J. Aquat. Plant Manage. 47: 1-15

Ecological Impact of Grass Carp: A Review of the Available Data

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ABSTRACT

The exotic grass carp (*Ctenopharyngodon idella*) has been used for almost a half a century in the United States as a biological agent to control and manage aquatic plants. This long-lived generalist herbivore consumes large amounts of vegetation and can considerably alter habitat and impact aquatic communities. We conducted a literature review to determine whether previous studies adequately addressed ecological impacts of grass carp and their underlying mechanisms. Our goal was to identify strengths and limitations of ecological assessment in the literature and suggest a trajectory of future research. The review yielded 1,924 citations on grass carp; however, data on ecological interactions were limited, and most research emphasized the biology of grass carp or eradication of aquatic plants rather than ecological mechanisms responsible for ecosystem-wide impacts. Very few studies addressed effects on habitat complexity or community-structuring processes. We provide a comprehensive tabulated overview of feeding preferences and environmental impacts of grass carp. We argue that ecology is paramount to evaluating grass carp impacts and thorough understanding of these impacts is essential for the appropriate management of aquatic communities. Current knowledge is not sufficient to accurately predict long-term effects of grass carp on freshwater ecosystems. We advise a more cautious approach to developing guidelines for grass carp use.

Key words: aquatic plant management, *Ctenopharyngodon idella*, habitat alteration, literature review.

INTRODUCTION

During the last 45 years, a considerable amount of information has been published on grass carp, *Ctenopharyngodon idella* (Val.). Reports of grass carp use in management started to proliferate in the mid 1970s, approximately 10 years after the first grass carp were stocked into Arkansas reservoirs with the hope that this large exotic herbivore would control growth of noxious aquatic plants (Pierce 1983). These first reports emphasized the biology and physiology of the fish and its feasibility as a tool for weed control (Sills 1970, Stott and Robson 1970, Shireman and Maceina 1981, Shireman 1984, Wiley et al. 1984, 1987, Leslie et al. 1987). Much of this literature was stimulated by the apparent success and efficiency grass carp demonstrated in reducing and even eradicating entire macrophyte communities. Encouraged by the enthusiasm of finding an effective management tool for an ever-increasing problem of invasive plant infestations, this emphasis prevailed in the literature for more than a decade. By the mid-to-late 1980s, the interest shifted toward addressing questions of the direct impacts these herbivores had on environmental parameters other than targeted aquatic plants.

Concurrently, literature was developing in the discipline of aquatic ecology that addressed indirect effects on the structuring of aquatic communities. Much of this literature emphasized effects of exotic introductions and dominant organisms on community structure (Pimm 1987, Ross 1991, Simberloff 1990, Soule 1990, Vitousek 1990) and provided evidence that a keystone species can alter environmental conditions and mediate community processes (Paine 1966), along with other indirect mechanisms responsible for altering community structure (Kerfoot and Sih 1987). Many of these mechanisms involve multi-species interactions, such as competition, predator-prey interactions, and aquatic plants as ecologically important components within aquatic ecosystems (Jeppesen et al. 1997). Submerged macrophytes are important for water quality, nutrient dynamics, and invertebrate-fish interactions (Jeppesen et al. 1997 and references therein). Spatial heterogeneity across a landscape is important for ecological interactions (Palmer and Poff 1997, Schaffer 1981). Like a landscape, a waterscape exhibits similar heterogeneity due to the differences in spatial complexity and structural habitat provided by aquatic plants. Habitat heterogeneity in aquatic systems mediates mechanisms responsible for determining trophic interactions, animal distribution (Werner and Hall 1979, Savino and Stein 1982, Mittelbach 1988, Diehl 1993), and community composition, such as species diversity and abundance (Gilinsky 1984, Adams and DeAngelis 1987). It was previously thought that macrophytes provide few functions other than physical structure, but now it is clear they are grazed by a variety of animals (Lodge et al. 1997) and also indirectly contribute to lake primary productivity by supporting large biomass of periphyton (Wetzel 2001). Vegetated habitats provide abundant food reserves for mammals, waterfowl, amphibians, reptiles, fish, and invertebrates (Swanson and Meyer 1973, Pardue and Nielsen 1979, Gilinsky 1984, Keast 1984, Eldridge 1990, Fredrickson and Laubhan 1996). Grass carp can cause major reduction or complete elimination of aquatic plants when introduced into aquatic systems (Van Dyke et al. 1984, Wiley et al. 1987, Klussman et al. 1988). Diversity of aquatic plant communities can be reduced considerably, even at carp

