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REVIEW

THE ECOLOGY OF *CLADOPHORA*

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ABSTRACT

Cladophora *is found in a variety of marine and freshwaters and provides habitat and food for numerous organisms. It may be the most ubiquitous macroalga in freshwaters worldwide. This filamentous green alga can reach nuisance levels as a result of cultural eutrophication. Taxonomic identification of* Cladophora *species is difficult. Taxonomy may be clarified by the simultaneous culture of known taxa and material derived from field collections under the same sets of culture conditions. This should eliminate ecotypic variations in morphology.* Cladophora *is predominantly benthic and is often found in regions of unidirectional flow or periodic wave action. Its metabolism and morphology are related to hydrodynamic conditions. Nitrogen and phosphorus are the most commonly reported limiting nutrients.* Cladophora *is a mid- to late successional species in freshwaters where it is grazer resistant. In marine communities, however, it is considered an early opportunist and relatively palatable to invertebrates.* Cladophora *is colonized by a wide variety of epiphytes and motile animals because it can offer protection from predation, food (in the form of epiphytes or* Cladophora *itself), or a substrate that is anchored against flow disturbance. Species interactions that occur within* Cladophora *communities include 1) competition with other primary producers, 2) top-down control of biomass, 3) association with nitrogen-fixing epiphytes, 4) grazing on epiphytes by invertebrates, and 5) complicated foodwebs in marine intertidal and freshwater communities. Because* Cladophora *is found in many different habitats, its ecology varies significantly with locale.*

Key index words: Cladophora; *competition; ecology; eutrophication; grazing; hydrodynamics; nutrients; species interactions*

Representatives of the genus *Cladophora* are distributed worldwide and often dominate the benthos in fresh and marine waters (Blum 1956, Söderstrom 1963, van den Hoek 1963, 1964, 1982, Collins 1970, Whitton 1970). *Cladophora* is a filamentous chlorophyte with varied degrees of branching (van den Hoek 1963, 1982). Generally, *Cladophora* is an attached benthic alga, but it can be found as floating mats or as loose masses on soft substrates. Members of the genus may occur in ultraoligotrophic lakes (Stanford and Prescott 1988) to highly eutrophic habitats, and they range from arctic to temperate marine waters (van den Hoek 1982). Some species in intertidal pools are capable of withstanding 5–30‰ salinity variations (Jansson 1974), and other species in saline lakes can survive up to 100‰ salinities (Borowitzka 1981).

Growths of *Cladophora* reach nuisance proportions at times, often as a result of eutrophication. Problems attributed to such blooms include clogging of water works, excessive diurnal swings in O_2, fouling of fish lines, unpleasant odors and appearance, lowering of property values, and danger of entanglement to young, inexperienced swimmers (Herbst 1969, Bolas and Lund 1974, Lembi et al. 1988). Eutrophication and excessive growth problems occur in freshwaters (e.g. Whitton 1970, Millner and Sweeney 1982) and shallow marine systems (e.g. Pogreboff and Ronnberg 1987, Kautsky et al. 1988, Lapointe and O'Connell 1989).

The purpose of this review is to update information on the ecology of *Cladophora.* Whitton (1970) wrote a comprehensive review on freshwater *Cladophora,* but because many new studies have been published in the last 20 years and because it is the dominant macroalga in many aquatic communities, a new review is warranted. We emphasize species interactions and hydrodynamics because of the recent advances in these areas of research. We also identify some differences and similarities in the ecology of the alga in marine environments versus in freshwaters.

Taxonomy

Taxonomic identification within the genus is difficult because, as van den Hoek (1982) states, "Almost all taxonomically valid criteria within *Cladophora* are of a quantitative nature, each criterion (e.g. diameter of apical cells) being represented by a graded series of variable expressions with overlaps between species." In addition there is a wide degree of morphological variation in response to environmental conditions and plant age (van den Hoek 1963, 1982, Ronnberg and Lax 1980). This stimulates a "lumpers" versus "splitters" debate, resulting in a range of the number of species that are recognized. For example, Phinney (1945) reduced the number of freshwater North American species to four, whereas Collins (1970) reported 12.

In the face of environmentally induced morphological variation, the most reasonable taxonomic approach appears to be to combine studies of field collections with observations of simultaneously collected material that is subsequently cultured in the laboratory. This is a good approach because culture conditions can be controlled to minimize phenotypic plasticity. For example, when van den Hoek (1982) cultured 13 marine species, only five of the cultures retained the characteristic morphology of the original material. In addition, *Cladophora jongiorum* van den Hoek greatly resembled *Cladophora montagneana* Kütz. in the field but clearly differed in culture. Cultures also were used to distinguish between *Cladophora vagabunda* van den Hoek and *Cladophora vadorum* (Aresch.) Kütz. (van den Hoek 1982). The taxonomy of European and North Atlantic species has been approached in this manner (van den Hoek 1963, 1964, 1982), and a similar approach may be useful elsewhere.

Alternatively, molecular and cytological techniques are beginning to be used in taxonomic studies of *Cladophora.* Such studies have shown a large degree of divergence between the few species studied. Deoxyribonucleic acid (DNA)–DNA hybridization has shown high interspecific divergence between *Cladophora sericea* (Huds.) Kütz. and *Cladophora rupestris* (L.) Kütz. (Bot et al. 1989b) and between *Cladophora albida* (Huds.) Kütz. and *C. rupestris* (Bot et al. 1989a). DNA–DNA hybridization has shown that subspecies of *Cladophora pellucida* (Huds.) Kütz. can diverge significantly in patterns probably related to Miocene closure of the Mediterranean–Indo-Pacific seaways (Bot et al. 1991). Verma (1985) distinguished *Cladophora crystalina* (Roth.) Kütz. from *Cladophora intermedia* Fosl. and *Cladophora crispata* (Roth.) Kütz. on the basis of chromosome numbers.

