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Phytoplankton and Catfish Culture: a Review

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ABSTRACT

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The profitability of aquaculture has been constrained by the difficulty of managing phytoplankton biomass and growth. This review examines problems caused by uncontrolled phytoplankton dynamics, considers causes of these problems, and assesses the effectiveness of methods used to manage phytoplankton in aquacultural ponds. Most algae-related problems can be attributed to excessive algal biomass (off-flavor, inefficient fish production, poor quality of discharge water) or to non-optimal growth conditions (insufficient dissolved oxygen, propensity to die off). Algal die-offs have been attributed to several causes: photolysis, pathogen attack, and severe nutrient depletion. Although conclusive evidence is lacking, evaluation of die-offs suggests that most algal die-offs result from severe nutrient depletion. The data on off-flavor are similarly limited, but suggest that many taxa, in addition to blue-greens, may cause off-flavor in fish. Most attempts to manage algal dynamics (i.e., herbicides, dyes, nutrient competition by macrophytes, biological control with fish, manipulation of nutrient ratios, and pathogenic control) are ineffective, and many may exacerbate problems associated with algal growth. Biological control appears the most favorable control mechanism, but controversy exists concerning the potential of fish to control algal biomass. Most attempts to control algal biomass with fish have failed. Of 46 trials, filter-feeding fish significantly increased algal biomass 22 times and had no effect in another 12 trials. Biological control of phytoplankton biomass remains a desirable but elusive goal.

INTRODUCTION

Unmanaged phytoplankton growth poses major constraints to the profitability of aquaculture in the U.S. and abroad (Meyer et al., 1973; Anonymous, 1975; Seymour, 1980; Boyd, 1982; Costa-Pierce et al., 1985). This review focuses on the major problems caused by uncontrolled phytoplankton dynamics and on the causes of these problems, beginning with a detailed review of algal die-offs. Other problems – inadequate dissolved oxygen, off-flavor of fish, reduced fish production, and pollution of downstream waters – are also reviewed. The effectiveness of methods used to manage phytoplankton in aquacultural ponds is addressed with an emphasis on the theory and experience pertaining to the biological control of phytoplankton. Because data are readily available

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from the U.S., the review will concentrate on intensive[1] catfish culture. It is hoped that these analyses will also apply to other aquacultural systems.

ALGAL DIE-OFFS

A major problem attributable to unmanaged algal growth is decline in water quality following algal die-offs. Phytoplankton populations periodically collapse; subsequent decomposition of the dead algae can cause oxygen deficits and toxic ammonia levels (Barica, 1975; Boyd et al., 1975; Seymour, 1980;

TABLE 1

Reports of algal die-offs in freshwater. Phylum refers to the general classification of the algae: BG = blue-green, DI = dinoflagellates, DM = diatoms, and GR = greens. Ecotype refers to edibility (ED) or inedibility (IN) to zooplankton grazing. Algae whose lengths usually exceed 25 μm were considered inedible (Vyhnalek, 1983). Habitat refers to the system from which the die-off was reported. Obs. are the number of different algal die-offs reported in a particular reference. *Refers to die-offs that occur with multi-species blooms, but when the mortality can be attributed to the decline of a single species

Genus	Phylum	Ecotype	Area	Habitat	Obs.	Reference
Die-offs of single species blooms						
Anabaena	BG	IN	So. U.S.A.	Catfish pond	1	Boyd et al., 1975
Anabaena	BG	IN	So. U.S.A.	Catfish pond	22	Boyd et al., 1978b
Aphanizomenon	BG	IN	Canada	Small lake	3	Barica, 1975
Aphanizomenon	BG	IN	Canada	Small lake	11	Barica, 1978
Aphanizomenon	BG	IN	Canada	Small lake	3	Healey and Hendzel, 1976
Aphanizomenon	BG	IN	Canada	Small lake	4	Coulombe and Robinson, 1981
Aphanizomenon	BG	IN	Canada	Small lake	1	Brownlee and Murphy, 1983
Aphanizomenon	BG	IN	France	Carp pond	1	Seymour, 1980
Microcystis	BG	IN	So. U.S.A.	Catfish pond	1	Tucker et al., 1984
Oscillitoria	BG	IN	Israel	Carp pond	1	Abeliovitch, 1967
Closterium	GR	IN	So. U.S.A.	Catfish pond	2	Tucker et al., 1984
Ceratium	DI	IN	Canada	Small lake	1	Nicholls et al., 1980
Die-offs of multi-species blooms						
Anabaena and	BG	IN	Canada	Small lake	2	Barica, 1975
Microcystis	BG	IN				
Microcystis and	BG	IN	Canada	Small lake	1	Barica, 1975
Merismopoedia	BG	IN				
Cyclotella and	DM	E	Canada	Small lake	1	Barica, 1975
Synedra	DM	IN				
**Microcystis* and	BG	IN	So. U.S.A.	Catfish pond	1	Tucker et al., 1984
Oscillitoria	BG	IN				
**Microcystis* and	BG	IN	So. U.S.A.	Catfish pond	1	Tucker et al., 1984
Closterium	GR	IN				
**Oscillitoria* and	BG	IN	So. U.S.A.	Catfish pond	2	Tucker et al., 1984
Closterium	GR	IN				

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[1] Aquacultural systems can be divided into extensive (no nutritional inputs), semi-intensive (addition of fertilizer and/or supplementary feed, natural foods still important), and intensive systems (fish are fed supplementary feed, and natural food has little or no nutritional importance).