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densities typically required to control a target plant species (Stott and Robson 1970, Stott 1977, Fowler and Robson 1978, Shireman and Maceina 1981). Because such changes in a plant community significantly alter the habitat and interactions of many aquatic organisms, it is prudent to first develop a thorough understanding of how an exotic herbivorous fish can influence the aquatic community before assessing its feasibility as a management tool.

Previous reviews have discussed mostly biology and feeding preferences of grass carp, management applications such as stocking rates, and effects on water quality (e.g., Bain 1993, Petr 2000, Cudmore and Mandrak 2004, Pipalova 2006). None of the previous reviews, however, emphasized ecological interactions or attempted to address potential mechanisms responsible for grass carp impacts. The goals of this review are to evaluate the availability of data in previous research on grass carp that attempt to validate community impacts, identify strengths and limitations of this research, and determine potential design and trajectory of future research, and protocol for use of grass carp as a biocontrol agent.

We used mainly BIOSIS previews and Cambridge Scientific Abstracts to search the literature and yielded 1,924 unduplicated citations on grass carp, 166 of which were pertinent to this review. Research topics and the type of response variables quantified in the research were summarized, and relative prevalence of each topic was determined by calculating the frequency of its occurrence. Publications were evaluated on the basis of whether they attempted to: (1) quantify impacts on community structure and process; (2) measure response variables at habitat, population and/or individual levels; and (3) investigate direct and indirect impacts on the aquatic community. A direct impact was defined as a single-level interaction such as immediate alteration of plant abundance due to grass carp feeding activities; indirect impacts were defined as multi-level interactions, such as changes in zooplankton composition as a result of the increase in phytoplankton abundance due to accelerated nutrient loading facilitated by grass carp foraging activities (Miller and Kerfoot 1987).

RESULTS AND DISCUSSION

Our review of the literature suggested that data are limited for a thorough assessment of grass carp impacts on the aquatic community. We found that most research is related to the eradication of aquatic plants rather than ecological mechanisms potentially responsible for the impacts. Limited data are available to validate long-term consequences and indirect impacts of system-wide introductions of grass carp. Fewer than 50 citations addressing grass carp impacts referred to the term “ecology,” and of these, only a few (<10) inferred ecological processes, yet did not validate causal mechanisms (Table 1). The two most common response variables measured in studies investigating potential impacts by the carp on aquatic communities were direct impact on aquatic plants and indirect alteration of water quality. Less than 2% of all studies investigated structural alteration of habitat or the dynamic processes responsible for structuring the aquatic community.

Direct impacts

Aquatic plant abundance

Changes in plant abundance and community composition occur due to immediate foraging activities as well as alteration of water transparency, disturbance of the sediment, and deposition of fecal matter by grass carp. Grass carp introductions may lead to unexpected and undesirable changes in the plant community. Hanlon et al. (2000) reported several cases of hydrilla (*Hydrilla verticillata* [L.f.] Royle) overgrowth after carp introduction. A shift in plant community composition to less palatable/grazing-resistant species has also been observed (Vinogradov and Zolotova 1974, Hanlon et al. 2000, Pipalova 2002). Several studies reported that grass carp eliminated native plants, leaving invasive vegetation intact (Van Dyke 1994, McKnight and Hepp 1995). Limited data are available to quantify the direct impact on non-target plants since many studies focused only on specific plant species targeted for control and did not assess other plants in the community. In addition, the impact on small and less conspicuous plant species was likely unnoticed because studies frequently used aerial photography to estimate changes in plant abundance.

