biovolume.	Holen (2000)
Lake Olgethorpe, Georgia, USA	<i>Strombidium viride</i> found during winter mixis and summer stratification; 0.9–51.1 % ciliate abundance, 0.1–13.4 % of ciliate biomass; ciliates with endosymbionts (<i>Paradileptus</i> , <i>Stokesia vernalis</i>) observed during stratification.	Pace (1982)
Lake McCloud (acidic, oligotrophic), Florida, USA	<i>Stentor niger</i> >90 % of ciliate biomass and estimated 30 % of total autotrophic biomass, <i>Strombidium viride</i> often numerically dominant.	Bienert et al. (1991)
Acidic, oligotrophic lakes, Florida, USA	<i>Stentor niger</i> comprised annual average of 64 % of ciliate biomass, dominant in spring and summer.	Bienert (1987, cited in Beaver & Crisman 1989b)
Humically colored lakes, USA	15 % of annual pelagic autotrophic biomass; most abundant during summer stratification, when often contribute >50 % of autotrophic biomass.	Beaver et al. (1988 cited in Beaver & Crisman 1989b)
Lake Alchichica (warm, monomictic), Mexico	<i>Euplotes cf daidaleos</i> and <i>Pelagothrix</i> sp. important in oxycline.	Macek et al. (2008), Peštová et al. (2008)
South America		
Temperate, oligotrophic lake, Chile	<i>Stentor araucanus</i> , <i>S. amethystinus</i> , <i>Ophrydium naumanni</i> combined: 16 % of ciliate abundance, 92 % of ciliate biomass, and 47 % of total zooplankton biomass. Estimated annually account for 4 % of autotrophic biomass, 6.5 % of total photosynthesis.	Woelfl & Geller (2002)

Table 1 (continued)

Location	Contribution/comments	Source
Ultraoligotrophic lake Moreno Oeste, Argentina	During summer stratification, <i>Ophyridium naumanni</i> formed deep chlorophyll max.; <i>Stentor araucanus</i> in upper epilimnion.	Quieimalinos et al. (1999), Modenutti & Balsiero (2002), Modenutti et al. (2005)
Australia Australian lakes	Large <i>Stentor</i> sp. 4–69% of total plankton photosynthesis in winter, spring and autumn.	Laybourn-Parry et al. (1997)
Antarctica Saline lakes	<i>Myrionecta rubra</i> dominant ciliate and an important component of phytoplankton, up to 2.7×10^5 cells l ⁻¹ .	Bell & Laybourn-Parry (1999), Laybourn-Parry (2002)
Freshwater lake, Vestford Hills	<i>Strombidium viride</i> most common ciliate sp.	Laybourn-Parry et al. (1991)

Table 2. Location and importance of ciliates that carry out acquired phototrophy in marine plankton assemblages. MR: *Myrionecta rubra*; PO: plastidic oligotrichs; chl: chlorophyll; ave.: average

Location	Contribution/comments	Source
POLAR		
Arctic		
Iceland, Greenland and Barents Seas	In surface waters 58–65% of ciliate abundance; ave. 4–15% of total chl in summer.	Putt (1990a)
Irminger Basin, open sea	MR 0–5 cells ml ⁻¹ at 5 m, winter, spring and summer.	Montagnes et al. (2008)
Disko Bay, coastal Greenland, 0–28 m	PO 13% of ciliate abundance and 30% ciliate biomass in summer; MR up to 34% of ciliate biomass in spring.	Levinsen et al. (1999, 2002), Levinsen & Nielsen (1999)
Western Bering Sea	Late spring-early summer, 30–40% of ciliate abundance on shelf	Sorokin et al. (1996)
Cobb Seamount, Eastern subarctic Pacific, 0–24 m	Ave. 40% of ciliate biomass.	Sime-Ngando et al. (1992)
Western subarctic Pacific, 0–30 m	Late spring–summer, 30–50% of ciliate abundance.	Booth et al. (1993, cited in Pitta & Giannakourou 2000)
Western Subarctic Pacific, 0 m	PO 28% of ciliate abundance and 48% of ciliate biomass in spring; 13% of ciliate abundance and 39% of ciliate biomass in fall	Suzuki & Taniguchi (1998)
Antarctic		
McMurdo Sound, 5 m	PO ~25% of 'oligotrichs' in bloom period; 47% of 'oligotrichs' in post-bloom during spring–summer.	Stoecker et al. (1995)
Weddell-Scotia Seas, 0–85 m	PO 10% of large ciliate abundance in fall and winter.	Gowing & Garrsion (1992)
Southern Ocean, 5 m	PO <5% of total ciliates, 0–5% of total chl in winter.	Froneman & Perissinotto (1996)
Kerguelen Plateau, Southern Ocean	Mixotrophic ciliate biomass 40–60% of total aloricate ciliate biomass.	Christaki et al. (2008)
TEMPERATE SEAS		
Baltic Sea		
Gdansk Basin	MR 58–73% of mean annual ciliate biomass; <15% of ave. total chl, but at some stratified stations contributed >24% of total chl.	Witek (1998)
Open North Baltic, surface layers	MR ~10% of total primary production during spring, dominant ciliate.	Leppänen & Bruun (1986)
Open Baltic	MR abundant in surface waters and at in deep layers down to 80 m.	Setälä & Kivi (2003)
Atlantic		
Southampton Water, UK	Recurrent MR red-tides in summer, over 1000 cells ml ⁻¹ ; chl <i>a</i> over 100 µg l ⁻¹ .	Crawford et al. (1997)
Estuary, Maine, USA	<i>Laboea strobila</i> up to 15% of annual ciliate biomass and up to 6% of annual primary production; MR up to 60% of annual ciliate biomass; <i>L. strobila</i> + MR up to 23% of estimated total primary production in winter	Sanders (1995)

Table 2 (continued)

Location	Contribution/comments	Source
Woods Hole, USA, coastal, surface	Annual ave. 31% of oligotrichs and choreotrichs; 45% of non-loricate ciliates; in summer up to 90% of oligotrichs had plastids.	Stoecker et al. (1987)
Salt Pond estuary, Cape Cod, USA	MR accounted for <1 to 100% chl <i>a</i> and <1 to >70% of the community primary production.	Stoecker et al. (1991)
Georges Bank, NW Atlantic, euphotic zone	In early summer, 30% of ciliate abundance at <100 m stations, ≤3% at deeper stations. Ave. ~9% total chl.	Stoecker et al. (1989)
Irish Sea, water column	Late spring, MR contribute >70% chl <i>a</i> at some stations.	Montagnes et al. (1999)
Norwegian fjord and poll, 0 + 7 m	Late spring, 3–7% of total ciliates.	Verity & Vernet (1992)
Open Ocean, North Atlantic, 0–20 m	Spring, 16–39% of total ciliates, 32–68% of total oligotrichs; often dominate ciliate biomass.	Sieracki et al. (1993), Stoecker et al. (1994)
Pacific		
Coastal Fjord, British Columbia, Canada	<i>Laboea</i> and <i>Tontonia</i> 1–2% of abundance and 7% of ciliate biomass.	Martin & Montagnes (1993)
Hiroshima Bay, Japan, surface layers	In summer, PO dominate ciliate assemblages.	Kamiyama et al. (2003)
San Francisco Bay, California, USA	Red tides of MR associated with strong stratification in estuary.	Cloern et al. (1994)
Coastal lagoon, Mexico	MR 0–420 cells ml ⁻¹ .	Bulit et al. (2004)
SUB-TROPICAL		
Mediterranean Sea		
Gulf of Naples	PO ~40% ciliate biomass and 27% of abundance; MR 13% of ciliate biomass and 17% of abundance. MR estimated to contribute 3% annual primary production.	Modigh (2001)
Blanes Bay, 0.5 m	18% of oligotrichs.	Vaque et al. (1997)
Ligurian Sea, 0–50 m	In spring, PO 46% of abundance and 39% of oligotrich biomass, MR 6–11% ciliate abundance and 1–2% ciliate biomass.	Perez et al. (2000)
Ligurian Sea, surface waters	Year round av. 51% of ciliate biovolume; in spring and summer ~60–100% of ciliate biovolume.	Bernard & Rassoulzadegan (1994)
Catalan Sea, oligotrophic	In early summer, 63% of ciliate biomass at 5 m; 21% of ciliate biomass integrated over 0–80 m; ciliates estimated to contribute <0.5% to 20% of total chl.	Dolan & Marrase (1995)
Open Mediterranean Sea, oligotrophic, upper 200 m	In late spring, 17% of integrated abundance and 18% of integrated ciliate biomass.	Pitta et al. (2001)
Aegan Sea, Oligotrophic, 0–100 m,	In spring, PO 17–54% of total ciliate abundance and 13–62% of ciliate integrated biomass.	Pitta & Giannakourou (2000)
Atlantic		
Sargasso Sea, surface waters	Late spring, PO 37% of ciliate abundance.	Stoecker et al. (1991)
Gulf Stream, surface waters	Late spring, PO 25% of ciliate abundance.	Stoecker et al. (1991)
Pacific		
Peru upwelling	Blooms of MR; 100–125 mg chl <i>a</i> m ⁻³ ; photosynthetic rates of 1000–2000 mg C m ⁻³ h ⁻¹ .	Smith & Barber (1979)
Hiroshima Bay, Japan, surface and near surface layers	In summer, dominant ciliates.	Kamiyama et al. (2003)
Yellow Sea, surface waters	Late spring, <i>Laboea strobila</i> , 0 to >400 cells l ⁻¹ .	Zhang et al. (2002)
East China Sea, 2 m to bottom or 100 m	In summer, in Yangtze (Chiangjiang) River plume, ≥50% of oligotrich and choreotrich ciliates; 7.7% chl <i>a</i> in plume.	Chiang et al. (2003)
East China Sea	PO 33% ciliate abundance and 44% of ciliate biomass in summer, 48% ciliate abundance and 44% ciliate biomass in fall, 28% ciliate abundance and 5% of ciliate biomass in winter; MR 11% abundance and 5% biomass in winter.	Ota & Taniguchi (2003)