Tucker et al., 1984). Insufficient oxygen and high ammonia levels may, in turn, kill fish outright, promote disease, and/or temporarily reduce the feeding and growth rates of fish (Meyer et al., 1973; Shilo and Rimon, 1982).

Reports of algal die-offs from freshwater systems show distinct patterns (Table 1). First, of 59 die-offs, 55 occurred when blue-greens dominated the phytoplankton community. Fifty-five occurred when the community was composed largely of a single species or when the die-off could be attributed to the mortality of a single species. In all but one observation in Table 1, the species that collapsed were large or colonial phytoplankton which are relatively immune to zooplankton grazing (Gliwicz, 1977; Vyhnalek, 1983). In addition, dense phytoplankton communities appear more prone to die-off than less dense communities (Boyd et al., 1978b; Barica, 1984). These patterns should be interpreted with caution because the characteristics listed above tend to correlate with hypereutrophy, and most of the data come from two temperate habitats – pothole lakes in Canada and catfish ponds in Alabama.

Photolysis

One hypothesis to explain algal die-offs maintains that photolysis, destruction of algae by high light levels, causes algal die-offs (Abeliovitch and Shilo, 1972; Eloff et al., 1976). However, several factors argue against photolysis as a general explanation for algal collapse. First, photolysis has been demonstrated experimentally only with laboratory cultures that had not been acclimated to pond conditions (Abeliovitch and Shilo, 1972) or with field populations that were first poisoned with Chloramphenicol, an inhibitor of protein formation (Eloff et al., 1976). In the latter study, pond phytoplankton, acclimated to high light levels, did not die off unless poisoned.

Second, some scum-forming blue-greens, the group thought to be most vulnerable to photolysis, grow moderately well under intense light at the water surface (Lewis, 1983; Paerl et al., 1983; Spenser and King, 1985). Blue-greens produce carotenoids for photoprotection, and scum formation may actually represent a formidable advantage in the competition for light, CO_2, and nitrogen rather than a hazard of the flotation mechanism gone awry (Reynolds and Walsby, 1975).

Third, die-offs occur when algal communities are not exposed to inordinately high light levels: to scum-forming species during cloudy weather (Swingle, 1966; Barica, 1978); to blue-greens which were not then forming scums (Coulombe and Robinson, 1981); and to algal taxa that never form scums, e.g., dinoflagellates (Swingle, 1966; Nicholls et al., 1980), greens (Swingle, 1966; Tucker et al., 1984), and diatoms (Barica, 1975). Consequently, photolysis does not seem to be a general explanation for phytoplankton die-offs.

Pathogens

Epidemics caused by pathogens might also cause algal die-offs (Saferman and Morris, 1964; Padan and Shilo, 1973; Desjardins, 1980; Coulombe and Robinson, 1981). Die-offs almost always occur to a single species, an observation consistent with the etiology of viral attack because viral pathogens are host specific (Desjardins, 1980). In addition, virus-like particles have been observed in the water after phytoplankton die-offs (Coulombe and Robinson, 1981), and experimentally induced epidemics cause algal biomass declines similar to algal die-offs (Desjardins and Olson, 1983).

However, die-off occurs with blue-greens and other algal taxa for which no pathogenic viruses have been found (Padan and Shilo, 1973), although no systematic study has actually looked for these viruses. Also, only one experiment (Desjardins and Olson, 1983) supports this hypothesis, and its experimental conditions are unlikely to occur in the field: the algal blooms consisted only of susceptible clones, and the viral density was initially restricted by sterile technique and then artificially enhanced by purposeful introduction. Because cyanophages (viruses that attack blue-green algae) are "ubiquitously distributed in freshwater" (Padan and Shilo, 1973), Desjardins and Olson (1983) concluded that cyanophages are more likely to prevent an algal bloom rather than destroy one that has already developed. Thus, there is little data to support the importance of viruses to algal die-offs in the field (Padan and Shilo, 1973). A similar criticism applies to hypotheses attributing algal die-offs to attack by pathogenic fungi and bacteria (Canter, 1979; Abeliovitch, 1980; Burnham, 1980; Shilo, 1980).

Pathogenic attack is also somewhat inconsistent with the chronology of algal die-offs. Die-offs almost always occur when the phytoplankton are dominated by one species which then collapses. Because even low levels of infection decrease competitive ability, it seems unlikely that an infected species could dominate the plankton.

Nutrient depletion

Phytoplankton might also collapse when they become severely nutrient limited (Lund, 1950; Reynolds and Walsby, 1975; Healey and Hendzel, 1976). Nutrient depletion could explain the chronology of an algal die-off: dominance of the community by the species that eventually collapses. As the dominant species approaches the carrying capacity of the system, this population would become very nutrient stressed. Since phytoplankton respond very rapidly to changes in their environment, a die-off could simply be a normal, albeit very rapid, bust portion of a boom-bust population cycle.

Unfortunately, evaluation of this hypothesis is hampered by confusion concerning the fate of nutrient-starved algae. Whether nutrient-stressed algae survive in a state of senescence or whether they die from nutrient deprivation has not been established (Golterman, 1960; Lund, 1965). However, phytoplankton, like other organisms, probably exhibit both behaviors depending on the severity and duration of privation (Reynolds, 1984).