Grass carp can be considered “selective generalists” in their foraging behavior because they eliminate species in order of decreasing palatability (Colle et al. 1978, Van Dyke et al. 1984, Leslie et al. 1987). More than 50 genera of food items, including aquatic macrophytes, algae, invertebrates and vertebrates, were reported to be eaten by grass carp (Table 2). Feeding preference is one of the best-studied aspects of grass carp biology; however, contradictory evidence exists for several plant species this fish consumes (Tables 2 and 3; also see Bonar et al. 1990, Cooke et al. 2005). Hydrilla and pondweeds (*Potamogeton* spp.) were the most common food items reported to be eaten by grass carp, and species most commonly avoided were in the genera *Nymphaea*, *Potamogeton*, *Myriophyllum*, *Nuphar*, and *Typha*. For the same set of macrophyte species, the order of preference changes under different environmental conditions, most likely determined by ease of mastication (Wiley et al. 1986, Pine et. al 1989, Bonar et al. 1990). Cellulose, silica, and iron content were shown to be the best predictors of unpalatability, whereas calcium and lignin were positively correlated with consumption rates (Bonar et al. 1990). Predictions of the order of plant elimination in the field still have a large degree of uncertainty; the situation may be improved by a series of field studies across a range of environmental conditions.

Habitat heterogeneity

Aquatic plants provide habitat heterogeneity important at both system (i.e., among plant beds) and micro (i.e., within plant beds) scales. The level of this heterogeneity is determined by the magnitude of available spatial “patchiness” constituted by unique plant attributes (i.e., stem-leaf morphology and architecture) found in the habitat (Dibble et al. 2006). Variability and juxtaposition among these different habitat attributes may collectively define the ecological value of habitat in a community or ecosystem as a whole (Wiens 1976, Stensen 1980, Holt 1984, Horne and Schneider 1995,

TABLE 1. GRASS CARP IMPACT ON THE COMMUNITY.

Topical emphasis	References[a]
Effects on Community Structure	
Algae biomass/phytoplankton	8, 11, 24, 30, 32, 41, 44, 48, 53, 55, 56, 61, 63, 65, 75, 110, 114, 123, 124, 137, 161
Crayfish	27, 41, 123
Detritus	61, 113
Fish	3, 4, 8, 9, 10, 11, 16, 19, 22, 26, 42, 46, 50, 52, 53, 54, 55, 56, 58, 61, 62, 63, 67, 73, 78, 80, 85, 86, 92, 94, 99, 100, 104, 105, 108, 113, 121, 123, 141, 143, 151, 157
Habitat alteration	3, 10, 11, 16, 43, 50, 112, 114, 119, 139
Grass shrimp	45, 143
Macroinvertebrates	6, 8, 10, 27, 32, 41, 53, 55, 63, 65, 73, 96, 97, 105, 108, 112
Native plants	30
Periphytic algae	30, 32, 115
Phytoplankton diversity	44, 61, 160
Plant abundance	8, 11, 12, 13, 19, 59, 58, 64, 65, 81, 91, 112, 127, 128, 135, 160
Plant biomass	19, 60, 61, 66, 70, 74, 81, 83, 90, 94, 97, 100, 104, 110, 121, 134, 160, 161
Plant composition	104, 127, 150, 161
Plant diversity	11, 12, 13, 19, 48, 81, 91, 97, 100, 161
Plants, percent coverage	55, 58, 60, 63, 64, 97, 108, 112, 135, 137, 155, 158, 160, 161
Standing crop	84
Seasonal effects on plants	19, 71, 72, 76
Snails	6
Zoobenthos	123, 160
Zooplankton	32, 44, 54, 55, 63, 65, 96, 97, 98, 101, 105, 108, 110, 115
Water quality	4, 7, 8, 11, 17, 18, 19, 30, 31, 32, 44, 47, 48, 53, 54, 55, 58, 61, 63, 65, 66, 67, 74, 75, 79, 94, 95, 96, 98, 100, 101, 104, 105, 106, 108, 110, 113, 114, 115, 121, 123, 124, 137, 143, 150, 160
Effects on Community Process	
Carbon flow	8, 19
Eutrophication	96, 114
Food chains	8, 10, 62, 123
Lake productivity	8, 19, 49, 55
Nutrient loading	18, 24, 86, 113, 114, 124
Photosynthesis	8, 53
Primary production	97, 98, 101, 104, 106, 107, 108, 121, 124
Reduction of buffer capacity	18
Shoreline erosion	33
Streamflow	96
Weevill activity	45