Antibodies produced in response to soluble protein fractions of algal extracts and used in cross-reaction experiments showed a high immunological distance between different species, supporting the possibility that *Cladophora* may actually be composed of several genera (Olsen-Stojkovich et al. 1986). As ribonucleic acid (RNA) and DNA probes become available for different species it may be possible to classify field collections relatively quickly and easily. Until such a time, taxonomic identification will remain difficult.

Factors Related to Distribution and Abundance

Substrate. Cladophora colonizes many different types of substrate. Solid substrates are usually preferred. Attachment to rocks is probably most common, but freshwater *Cladophora* has also been reported attached to clams (Curry et al. 1981) and fish (Vinyard 1953, as cited by Whitton 1970), as an inhabitant of rice fields (Pantastico and Suayan 1973), and as an epiphyte (Utermöhl 1982). Marine species of *Cladophora* usually attach to solid substrates, but some species form indefinite masses that float to the surface of saltmarsh pools or lie loose on sediment bottoms (van den Hoek 1982).

The slope of hard substrates was identified as important by Konno (1985), who established that at greater than 120° inclination, the dominance of the marine *Cladophora wrightiana* decreased. This might be related to the fact that there is less light beneath an overhang.

Large streamers can become detached from substrates and form floating masses in marine (Dethier 1982) and freshwaters (Power 1990a). Some species exist as loose aggregates or balls on soft substrates in both marine and freshwater habitats (Nakazawa 1974, Gordon et al. 1980, Niiyama 1989). *Cladophora* has been found associated with marine stromatolites where it forms mixed communities with cyanobacteria (Braithwaite et al. 1989). In these mixed communities, indirect precipitation of high-magnesium calcite and trapping of sediment by *Cladophora* actually build the substrate on which it is located.

In streams and rivers, *Cladophora* is abundant on some rocks but not on all adjacent rocks. Although the factors related to substrate suitability are not well known, factors that may be important include inclination, surface roughness, chemical composition, substrate stability, and hydrodynamic factors.

Hydrodynamics. Part of the success of *Cladophora* is undoubtedly related to its ability to withstand the shear stress found in benthic regions of rivers and rocky intertidal habitats. The thallus is tough, but flexible, and allows flow to occur through and around it (Dodds 1991a). The thallus spreads out at low current velocities and becomes more streamlined as flow increases (Fig. 1). The streamlining may be a general adaptation to flow; it has been observed in other macroalgae and terrestrial plants (Vogel 1981, 1988). Description of the hydrodynamic conditions associated with growth is very difficult because such conditions may vary considerably over time (seconds to years in both freshwater and marine habitats), but it is important to understand these relationships because, as described below, the connection between physiological rates and transport of materials by flow may be significant.

Cladophora is found mainly outside of the diffusion boundary in the area dominated by turbulent transport (i.e. outside the area dominated by molecular diffusion). However, very short tufts may reside primarily within the boundary. The fact that there can be significant current inside tufts attached to rocks (Fig. 2) and streamers (Dodds 1991a) of *Cladophora* suggests that transport of materials to and away from the thallus is not constrained by molecular rates of diffusion. Position relative to flow boundary is pertinent because chemically mediated interactions of benthic species are constrained by their location relative to the diffusion boundary (Dodds 1990).

Hydrodynamic conditions can influence, to some degree, the biomass that is attained on a particular substrate. A weak positive correlation between rock size and algal abundance in a river was demonstrated in *Cladophora* by Dodds (1991b) and in the closely related *Rhizoclonium* by Power and Stewart (1987). This correlation probably occurs because larger

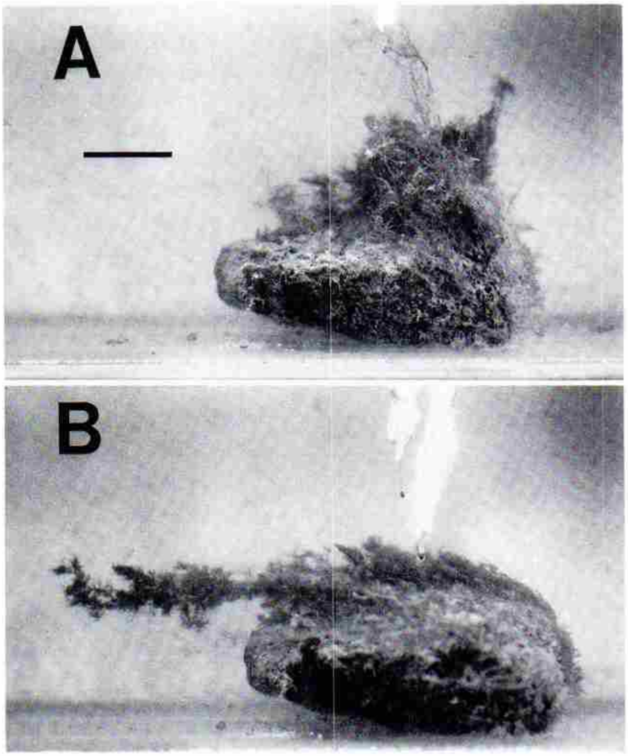

FIG. 1. Streamlining of *Cladophora* with flow. The rock with attached *Cladophora* was subjected to a A) 0 and B) 4.5-cm·s^{-1} open channel current. Scale bar = 2 cm. A thermistor current probe is above the rock.

rocks are less likely to be overturned by flooding, and consequently their upper surface may be subjected to less disturbance than smaller rocks. Flooding has been identified as a factor that can decrease *Cladophora* biomass in rivers (Fisher et al. 1982, Freeman 1986, Entwisle 1989, Sand-Jensen et al. 1989), and resistance to abrasion in filamentous algae may relate to the ability to withstand hydrodynamic disturbance (Power and Stewart 1987). Small-scale abundance patterns may also be determined by hydrodynamic conditions, but little is known about zoospore preference for, or success within, specific subhabitats.