Assuming that phytoplankton do die when severely stressed, most algal die-offs may result from severe nutrient depletion. Evidence supporting this hypothesis can be found in studies (Barica, 1975; Healey and Hendzel, 1976; Pabst et al., 1980) which suggest that nutrient depletion is a necessary condition for phytoplankton collapse. Nutrient-stressed populations apparently come very close to dying. Collapse is proximally triggered by meteorological changes such as cloudy weather or a decline in water temperature (Barica, 1978; Van Nguyen and Wood, 1979).

These meteorological changes may trigger die-offs by quickly exacerbating nutrient deprivation. Cloudy weather could increase nitrogen deprivation of nitrogen-fixing blue-greens, because their rate of fixation varies with light intensity (Lewis and Levine, 1984). In addition, reduced light and lowered temperature raise the cell quota, the minimum amount of nutrients necessary for algal growth (Rhee and Gotham, 1981a,b). Calm weather, which has been associated with other die-offs (Boyd, 1982), reduces mixing with bottom waters that are often an important nutrient source for phytoplankton growth in vertically stratified systems (Margalef, 1978). Thus, meteorological shifts might, on a very short time scale, dramatically worsen nutrient deprivation, pushing phytoplankton to the point of privation at which death occurs. Brownlee and Murphy (1983) describe an algal die-off that was precipitated by a sudden reduction of nutrients, although this nutrient reduction was achieved by chemical co-precipitation of orthophosphate and calcium carbonate.

Three lines of reasoning support the hypothesis that algal die-offs result from severe nutrient depletion.

1. Empirical observations. A causal mechanism of nutrient depletion could explain the interaction of weather and nutrient status. Nutrient depletion also explains die-offs of all algal taxa, not just scum-forming species or those susceptible to viral attack. A nutrient-depletion hypothesis explains why multi-species die-offs are rarely observed (Table 1), and when observed, are described as "smoother and slower" than collapses of a single species (Barica, 1975). Few species of algae will simultaneously face very severe nutrient depletion, because critical nutrient levels are species specific (Tilman et al., 1982). Since dense populations are more likely to be nutrient- or light-limited, nutrient depletion also explains why dense populations are more likely to collapse than less dense communities. Finally, the observed relationship between a species' reduced vulnerability to zooplankton grazing and its tendency to die off (Table 1) supports this hypothesis. Populations of large, relatively inedible phytoplankton could be more susceptible to nutrient depletion, because zooplankton excretion, which can be an important nutrient source for phytoplankton growth, falls as consumption decreases (Peters, 1975). Predation by zooplankton would also prevent phytoplankton from reaching the carrying capacity of the environment.

2. *Accommodation of competing hypotheses.* Scum formation and exposure to possibly lethal levels of light may ultimately be triggered by nutrient depletion (Lewis, 1983; Paerl et al., 1983). Severe nutrient depletion stops protein formation, mimicking the action of Chloramphenicol that induced photolysis in the experiment of Eloff et al. (1976). In addition, nutrient-limited, stationary-phase phytoplankton may succumb more easily to viral and bacterial attack (Daft et al., 1975; Desjardins, 1980).

3. *Experimental evidence.* Fertilization reduced the incidence of algal die-offs in experiments by Barica et al. (1980), and the nutrient excretion of silver carp reportedly increased the stability of phytoplankton populations in prawn ponds (Costa-Pierce et al., 1985).

Despite limitations of the data, aquaculturists might profitably assume that nutrient depletion is involved in most algal die-offs. Unlike other factors (pathogen prevalence and scum formation), nutrient levels are easily controlled by fertilizing or by maintaining algal biomass below levels at which nutrients become limiting. Given that nutrient depletion may induce scum formation and may increase susceptibility to pathogenic attack, maintaining high inorganic nutrient levels seems prudent.

If nutrient depletion causes most die-offs, promoting algal species diversity might also reduce the frequency of algal die-offs. Several species would rarely collapse simultaneously, because nutrient limitation is to some extent species specific. Few algal species undergo critical nutrient depletion at the same time (Tilman et al., 1982). Diverse algal communities would also be less vulnerable to attack by pathogens, which are also often host specific.

Costs of algal die-offs

Algal die-offs cause serious economic losses to aquaculture (Boyd et al., 1978b) in both intensive and extensive aquacultural systems growing both fish and invertebrates: in Hong Kong (Sin and Chiu, 1982); China (Anonymous, 1975), France (Seymour, 1980), Israel (Shilo and Rimon, 1982), Canada (Barica, 1975, 1978) Hawaii (Costa-Pierce et al., 1984), and the continental U.S. (Boyd et al., 1975, 1978b). Two studies (Boyd et al., 1978b; Barica, 1984) assessed the frequency of phytoplankton die-offs. In the first, catfish ponds in Alabama, U.S.A., were observed throughout the spring of three consecutive years (Boyd et al., 1978b). On average, 30% of ponds had phytoplankton die-offs each spring. However, of the ponds having algal densities greater than 1000 *Anabaena* filaments per ml (approximately 50 μg/l chlorophyll a)[2], 81% (22 of 27) had phytoplankton die-offs. Barica (1984) found a similar frequency of algal die-offs in Canadian pothole lakes used for trout culture. Of 20 lakes with algal densities exceeding 100 μg/l chlorophyll a, 80% had phytoplankton die-offs.