[a]Reference numbers correspond to the number preceding citations in the bibliography listed in the appendix.

Moloney and Levin 1996). Species diversity is positively correlated with habitat complexity, and increasing heterogeneity among habitats at a landscape scale is a common objective in ecosystem management (Bookhout 1996). Direct impacts by grass carp on habitat heterogeneity, even though ecologically important, were not adequately assessed in the research we reviewed.

Similarly, the heterogeneity at a smaller scale within aquatic plants is just as important for habitat structure (Dionne and Folt 1991, Lillie and Budd 1992, Budd et al. 1995), yet grass carp impacts on structure have gone unmeasured. This level of habitat heterogeneity can be determined as spatial complexity (e.g., plant stem density or frequency of interstices; Lynch and Johnson 1989, Dibble et al. 1996) and is equally important to individual organisms (Anderson 1984, Diehl 1988, Dibble and Harrel 1997, Pedlow et al. 2006) and collectively to populations (Persson and Eklov 1995). Spatial complexity in aquatic habitats is important for predator avoidance and ontogenetic niche shifts (Werner et al. 1977, Lodge et al. 1988, Persson and Crowder 1997) and, at least theoretically, greater macrophyte densities allow higher equilibrium densities of both fish and macroinvertebrates (Diehl and Kornijów 1997). A few investigations on grass carp hypothesized mechanisms of trophic interactions and population dynamics (Bettoli et al. 1991, 1992, 1993), yet no attempt was made to measure heterogeneity at this level or validates the mechanism that explained the effects. Even without complete vegetation removal, preferential feeding may significantly affect habitat heterogeneity.

The problem of reaching the desired habitat heterogeneity is complicated by the inability to accurately predict effective stocking densities. Despite a relatively high number of studies published on this topic, specific stocking densities that would result in complete elimination of a specifically targeted plant cannot accurately be predicted across a range of different plants and environmental conditions. Partial control of vegetation is rarely achieved with grass carp (Petr 2000, Bonar et al. 2002. After studying 38 lakes in Florida, Hanlon et al. (2000) concluded that the relationship between stocking density and plant abundance was unpredictable except for maximum stocking density that consistently resulted in complete eradication of macrophytes. The prob-

TABLE 2. LIST OF FOOD ITEMS (GENERA) REPORTED EATEN BY GRASS CARP.