Table 2 (continued)

Location	Contribution/comments	Source
Subtropical Western Pacific, 0 m	In spring, PO 45% of abundance and 35% of ciliate biomass.	Suzuki & Taniguchi (1998)
Baja California upwelling system	MR red water patches with up to 538 cells ml ⁻¹ , sometimes subsurface max.	Packard et al. (1978)
TROPICAL		
Lime Cay, Jamaica, 5 m	Annually, <i>Laboea</i> and <i>Tontonia</i> 12% of ciliate abundance and 25% of ciliate biomass; MR 3% of abundance and 1% of ciliate biomass.	Lynn et al. (1991, cited in Pitta & Giannakourou 2000)
Equatorial Pacific, 140° W, 0–120m	El nino conditions- plastidic ciliates 30% of ciliate biomass; relaxation of El Nino-7% of ciliate biomass	Stoecker et al. (1996)
Continental Shelf off Brazil	Subsurface layers MR with abundances >4000 cells ml ⁻¹ , chl <i>a</i> up to 79 µg l ⁻¹ .	Owen et al. (1992)

(3) Planktonic, free-swimming ciliates that use photosynthesis primarily to cover some or all of their respiratory demand for carbon are common in the mixed layer, particularly under stratified conditions, in marine and freshwater ecosystems (Tables 1 & 2). Kleptoplastidic oligotrichs are the most common and abundant photosynthetic ciliates in this niche (Table S2).

Most mixotrophic oligotrichs ingest nanophytoplankton and retain algal plastids derived from their prey (Table S2). However, some tide pool oligotrichs ingest swimmers of green macroalgae and retain their plastids and eyespots (McManus et al. 2004). Mixotrophy in plastidic oligotrichs is obligate and non-plastidic individuals are not observed (Stoecker et al. 1988, Stoecker & Silver 1990) (Fig. 2). In the marine species, plastids from a variety of chromophytic and chlorophytic algae can be retained and many types of plastids can be observed within an individual ciliate. Little is known about plastid specificity in freshwater oligotrichs (Table S2). Plastid turn-over is rapid (usually hours) in the light, with plastids being continuously replaced through ingestion of algae (Stoecker & Silver 1990).

Some mixotrophic oligotrichs have algal endosymbionts instead or in addition to retained plastids (Table S2). Most of the identified algal endosymbionts are prasinophytes or other green algae (Table S2). Jonsson (1987) observed 2 wk survival of *Pyramimonas* sp. endosymbionts in cultures of the estuarine oligotrich *Strombidium reticulatum*. This may indicate that endosymbionts turnover much more slowly than isolated plastids in oligotrichs. In freshwater ciliates, algal endosymbionts are observed in some planktonic Heterotrichea, Oligotrichida, Stichotrichia, Litostomatea, Prostomatea and Penicula (Table S2). Of these, *Stokesia vernalis* and *Askenasia chlorelligera* (Table S2) can be abundant in the epilimnion of lakes during summer stratification (Berninger et al. 1986, Sommaruga & Psenner 1995).

Mixotrophic oligotrichs vary in their chlorophyll contents, photosynthetic capacities and probably in their reliance on phototrophy as a source of fixed carbon. One of the largest and most photosynthetic, *Laboea strobila*, is found in estuaries and oceans world-wide (Table S2) and its physiological ecology has been investigated in the laboratory and field (Table 3). Photosynthesis can contribute an estimated 6% of cell C h⁻¹, while maximum ingestion is about the same (recalculated from Stoecker et al. 1988, Stoecker & Michaels 1991). Photosynthate is used primarily to meet respiratory demand for carbon (Putt 1990b). In the light, in addition to the carbon fixation measured in ¹⁴C incubations, respiratory loss of cell carbon may be spared (Stoecker & Michaels 1991).

The effect of mixotrophy on the ability to survive starvation is light dependent. In culture, some plastid retaining oligotrichs can have high survival without food for at least 2 d, with some individuals surviving as long as 4 to 6 d on a light:dark cycle (Stoecker et al. 1988–1989). Most heterotrophic ciliates quickly go into starvation mode, reducing their rates of respiration or encysting (Crawford & Stoecker 1996). However, in the dark, plastid-retaining ciliates may be more susceptible to starvation than heterotrophic ciliates, since they do not appear to be able to reduce their dark respiration rates (Crawford & Stoecker 1996). Their dependence on both light and prey may make them particularly vulnerable to mixing below the euphotic zone.

Among the marine and perhaps also freshwater planktonic oligotrichs, acquired photosynthesis appears to be a strategy to take advantage of algal blooms that occur at the onset of thermal stratification or that are associated with ice or ice melt (Macek et al. 1996, 2001). By storing and using photosynthetic machinery (plastids) and recycling nutrients within themselves, they may be able to functionally prolong their coupling to an algal bloom. Although mixotrophic oligotrichs may not be able to grow as fast as heterotro-

Table 3. *Myrionecta rubra* and *Laboea strobila*. Cell size, chlorophyll *a* content and rates of photosynthesis, ingestion and respiration in 2 marine planktonic ciliates with acquired phototrophy — the obligate phototroph *M. rubra* and an obligate mixotroph, the plastid-retaining ciliate *L. strobila*. Sources are given in the footnote; rates measured on cultured (Cul.) or wild populations (W)

Species	Cell size	Chl <i>a</i> (pg cell ⁻¹)	Photosynthesis (pg C cell ⁻¹ h ⁻¹)	Cell specific rates (C cell ⁻¹ h ⁻¹)		
				Photosynthesis	Ingestion	Respiration
<i>Myrionecta rubra</i> (at 15–20°C)	~600 pg C; ~3300 μm ³ a	8–13 ^a	75–85 ^a	2–14 % (at P _{max}) ^a	0.02–0.2 % ^b	~0.1 % ^{a,c}
<i>Myrionecta rubra</i> (at 0–5°C)	3000–4200 μm ³	8–58 ^e	10–55 ^e	1.8–10 % (at P _{max}) ^f	0–0.4 % ^{d,g}	
<i>Laboea strobila</i>	9–14 ng C ^{h,i} ; ~110 × 10 ³ μm ³	187–248 ^{h,j}	925 (at P _{max}) ^{j,k} ; 260–277 (at P _{max}) ^{k,m}	6.4 % (at P _{max}) ^l ; ~2.8 % (at P _{max}) ^k	5.9 % (food saturated) ^j	av. 2.1 % ⁱ

^aStoecker et al. (1991), W; ^bYih et al. (2004), Cul.; ^crecalculated from Smith & Barber (1979); ^dJohnson et al. (2006), Cul.; ^eJohnson & Stoecker (2005), Cul.; ^frecalculated from Johnson & Stoecker (2005), Cul.; ^grecalculated from Gustafson et al. (2000); ^hStoecker et al. (1987); ⁱStoecker & Michaels (1991), W & Cul.; ^jStoecker et al. (1988); ^kPutt (1990b), Cul.; ^lrecalculated from Stoecker et al. (1988); ^mfor measurements on wild populations refer to Stoecker et al. (1989), Putt (1990b)

phic ciliates (Dolan & Perez 2000), by being able to temporarily withstand food-limiting conditions without stepping-down their metabolism, they may be able to take better advantage of nanophytoplankton blooms that are temporally and spatially patchy.

Plastidic oligotrichs are relatively abundant in oligotrophic, mesotrophic and sometimes eutrophic surface waters (Tables 1 & 2). Total oligotrich abundance is positively correlated with chlorophyll in the sea and the percentage of oligotrichs that are photosynthetic is relatively constant, averaging 30% (Dolan & Perez 2000). At a coastal Mediterranean site, about 41% of all oligotrich species were observed to be plastidic (Laval-Peuto & Rassoulzadegan 1988). In some oligotrophic lakes, plastidic oligotrichs dominate the ciliate assemblage during stratification (Beaver & Crisman 1989b, Pirlot et al. 2005). In both marine and fresh waters, peak abundances coincide with stratification.

(4) Acquired phototrophy in *Myrionecta rubra* (*Mesodinium rubrum*) is cellularly and physiologically unique among ciliates. In contrast to the other photosynthetic ciliates, it is an obligate phototroph and obtains almost all its carbon from photosynthesis, and nitrogen and phosphorus from uptake of dissolved inorganic nutrients (Fig. 2). It appears to alternate between 'bloom' and 'slow growth-maintenance' life styles in the marine plankton.