Cladophora biomass in tidepools is affected by waves; large, loosely attached mats slough off with wave action as they become thick (Dethier 1982). Different marine species appear to have varied tolerances for surf exposure (Kapraun 1980), but it is unclear if this is related to stronger holdfasts, more flexible thalli, or other factors. As may be expected, complete submersion in a river allows for greater growth than that which occurs in a splash zone (Oertel 1991).

Photosynthetic rates of freshwater *Cladophora* have been related to water velocity. An increased rate of photosynthesis was observed as velocity increased from 0 to 2.1 cm·s^{-1} (Pfeifer and McDiffett 1975). A doubling of photosynthetic rates in small tufts accompanied an increase in water velocity from 0 to 8 cm·s^{-1}, but a subsequent decrease in rates occurred with velocities higher than 8 cm·s^{-1} (Dodds 1991c). Transport of CO_2 into *Cladophora* tufts may relieve C depletion by increasing CO_2 availability and lowering the reliance upon HCO_3^- as a carbon source (Raven et al. 1982). The increase in photosynthetic rates is consistent with the idea that transport of material with increased current can enhance algal productivity (Whitford 1960, Schumacher and Whitford 1965, Westlake 1967, Pasciak and Gavis 1974, Lehman 1978, Wheeler 1980, Dodds 1989). Increased transport is directly related to a thinner diffusion boundary as current increases (Carlton and Wetzel 1987).

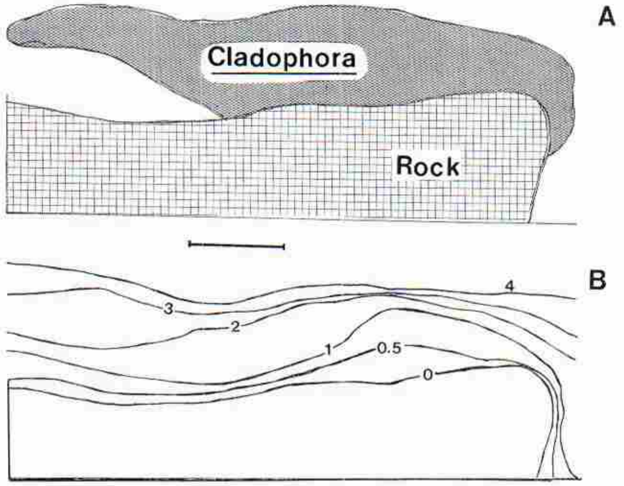

FIG. 2. Profiles of water velocity through a tuft of *Cladophora* attached to a rock. A) Extent of *Cladophora*. B) Velocity contours (in cm·s^{-1}). Scale bar = 1 cm. The profiles are from the same rock as in Figure 1. Velocity measured with a thermistor current probe (LaBarbara and Vogel 1976).

A decrease of photosynthetic rates above 8 cm·s^{-1} may be related to the streamlining effect of increased current. As tufts become more compact with higher current, transport of materials into and away from the tufts may be inhibited or self-shading may increase, leading to an overall decrease in photosynthesis. Small-scale profiles of water velocity do show locally decreased current velocities within masses of *Cladophora*, suggesting that compaction of the tufts could indeed lower transport (Dodds 1991a; Fig. 2). Biomass-specific photosynthetic rates decrease as biomass per unit area increases (Pfeifer and McDiffett 1975), suggesting lower *Cladophora* photosynthesis as individual filaments become more tightly packed. Lowered photosynthesis associated with denser growth may result from increased self-shading, decreased transport, or both.

Morphology of *Cladophora* also has been linked to hydrodynamic factors. Branching of marine *Cladophora* may become more pronounced with increased wave energy (van den Hoek 1964, 1982).

Cells may become shorter with more turbulence (Ronnberg and Lax 1980). Branching of freshwater *Cladophora* may increase with increased water velocity (Parodi and Cáceres 1991), and the angle of branches from the main axis decreases with increased current (Whitton 1975). The mechanisms by which increased turbulence alters growth patterns are unclear; flume experiments could be used to clarify the mechanisms.

Water motion has been implicated in the formation of spherical aggregations of *Cladophora*. Such aggregations are known as "lake balls" but also occur in brackish waters (Gordon et al. 1980, 1985). Water motion can cause similar aggregations of nonliving material (Smith 1933), so it is unlikely that formation of these balls is an active biological process. Both vertical and horizontal rotations, in addition to species-related growth form, are required for formation of lake balls (Nakazawa 1976). Growth of highly branching species in these spherical aggregations may cause the filaments to become more entangled, resulting in decreased dispersion.

Light. In nature, *Cladophora* is found in high- and low-light habitats. As thallus size increases, self-shading increases. In turbulent waters, this results in a very uneven light field, with thallus movement constantly changing the degree of shading. Filaments other than those at the very top of the tuft may rarely experience photoinhibition. Even though *Cladophora* is often located in highly exposed shallow benthic habitats, self-shading and epiphyte cover may relieve photoinhibition (Wiencke and Davenport 1987).

There has been extensive laboratory study of the photosynthesis–irradiance relationships of freshwater species. Quantum use efficiency was shown to vary significantly in *Cladophora* samples collected from two shallow rivers (within 20 km of each other) when $^{14}CO_2$ incorporation was determined in bottles with natural sunlight attenuated by neutral density filters (Dodds 1991c). Extensive physiological measurements were made in a controlled environment facility using *Cladophora* isolated from Lake Huron as part of research on nuisance growths in the Great Lakes (Graham et al. 1982). These experiments established that optimum rates of photosynthesis occurred between 300 and 600 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1}, and a positive net photosynthesis resulted when temperatures exceeded 5° C and light was above 35 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1}.

Similar photosynthesis–irradiance determinations made with fresh *Cladophora glomerata* collected from Green Bay, Lake Michigan, showed that saturation occurred at 345 (July) to 1125 (August) μmol quanta$\cdot$m$^{-2}\cdot$s^{-1}. Compensation points in July and August were 44 and 104 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1}, respectively (Lester et al. 1988).