Genus	Reference[a]
Alisma	132
Alternanthera	112
Anax[b]	113
Azolla	35, 123, 131
Bacopa	142
Bimaslur[b]	113
Brasenia	112
Bufo[b]	113
Cabomba	31, 107, 108, 112, 155
Callitriche	15, 123, 132
Carex	123, 126, 142
Ceratophyllum	4, 10, 19, 35, 48, 55, 60, 64, 79, 93, 95, 98, 101, 104, 107, 121, 123, 126, 127, 131, 132, 134, 150, 155
Chara	15, 35, 48, 66, 72, 75, 81, 95, 99, 123, 126, 128, 130, 142, 143, 146, 160, 164
Cladophora	131, 160, 161
Egeria	84, 91, 95, 134
Eichhornia	26, 35, 45, 112, 131
Eleocharis	40, 84, 87, 112, 142, 143, 161
Elodea	15, 19, 71, 81,93, 95, 99, 104, 107, 121, 123, 126, 131, 143, 163
Ephemera[b]	113
Glyceria	99
Halophila	123
Hydrilla	2, 4, 7, 10, 13, 17, 18, 20, 31, 33, 35, 44, 48, 49, 54, 55, 58, 62, 63, 64, 70, 78, 79, 91, 95, 96, 98, 105, 108, 120, 123, 133, 135, 155, 158
Hydrocharis	123, 126
Hygrophila	35
Juncus	123, 126
Lagarosiphon	119
Lemna	15, 35, 74, 107, 123, 126, 131, 132
Limnobium	131
Limnophila	123
Mayaca	155
Myriophyllum	4, 10, 15, 18, 35, 48, 55, 64, 66, 71, 75, 93, 95, 96, 99, 101, 107, 123, 126, 130, 132, 134, 142, 155
Nuphar	112
Najas	11, 19, 35, 60, 104, 107, 121, 123, 131, 142, 143, 155, 164
Nasturtium	123, 126
Nechamandra	123
Nitella	15, 84, 123
Notropis[b]	113
Nymphaea	131
Ottelia	123
Phragmites	110, 123, 126
Pistia	35, 131
Pithophora	123
Polygonum	99, 142, 143
Potamogeton	11, 12, 15, 18, 19, 54, 66, 71, 72, 74, 75, 83, 84, 93, 95, 96, 99, 104, 107, 121, 123, 126, 127, 128, 130, 131, 132, 143, 150, 161, 164, 166
Ranunculus	99
Rhizoclonium	15
Ruppia	131
Sagittaria	40, 142
Salomia	123
Salvinia	123
Sparganium	123, 132
Spirodela	123
Spirogyra	123, 131
Trapa	101, 123
Typha	99, 123, 126, 132
Utricularia	87, 107, 123
Vallisneria	123
Wolffia	35, 123
Zannichellia	132
Zygnema	160

[a]Reference numbers correspond to the number preceding citations in the bibliography listed in the appendix.
[b]Non-plant food item.

TABLE 3. AQUATIC PLANTS REPORTED AVOIDED BY GRASS CARP.

Plant Genera	Reference[a]
Alternathera	123
Brasenia	107
Cabomba	131
Ceratopohyllum	40, 161, 164
Chara	60
Cladium	96
Echinodorus	107
Egeria	35
Eichhornia	123
Eleocharis	107
Jussiaea	165
Lemna	166
Myriophyllum	54, 81, 123, 131, 161, 164
Najas	40
Nelumbo	107
Nuphar	31, 81, 108, 109
Nymphaea	31, 93, 107, 108, 109, 123
Nymphoides	109, 123
Orontium	107
Phragmites	160
Pistia	123
Polygonum	107, 123
Potamogeton	35, 40, 107, 166
Ranunculus	109, 165
Sagittaria	107, 131
Salvinia	35
Scirpus	107
Typha	31, 107, 108
Vallisneria	48

[a]Reference numbers correspond to the number preceding citations in the bibliography listed in the appendix.

lem of appropriate vegetation control is exacerbated by the long life span of this fish; grass carp live longer than 10 years, and they have been shown to persist in a lake for at least 2 years after complete removal of the invasive plant it was stocked to control (Kirk et al. 2000, Kirk and Socha 2003). Long persistence in the environment may also hinder future native macrophyte revegetation efforts if the policy or stakeholder interests change.

Early life stages

Most literature discussed only direct impacts relevant to adult grass carp and neglected potentially important direct impact of early life stages of carp on other fishes. Grass carp stocked for plant control is usually >200 mm in length to reduce mortality due to predation (Pierce 1983, Cassani 1996); however, mounting evidence suggests that naturalized populations of grass carp are reproducing in the United States (Connor et al. 1980, Pflieger and Grace 1987, Brown and Coon 1991, Raibley et al. 1995). In fact, one recent study reported juvenile grass carp in two rivers in Oklahoma previously deemed unsuitable for grass carp reproduction (Hargrave and Gido 2004).