Myrionecta rubra has cryptophyte plastids or endosymbionts, which give it a reddish color (Taylor et al. 1971, Smith & Barber 1979, Hansen & Fenchel 2006, Johnson et al. 2006, Johnson et al. 2007). It can survive and grow for long periods without feeding, but periodic ingestion of suitable cryptophytes (*Teleaulax/ Geminigera* clade) is necessary to maintain high photosynthetic and growth rates (Gustafson et al. 2000, Johnson & Stoecker 2005, Park et al. 2007). Although most of its body carbon comes from photosynthesis, it requires cryptophytes as a source of plastids, nuclei and/or or-

ganic growth factors (Johnson & Stoecker 2005, Hansen & Fenchel 2006, Johnson et al. 2007). In the absence of suitable prey it can remain photosynthetic and survive for prolonged periods (months) at low irradiance (Johnson & Stoecker 2005, Smith & Hansen 2007).

Myrionecta rubra is well known for its ability to form 'red water' surface or subsurface blooms and to migrate vertically (Lindholm 1985, Crawford 1989) (Table 2). *M. rubra* blooms in the coastal ocean are usually associated with upwelling events and estuarine blooms with nutrient delivery followed by stratification. *M. rubra* blooms can reach densities of over 10⁶ cells l⁻¹ with chlorophyll values of over 100 mg chl *a* m⁻³ and rates of primary production of over 1000 mg C m⁻³ h⁻¹ (Smith & Barber 1979, Owen et al. 1992, Crawford et al. 1997). Some of the highest rates of primary production in the sea have been measured in red waters caused by this ciliate (Crawford 1989). *M. rubra*, when well supplied with suitable cryptophyte prey and nutrients, is capable of high rates of photosynthesis and spurts of rapid population growth (Johnson & Stoecker 2005, Smith & Hansen 2007). It may be only under these conditions that *M. rubra* inhabits well-lit, surface waters.

Myrionecta rubra occurs more routinely at low densities and can be found year-round in most estuarine and coastal waters (Crawford 1989, Montagnes & Lynn 1989, Smith & Hansen 2007). It is often an important member of the microplankton in winter, in turbid waters, and at or near the base of the euphotic zone, all of which are relatively low light environments (Table 2) (Lindholm & Mork 1990, Stoecker et al. 1991, Sanders 1995, Levinsen et al. 2000, Levinson & Nielsen 2002, Setälä & Kivi 2003). Peak population densities can be below its compensation depth for photoautotrophy (Crawford & Lindholm 1997). Laboratory studies show that *M. rubra* is well adapted to survive and grow slowly at low irradiances (which reduces plastid

turnover) when cryptophyte prey is scarce (Johnson & Stoecker 2005).

We speculate that high populations of suitable cryptophytes in the water column are a necessary antecedent to *Myrionecta rubra* surface blooms. Ingestion of suitable prey may result in a 'switch' in physiology, behavior and growth, resulting in surface and near surface accumulations of cells. When cryptophytes are depleted, rates of photosynthesis and growth in *M. rubra* decline and this decline is much more rapid in high than low light (Johnson & Stoecker 2005). These physiological changes may trigger a change in photo-behavior and locomotion resulting in aggregation of 'starved' *M. rubra* cells in low light environments where plastid life is extended. However, this hypothesis remains to be tested.

Dinoflagellates

Dinoflagellates are a physiologically diverse group of protists, with about half of all species carrying out strict heterotrophy and the rest capable of phototrophy. Both heterotrophic and photoautotrophic dinoflagellate species include members that are parasites, and many of the phototrophs are mixotrophic (phagocytic). Phototrophic dinoflagellates have the highest diversity of plastid types of any eukaryote lineage. In addition to their major peridinin-chlorophyll *c* containing plastid, various dinoflagellate species may possess a permanent chlorophyll *b* containing plastid or a chlorophyll *c*-fucoxanthin containing plastid (Delwiche 1999). Furthermore, there are at least 6 species that possess a permanent diatom endosymbiont, lacking its own cell wall, but still having an apparently unreduced second eukaryotic nucleus (Tomas & Cox 1973, Chesnick et al. 1997). In spite of this high diversity of plastids and permanent endosymbionts, it is perhaps surprising that the dinoflagellates have relatively few examples of acquired phototrophy when compared to the ciliates or Rhizaria (see Tables S1, S2 & S3 available as supplementary material at www.int-res.com/articles/suppl/a057p279_app.pdf). While only about 1% of all dinoflagellates can be classified as carrying out acquired phototrophy, and nearly all these are rare or generally low in abundance, several species may be conspicuous due to their potential impact on human health (Table 4). The toxin producing *Dinophysis* spp. and the controversial harmful species *Pfiesteria piscicida* are both organelle-retaining dinoflagellates with global distributions in estuarine and coastal oceanic waters. Another species, *Noctiluca scintillans*, may possess prasinophyte endosymbionts in tropical waters and form periodic non-toxic blooms in coastal waters (Sriwoon et al. 2008).

Most dinoflagellates that carry out acquired phototrophy do so by sequestering plastids or multiple organelles from their algal prey for temporary use. Only 2 dinoflagellate species, *Noctiluca scintillans* and *Podolampus bibes*, which host endosymbionts are also capable of a free-living existence (Table S3). Thus, dinoflagellates appear to be more adapted to carrying out organelle retention than to endosymbiosis per se. Most dinoflagellates that sequester foreign organelles belong to the Gymnodiniaceae or Dinophysiaceae families. Organelle retaining members of both families were at one time misidentified as being phototrophic, due to their specific prey selection and feeding habits, which in nature results in a nearly constant presence of sequestered organelles from one type of prey. All members of the Gymnodiniaceae sequester multiple organelles from their prey and generally maintain them for 2 to 12 d (Fields & Rhodes 1991, Skovgaard 1998). Laboratory research on *Gymnodinium gracilentum* and *Amphidinium poecilochroum* has shown that these species are capable of growing in the dark, albeit with reduced growth rates (Jakobsen et al. 2000).

Little is known about the ecology of Gymnodiniaceae that carry out acquired phototrophy. *Gymnodinium acidotum* has been described as excysting as colorless cells from sediment samples, before acquiring their cryptophyte organelles from free-living cells (Fields & Rhodes 1991). While *G. acidotum* may be the dominant 'phytoplankter' in natural freshwater systems (Farmer & Roberts 1990), high abundance in nature is most likely transient and linked to the availability of cryptophyte prey. *Amphidinium latum* and *A. poecilochroum* both have cryptic distributions in coastal marine environments, and appear to be associated with sediments (Larsen 1988, Horiguchi & Pienaar 1992). *A. salinum* has also been suspected of carrying out kleptoplasty due to irregularities in plastid size and position (Al-Qassab et al. 2002); however, no molecular or electron microscopy data are available that support this observation. The freshwater dinoflagellate *A. wigrense* (Table S3) has also been described as possessing cryptophycean plastids (Wilcox & Wedemayer 1985); however, it appears to be rare in lakes and ponds and its distribution is poorly known. In general, the phylogenetic positions of *Amphidinium* spp. that carry out acquired phototrophy are not well understood, and at least 7 additional obscure species with blue-green plastids (cryptophycean) have been reported: *A. amphidinioides*, *A. bourrellyi*, *A. caerulecens*, *A. glaucum*, *A. lacunarum*, *A. oculatum*, and *A. phthartum* (Calado & Moestrup 2005).

In contrast, *Dinophysis* species that carry out organelle retention sequester only the plastids of their prey and have extraordinarily long retention times. While *Dinophysis* is a mixotroph (Jacobson & Ander-

Table 4. Importance of dinoflagellates that carry out acquired phototrophy in plankton assemblages