Gordon et al. (1980) showed that the estuarine *Cladophora albida* had positive net photosynthesis rates above 25 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1}. Photosynthesis rates were saturated at 100 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1} at 12° C and at 750 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1} at 30° C, with no observed photoinhibition. Characteristics of photosynthesis–irradiance curves varied with light history and culture media in these experiments.

Temperature. Responses to temperature are often used to describe the seasonal abundance of freshwater *Cladophora* (Whitton 1970, Wong et al. 1978, Muller 1983, Robinson and Hawkes 1986), and thermal effluent has been shown to be related to increased biomass (Squires et al. 1979). In many rivers and lakes, *Cladophora* dies off in midsummer, which could be caused by an inability to maintain dominance above 23.5° C (Wong et al. 1978). However, photosynthesis can occur in some freshwater species, at least over a short period, at temperatures up to 35° C, with optimum rates at 27° C (Brock and Hoffmann 1974). Maximum photosynthetic oxygen production occurred at about 30° C for the marine *C. albida* (Gordon et al. 1980). There is a summer die-off in Lake Huron, and laboratory experiments on *Cladophora* showed that net photosynthetic O_2 production decreased above 25° C, establishing a clear correlation between temperature and summer die-off (Graham et al. 1982). High temperature may not cause midsummer die-off in Lake Erie because gross photosynthetic oxygen production and dark respiration acclimate to the seasonal temperature highs, allowing growth to continue (Mantai 1987). Lester et al. (1988) recorded maximum net photosynthetic oxygen production between 28 and 31° C for *C. glomerata* from Lake Michigan, suggesting that midsummer die-off is not attributable to temperature in the population they studied. However, studies of photosynthesis at sustained high temperatures are needed to determine the influence of temperature on growth via its effects on photosynthesis.

Several factors may explain why high temperatures cause summer die-offs in freshwaters in some cases but not in others: 1) There are certainly variations in the growth responses of different species to temperature. 2) Interaction may occur between photosynthetic response to irradiance and temperature (Graham et al. 1982); what is an inhibitory temperature at one light level may allow growth at another light level. 3) Low nutrients associated with higher temperature may partially explain midsummer die-offs of *Cladophora* in rivers (Muller 1983). 4) Grazers may lower biomass in late summer (Feminella and Resh 1991).

Geographic distribution of marine species of *Cladophora* often seems to be limited by temperature (van den Hoek 1982, Bot et al. 1990, Cambridge et al. 1990a, b, c), so cases where temperature appears to be unrelated to distribution may indicate that more complete distributional records are necessary (Cambridge et al. 1991). Distribution on smaller spatial scales in the intertidal zone may also be a function of temperature, but this has not been studied.

Inorganic chemistry. Cladophora growths have been associated with many marine and freshwater eutrophication events. These include nutrient enrichments in the Great Lakes (see *J. Great Lakes Res.*, 1982, Vol. 8, for extensive research on this area), in Bermuda (Schramm and Booth 1981, Lapointe and O'Connell 1989), in the Peel Inlet, Western Australia (Gordon et al. 1980, Birch et al. 1983, Lavery et al. 1991), near marine fish farms (Ruokolahti 1988), in pulp mill effluent in the Bothnian Sea (Pogreboff and Ronnberg 1987), in wetlands (Richardson and Schwegler 1986), and in streams or rivers (Bolas and Lund 1974, Sand-Jensen et al. 1989, Dodds 1991b). Because nutrient loading events often involve enrichment with several nutrients, the correlation between cultural eutrophication and increased biomass cannot necessarily be ascribed to a single nutrient.

The most commonly published observation is that excessive *Cladophora* biomass or production in freshwaters is stimulated by phosphorus additions (Herbst 1969, Pitcairn and Hawkes 1973, Bolas and Lund 1974, Wong and Clark 1976, Birch et al. 1981, Auer and Canale 1982, Neil and Jackson 1982, Freeman 1986, Painter and Kamaitis 1987, Jackson 1988, Painter and Jackson 1989). *Cladophora* also can be abundant in habitats where nitrogen supply limits primary production (Adams and Stone 1973, Moore 1977a, Millner et al. 1982, Muller 1983, Lapointe and O'Connell 1989, Dodds 1991b). In some situations, there seems to be no correlation between dissolved nutrient levels and biomass (Schramm and Booth 1981, Lorenz and Herdendorf 1982, Cheney and Hough 1983). This lack of correlation may be explained by adjusting for changes in growth rates driven by variations in ambient light fields (Wong et al. 1976).

There has been considerable study of phosphorus uptake by freshwater *Cladophora*. Some members of this genus appear to be able to survive with low ambient (extracellular) phosphate concentrations in marine (Schramm and Booth 1981) and freshwater habitats (Stanford and Prescott 1988). Relatively high half-saturation uptake constants (50–250 $\mu g\ P \cdot L^{-1}$) have been reported for *Cladophora glomerata* (L.) Kütz. (Auer and Canale 1982). In other freshwater studies of *C. glomerata*, slightly lower half-saturation uptake constants (15–86 $\mu g\ P \cdot L^{-1}$) were observed by Lohman and Priscu (1992), and half-saturation uptake constants from 8 to 15 $\mu g \cdot L^{-1}$ were observed by Wallentinus (1984). Half-saturation constants for growth of *C. glomerata* are within the ranges reported for uptake (Rosemarin 1982). Uptake was saturated at 2 $mg \cdot L^{-1}$, and half-saturation constants for uptake by the marine *C. albida* ranged from 2 to 55 $\mu g \cdot L^{-1}$, well within the ranges reported for *C. glomerata* (Gordon et al. 1981). *Cladophora* also produces phosphatase, which may allow it to take advantage of dissolved organic phosphorus (Lin 1977).

Critical cell concentrations (the minimum cell concentrations that permit maximum yield) for N (1.10%) and P (0.06%) have been identified for freshwater *Cladophora glomerata* (Gerloff and Fitzgerald 1976). When the algal tissue falls below the critical concentration for a nutrient, it is presumably limited by that nutrient. The ranges of N and P tissue concentrations in *C. glomerata* have been reported as 0.83–4.89% N and 0.04–0.54% P (Gerloff and Fitzgerald 1976). Critical cell concentrations for marine *C. albida* for N and P have been reported as 1.5 and 0.05%, respectively (Gordon et al. 1981); these are similar to the values identified for freshwater *C. glomerata*.