Thus, these observations suggest that algal die-offs, at least in temperate regions, are a relatively frequent event. Moreover, 80% probably underestimates the actual incidence of die-offs in temperate fish ponds because fish ponds regularly exceed 100 μg/l chlorophyll a; the observation periods of both studies were considerably shorter than normal growing seasons; and Barica reported the number of lakes with at least one die-off, not the total number of algal die-offs. A single lake may have had two or more die-offs per summer (Barica, 1975).

Estimating economic losses resulting from algal die-offs, however, is difficult. The major negative effect of die-offs, oxygen depletion, can be remedied by emergency aeration (Boyd and Tucker, 1979; Boyd, 1982). The remaining costs are subtle and difficult to quantify, but include costs due to increased supervision; costs resulting from the purchase, maintenance, and operation of emergency aeration devices; and costs due to reductions in fish health and growth.

A minimal estimate of the costs of algal die-offs can be obtained by considering losses resulting from reduced feeding and growth of fish. Die-offs often produce high levels of ammonia which can discourage fish feeding and growth for periods of 10–15 days (Seymour, 1980; Shilo and Rimon, 1982; Tucker et al., 1984). Since total fish production depends on the length of the growing season, each severe algal die-off can reduce fish production in a 180-day growing season by 6–8% (e.g., 10/180 to 15/180). Assuming that 80% of ponds have one algal die-off per growing season (Boyd et al., 1978b; Barina, 1984), die-offs cause an estimated 4–7% reduction in annual fish production in temperate regions. This minimal estimate does not include costs of emergency aeration, or losses due to fish killed or sickened by the die-off.

OTHER PROBLEMS RESULTING FROM UNMANAGED PHYTOPLANKTON GROWTH

Insufficient oxygen production

As algal densities rise, net oxygen production per unit algal biomass falls as nutrients or light become limiting (Goldman, 1979b; Javornicky, 1980), and dissolved oxygen levels generally peak at intermediate algal densities (Gold-

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[2] Boyd et al. (1978b) reported only numbers of filaments per ml and Secchi disc depths. Secchi disc depths were converted to chlorophyll a values using the equation of Almazan and Boyd (1978).

man, 1979a,b; Steel, 1980; Laws and Malecha, 1981; Colman and Edwards, 1987; Smith and Piedrahita, 1988). Oxygen production by dense standing stocks of algae often fails to compensate for total pond respiration, causing oxygen shortages than can stress and sometimes kill fish (Boyd et al., 1978a; Laws and Malecha, 1981). Hence, insufficient dissolved oxygen is generally attributed to excessive phytoplankton biomass.

However, the relationship between algal biomass and dissolved oxygen levels is complex and indirect. Low dissolved oxygen tends to co-occur with high algal biomass because inorganic nutrients and light, which affect dissolved oxygen directly through their effects on Net Primary Production (NPP), tend to become depleted as algal biomass rises. However, nutrient depletion can occur at any biomass level, and light levels depend on site-specific levels of non-algal turbidity as well as levels of ambient light and algal biomass. NPP has a more direct relationship to dissolved oxygen levels and, therefore, seems a better target of management than algal biomass (Smith and Piedrahita, 1988).

Although no data estimate the economic benefits of maximizing NPP in fish ponds, models discussed in Smith and Piedrahita (1988) predict that current stocking rates could be increased two to three times if NPP could be maintained at optimal levels. Increasing stocking levels and fish yields would decrease costs of fish production because only costs due to feed and fingerlings would rise appreciably. Feed and fingerlings comprise about 60% of the total cost of catfish production (Pillay, 1973). Therefore, tripling fish yields without expanding pond acreage could pare the costs per production by about 25%[3]. Annual catfish production in the U.S. totals almost 100 million dollars (Anonymous, 1985), so optimal phytoplankton management could save about $25 million.

Off-flavor

Blue-green algae exude chemicals – geosmin and methylisoborneol – that taint fish flesh causing what is commonly termed "off-flavor" (Lovell and Sackey, 1973; Tabachek and Yurkowski, 1976; Persson, 1980, 1981; Lovell, 1983). Because of this and because fish with off-flavor tend to be found in ponds dominated by blue-green algae, blue-greens are sometimes thought to be the sole source of off-flavor. However, correlations between the density of blue-green algae and the occurrence of off-flavor yield inconsistent results (Persson, 1981; Brown and Boyd, 1982; Armstrong et al., 1986).

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[3] Let the current cost (C) of production (P) be C/P. If only costs due to fingerlings and feed increase appreciably, tripling fish stocking raises the costs to $(1+0.6+0.6)\times C$, or 2.2 C. Since production would be $3\times P$, the new cost per production would be $(2.2\times C)/(3\times P)$, or 73% of current costs per production.

A body of evidence suggests that blue-greens may not be the sole cause of off-flavor in fish:

(1) decomposing phytoplankton of all taxa can serve as a carbon source for actinomycetes, fungi which also produce off-flavor chemicals (Lovell, 1979);

(2) ponds producing fish with severe off-flavor are often dominated by other taxa of algae (Brown and Boyd, 1982; Armstrong et al., 1986);

(3) total algal biomass is sometimes a better predictor of off-flavor than density of blue-green algae (Brown and Boyd, 1982);

(4) many algal taxa produce odorous compounds (Juttner, 1983) that might cause off-flavor;

(5) the descriptions of several recently identified off-flavors closely resemble descriptions of odors and tastes of drinking water that are produced by many algal taxa (Table 2).