Location	Contribution/comments	Source
POLAR/SUB-POLAR		
Arctic		
Kandalaksha Gulf, White Sea	<i>Dinophysis acuminata</i> and <i>D. norvegica</i> up to 1550 cells l ⁻¹ during summer.	Vershinin et al. (2006)
Arctic Ocean	<i>Amylax triacantha</i> and <i>Dinophysis norvegica</i> widespread.	Okolodkov & Dodge (1996)
Antarctic		
Ross Sea	Unidentified dinoflagellate with Kleptoplastids (RS-Dino) maximum of 3 × 10 ⁴ cells l ⁻¹ in sea surface and 9 × 10 ⁵ cells l ⁻¹ in slush; estimated using qPCR.	Gast et al. (2007)
TEMPERATE		
Baltic Sea		
Gulf of Gdańsk, Poland	0.1–4000 cells l ⁻¹ ; 0.5–21 % of phytoplankton biomass between July–October.	Żmijewska et al. (2000)
Cental Baltic Sea, east of Gotland	Subsurface thermocline maximum of 40–150 × 10 ³ cells l ⁻¹ ; surface < 5 cells l ⁻¹ .	Carpenter et al. (1995)
Atlantic		
German Bight, North Sea	<i>Dinophysis norvegica</i> , max. of 400 cells l ⁻¹ ; <i>D. acuminata</i> summer max of 4000 cells l ⁻¹ .	Klöpper et al. (2003)
Galician Rías Bajas, NW Spain	<i>Dinophysis acuminata</i> , up to 500–28 000 cells l ⁻¹ during September.	Maneiro et al. (2000)
Nycklebyviken, North Sea, NW Sweden	<i>Dinophysis</i> spp. 0–14000 cells l ⁻¹ during October–November.	Godhe et al. (2002)
Dutch Coast, North Sea	<i>Noctiluca scintillans</i> (non-symbiotic) summer abundance peaks at 35–240 cells dm ⁻³ .	Daan (1987)
Estuarine and coastal western North Atlantic	<i>Pfiesteria piscicida</i> < 2000 cells l ⁻¹ .	Lin et al. (2006)
Pacific		
Okkirai Bay, northern Japan	<i>Dinophysis fortii</i> reached ~200 cells l ⁻¹ in June; max. densities were preceded by cryptomonad blooms.	Koike et al. (2007)
SUB-TROPICAL		
Mediterranean Sea		
Greek coastal waters	<i>Dinophysis acuminata</i> max. in February of 85.4 cells l ⁻¹ ; blooms found above pycnocline.	Koukaras & Nikolaidis (2004)
Alfacs Bay, Catalonis Spain	<i>Dinophysis sacculus</i> is most abundant in fall, winter and spring months; to 4000 cells l ⁻¹ .	Garces et al. (1997)
Varano Lagoon, SE Italy	<i>Dinophysis sacculus</i> maximum abundance in late June and November; up to 5840 cells l ⁻¹ .	Caropo (2001)
Balear-Provençal, Ioian, Adriatic Sea basins	<i>Amphidinium latum</i> present.	Gómez (2003)
All Mediterranean sub-basins	<i>Podolampas bipes</i> present.	Gómez (2003)
Gulf of Trieste	<i>Dinophysis</i> spp. max. in June of 2000 cells l ⁻¹ .	France & Mozetič (2006)
Atlantic		
Gulf of Mexico	<i>Dinophysis mitra</i> present.	Balech (1967)
TROPICAL		
Andamen Sea, Indian Ocean	<i>Noctiluca scintillans</i> present at ~1 cell l ⁻¹ .	Eashwar et al. (2001)
SE India, Indian Ocean	<i>Noctiluca scintillans</i> red tide reached 9 × 10 ⁵ cells l ⁻¹ .	Sahayak et al. (2005)
Manila Bay, Philippines, Western Pacific	<i>Noctiluca scintillans</i> (symbiotic) red tide (February–April) reached ~5000 cells l ⁻¹ .	Furuya et al. (2006)
Gulf of Thailand, South China Sea	<i>Noctiluca scintillans</i> (symbiotic) abundance exceeded 100 cells l ⁻¹ from January to August at 0.5 m depth; max. of 18.7 × 10 ³ cells l ⁻¹ .	Sriwoon et al. (2008)

sen 1994), some species may grow for prolonged periods as a phototroph before needing to feed (Park et al. 2008). Plastid sequestration in *Dinophysis* is unique, because rather than feeding directly on cryptophyte

algae, it sequesters cryptophyte organelles from its ciliate prey *Myrionecta rubra* (Park et al. 2006). Plastid sequestration from cryptophyte algae to *M. rubra*, and then from *M. rubra* to *Dinophysis* is a fascinating

example of the complexity of microbial food webs and their often non-hierarchical trophic dynamics. Plastids in *D. fortii* may persist for 40 d or more (Nagai et al. 2008), while plastids in *D. caudata* persist for over 2 mo (Park et al. 2008). While most photosynthetic *Dinophysis* species sequester plastids from cryptophyte algae, *D. mitra* has been shown to possess prymnesiophyte plastids belonging to the class Prymnesiophyceae (Koike et al. 2005). The precise identification of their haptophyte prey, however, remains elusive and the feeding and sequestration mechanism of *D. mitra* has not been described.

Plastid-retaining *Dinophysis* spp. are globally distributed in coastal marine environments and are known to produce diarrhetic shellfish toxins (Hallegraeff & Lucas 1988, Lee et al. 1989). Typical 'blooms' of *Dinophysis* spp are <100 cells ml^{-1} (Hallegraeff & Lucas 1988), which is a much lower abundance than most bloom-forming dinoflagellates. The reasons for high abundance of *Dinophysis* spp. are not well understood, but have been connected to chemical and/or physical environmental factors as well as life history dynamics (Caroppo 2001). In a 3 yr study in Okkirai Bay, Japan, high abundance of *D. fortii* was always preceded by blooms of *Teleaulax* spp. cryptomonads (Koike et al. 2007). The connection between these events is likely bridged by elevated abundance of *Myrionecta rubra*, but there was no discussion of such a link in Koike et al. (2007).

Perhaps the most basic form of organelle sequestration is carried out by the dinoflagellates *Pfiesteria piscicida* (Lewitus et al. 1999) and *Cryptoperidiniopsis* sp. (Oodiniaceae) (Eriksen et al. 2002). *P. piscicida*, known for its controversial association with estuarine fish kills, retains photosynthetically active plastids from cryptophyte prey (Lewitus et al. 1999). Unlike most organelle-retaining dinoflagellates, *P. piscicida* does not selectively graze one type of prey; rather they are extraordinarily opportunistic grazers that even resort to cannibalism (Burkholder & Glasgow 1997, Feinstein et al. 2002, Vogelbein et al. 2002). The ability of *P. piscicida* to maintain sequestered plastids is low compared to other organelle retaining dinoflagellates, losing plastids in moderate light levels in 1 to 2 d (Feinstein et al. 2002, Lewitus et al. 2006). Less information is available on the mixotrophic capacity of *Cryptoperidiniopsis* spp., however, growth of the dinoflagellate is more influenced by light levels than *P. piscicida* (Eriksen et al. 2002).

The organisation of multiple sequestered prey organelles appears to be a conserved trait amongst groups of dinoflagellates. Both *amylax buxus* and *A. triacantha* (Gonyaulaceae) possess foreign organelles of cryptophyte algal origin, organized in complexes resembling those found in the dinoflagellates *Gymnodinium acidotum* and *Amphidinium latum*. These complexes

typically house plastids, mitochondria, and cytoplasm from their prey, and may or may not have an associated prey nucleus (Farmer & Roberts 1990, Horiguchi & Pienaar 1992, Koike & Takishita 2008). The phototrophic ciliate *Myrionecta rubra* also maintains organelle complexes from its cryptophyte prey (Taylor et al. 1969, Hibberd 1977, Johnson et al. 2006). *M. rubra*, however, is unique in its organization of foreign organelles, as the associated prey nucleus is relatively stable and has been shown to be functional (Johnson et al. 2007). The organelle-retaining Antarctic dinoflagellate (RS-Dino) also appears to maintain a stable prey nucleus for some time (Gast et al. 2007), although the nucleus has not yet been shown to be transcriptionally active.

The dinoflagellate *Podolampus bipes* (Podolampaceae) has been described as possessing intact endocytobionts of dictyochophyte origin (Schweiker & Elbrächter 2004); however, nothing is known of the nature of the potential symbiotic relationship. The heterotrophic parasite of diatoms *Paulsenella* cf. *chaetoceratis* harvests plastids from diatom cells using a feeding tube (Drebes & Schnepf 1988) but the stability or function of these plastids are unknown.

At least 6 species of dinoflagellates possess permanent diatom endosymbionts composed of plastids, mitochondria, cytoplasm, and a nucleus (Inagaki et al. 2000, Tamura et al. 2005, Horiguchi & Takano 2006, Pienaar et al. 2007). These dinoflagellates are phototrophic, found in freshwater or coastal regions and embayments, may either be pelagic or mostly benthic (Tamura et al. 2005), and in some cases are known to produce non-toxic red tides (Kempton et al. 2002). These dinoflagellates do not fit within the classification scheme of acquired phototrophy, rather they represent stable tertiary endosymbiotic associations, falling somewhere between acquired phototrophy and stable plastid acquisition.

DOES ACQUIRED PHOTOTROPY MATTER TO AQUATIC ECOSYSTEMS?

Not all types of acquired phototrophy are important in all aquatic ecosystems (Fig. 4). In marine ecosystems, obligate mixotrophy in plastid-retaining oligotrich ciliates and obligate phototrophy in *Myrionecta rubra* is important at all latitudes, whereas mixotrophy in planktonic Rhizaria is important in tropical and subtropical oceans. Mixotrophy in benthic marine protists (primarily in foraminifera) is important on tropical reefs. Acquired phototrophy in dinoflagellates is rarely of quantitative significance in marine ecosystems. However, *Dinophysis* spp. with acquired phototrophy are of concern in marine food webs because of their toxicity.

In fresh water, acquired phototrophy in ciliates is important in many lakes and ponds, with plastid retention by oligotrichs particularly important in mesotrophic and oligotrophic lakes. Ciliates with green algal endosymbionts are important in the 'oxycline' in eutrophic lakes and ponds. Sessile and colonial ciliates with algal endosymbionts dominate in some oligotrophic lakes. Although dinoflagellates with acquired phototrophy occur in fresh water, there are no reports of them being quantitatively significant in food webs or in carbon flow. Freshwater foraminifera are not reported to have algal endosymbionts or plastids.