A significant correlation between the tissue's phosphorus content and the extracellular concentration of phosphorus was found in streams in southern Ontario, but no similar nitrogen correlation was found (Wong and Clark 1976). In contrast, a correlation between nitrogen content and dissolved inorganic nitrogen was observed for *Cladophora* in the Clark Fork of the Columbia River (Montana), whereas no relationship was found for phosphorus. In this case, luxury uptake of phosphorus may have allowed the alga to take advantage of sporadic phosphate availability, a factor that can decouple the relationship between tissue phosphorus content and ambient phosphorus concentration (Lohman and Priscu 1992).

Given the wide variety of conditions under which *Cladophora* occurs, it is probably unwise to assume that any single nutrient limits growth in all cases. For example, the ability of marine *Cladophora prolifera* mats to dominate in eutrophic conditions has been ascribed to an ability to withstand high levels of H_2S, rather than as a direct consequence of increased P-loading (Schramm and Booth 1981). Very high levels of sewage can eliminate *Cladophora* (Edwards et al. 1984). Other nutrients required for growth of *Cladophora glomerata* include silicon (Moore and Traquair 1976), boron, thiamine, and zinc (Moore and McLarty 1975), and vitamins B_1 and B_{12} (Hoffman and Graham 1984, Hoffman 1990); certainly nutrients other than nitrogen and phosphorus play important roles at times.

Salinity restricts the range of some species (Thomas et al. 1990). *Cladophora rupestris* found in intertidal rock pools can stand 5–30‰ salinity (Jansson 1974). It is likely that most *Cladophora* species that are successful in the high intertidal zone have a broad salinity tolerance. Indeed, the marine *C. rupestris* tolerates a considerably higher range of salinities than does the freshwater *C. glomerata* (Thomas et al. 1989).

Reproduction and Propagation

Information on the ecology of reproduction and propagation is limited, even though this may be a key factor in the *Cladophora* life history. *Cladophora* commonly exhibits a diplohaplontic life history (van den Hoek 1963, 1982). In some species sexual reproduction has never been observed, only asexual reproduction by biflagellate or quadraflagellate zoospores (Whitton 1970, van den Hoek 1982). Some species of *Cladophora* form akinetes (Bold and Wynne 1985). However, neither the factors that stimulate akinete production nor the ecological importance of akinetes are understood. Factors that promote zoosporogenesis in *C. glomerata* include high temperatures, vitamin limitation, and shortened photoperiod (Hoffman and Graham 1984). That temperature can stimulate zoosporogenesis may explain why summer die-off occurs in some freshwaters. Production of zoospores lyses the mother cells and may cause a temporary decline in biomass. Hällfors et al. (1975) suggested that distinct bands of *Cladophora* in the intertidal zone were caused by the settlement of zoospores at distinct levels. Lorenz et al. (1991) suggested that zoospores cannot establish new plants when light is below 25 μmol quanta$\cdot$m$^{-2}\cdot$s^{-1} because growth would be light-limited. Mason (1965) showed that propagation by overwintering filaments reestablished most of the biomass of *Cladophora glomerata* found in a farm pond; akinetes and zoospores germinated in the spring but contributed less to propagation of the population.

Most species of *Cladophora* attach by multicellular, branching rhizoids (van den Hoek 1982); these basal holdfasts may serve as resistant structures from which new growths can arise. Basal portions of *Cladophora glomerata* may be resistant to temporary drying, which is known to lower standing crop (Usher and Blinn 1990). Freshwater *Cladophora* does not appear to be able to withstand drying for more than several days (Dodds 1991b).

Our observations (unpubl.) suggest that *Cladophora* in rivers can become detached from its original substrate, drift until it becomes wrapped around a rock or a branch, and continue to be photosynthetically active. Such drift may account for a major portion of biomass in some locations, but this passive mechanism only allows for colonization of downstream habitat.

Species Interactions

Competition. *Cladophora* can be considered a late- or midsuccessional species in flowing freshwaters (Fisher et al. 1982, Sand-Jensen et al. 1989, Simons and van Beem 1990, Dudley and D'Antonio 1991) and an early-successional, opportunistic species in marine waters (Wanders 1977, Taylor and Littler 1982, Menge et al. 1983). These generalizations about successional state are probably overly simplistic; the midsummer die-off in freshwater may be inconsistent with a "successional dominant," and the prominence of *Cladophora* belts (e.g. Jansson 1967) implies that *Cladophora* can be the competitive dominant in marine habitats. However, the generalization regarding the differences in successional position of *Cladophora* in marine and freshwaters may reflect real differences between the ecology of marine and freshwater *Cladophora* species. There are probably several different reasons for this dichotomy. One possibility is that rhodophytes and phaeophytes, which are not large components of algal biomass in freshwaters, are better competitors for light or space. Marine invertebrates are also more likely to compete for benthic space than freshwater invertebrates. *Cladophora* may be less palatable to grazers compared with other common benthic freshwater algae, but more palatable relative to other benthic marine species. These differences and/or others may explain why *Cladophora* is opportunistic in marine habitats and is a climax species in freshwaters.

Because *Cladophora* provides substrate for epiphytic growth, there are numerous descriptions of attached epiphyte communities (e.g. Jansson 1966, 1969, Moore 1977b, c, Lowe et al. 1982, Sheath and Morison 1982, Stevenson and Stoermer 1982, Huang and Boney 1985). Competition between *Cladophora* and its epiphytes is a strong possibility (Jansson 1969, 1975). Nutrients or light must first pass through a layer of epiphytes before reaching *Cladophora.* Water-soluble extracts from freshwater *Cladophora* can inhibit photosynthesis of epiphytic diatoms, implying that competition with epiphytes has resulted in selective pressure for synthesis of these compounds (Dodds 1991c). However, the case for competition between *Cladophora* and its epiphytes may be highly dependent on variable environmental conditions. For example, competition with epiphytes for light may be important only at low ambient light levels (Dodds 1991c). Freshwater *Cladophora* can benefit epiphytes by providing attachment space and refuge from high flow (Moore 1976). High epiphyte biomass has been ascribed to temperature increases (Moore 1977b), high nitrogen supply (Fitzgerald 1969), and lack of grazing (Dodds 1991c).