Vegetated habitats provide important nursery grounds for many native fishes (Gregory and Powles 1985, Chubb and Liston 1986, Dibble et al. 1996b), and competition for available food and habitat among and between early life stages of these fishes can be intense and critical to growth and survival (Werner and Hall 1979, Mittelbach 1981, Diehl 1993). Increases in the number of young non-native fish may exacerbate competition and niche overlap. Larval and juvenile grass carp are not herbivorous and have been shown to feed on zooplankton, insect larvae, chironomids, cladocerans, and copepods (Chilton and Muoneke 1992, Cudmore and Mandrak 2004). Young grass carp may therefore alter trophic dynamics within communities by directly competing for food with native fishes and their larvae.

Indirect impacts

Community structure

Secondary effects from a primary disturbance may be stronger in aquatic communities than the more easily measured direct impacts (Kerfoot and Sih 1987). There is indisputable evidence for presence of trophic cascades in aquatic systems (Brett and Goldman 1996), and some of the strongest cascades are observed in benthic habitats of lakes (Shurin et al. 2002). Presence of novel phytophagous fish exceeding gape size of predator has a potential to involve novel energy pathways (e.g., with more energy flowing towards detrital food chain), which may strongly affect rates of nutrient cycling. Increase in nutrient cycling leads to reduced resilience of an ecosystem (Wetzel 2001), often manifested in population explosions and subsequent crashes of dominant taxa. Because macrophytes play an important role in benthic-pelagic coupling by subsidizing pelagic fish populations and affecting nutrient loading (Schindler and Scheuerell 2002), it is natural to expect that effects of grass carp would propagate beyond the littoral zone and change the role of benthic subsidies to the pelagic habitat of lakes. Mitzner (1978) demonstrated that introduction of grass carp resulted in reduced primary production, possibly due to decreased littoral-pelagic coupling (Lodge et al. 1988).

Grass carp may be viewed as a novel keystone species that reduces spatial heterogeneity, and the resulting loss of complex habitat can potentially influence exploitative competition and other interactions among resident species. This is an example of how the indirect effect of a large herbivore may be transmitted through a resource base, consequently altering the community structure. Other behavioral alterations due to the presence of large fish, whether they are direct predators or not, can impact populations (Sih 1980, Sih et al. 1985, Miller and Kerfoot 1987) and potentially alter ecosystem processes. Secondary changes in aquatic vertebrate and invertebrate communities have been documented after grass carp introductions (see next section). Some observed effects are not consistent across different studies, which may be an indication of our limited understanding of the underlying mechanisms.

Macroinvertebrate populations

Aquatic plants form a base for macrophyte-periphyton-grazer complex (Carpenter and Lodge 1986) and support high densities of macroinvertebrates by providing them with food, habitat, and refuge from predation (reviewed in Diehl and Kornijów 1997). Changes in vegetation due to grass carp foraging lead to decreased macroinvertebrate diversity and abundance (Vinogradov and Zolotova 1974). Due to decrease in attachment substrate typically provided by vegetated habitat, richness and abundance of epiphytic macroinvertebrates can decrease, whereas the number of benthic invertebrate species can increase (Martin and Shireman 1976, Leslie and Kobylinski 1985, Klussman et al. 1988, Kirkagac and Demir 2004). However, Fedorenko and Frazer (1978) reported that benthic invertebrates also decreased after vegetation removal by grass carp, possibly due to direct competition, low food availability, and increased predation due to the loss of refuge.

Fish populations

In general, when vegetated habitats become too spatially complex, fish growth is negatively impacted due to reduced food availability and decreased feeding efficiency (Crowder and Cooper 1982, Savino and Stein 1982, Anderson 1984). Moderate (20%) removal of overly dense vegetation resulted in improved growth of some age classes of bluegill (Olson et al. 1998); however, further reduction in aquatic plant density and the corresponding decrease in spatial complexity results in increased competition for limited food sources and refugia (Mittelbach 1988). Thus, plant levels at either extreme of the density spectrum may decrease fish growth and survival and, ultimately, alter population dynamics within the community (Adams and DeAngelis 1987, Savino et al. 1992, Diehl 1993).