Perhaps then, off-flavor should be attributed to dense algae rather than to blue-green domination. Unfortunately, two factors complicate evaluation of the relationship between algal biomass and off-flavor. Once acquired, fish may retain off-flavors for several days or weeks (Lovell and Sackey, 1973; Persson, 1980); hence, the source of off-flavor can substantially precede the observation of poor-tasting fish. Lag times between the observation of off-flavor and the ultimate source could be even longer when detritus of algal origin serves as a carbon source for actinomycetes which then produce off-flavor chemicals. A second complication arises, because production of off-flavor chemicals may depend on the physiological state of the phytoplankton as well as their biomass and taxonomic composition (Persson, 1981). Conditions used for algal culture affect the production of off-flavor chemicals in the laboratory (Persson, 1981), and excretion of other organic compounds increases when phytoplankton are stressed (Fogg, 1977; Sharp, 1977).

No economic study has estimated the cost of off-flavor. However, off-flavor

TABLE 2

Correspondence of off-flavors in fish (from Lovell, 1983) and descriptions of odors from drinking water (Palmer, 1962)

Off-flavor	Odor	Taxa of algae causing odor
Sewage	Septic	Blue-green, dinoflagellate, green
Earthy-musty	Musty	Blue-green, diatom, green
Rancid	Spoiled	Green
Metallic	Metallic*	Dinoflagellate
Moldy	Musty	Blue-green, diatom, green
Weedy	Grassy	Blue-green, green
Petroleum	Aromatic	Diatom
Stale	No similar odor	

*This was a corresponding taste.

can cause severe economic losses and may be, according to Lovell (1981), "the most serious problem facing pond culture of fish in the U.S."

Lost production

It is ironic that dense phytoplankton cause so many problems, because primary production is the ultimate source of most fish production in extensive aquacultural systems (Anonymous, 1975). Positive relationships have been found between fish production and algal biomass (Almazan and Boyd, 1980) and between fish production and measures of algal growth (Melack, 1976; Edwards et al., 1981; Liang et al., 1981; Barthelmes et al., 1988). These relationships imply that dense algae found in intensive fish ponds could support the growth of more fish if phytoplanktivorous species were stocked (Pretto-Malca, 1976; Dunseth, 1977). Thus, very dense phytoplankton should be viewed both as a vast, underutilized resource as well as the source of the numerous problems discussed in this literature review.

Discharge problems

Effluent from fish ponds may sometimes violate standards for discharge into natural stream courses and rivers. Early work from Auburn University suggested that aquacultural discharges were usually not of sufficient volume nor of sufficient organic load to cause major problems (Boyd, 1978). Auburn ponds at that time, however, had phytoplankton densities ranging from 100 to 300 μg/l chlorophyll a, relatively low values by today's standards (Rimon and Shilo, 1982; Tucker et al., 1984). The number of ponds has also increased as the industry has expanded. Thus, Boyd's early work may underestimate the discharge problem today.

Miscellaneous problems

Unmanaged phytoplankton growth also causes a host of other problems that will be briefly mentioned here. Primary production by very dense phytoplankton can raise pH to levels that can directly, or indirectly through ammonia toxicity, affect fish growth and health (Swingle, 1961; Soderberg et al., 1983; Meade, 1985). High levels of photosynthesis can also produce toxic levels of oxygen supersaturation (Weitkamp and Katz, 1980). Losses from supersaturation have only rarely been reported for natural systems and aquacultural operations (Supplee and Lightner, 1976; Weitkamp and Katz, 1980; Motzkin et al., 1982), yet ponds regularly reach levels of supersaturation that kill fish under laboratory conditions. Shading by very dense phytoplankton reduces dissolved oxygen at the pond's bottom which limits growth rates of fish food (e.g., chironomids, oligochaetes) and some aquaculture species (e.g., *Macro-*

brachium) which are confined to the benthos. Anoxic bottom sediments may produce excessive ammonia, nitrite, and hydrogen sulfide that can kill or stress fish even in aerated systems (Rimon and Shilo, 1982; Torrans and Clemens, 1982; Avnimelech and Zohar, 1986). These toxic metabolites may also cause the cessation of fish growth found in intensively managed ponds in Israel (Avnimelech et al., 1981; Rimon and Shilo, 1982; Motzkin et al., 1982).

METHODS OF MANAGING PHYTOPLANKTON

Fish culturists and aquacultural researchers have attempted to manage phytoplankton growth in several ways. These methods are discussed briefly below in terms of their potential success and limitations. Following this is a detailed discussion of biological management techniques, which have the potential to redress many of the problems inherent in the other techniques.

Aquaculturists commonly use two methods to manage phytoplankton: herbicides and reduction of nutrient inputs. The latter, whether by cessation of feeding or reduction of fertilization (Anonymous, 1975), maintains water quality at the expense of slowing the rate at which food is provided to the fish. This method may also be incompatible with attempts to manage NPP and to minimize algal die-offs, both of which may rely on maintenance of excess nutrient levels. Herbicides are difficult to administer properly, are expensive, and may be environmentally unsound (Janik et al., 1980). Moreover, herbicides reduce NPP and, worse, often induce algal die-offs; thus, herbicides can cause more problems than they solve (Tucker and Boyd, 1978; Smith and Piedrahita, 1988).

Researchers have also attempted to control algal biomass by promoting growth of macrophytes (McVea and Boyd, 1975; Costa-Pierce et al., 1985) which compete with phytoplankton for nutrients and light. Nutrient and light depletion, however, reduces NPP (Smith and Piedrahita, 1988), so macrophyte growth often exacerbates insufficient dissolved oxygen (McVea and Boyd, 1975; Pokorny and Rejmankova, 1983; Gopal et al., 1984; Costa-Pierce et al., 1985).