Cladophora can also occur as an epiphyte. It has been observed attached to *Potamogeton pectinatus* L. (Howard-Williams and Allanson 1981) and to *Phragmites australis* (Lav.) Trin. ex Stevd, increasing the susceptibility of *Phragmites* to breakage (Utermöhl 1982). When *Cladophora* decomposes, it releases an unknown type of water-soluble compound that inhibits formation of new shoots of *Phragmites* (Schröder 1987).

Cladophora glomerata is also found associated with the macrophyte *Elodea canadensis.* Carbon fixation was inhibited by O_2 in *Elodea* to a greater degree than in *Cladophora* under high pH and low CO_2 concentrations. Simpson and Eaton (1986) have speculated that this may explain why *Cladophora* can replace *Elodea* in some locations. Ozimek et al. (1991) showed that *Cladophora glomerata* had negative effects on growth of both *Elodea canadensis* and *Potamogeton pectinatus,* mainly as a result of competition for light. *Cladophora glomerata* as a marine epiphyte has also been associated with the decline of *Fucus vesiculosus.* Increases in salinity and nutrients off the southern coast of Finland increased production of periphyton, including *Cladophora,* and consequently reduced the growth of *Fucus* through competition for both light and nutrients (Kangas et al. 1982).

An interesting case has been made regarding dominance of *Cladophora* in the eutrophic Peel–Harvey estuary (Australia) until 1979, after which time it was replaced by *Chaetomorpha* (Lavery et al. 1991). Prior to 1979, *Cladophora* formed loose aggregates covering anoxic, highly organic sediment in deep areas of the estuary. These aggregates were able to withstand disturbance by water motion; some aggregates floated when oxygen bubbles from photosynthesis accumulated, were transported to shallow areas, and prohibited other species of algae from receiving sufficient light. Following a large winter storm in 1978, much of the biomass was removed from the deep areas, and the anoxic sediments became exposed to oxygen. With formation of an oxidized zone at the surface of the sediments, nutrient regeneration was insufficient to resupply *Cladophora* growth, and the population subsequently declined. During the following year, there was reduced nutrient input and increased light attenuation by a *Nodularia* bloom. Subsequently, there was an increase of *Chaetomorpha* biomass, possibly because it was released from competition by *Cladophora.*

Diseases. Patrick et al. (1983) reported on studies of biological control of freshwater *Cladophora.* Of the grazers investigated (the pond snail *Physa heterostropha,* the crayfish *Orconectes propinquus,* the tadpole *Rana pipiens,* the catfish *Ictalurus punctatus,* and the fathead minnow *Pimephales promelas*), none preferred *Cladophora.* Patrick et al. did find, however, that the fungus *Acremonium kiliense* had a detrimental effect on *C. glomerata.* This effect was more pronounced in the summer months than in the fall. Other investigations have shown that *A. kiliense* produces a water-soluble, dialyzable, heat-stable agent that rendered *C. glomerata* chlorotic and inhibited its growth (Bott and Rogenmuser 1980).

The specificity of fungal pathogens varies. Raghukumar (1986) described a fungus (*Coenomyces* sp.) that could infect *Cladophora repens* (Agardh.) Harvey and *Rhizoclonium* sp. Two other fungi (*Sirolpidium bryopsidis* and *Olpidium rostiferum*) could infect *Cladophora frascatii* Collins et Harvey but not *Rhizoclonium* or other *Cladophora* species. Conversely, species of marine *Lyngbya, Cladophora* sp., and *Rhizoclonium* were susceptible to severe infection by a *Labyrinthula* sp. (Raghukumar 1987). The fungus *Blodgettia bornetii* can penetrate the cells of *Cladophora catenata* (L.) Kütz. and *Siphonocladus rigida* (TeStrake and Aldrich 1984). However, this may represent obligate symbiosis rather than a parasitic interaction.

Viral pathogens that infect *Cladophora* have not been identified, but they probably exist. Viral and fungal pathogens might be used for future biotic control of excessive growths. However, questions such as pathogen specificity and the conditions required for successful infection in the field need to be addressed before such approaches can be used to control the growth of *Cladophora* in nature.

Grazing. Members of *Cladophora* are generally considered to be poor, nonpreferred food sources for freshwater grazers (Gregory 1983, Patrick et al. 1983, Bronmark et al. 1991). In marine systems, consistent with its position as an early successional species, *Cladophora* is considered relatively palatable (e.g. Lubchenco 1978). But *Cladophora* sp. is not eaten extensively by the grazers found in the high intertidal zone in Washington State (Dethier 1982). In any case, many species from varied taxonomic groups graze *Cladophora* in marine habitats and freshwaters (Table 1). One should not assume that the alga is used for food simply because it is found in the guts of organisms. The most efficient way to harvest the organisms affiliated with *Cladophora* may be to ingest the alga. *Cladophora glomerata* has a low content of amino acids relative to freshwater periphyton assemblages that are rich in diatoms, and it contains toxic fatty acids (capric, lauric, myristic, and palmitoleic acids) (LaLonde et al. 1979). Such toxicity may explain why *Cladophora* is not consumed by many freshwater grazers (Patrick et al. 1983).

Decaying *Cladophora* is an adequate food source for mayfly nymphs (Bird and Kaushik 1985). However, the amphipod *Gammarus pseudolimnaeus* and the mayfly larva *Ephemerella subvaria* preferred decaying *Potamogeton* and maple leaves for food over decayed *Cladophora* (Bird and Kaushik 1984). Decaying marine *Cladophora* in the intertidal zone was an adequate food source for the harpacticoid *Tachidius discipes* (Jansson 1967).