As a general tendency, a decrease in the abundance of fish species are dependent on aquatic plants, such as largemouth bass (*Micropterus salmoides*) and other sunfishes (*Lepomis* spp.), whereas non-phytophyllic species, such as gizzard shad (*Dorosoma cepedianum*) and silversides (*Labidesthes* spp.), tend to increase in abundance (Ware and Gasaway 1978, Klussman et al. 1988, Maceina et al. 1991, Bettoli et al. 1992,). Bettoli et al. (1993) observed a radical change in fish community following grass carp introduction, with a decline in the total number of species over a 7-year period (Table 4). Most notable declines were observed for *Lepomis* spp., crappie (*Pomoxis* spp.), brook silversides (*Labidesthes sicculus*), and juvenile largemouth bass. Colle and Shireman (1994) reported that after complete elimination of vegetation by grass carp, fish harvest declined, and several species had disappeared.

In contrast, Killgore et al. (1998) observed no change in the number of littoral species and an increase in the total fish catch after hydrilla control by grass carp, although the mean total length of the largemouth bass declined (Table 4). This study was unusually successful in achieving intermediate levels of vegetation control, a result that may not be easily extrapolated to many other situations.

Other aquatic vertebrates

Previous work has evaluated indirect impacts of grass carp on waterfowl, suggesting that abundance of bird species can be reduced in the presence of grass carp due to shifts in plant community and competition for preferred food plants (Gasaway and Drda 1976, Johnson and Montalbano 1984, 1987, Leslie et al. 1987, McKnight and Hepp 1995). However, no study specifically addressed grass carp impact on other vertebrates (e.g., aquatic mammals, reptiles, and amphibians). Many of these animals are highly dependent on vegetated habitats for food and protection from predators, and macrophytes are critical to their survival. Salamanders feed on small prey species living in aquatic plants, and larval stages of amphibians rely on these habitats to avoid predation (Brophy 1980, Zaret 1980).

Muskrats (*Ondatra zybethicus*), beaver (*Castor canadensis*), and nutria (*Myocastor coypus*) rely heavily on aquatic plants (Chabreck 1988, Fredrickson and Laubhan 1996), and more research is needed to quantify how changes in aquatic plants alter habitat and distribution of these animals. A better understanding of how grass carp impact animal distribution will improve the management of these ecosystems; this is especially important for controlling exotic species such as nutria.

Indirect effects operate at different temporal and spatial scales. Parameters that validate those mechanisms are not easily measurable and usually require a period of time before response is detected (Miller and Kerfoot 1987), which may explain why these effects are frequently ignored or inadequately tested. Nevertheless, they need to be incorporated into the designs of future experiments attempting to predict and explain how grass carp impact aquatic communities.

TABLE 4. IMPACT OF GRASS CARP ON OTHER FISHES.

Topical emphasis	References[a]
Populations	4, 8, 9, 10, 11, 16, 46, 50, 52, 53, 54, 78, 92, 116, 141
Density/abundance	53, 55, 56, 58, 62, 67, 85, 92, 108, 123, 141, 151, 157
Biomass	8, 50, 55, 58, 61, 78, 81, 92, 100
Diversity	50, 55, 56, 62, 100, 157
Production (kg/ha)	53, 80, 123
Total stand. crop (kg/ha)	58, 62, 63, 73, 78, 108, 123
Weight	92, 105
Relative weight	58
Length	92, 105, 157
Distribution	85, 151
Vulnerability to predation	85
Diets	3, 10, 26, 85, 92, 110, 113
Growth	11, 22, 26, 42, 67, 80, 85, 86, 99
Condition	50, 54, 78, 85, 92, 105, 143
Recruitment	42, 67, 78, 92, 99
Reproductive success	62, 73, 92, 123
Male/female ratio	92
Spawning impacts	16, 81, 123
Angler success	19, 50, 62, 94, 99, 104, 121

[a]Reference numbers correspond to the number preceding citations in the bibliography listed in the appendix.