Other control measures are largely untested. Modifying N/P ratios to exclude blue-greens (as suggested by Seymour, 1980) would affect only species composition which would have little impact on the water quality problems discussed above, unless off-flavor really results only from blue-green algae. For the same reason, controlling phytoplankton with species-specific viruses or pathogens would have little utility. Algal pathogens (e.g., myxobacteria) that are not species specific suffer from many of the same problems as broad-spectrum herbicides, i.e., expense, difficulty of use, and tendency to induce algal die-offs. Shading phytoplankton by increasing turbidity or with dyes solves relatively minor problems due to excessive algal production (supersaturation and excessively high pH) but exacerbates major problems due to insufficient NPP (Boyd, 1982; Smith and Piedrahita, 1988).

Before adopting any method to manage phytoplankton growth or biomass, fish culturists must consider potential effects on other water quality factors also controlled by phytoplankton dynamics. For example, it has been suggested (Smith and Piedrahita, 1988) that managers fertilize ponds when low dissolved oxygen occurs at intermediate algal densities. Without some mechanism of harvesting, however, fertilization might increase algal biomass, exacerbating problems caused by excessive algal biomass – off-flavor, discharge, and stratification. Managers must consider all possible impacts of a strategy and weigh the benefits against potential side-effects (Smith, 1987).

Biological management with filter-feeding fish

Biological control with fish redresses many of the major problems associated with unmanaged algal growth and also increases fish yields by utilizing another niche. Unfortunately, most attempts to manage phytoplankton with filter-feeding fish have failed (Table 3). Of 46 trials found in the literature, 22 resulted in significant increases in algal biomass due to the addition of algae-eating fish; only 12 produced significant decreases in algal biomass. Of the 21 trials conducted in experimental ponds, only three, all from Dunseth (1977), report a decrease in algal biomass after the addition of algae-eating fish. In pond trials in which primarily phytoplanktivorous fish (e.g., tilapia and silver carp) were added, 13 of 16 trials produced either increases in algal biomass or no effect. Negative trials (i.e., those having no effect or increasing biomass) cover a wide range of stocking densities, suggesting that the failure of fish to control phytoplankton was not due to an imperfect stocking level (Burke et al., 1986).

These experimental data agree with studies of the feeding of filter-feeding fish. Despite some confusion (Colman and Edwards, 1987), most studies suggest that these fish consume primarily large phytoplankton (Kajak, 1979; Cremer and Smitherman, 1980; Drenner et al., 1984a,b; Smith, 1986, 1987; Drenner et al., 1987). Since these fish also eat zooplankton (Grygierek, 1978; Drenner et al., 1984a,b; Smith, 1986), which consume small phytoplankton, filter-feeding fish remove both the competitors (large phytoplankton) and predators (zooplankton) of the small algae (Opuszyński, 1972; Kajak, 1979). Small algae generally outcompete and grow faster than large algae (Smith and Kalff, 1983); therefore, grazing by filter-feeding fish may reinforce the tendency of small algae to dominate aquatic systems (Milstein and Hepher, 1985; Smith, 1986). Grazing by these fish will probably only alter the size structure of the algal community, not control its biomass.

Filter-feeding fish can also affect algal biomass indirectly. For example, they might increase algal biomass by enhancing nutrient recycling (Opuszyński, 1979; Costa-Pierce et al., 1985; Drenner et al., 1986). Conversely, they could reduce nutrients by incorporating them into fish biomass (Prowse, 1969; Dunst et al., 1974; Barthelmes et al., 1988) or by the sinking of fish feces to the bottom (Kajak, 1979; Drenner et al., 1987). In addition, fish might reduce final biomass by disturbing sediments and clouding the water (Kajak, 1979; Drenner et al., 1984a).

Four studies (Kajak et al., 1975; Dunseth, 1977; Pierce, 1983; Drenner et al., 1987) demonstrate significant reductions in algal biomass after the stocking of filter-feeding fish (Table 3). Kajak et al. (1975) report a decrease in algal biomass after silver carp were added to enclosures in a eutrophic lake. Although the authors supplied no statistics, differences were large and consistent over time and were assumed to be significant. Kajak (1979) attributed this reduction to nutrient losses resulting from sedimentation of feces, not to fish grazing. Sinking feces could reduce nutrients in the water column under conditions found in their experimental enclosures: minimal water circulation, relatively low nutrient levels, and absence of bottom-feeding fish. These conditions, however, are rarely found in aquacultural ponds (Kajak, 1979). (Kajak's explanations appear to be based on his belief that the fish cannot control algal biomass, because he presents no data on nutrient levels in his enclosures.)

In a study at Auburn University (Dunseth, 1977), ponds stocked with silver carp or silver carp and tilapia (*Oreochromis* spp.) had less algae compared to control ponds with catfish alone. This effect was not, however, persistent. No effect was found when the entire experimental period was considered ($P > 0.10$, Behrends, 1977). In addition, Dunseth counted phytoplankton at 200×, an insufficient magnification to accurately count small phytoplankton (personal observation) that may dominate ponds stocked with silver carp (Schroeder, 1978; Milstein and Hepher, 1985; Smith, 1986, 1987). Also, phytoplankton in his control ponds may have had access to more nutrients than phytoplankton in ponds with filter-feeding fish. All treatments were provided with the same amount of fish food, but "catfish in the control ponds were not consuming all of the daily ration" just prior to the significant divergence between treatments (Behrends, 1977). Uneaten food could have supplied more nutrients to algae in control ponds, because catfish assimilate up to 40% of the nitrogen and 65% of the phosphorus that they consume (Boyd, 1982).