To evaluate the significance of acquired phototrophy to ecosystem processes we have chosen 3 types that are common in marine ecosystems: (1) obligate mixo-

trophy in marine foraminifera and radiolaria; (2) obligate mixotrophy in plastid-retaining oligotrichous ciliates; and (3) photoautotrophy in the ciliate *Myrionecta rubra*.

Foraminifera and Radiolaria

The vast majority of symbiotic foraminifera, Polycystinea, and Acantharea inhabit oligotrophic tropical and subtropical oceans (Table 5 and also see Table S1). A major issue for accurate biomass, primary production, and ecosystem function estimates is the wide size range these organisms can exhibit (juveniles to colonies), their delicateness, and their patchy distribution. Indeed, sampling techniques introduce strong biases for such measurements, as has been demonstrated between Niskin bottles, net tows, and *in situ* imaging (Michaels 1988, 1991, Stoecker et al. 1996, Dennett et al. 2002).

Most planktonic foraminifera species are cosmopolitan and occupy circum-global latitudinal climatic provinces. Species such as *Globigerinoides sacculifer* (Brady) usually make up 20% or more of tropical planktonic foraminiferan populations (Bé & Tolderlund 1971). Research examining the biogeography of planktonic foraminifera has observed that *Orbulina universa* morphospecies, one of the most common planktonic foraminifera inhabiting the surface waters of the World Ocean between 60° N and 50° S, show a clear correlation between genotype distribution and chlorophyll concentration from surface waters suggesting that species distribution is controlled by variations in surface ocean productivity (de Vargas et al. 1999). Such associations could be explained by specific differences between *Orbulina* genotypes and feeding behavior or symbiotic association. This latter hypothesis has been proposed to explain the faunal provincialism known from the fossil record of *G. rubber* (Thompson et al. 1979).

Polycystinea with acquired phototrophy are found in most marine environments but are generally more restricted to the warm oligotrophic waters of the tropical and subtropical regions. Although some symbiotic Polycystinea are found in surface water of Norwegian fjords (Dolven et al. 2007), little information is available with respect to the quantitative contribution and geographical extent of symbiotic Polycystinea. Overall, total Polycystinea production and diversity decline with increasing latitude (Anderson 1983b). In the Equatorial Pacific (140°W, equator), up to 50% of solitary Polycystinea have algal endosymbionts and contribute to over 60% of Polycystinea biomass (Stoecker et al. 1996). Maximum standing stocks of living Polycystinea bearing algal endosym-

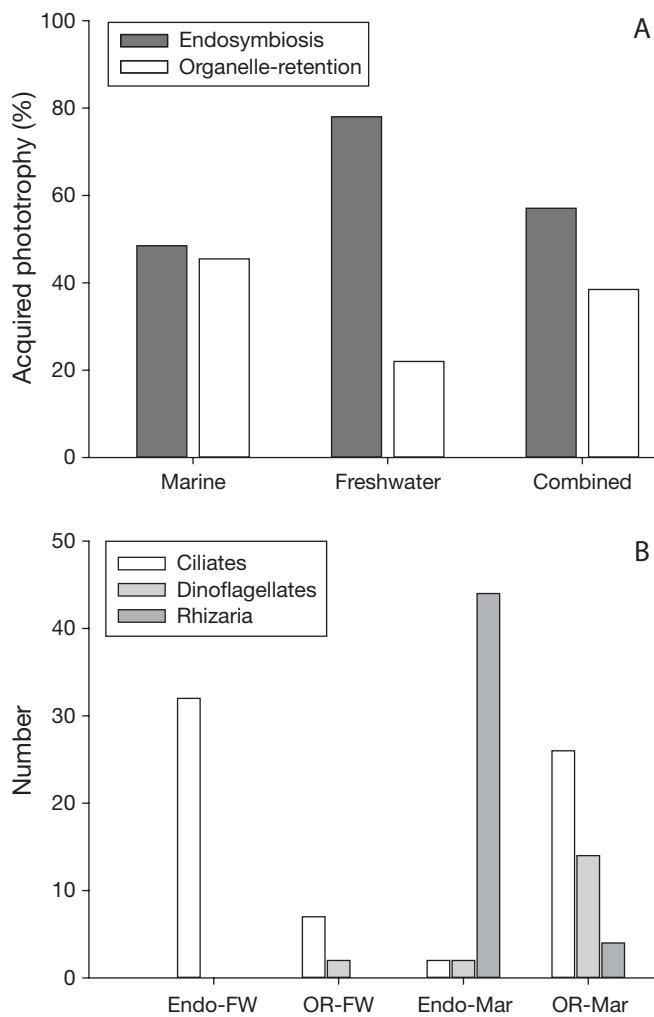


Fig. 4. (A) Percentage of the acquired phototrophic processes (endosymbiosis and organelle-retention) versus aquatic ecosystem; (B) number of species of acquired phototrophs in ciliates, dinoflagellates and rhizaria (foraminifera, radiolaria) according to ecosystem (FW: freshwater; Mar: marine) and process of acquired phototrophy (Endo: endosymbiosis; OR: organelle-retention)

Table 5. Location and importance of Polycystinea (Po), Acantharea (Ac), and Foraminifera (Fo) carrying out acquired phototrophy in plankton assemblages. PP: primary production; TPP: total primary production; ave.: average

Location	Contribution/comments	Source
SUB-TROPICAL		
Sargasso Sea, Bermuda	Ac and Fo accounted respectively for 0.41 and 0.06% of TPP in surface water over a 2 yr ave.; sarcodines ave. 21 % of PP for the >70 μm cell size fraction.	Caron et al. (1995)
Central North Pacific, VERTEX station	Over 18 mo, Ac abundances reached up to 4 cells l^{-1} and their PP was <4% of the TPP; they accounted for 6–35 % of PP by plankton >100 μm .	Michaels (1991)
Central North Pacific and Atlantic	Data integrated over 150 m depth demonstrated that colonial Radiolaria contributed up to 10% of the living microbial biomass (>2 μm) and 6–12% of the total living biomass in the Atlantic and Pacific; they contributed up to 9% of the TPP in the eastern North Pacific gyre.	Dennett et al. (2002)
Central North Pacific, CLIMAX station	Ac abundances reached 10–40 cells l^{-1} ; their integrated abundances up to $2 \times 10^6 \text{ m}^{-2}$.	Beers et al. (1975)
Sargasso Sea, Bermuda Atlantic Time Series (BATS)	Integrated over the upper 150 m, Fo abundance was $\sim 10^5 \text{ m}^{-2}$ and their ave. biomass 1.4 mg C m^{-2} ; Ac abundance was $\sim 10^6 \text{ m}^{-2}$ and their biomass 2.8 mg C m^{-2} ; Po were mostly colonial and too sparse for accurate abundance estimates, their ave. integrated biomass was 2.6 mg C m^{-2} .	Michaels et al. (1995)
Gulf of Aden	Colonial Po of the <i>Collozoum</i> genus reached abundances of 16 000 to 20 000 colonies m^{-3} .	Khmeleva (1967)
Gulf of Eilat, Red Sea	Benthic Fo genera <i>Amphisorus</i> and <i>Amphistegina</i> were found at abundances of 10^5 to 10^6 cells m^{-2} in patches.	Lee & McEnery (1983)
TROPICAL		
South China Sea	Several solitary Po genera presented ave. abundances of 2234 ind. m^{-3} at 0 to 75 m depth, 939 ind. m^{-3} at 75 to 150 m depth and 157 ind. m^{-3} at 150 to 250 m depth.	Zhang et al. (2002)
Equatorial Pacific, 140° W, integrated data 0 to 120 m	During El Niño conditions plastidic Ac, Radiolaria, and Fo contributed to ~45, 60, and 85 % of Ac, Radiolaria, and Fo biomass, respectively; during the relaxation of El Niño plastidic Aca, Radiolaria and Fo contributed to ~85, 70, and 75 % of Ac, Radiolaria, and Fo biomass, respectively.	Stoecker et al. (1996)
Equatorial Pacific, Galapagos	Fo, Radiolaria and Ac abundances reached up to 3.3, 6, and 30 cells l^{-1} , respectively; integrated abundance of Ac over the upper 150 m was on av. 3.41×10^5 cells m^{-2} with the highest concentration in the upper 20 m; at most they accounted for 4 % of total chl <i>a</i> and up to 41 % of the PP.	Michaels (1988)
Western Sargasso sea, cape Florida	Radiolaria, Ac, and Fo integrated abundances over the upper 50 m were 0.24 to 0.34×10^5 , 1.71×10^5 , and 0.08 to 0.32×10^5 cells m^{-2} , respectively.	Michaels (1988)
Hawaii and central pacific atoll	Benthic foraminifera genus <i>Amphistegina</i> represented 25 to 90 % of sand-sized sediments.	Hallock Muller (1976), McKee et al. (1959)

bionts are usually found at around 75 to 100 m (central sub-arctic Pacific) (Tanaka & Takahashi 2008). In contrast, colonial radiolarians can be abundant in the subsurface on calm days (Anderson 1983b, Dennett et al. 2002), with extreme abundances of *Collozoum* sp. reaching up to 20 000 colonies m^{-3} reported in the Gulf of Aden (Khmeleva 1967). Notably, several species have been observed in Antarctic and Arctic waters, as well as boreal zones of the Atlantic, but in less abundance than in tropical waters (Anderson 1983b).