Complex species interactions. An interesting feature of the ecology of *Cladophora* is that these algae are found associated with nitrogen-fixing organisms. The biomass of marine *Cladophora* increases after decomposition of blooms of the nitrogen-fixing cyanobacterium *Nodularia spumigena* (Birch and Gabrielson 1984), possibly in response to nitrogen released from the decomposing cyanobacteria. Nitrogen fixation by epiphytes on freshwater *Cladophora* also has been observed (Dodds 1991c). These epiphytes include heterocystous *Nostoc parmelioides* Kützing and *Epithemia sorex,* a diatom with nitrogen-fixing endosymbiotic cyanobacteria (Bahls and Weber 1988). Nitrogen-fixing cyanobacteria (*Nostoc* spp.) also occur within other populations of freshwater *Cladophora* (Whitton et al. 1986, Power 1990b). *Cladophora* can survive in nitrogen-deficient waters; nitrogen-fixing cyanobacteria are common in such waters, and the ability of *Cladophora* to survive there may be enhanced because it can utilize the nitrogen that is fixed and released by the cyanobacteria.

Cladophora and phytoplankton may compete in lakes. The phytoplankton can intercept light, but benthic mats of filamentous periphyton can intercept nutrients from the sediments (Hansson 1988). In one lake, controlling the growth of phytoplank-

TABLE 1. *Species reported to consume* Cladophora *in marine and freshwater habitats.*

Species	Comments	Reference
Freshwater		
Asellus aquaticus (Isopoda)	Slow growth on *Cladophora* in laboratory experiments	Marcus et al. 1978
Hydropsyche occidentalis (Trichoptera), *Baetis tricaudatis* (Ephemeroptera), *Hyalella azteca* (Amphipoda), *Simulum argus* (Diptera), *Trycorythodes minitus* (Ephemeroptera), *Ophiogomphus severus* (Odonata), *Argia vivida* (Odonata), *Sigara* (sp.) (Hemiptera)	Present in gut contents	Koslucher and Minshall 1973
Gumaga nigricula (Gastropoda)	Removed *Cladophora,* grazer exclusion/inclusion experiments	Feminella and Resh 1991
Theodoxus fluviatilis (Osteichthyes)	Lowered relative abundance of *Cladophora* in chambers	Jacoby 1985
Gila robusta seminuda (Osteichthyes)	Consumed with *Spirogyra* and diatoms	Greger and Deacon 1988
Orconectes propinquus (Decapoda)	Found in guts	Capelli 1980
Lymnaea stagnalis, Lymnaea peregra (Gastropoda)	Only when competing for food with tadpoles, diatoms preferred otherwise	Bronmark et al. 1991
Carp hybrids (Osteichthyes)	Aquarium studies	Duthu and Kilgen 1975
Tilapia (Osteichthyes)	As a food supplement	Appler and Jauncey 1983
Brachycentrus occidentalis (Trichoptera)	Only after removing epiphytes	Dodds 1991b
Triops longicaudatus (Notostraca)	Food supplement	Scott and Grigarick 1978
Hydropsyche oslari (Trichoptera), *Hesperophyalax consimilis* (Trichoptera), *Tipula commiscibilis* (Diptera), *Capnia* spp. (Plecoptera), *Eukiefferiella* sp., *Pseudodiamesa* sp. (Chironomidae)	4–20% of gut contents were *Cladophora*	Gray and Ward 1979
Gammarus pulex (Amphipoda), *Asellus aquaticus* (Isopoda)	Never more than 20% of gut contents	Moore 1975
Agapetus celatus (Trichoptera)	Exclusion experiments	Dudley and D'Antonio 1991
Macrobrachium rosenbergii (Decapoda)	Freshwater prawn can grow on *Cladophora* in culture	Nelson et al. 1977
Marine		
Hermaeina smithi (Sacoglossa)	May use chloroplasts symbiotically	Greene 1970
Idotea chelipes (Isopoda)	Laboratory feeding experiments	Jansson and Matthiesen 1971
Littorina littorea (Gastropoda)		Lubchenco 1978
Idotea baltica (Isopoda), *Gammarus oceanus* (Amphipoda)	Older *I. baltica* eat *Cladophora,* younger prefer diatoms	Jansson 1967
Lymnea peregra (Gastropoda)	Poor growth	Skoog 1978
Limapontia capitata (Sacoglossa)	Several *Cladophora* spp. consumed	Jensen 1975

ton increased the penetration of light and promoted an excessive growth of *Cladophora* (Spencer and King 1984).

Complex community interactions involving grazers, *Cladophora,* and its epiphytes occur in lotic communities. Fish in a northern California river consume fish fry and insects that prey upon the larvae of chironomid midges that graze upon and weave their retreats in *Cladophora* (Power 1990b). This trophic control is made more complex by the fact that *Cladophora* offers protection from fish predation but not invertebrate predation (Power et al. 1992). In addition, floods may decrease the numbers of invertebrate grazers, potentiating *Cladophora* blooms during the next growing season (Power 1992). The midge larvae appear to lower algal biomass when they first colonize *Cladophora,* but the larvae stimulate growth later when they approach pupation, possibly by regenerating nutrients (Power 1991). Chironomid larvae and mayfly nymphs that eat *Cladophora* have higher emergence rates and populations in floating mats than in attached streamers. Insects are less susceptible to fish predation in the floating masses, and floating *Cladophora* mats may provide thermally favorable microhabitats for insect growth and development (Power 1990a).

Freshwater snails (*Lymnaea*) will graze *Cladophora* only when exposed to competition from *Rana temporaria* tadpoles. The snails prefer other types of periphyton but are unable to compete with the tadpoles when they co-occur and are forced to rely upon *Cladophora* (Bronmark et al. 1991).