Pierce (1983) found that *Oreochromis aurea* significantly reduced algal biomass in experiments conducted in large tanks. (A significant effect was obtained by combining data from both experimental treatments.) Pierce added nutrients in excess; thus, phytoplankton within his experimental cultures were apparently light limited. Because fish can dramatically increase turbidity by stirring sediments (Kajak, 1979; Drenner et al., 1984a), the observed reduction in algal biomass could have resulted from reduced light levels rather than from grazing. In addition, Pierce's experimental containers differed from ponds in one very important aspect: "due to wide pH fluctuations ... zooplankton were always insignificant or absent" (Pierce, 1983). Because the effect of filter-

TABLE 3

Studies of the effect of filter-feeding fish on phytoplankton biomass. Fish codes: sc = silver carp (*Hypophthalmichthys molitrix*), bh = bighead (*Aristichthys nobilis*), gs = gizzard shad (*Dorosoma cepedianum*), pf = paddlefish (*Polyodon spathula*), oa = *Oreochromis aurea*, og = *O. galilaea*, os = mixture of *Oreochromis aurea, O. nilotica*, and *O. nilotica* and *O. hornorum* hybrids. Effect is the ratio of algal biomass in systems stocked with filter-feeding fish compared to algal biomass in systems without these fish. Note: many of the studies below were not explicit attempts to control algal biomass.

Study	Fish	Experimental conditions	Fish stocking density (no./ha)	Effect
I. Studies showing significant increases in algal biomass				
Janusko, 1974	bh	Ponds	1 500	2.1
	sc+bh	Ponds	1 500ea	1.5
Perschbacher, 1975	oa	Ponds	?[a]	2.1
	oa	Ponds	2 470	15.2[b]
	oa	Pools	34 600	3.5
	oa	Pools	24 600	2.4
Barthelmes and Kliebs, 1978	sc	Ponds	1 000	1.3
Janusko, 1978	sc	Ponds	12 000	1.3
Costa-Pierce et al., 1985	sc	Ponds	1 000	2.2
Rea, 1986	sc	Ponds	2 470	2.1
	sc	Ponds	9 880	2.1
	bh	Ponds	2 470	2.1
	bh	Ponds	9 880	2.1
	pf	Ponds	990	2.1
Drenner et al., 1986	gs	Tanks	359[c]	10.3[c]
	gs	Tanks	387[c]	14.0
	gs	Tanks	271[c]	3.0
	gs	Tanks	247[c]	3.0
	gs	Tanks	211[c]	4.5
	gs	Tanks	178[c]	4.5
	gs	Tanks	112[c]	8.0
	gs	Tanks	119[c]	5.3
II. Studies showing no effect on algal biomass				
Janusko, 1974	bh	Ponds	1 500	2 4
	sc	Ponds	1 500	1.1
	sc	Ponds	3 000	0.9
Janusko, 1978	sc	Ponds	4 000	1.3
	sc	Ponds	8 000	1.1
Drenner et al., 1984b	gs	Tanks	245[d]	0.7
Smith, 1985	sc	Tanks	110 000	1.3
Costa-Pierce et al., 1985	sc	Ponds	1 000	1.2
Threlkeld, 1987	gs	Tanks	4 300	0.9
	gs	Tanks	4 300	1.4
	oa	Tanks	21 500	0.9
	oa	Tanks	21 500	1.5

TABLE 3 (continued)

Study	Fish	Experimental conditions	Fish stocking density (no./ha)	Effect
III. Studies showing significant decreases in algal biomass				
Kajak et al., 1975	sc	Enclosures	10 000	0.2
	sc	in lake	30 000	0.2
Dunseth, 1977	sc	Ponds	2 470	0.8
	os	Ponds	1 950	0.8
	os + sc	Ponds	1950 + 2470	0.7
Pierce, 1983	oa	Tanks	70 000	0.6
	oa	Tanks	160 000	0.2
Drenner et al., 1987	og	Tanks	250[e]	0.3
	og	Tanks	500[e]	0.2
	og	Tanks	1 000[e]	0.2
	og	Tanks	2 000[e]	0.1
	og	Tanks	4 000[e]	0.05
IV. Studies with insufficient replication				
Janusko, 1972[f]	sc	Ponds	10 000	2.0
Barthelmes and Kliebs, 1978	sc	Ponds	10 000	0.8

[a] Perschbacher (1975) compared 30 ponds with and without *O. aurea*. He gave no stocking densities.

[b] Phytoplankton counts. No data on biomass given.

[c] Weights of fish are in kg dry weight per ha. Drenner et al. (1986) performed four separate experiments, the first three using an experimental design with two stocking levels of gizzard shad and a control with no shad. The fourth experiment tested only presence and absence of shad. All treatments were repeated with and without another fish, *Menidia beryllina*. As shown by ANOVA, shad always significantly increased algal biomass compared to controls with no shad, when stocked alone or with *Menidia*. Experiments with three levels of shad were treated as a single trial, and stocking densities and effects reported above are for the treatment with the higher shad stocking level.