In contrast to solitary Polycystinea, Acantharea clearly predominate in subsurface water where they

are frequently more abundant than Polycystinea and Foraminifera (Beers & Stewart 1970). Acantharea could occasionally account for up to 20 % or more of the carbon fixation in the upper euphotic zone of the oligotrophic ocean (Michaels 1988). In the Equatorial Pacific, Acantharea reached abundances of up to 30 cells l^{-1} at the surface but declined sharply below 20 m (90 % of cells were at the surface). Acantharea densities ranged from 4 to 7 cells l^{-1} in the Equatorial Atlantic and North Pacific central gyre (Bishop et al. 1977, Bishop et al. 1978, Michaels 1991), and up to 30 cells l^{-1} in the Southeast Atlantic (Graham et al. 1976, Bishop et al. 1978). In the North pacific central gyre, the biomass

of *Acantharea* reached 6.8 to 56.7 mg C m⁻² and did not show a seasonal pattern (Michaels 1991). In the upper 20 m, symbiont carbon fixation in *Acantharea* was <4 % of the total primary production and 6 to 35 % of primary production by plankton >100 µm.

Plastid-retaining oligotrichs

Plastid-retaining ciliates are grazers and consume small phytoplankton, and as such are a component of the microzooplankton. In polar and temperate seas, they can contribute up to 40 to 60 % of ciliate abundance and biomass in late spring and summer (Table 2). They are also important in subtropical seas (Table 2); for example, in the Gulf of Naples on an annual basis they contribute ~27 % of ciliate abundance and 40 % of ciliate biomass (Modigh 2001) and in surface waters of the Ligurian Sea they contribute ~51 % of ciliate biovolume (Bernard & Rassoulzadegan 1994). In the East China Sea, plastidic oligotrichs account for 33 to 48 % of ciliate abundance and 44 % of ciliate biomass in summer and fall (Ota & Taniguchi 2003). Less information is available on their abundance in tropical seas. In the equatorial Pacific, plastidic ciliates contribute ~30 % of ciliate biomass during El Niño conditions and ~7 % during relaxation of El Niño conditions (Stoecker et al. 1996).

Plastidic oligotrichs usually contribute <10 % of total chlorophyll in the marine plankton (Stoecker et al. 1989, Putt 1990a, Dolan & Marrase 1995, Sanders 1995, Froneman & Perissinotto 1996, Perez et al. 2000, Chiang et al. 2003). The average annual contribution is probably <1 %. Assuming plastidic ciliates have chlorophyll-specific photosynthetic rates similar to phytoplankton (Stoecker et al. 1988) (Table 3), in most marine planktonic ecosystems they are estimated to make a small contribution to total annual primary production (Table 2). During stratification, when the phytoplankton biomass is low and dominated by pico- and nanophytoplankton, photosynthesis by ciliates can be important in the >20 µm size class (Stoecker et al. 1989, Putt 1990a).

Planktonic ciliates are an important source of food for copepods in marine ecosystems (reviewed in Calbet & Saiz 2005). Although phytoplankton biomass is at least 10× higher than planktonic ciliate biomass, ciliates comprise on average 30 % of copepod daily rations in marine ecosystems (Calbet & Saiz 2005). In the upper layers of the sea, oligotrichs usually dominate the planktonic ciliate assemblage and about 30 % of the oligotrichs retain plastids (Dolan & Perez 2000). Plastid retention, by influencing the gross growth efficiency of ciliates, could have a significant impact on ciliate production and transfer of phytoplankton-

derived carbon from the microbial food web to copepods and the 'classical' food chain.

Plastidic oligotrichs may have higher trophic efficiencies for ingested carbon than heterotrophic ciliates because respiratory and excretory needs for carbon are supplemented by photosynthesis (Putt 1990b). Assimilation efficiencies of 80 to close to 100 % and gross growth efficiency (GGE) of ~30 % are commonly assumed for heterotrophic ciliates (Straile 1997, Landry & Calbet 2004). Based on these efficiencies, we can assume that ~70 % of ingested C is respired in heterotrophic ciliates. In some plastid retaining oligotrichs, up to 100 % of the respiratory demand for carbon can be met by photosynthesis in the light (Stoecker & Michaels 1991) (Table 3). Stored photosynthate (mostly polysaccharide) is preferentially respired by the ciliates in the dark (Putt 1990b). If we assume that plastidic ciliates can cover respiratory demand for carbon for 12 h d⁻¹ (sparing ~35 % of ingested carbon from respiration), it is possible that under ideal conditions the GGE of plastidic ciliates for ingested carbon could be as high as 65 %. Plastidic oligotrichs comprise ~30 % of the marine planktonic ciliates, so plastid retention may increase average trophic efficiency of the total ciliate assemblage for ingested carbon from 30 to 40 %.

An increase in GGE from 30 to 40 % potentially has a substantial effect on microzooplankton production and on transfer of carbon to mesozooplankton (Landry & Calbet 2004). Under average conditions, ciliates are estimated to provide about 30 % of the diet of copepods (Calbet & Saiz 2005); under these conditions we calculate that plastid-retention would only boost trophic transfer of fixed carbon to copepods by ~1 %. In low chlorophyll waters approximately 50 % of the diet of copepods is ciliates (Calbet & Saiz 2005); we calculate that acquired phototrophy in marine oligotrichs could boost trophic transfer of carbon from primary production to copepods under these conditions by ~7 %. This potential boost has not been considered in most pelagic food web and biogeochemical models.

An increase in the average GGE of planktonic ciliates should also influence nutrient regeneration. If GGE of the ciliate trophic link is increased by 10 %, then it is likely that regeneration of inorganic nutrients and net respiration of carbon by the ciliates in the euphotic zone should be decreased by 10 %. During stratification, regeneration of nitrogen by grazers is important for growth of small phytoplankton. Thus, mixotrophy in ciliates may slightly decrease gross 'algal' primary production. However, this is unlikely to have a negative effect on metazoan tropho-dynamics, because of the number of trophic transfers (and hence losses of carbon due to respiration and excretion) between small phytoplankton and metazoan grazers.

Myrionecta rubra

Myrionecta rubra is likely one of the most widespread and abundant ciliates in marine ecosystems, with a nearly constant presence in coastal plankton assemblages (Lindholm 1985, Crawford 1989) (Tables 2 & S2). It has a global distribution, and is commonly found within estuaries, fjords, continental shelf environments, and upwelling zones (Taylor et al. 1971, Lindholm 1985). For many years *M. rubra* was misidentified in plankton studies, and in fact is still frequently grouped as heterotrophic microzooplankton in trophic studies (Crawford 1989, McManus et al. 2007, van Beusekom et al. 2007). *M. rubra* is mostly phototrophic in its physiology, but feeds on cryptophyte algae to acquire organelles or growth factors (Gustafson et al. 2000, Hansen & Fenchel 2006, Johnson et al. 2007). Ingestion of cryptophyte algae represents a negligible (<5%) contribution to its carbon growth requirements (Yih et al. 2004) and cellular chlorophyll content (Johnson & Stoecker 2005). The phototrophic capabilities of *M. rubra* are well described in both field (Smith & Barber 1979, Stoecker et al. 1991) and laboratory settings (Johnson & Stoecker 2005, Johnson et al. 2006).

One of the most striking features of *Myrionecta rubra* is its extremely high motility (Lindholm 1985). *M. rubra* cells can obtain a velocity of up to 1.2 cm s^{-1} during its 'jumps', propelled by cilia on the posterior end of the cell (Fenchel & Hansen 2006). This capacity for motility allows the ciliate to move extraordinary distances during a diel vertical migration, and explains why the ciliate is routinely found in discrete layers (Lindholm & Mork 1990, Olli 1999). In stratified fjords, *M. rubra* has been shown to accumulate near anoxic boundaries (Lindholm 1985, Lindholm & Mork 1990). Such vertical migrations are likely critical for the ciliate to acquire inorganic nutrients near the base of the mixed surface layer.

In upwelling zones off Peru, discrete populations of *Myrionecta rubra* can move between 30 m and the surface between early morning and midday (Sorokin & Kogelshatz 1979). Dugdale et al. (1987) surmised that vertical migrations of motile bloom forming phytoplankton such as *M. rubra* might play a key role in the transport of heat in the eastern boundary Peruvian system, absorbing upward of 99% of incoming radiation. During *M. rubra* blooms the ciliate is often observed forming discrete subsurface patches or lenses (Lindholm 1985). The formation of subsurface layers may be a phototaxic response to optimal light levels, while avoiding the surface may be a negative phototaxic response to saturating light intensities. In a red water event off Brazil, *M. rubra* formed a subsurface layer exceeding 4000 cells ml^{-1} 1 to 2 m below the surface, and was associated with slight changes in temperature

directly above the ciliate (Owen et al. 1992). The subsurface lens was thought to be the cause of temperature variation in the mixed surface layer, absorbing nearly all incoming surface radiation and shading the photic zone below the layer of cells (Owen et al. 1992). Thus, blooms of *M. rubra* are dynamic events, influencing heat and nutrient distribution, and creating microscale patches of food for grazers in upper mixed layers.