Cladophora may serve as a preferred habitat for marine organisms. Exudates of *Cladophora gracilis* (Griffiths ex Mackay) Kütz. increased survival of the ciliate *Vorticella marina* and enhanced telotroch settlement (Langlois 1975). *Cladophora* serves as the preferred spawning substrate for the Baltic herring *Clupea harengus membras* (Rajasilta et al. 1989).

Extensive research (including systems analysis, food web structure, and studies of epiphytes) has been conducted on *Cladophora* belt communities in the Baltic Sea. Results from these studies include 1) *Cladophora* forms an important habitat for juvenile isopods and amphipods that are a major component of fish diets (Jansson 1967), 2) the bivalve *Cardium* *lamarcki* metamorphoses on *Cladophora* and employs it to concentrate suspended particles (Jansson 1967), 3) fluctuations within communities can be driven by biotic as well as abiotic factors (Jansson 1975), 4) mean abundance of epiphytes was negatively correlated with invertebrate abundance (Jansson 1969), 5) isopods found on *Cladophora* compete for epiphytic diatoms as a food source (Jansson and Matthiesen 1971), 6) seasonal variation in the composition of invertebrate species occurs (Jansson 1974), 7) a distinct successional pattern of epiphytic diatoms exists (Jansson 1969), 8) formation of discrete bands of *Cladophora* in the intertidal zone was related to zoospores settling at distinct levels or formation of new communities from older ones immediately above (Hällfors et al. 1975), and 9) slight eutrophication may favor a high biomass of *Cladophora* (Hällfors et al. 1975).

Many freshwater organisms prefer *Cladophora* as a substrate, often because it provides protection from larger predators. *Cladophora* removal experiments have shown that invertebrate community structure is a function of the presence or absence of the alga (Dudley et al. 1986). Species of nematodes (Croll and Zullini 1972), caddis larvae (Feminella et al. 1989), and isopods (Holomuzki 1989) prefer *Cladophora* as habitat. Small-mouthed salamander larvae (*Ambystoma texanum*) prefer *Cladophora* as a refuge from predation and because it is inhabited by increased levels of their isopod prey (Holomuzki 1989). The isopod *Lirceus fontinalis* was significantly more abundant on *Cladophora* than on bare substrates. Presence of predatory green sunfish, or water recently inhabited by the sunfish, increased the preference of the isopods for *Cladophora* (Holomuzki and Short 1988). Some invertebrates prefer *C. glomerata* over *Bangia atropurpurea* (Roth) Ag., possibly because the cellulosic cell wall of *Cladophora* provides a firmer substrate for attachment than the mucilage surrounding *Bangia* (Chilton et al. 1986). Tadpole shrimp (*Triops longicaudatus*) prefer *Cladophora* over mud for egg deposits (Scott and Grigarick 1978). The flatworm *Meostoma lingua* frequents *Cladophora* because its filaments entangle *Daphnia*, making them easier to capture (MacIsaac and Hutchinson 1985).

Many questions remain regarding the invertebrates that inhabit *Cladophora*. *Cladophora* often harbors large numbers of invertebrates and is often nutrient limited, suggesting that invertebrates could remineralize nutrients from epiphytes and have a positive effect on *Cladophora*. This possibility has been investigated superficially for freshwater species (Dodds 1991c), but its importance remains unknown. The general importance of nutrient regeneration by stream invertebrates has been documented (Mulholland et al. 1991). Situational factors such as invertebrate density and activity, the rate of flow-related nutrient transport, and the degree of nutrient deficiency are probably all factors controlling the relative significance of nutrient regeneration by invertebrates.

Invertebrates may also alter the hydrodynamic properties of *Cladophora*. Not only do invertebrates remove epiphytes, but their activities can dislodge sediments trapped in masses of *Cladophora* filaments. Both sediments and epiphytes tend to lower flow inside freshwater *Cladophora* streamers and consequently decrease drag on the filamentous masses (Dodds 1991c). Furthermore, selective grazing on newly formed growing tips of lateral branches may decrease branching (Dodds 1991c) and thus affect hydrodynamic properties. Alternatively, selective grazing on apical tips by the mayfly nymph *Ephemerella needhami* may increase branching (McShaffrey and McCafferty 1991). The importance of invertebrates to hydrodynamic response remains to be demonstrated in a natural situation.

Much of the invertebrate attraction to *Cladophora* may be related to the heterogeneous substrate it provides. That such diverse communities of organisms inhabit *Cladophora* in marine and freshwater habitats is not surprising because any habitat that offers protection from predation, a place to anchor against flow, and a potential food source (either *Cladophora* itself, its epiphytes, or invertebrate prey) would be expected to be important.

Conclusions and Recommendations for Future Research

Cladophora is a generalist with different roles in different systems, and its ecology is difficult to explain with examples from only one system. Success in such widely divergent habitats is probably connected to the variety of functional roles *Cladophora* can fill. The wide divergence between different species within the genus (as shown by molecular taxonomy) may be related to this diversity of functional roles, as may the morphological plasticity that is observed within a species.

This review suggests several areas for future research on *Cladophora* that may be fruitful: 1) Development of rapid, molecular methods of taxonomic identification may enhance the ability of field ecologists to establish which species they are studying, 2) studies of both sexual and asexual reproduction in the field will help to explain colonization potential and abundance, 3) small-scale measurements of hydrodynamic conditions associated with a variety of *Cladophora* growth forms and concurrent determination of metabolic rates may help to explain the functional significance of morphological variation, 4) further research on fungal and viral pathogens in natural populations of *Cladophora* may be fruitful, 5) the relative importance of competition with epiphytes has yet to be established and probably varies between systems, and 6) ecosystem-level significance of primary production by *Cladophora* is not clear because it may not be a preferred food when living, but it may supply detrital feeders upon decomposition. *Cladophora* undeniably provides habitat for other organisms, which may be its most important function at the community/ecosystem level. Integrative studies of complex interactions involving *Cladophora* in many systems are needed to delineate the ecological importance of the genus.

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