[d] Weights of fish are in kg dry weight per ha.

[e] Weights of fish in kg wet weight per ha.

[f] Determined from Fig. 4 in Opuszyński (1972).

feeding fish on phytoplankton may result largely from the fish's effect on zooplankton (Opuszyński, 1972; Kajak, 1979; Drenner et al., 1986), Pierce's experimental results may not apply to aquacultural ponds that invariably contain zooplankton.

Drenner et al. (1987) found that the addition of *Oreochromis galilaea* reduced algal biomass in experiments conducted in large tanks. This species appears to take very small particles (down to 10 μm and somewhat less) with high efficiency, suggesting that this species may be able to control both netplankton and nanoplankton. However, the initial plankton community consisted primarily of large phytoplankton that *O. galilaea* grazes efficiently, and the experiments may have been too short (7 days) to have allowed sufficient time for smaller, less vulnerable plankton to respond. This fish's filtration rates on microplankton (<5 μm) were effectively zero; future experiments must determine whether *O. galilaea* can control microplankton as well as the larger phytoplankton that predominated in these experiments. Future work must also determine whether algal biomass can be controlled by *O. galilaea* at densities that allow the growth of other fish species in the pond.

Overall, experimental work to date and consideration of the feeding ecology of filter-feeding fish presents a pessimistic picture for prospects of biological control using filter-feeding fish. Experimental results (Kajak et al., 1975; Dunseth, 1977; Pierce, 1983; Drenner et al., 1987) suggesting otherwise should be treated with caution, because the reduction in algal biomass reported in these studies may have resulted from artifact or experimental conditions unlikely to be realized in aquacultural ponds.

Caution should also be used when evaluating some of the experimental data that suggest that fish cannot control algal biomass (Table 3). Trials with gizzard shad (Drenner et al., 1984b, 1986; Threlkeld, 1987), bighead (Janusko, 1974; Rea, 1986), and paddlefish (Tea, 1986) should be accorded less weight, because these fish may be primarily zooplanktivorous. Perschbacher's (1975) data are also limited. In one trial, he reports only phytoplankton cell numbers, which is not a good indicator of biomass. However, ponds with *Oreochromis* spp. had an average of 15 times more phytoplankton cells than ponds with no *Oreochromis*, the "species composition of the dominant forms were not appreciably altered" by the treatment, and COD (Chemical Oxygen Demand) and primary production were higher in ponds with *Oreochromis*. While each of these observations could be subject to an alternative view, all support the assumption that algal biomass responded significantly to treatment. Perschbacher also found significantly more algal biomass in a survey of 30 catfish ponds stocked with and without *Oreochromis*, but he provides no other information about the management of these ponds. The results of Janusko (1974) are confounded by differential nutrient additions. Common carp, which were stocked in all ponds, fed ad libitum during these trials and consumed less artificial feed when stocked in ponds with filter-feeding fish. This last is, however, a conservative artifact, because ponds with filter-feeding fish had higher or equal algal densities despite receiving less nutrients.

Several studies were omitted from Table 3 although they have data that could be interpreted as evidence that fish alone can affect algal biomass. Prowse (1969) suggests that silver carp can retard eutrophication, but his work addressed the size structure and taxonomic composition of the phytoplankton, not the biomass. Spartaru et al. (1983) and Schroeder (1978) both report that silver carp reduced algal biomass, but both works intended to measure the biomass of larger phytoplankton, not total algal biomass. In addition, authors of several experimental studies (Cooper, 1973; Cohen et al., 1983; Dickman and Nanne, 1987) stated that their results demonstrated an effect of herbivorous fish on algal biomass, the last study claiming an increase. None, however, provides data on algal biomass.

Future experimental approaches

Future attempts at biological control could try other methods and other filter-feeders. Some fish species may consume all sizes of phytoplankton at an efficiency adequate for control (e.g., *O. galilaea*). Experiments with other species of fish should, however, begin with a systematic study of their feeding ecology.

Non-piscine filter-feeders might also be used. Zooplankton consume phytoplankton, but they consume primarily small phytoplankton less than 25 μm in diameter (Gliwicz, 1969, 1977; McCauley and Downing, 1985) and are apparently unable to control algal biomass in fish ponds (Vyhnalek, 1983). The feeding spectra of bivalves have not been rigorously studied. They, like the zooplankton, may specialize on small algae (Mohlenberg and Riisgard, 1979) or may take an even wider range of particle sizes. Bivalves may control phytoplankton in some natural ecosystems (Cloern, 1982; Officer et al., 1982); therefore, their potential as biological control agents should be investigated more thoroughly. Preliminary work with *Corbicula*, a freshwater Asian clam, suggests that this bivalve might control algal biomass (Buttner, 1986).

Another strategy combines complementary filter-feeders, two or more herbivores that together eat all algal sizes. One such technique using filter-feeding fish and zooplankton was successful when tested in tanks, reducing algal biomass by 99% and increasing algal diversity (Smith, 1985). This technique, however, has not been extensively tested and may be difficult to apply to ponds (Smith, 1987). Moreover, while zooplankton and fish may eat all sizes of phytoplankton, phytoplankton escape herbivory with other defenses, primarily toxicity and indigestibility (Porter, 1977; Lampert, 1981).

In summation, experimental work suggests that fish alone may be unable to provide persistent control of phytoplankton growth. It is possible that no biological control method will work. Biological control of phytoplankton biomass in fish ponds remains a desirable but elusive goal.

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