Myrionecta rubra is an abundant and important phototroph in numerous near shore aquatic ecosystems (Table 2). In the open northern Baltic sea *M. rubra* is the dominant ciliate species during spring, representing 10% of total phytoplankton production and 2% of the total biomass (Leppänen & Bruun 1986). Similar values of 6 to 9% of phytoplankton biomass and production have also been shown for *M. rubra* in the Gdańsk Basin of the southern Baltic Sea (Witek 1998). In the Georges Banks and Gulf of Maine, *M. rubra*, along with the oligotrich ciliate *Laboea strobila*, contributes 1 to 7% of total phytoplankton fixed carbon, and 14 to 90% of microplankton fixed carbon (Stoecker et al. 1989). In shallower stations, *M. rubra* represents 30% of total ciliate biomass while at deeper stations it is rare (3%) (Stoecker et al. 1989). Similar low levels of *M. rubra* have been reported in offshore environments of the North Atlantic (Montagnes et al. 2008) and western Pacific Ocean (Gómez 2007). In a tropical upwelling region of the South Brazil bight, *M. rubra* was consistently present during a winter cruise, representing one third of total ciliate abundance, and >20% of the total microzooplankton biomass (McManus et al. 2007).

Myrionecta rubra has a high photosynthetic rate that is comparable to or higher than other phytoplankton groups. *M. rubra* cells isolated from a temperate salt pond in Massachusetts, USA, had chlorophyll-specific rates of around $10 \text{ pg C (pg chl a)}^{-1} \text{ h}^{-1}$, while samples of a red water bloom of the ciliate off Peru reached $16.8 \text{ pg C (pg chl a)}^{-1} \text{ h}^{-1}$ (units recalculated from Smith & Barber 1979). While the mixotrophic oligotrich ciliate *Laboea strobila* has a much higher cellular photosynthetic rate (Table 3) than *M. rubra* due to its large size, its chlorophyll-specific rate is lower, at $3.7 \text{ pg C (pg chl a)}^{-1} \text{ h}^{-1}$ (Stoecker et al. 1988). An Antarctic culture of *M. rubra* has been shown to have a much lower chlorophyll-specific rate of 0.6 to $1.25 \text{ pg C (pg chl a)}^{-1} \text{ h}^{-1}$ (Johnson & Stoecker 2005, Johnson et al. 2006); however, lower values are typical for $P_{\text{max}}^{\text{chl}}$ in polar phytoplankton (Cota et al. 1994). Respiration rates for *M. rubra* are relatively low (Table 3) compared to other ciliates (Crawford 1989, Stoecker & Michaels 1991, Stoecker et al. 1991); however, Fenchel & Hansen (2006) estimated that at high jumping frequencies, *M. rubra* may use 30% of its energy for motility and only 3% when resting. Maximum growth rate of temperate *M. rubra* strains has been

measured at around 0.5 d^{-1} (Smith & Barber 1979, Yih et al. 2004); for a polar strain this is around 0.2 d^{-1} (Johnson & Stoecker 2005).

Although *Myrionecta rubra* has been described as lacking an oral cavity (Lindholm et al. 1988) and thought to be incapable of feeding (Crawford 1989), studies on cultures of the ciliate have revealed a capacity for ingesting cryptophyte algae (Gustafson et al. 2000). *M. rubra* is also known to feed on bacteria (Myung et al. 2006), but neither cryptophyte algae nor bacteria appear to be an important source of carbon for growth in non-limiting light irradiances. Hansen & Fenchel (2006) found that 1 prey cell ingested per generation of *M. rubra* is sufficient for maintaining maximum growth rates in culture. While temperate strains of *M. rubra* can ingest up to 9 cryptophyte cells per day, such ingestion rates do not further enhance growth rates (Yih et al. 2004, Hansen & Fenchel 2006). Both temperate and polar strains of *M. rubra* can survive for 50 d without feeding, although the temperate strain experiences greater mortality (Smith & Barber 1979, Johnson & Stoecker 2005). *M. rubra*'s capacity for ingesting bacteria increases in low light (to $150 \text{ bacteria grazer}^{-1} \text{ h}^{-1}$), potentially acting as an important source of organic material in light-limited conditions (Myung et al. 2006). Supplementation of growth with ingested bacteria may be important in deep low-light populations of *M. rubra* and in over-wintering polar populations.

Grazing on *Myrionecta rubra* has received relatively little attention, and it is thought that the high motility of *M. rubra* assists in its escape from potential grazers (Fenchel & Hansen 2006). However, *M. rubra* is the main prey of photosynthetic members of the dinoflagellate *Dinophysis* (Nagai et al. 2008), which probably capture *M. rubra* through ambush, considering their much lower motility. The copepod *Oithona* spp. ingests ciliates (including *M. rubra*) and flagellates preferentially over other nano-microplankton in the spring, while during summer and winter, clearance rates are highest for *Strombidium* spp. and *M. rubra* (Castellani et al. 2005). In a Baltic Sea inlet, Lindholm & Mörk (1990) observed apparent grazing on *M. rubra* by rotifers and the ciliate *Didinium* sp. During red water events of *M. rubra*, digestive glands of bivalves are frequently observed to turn pinkish due to filter feeding on the ciliate (Carver et al. 1996). In certain regions, persistent red water blooms of *M. rubra* have been associated with fish and invertebrate mortality due to declines in dissolved oxygen (Horstman 1981).

IMPORTANCE IN BIOGEOCHEMICAL CYCLES

Planktonic Rhizaria are large protists some of which possess exoskeletons made of calcium carbonate

(Foraminifera), silicate (Polycystinea), or strontium sulfate (Acantharea). Acquired phototrophy (mixotrophy) allows these large protists to thrive in oligotrophic areas, which are otherwise dominated by very small eukaryotes. Therefore, these mixotrophs are important contributors to sinking material, enhancing particle flux to the deep ocean. The size of an organism is a major factor determining its sinking rate and hence its influence on carbon flux and, depending on the composition of its exoskeleton, on the cycles of particular elements. Food webs, sedimentation and biogeochemical cycles would be very different in the world's ocean without these large Rhizaria that are dependent on acquired phototrophy.

Foraminifera and Polycystinea present an excellent fossil record and are widely used by geologists and paleo-oceanographers in reconstruction of past climates and oceanic conditions (Steineck & Casey 1990). The impact of Rhizaria on oceanic biogeochemical cycles is significant; however, although their fluxes have been studied by geologists, the underlying biology and ecology of Rhizaria responsible for these fluxes is not well known.

Carbon

Rhizaria inhabiting vast areas of the oceans represent a substantial biomass of organic matter and their implication in the global carbon cycle is significant. The sinking of a few, very large cells can constitute a large fraction of the carbon flux (Goldman 1988). Although, Acantharea, Polycystinea and Foraminifera contribute significantly to carbon flux. On average (over 3 cruises), they accounted for 15.5% of total carbon flux during short-term trap deployment at the BATS sampling station near Bermuda, and up to 43% when large Radiolaria and Foraminifera were present (Michaels 1988). Over an 18 mo period in the central north Pacific gyre, exports of Acantharea by sinking of intact cells from the euphotic zone were at least 2 to 6% of standing stock per day and represented up to 9% of the total sinking organic carbon flux (Michaels 1991).

Acantharea can contribute significantly to the primary productivity of oligotrophic seas. Rates of carbon export are comparable to the rate of carbon fixation by the symbionts in the Acantharea population (Michaels 1991). Combined production rate and seasonal abundances of Acantharea and Foraminifera reached ~5% of total annual primary production in Sargasso Sea waters. Symbiont carbon production was equivalent to 9, 39, 84, and 19% of the total organic carbon weights of Acantharea, Foraminifera, solitary Radiolaria, and colonial Radiolaria, respectively (Caron et al. 1995).

Spero & Parker (1985) estimated that the contribution from foraminifera symbionts to total primary production would amount to ~1%, reaching 25% in patches (Spero & Parker 1985). In the Gulf of Aden, colonial Radiolaria were estimated to fix 3 times as much carbon as the phytoplankton (Khmeleva 1967, Taylor 1990).

In addition to the organic carbon export, Foraminifera have a calcium carbonate exoskeleton which makes them particularly relevant to the carbon cycle. The symbiont-bearing Foraminifera are estimated to presently produce at least 130 million tons of calcium carbonate per year and to contribute ~5% of the annual carbonate production in reef and shelf areas and ~2.5% of the total calcium carbonate in the global ocean (Langer 2008). Investigations of sinking speeds for various foraminifera species demonstrated that most planktonic foraminifera with a cell size >150 µm reach 3800 m depth in 3 to 12 d depending upon shell weight and presence or absence of spines (Takahashi & Bé 1984). Foraminifera depend on their symbionts for growth and carbonate production. Photosynthesis and calcification are directly proportional to light intensity and 2 to 3 times higher than in the dark (Duguay & Taylor 1978, ter Kuile & Erez 1987).

Benthic foraminifera are abundant in the euphotic shallow benthic zones of tropical and semi-tropical seas, they are ubiquitous members of coral-reef associated ecosystems worldwide and play important roles in biogeochemical mineral cycling (Sournia 1976, Lee & McEnery 1983, Langer 2008). Larger foraminifera are so abundant that they were called 'living sands' (Lee 1998). The *Amphistegina* genus is one of the most abundant and widespread larger foraminifera and produces nearly a quarter of beach sands in Hawaii (Hallock Muller 1976) and >90% of the sand-sized sediments in a central Pacific atoll (McKee et al. 1959).

Silica

The silica cycle is strongly dominated by diatoms in eutrophic and coastal ecosystems. However, in the vast majority of the ocean surface Polycystinea, together with Phaeodarea (non-symbiotic rhizarian taxa), have a major impact on the silica cycle (Silver & Gowing 1991). To our knowledge, no studies have focused specifically on the impact of species carrying algal endosymbionts on the silica cycle.

Noteworthy, the silica cycle is tightly coupled to the Barite cycle, the latter being formed by decaying silica. Thus, there is a strong correlation between the dissolved Barite and Silica cycle in the ocean. Particulate Barite is used as a proxy for organic carbon remineralization and is extensively used in paleo-oceanography (Bishop 1988, Dehairs et al. 2008).

Strontium

The strontium cycle in the ocean is not well known. However, because the strontium-90 isotope is a long life waste product of uranium fission, some studies carried out after World War II focused on strontium accumulation in marine organisms (Bowen 1956). As previously mentioned, Acantharea are abundant in oceanic subsurface water and hence play an important role in the ocean's Strontium budget (Bernstein et al. 1987). However, very little is known with respect to their quantitative impact on the Strontium cycle. Probably one reason for this lack of research is that the Strontium sulfate exoskeleton of Acantharea is prone to dissolution which renders their enumeration in traps difficult; their contribution to sinking flux is usually underestimated.

ECOSYSTEM MODELING

Marine protists with acquired photosynthesis (except for *Myrionecta rubra* which is primarily a photoautotroph) are mixotrophs and generally fit the conceptual model for Type III mixotrophy (Photosynthetic 'Protozoa' that gain most of their carbon, nitrogen and phosphorus from ingestion of prey) (Stoecker 1998). Type III includes all the categories of acquired phototrophy illustrated in Fig. 2 with the possible exception of the 'obligate-obligate' category solely occupied by *M. rubra*. Type III mixotrophy has been considered in an idealized, steady state model of marine planktonic processes by Stickney et al. (2000). In this model, co-existence of mixotrophs with phytoplankton and zooplankton occurred, suggesting that mixotrophy represents a unique niche in the plankton even under summertime, quasi-steady-state conditions. This model also suggested that mixotrophy leads to decreased primary production based on uptake of dissolved inorganic nitrogen (new production) but that for mixotrophs which only feed on phytoplankton and other mixotrophs (e.g. plastidic oligotrichs) the total amount of photosynthesis, including that based on nitrogen from secondary sources, tends to increase. Essentially, the planktonic ecosystem becomes more efficient in terms of nitrogen because of nitrogen recycling within the mixotrophic cells.

In contrast to the Stickney model, Hammer & Pitchford (2005) examined the Type III mixotrophy in a simplified model of predator-prey interactions. In their model, even low levels of Type III mixotrophy (a small fraction of the zooplankton being involved in primary production) had a stabilizing effect on the ecosystem by reducing the propensity for blooms while at the same time increasing overall productivity of the sys-

tem. These results suggest that plastid retention among ciliates and other Type III mixotrophs (such as Rhizaria with endosymbionts) may increase stability as well as total primary and secondary production in planktonic food webs.

The lack of quantitative data on the effects of mixotrophy on GGE and trophic transfer, as well as the lack of basic information on the trophic level of both micrograzers and copepods, impedes realistic modeling of microbial food webs and their linkage to the metazoan food web. The example of photosynthesis meeting all or a substantial portion of respiratory demands for carbon in the plastid-retaining oligotrichs (Putt 1990b, Stoecker & Michaels 1991) suggests that acquired phototrophy in other protists, including foraminifera, radiolaria and dinoflagellates, may also spare ingested carbon from respiration and thus potentially increase GGE. An increase in average protistan GGE in the euphotic zone could have substantial positive effects on secondary production and on transfer of carbon from the microbial food web to metazoan grazers (Landry & Calbet 2004). This potential boost to food web efficiency has rarely been considered.

Acquired phototrophy (Type III mixotrophy) may have important roles in moderating ecosystem responses to perturbations such as increased stratification. Mainly because of the patchiness of the large protists bearing algal endosymbionts, their accurate impact on trophic transfer and incorporation in finer models is difficult to assess. This is particularly true for the colonial polycystines which may have one of the most significant impacts (Caron et al. 1995, Michaels et al. 1995, Dennett et al. 2002).

ENVIRONMENTAL PERTURBATIONS

Some protists with acquired phototrophy may be particularly susceptible to environmental perturbations. One very important group in ocean biogeochemistry and carbon flux, the Foraminifera, may be particularly vulnerable to ocean acidification because of their reliance on calcification (Russell et al. 2004, Fabry et al. 2008). In laboratory experiments, it has been shown that foraminifera shell mass decreases with decreases in seawater pH (Spero & Parker 1985). Field observations of particular benthic foraminifera have demonstrated mottling and bleaching (Tagle et al. 1997) while other physiological perturbations have been observed in response to the current environmental changes and are likely to impact foraminifera communities in the near future (Hallock 2000). In tropical and subtropical pelagic ecosystems, shelled Foraminifera are particularly important in the flux of organic carbon out of surface waters and in the formation of cal-

careous foraminiferan oozes that cover vast areas of the ocean floor (Kennish & Lutz 1992). Benthic calcareous Foraminifera that depend on acquired phototrophy are important in carbonate deposition and reef building in shallow, warm seas (Lee 1998). The Foraminifera, Acantharea, and Radiolaria, important in carbon flux out of the mixed layer and biogeochemical cycling in oligotrophic waters, are all susceptible to increasing biologically damaging UVB and eutrophication, and may be negatively impacted by attempts at ocean fertilization to increase carbon sequestration.

EVOLUTIONARY AND ECOLOGICAL ROLES OF 'EXCESS' CARBON FROM ACQUIRED PHOTOTROPHY

Biological oceanographers and limnologists tend to focus on abiotic conditions and resource availability (bottom-up controls) in explaining the structure and function of aquatic ecosystems, but it is clear that species interactions are also important (Strom 2008). Net growth of populations and accumulation of biomass depend on the balance between growth and mortality. Adaptations that reduce mortality are hypothesized to have a large effect in 'reshaping' protistan communities and their roles in biogeochemical cycling and trophic transfer (Strom 2008).

It can be argued that acquired phototrophy has been important in supporting evolutionary innovation, including complex structural and behavioral adaptations that reduce mortality in aquatic protists. In most protists with acquired phototrophy, photosynthesis supplies carbon stoichiometrically in excess to nitrogen or phosphorus. Organisms have evolved fitness-promoting purposes for 'excess carbon' such as energy/food storage (e.g. in mixotrophic ciliates), structures that reduce mortality due to predation (e.g. calcareous shells in Foraminifera, silicate tests of Polycystinea, polysaccharide plates covering mixotrophic oligotrichs, and gelatinous sheathes on some photosynthetic sessile ciliates), structures that increase food gathering capability and/or reduce sedimentation (e.g. spines on planktonic Foraminifera), and chemical as well as morphological defenses against predators (Hessen & Anderson 2008).

An important adaptation that may rely on 'excess carbon' from photosynthesis is rapid movement (Crawford 1992, Dolan & Perez 2000). All free-living ciliates are motile, but rapid movement in large ciliates with compound cilia (e.g. oligotrichs) is calculated to be energetically costly, perhaps requiring 42% of basal respiration (Crawford 1992). Some photosynthetic ciliates swim rapidly for their size and undergo extensive vertical migration (e.g. *Myrionecta rubra*). Some cili-

ates have rapid escape responses from predators (e.g. in *M. rubra* and some oligotrichs) (Crawford 1992, Dolan & Perez 2000). Rapid swimming may also allow exploitation of habitats with low prey concentrations because it should increase maximum clearance rates and, at low food concentrations, facilitate dispersal into new food patches.

CONCLUSIONS

Acquired phototrophy is at the root of much of the beauty and diversity that we observe among large aquatic protists, for example, the golden radiolarians, the green ciliates and the structurally complex shells of large benthic Foraminifera. Our understanding of how this diversity in form and function influences trophic dynamics and biogeochemical cycles in most aquatic ecosystems is rudimentary, but it is clear that we have to go beyond traditional classifications of aquatic protists as 'phyto' or 'zoo' and alter our concepts of 'trophic levels' to progress in our understanding of aquatic microbial ecology. This is a rich area for exploration using a combination of classical and molecular techniques, laboratory and field research and modeling.

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