Water quality

Aquatic plants decrease sediment resuspension, play an important role in nutrient cycling (Carpenter and Lodge 1986, Barko and James 1997), and create microclimates in the littoral zone (Lodge et al. 1988). Submerged macrophytes are responsible for several positive feedback mechanisms promoting retention of the vegetated state (Scheffer and Jeppesen 1997, Van Donk 1997), particularly important under the conditions of increasing eutrophication. Shallow lakes provide one of the most dramatic examples of a catastrophic shift when they suddenly change from clear-water vegetated state to an alternative stable state, turbid and unvegetated, in response to gradual changes in conditions, such as nutrient loading or macrophyte removal (Scheffer et al. 2001).

Detrimental changes in water quality parameters (increase in nitrite, nitrate, phosphate concentrations) following vegetation control by grass carp were reported in most studies that evaluated water quality (Table 5; Shireman and Smith 1983, Kirkagac and Demir 2004). These changes result from sediment resuspension during feeding and fecal matter deposition by carp as well as collapse of mechanisms responsible for maintenance of the vegetated state due to removal of macrophytes. The rate at which aquatic plants are eliminated determines the magnitude of impact (Hestland and Carter 1978, Lembi et al. 1978, Leslie et al. 1983, 1987, Richard et al. 1984, 1985). These changes in water quality are often followed by algal blooms (Vinogradov and Zolotova 1974, Canfield et al. 1983, Klussman et al. 1988, Shireman and Smith 1983), which in most lakes signal a shift to an alternative stable state (Scheffer and Jeppesen 1997). Increased rates of nutrient cycling after resuspension of sediments lead to decreased ecosystem stability (Wetzel 2001). When weighing pros and cons of complete macrophyte eradication, note that these water quality changes are often irreversible on relatively long time scales, even after herbivorous fish are removed (Scheffer et al. 2001).

Other considerations

Many natural freshwater lakes were isolated for some period of time and may harbor genetically distinct and/or locally rare populations of plants and animals. While it is not clear whether other methods of vegetation control or the invasion itself may have an effect just as detrimental as vegetation control by grass carp, the issue of potential impact on such populations needs to be addressed in the future if carp is to be used in systems other than ponds.

According to the invasional meltdown hypothesis, as more non-native species are introduced into the system, populations of resident native species are increasingly disrupted, and the community becomes more susceptible to future invasions (Simberloff and Von Holle 1999, Ricciardi 2001). As the history of biological introductions has shown, these aspects are very difficult to forecast and assess (Simberloff and Stiling 1996). Until proven otherwise, such possibility exists for grass carp introductions; for instance, frequent disturbance of sediment and vegetation may in fact promote further plant invasions. This may be especially true when grass carp is used without simultaneous mitigation of factors causing nuisance species overgrowth (e.g., eutrophication or frequent disturbance).

Current stocking practices

Grass carp are now recorded in 45 states (Mitchell and Kelly 2006). In some states, only triploid carp can be stocked

Table 5. Physical parameters measured to determine impacts by grass carp on water quality.

Parameter	References[a]
Alkalinity	7, 17, 19, 47, 53, 54, 55, 58, 63, 66, 75, 94, 95, 104, 114, 121, 143
Ammonia nitrogen	55, 75, 108, 113, 114, 123, 137
Calcium	17, 47, 48, 58
Carbonates	11, 44, 55, 58, 63, 66, 75, 95, 115
Chlorophyll	4, 17, 18, 30, 31, 32, 44, 54, 58, 65, 67, 114, 137, 143, 150, 160
CO_2	110
Conductivity	7, 17, 54, 55, 58, 63, 66, 95, 108, 114, 115
Dissolved oxygen	7, 44, 47, 18, 54, 66, 95, 96, 100, 101, 105, 110, 114, 116
Dissolved organic matter	8, 79, 98, 106, 115
Iron	115, 123
Kjeldahl nitrogen	18, 54, 66, 95, 96, 115
Light compensation point	105
Magnesium	17, 47, 48, 58, 115, 123
Nitrates/Nitrites	19, 31, 44, 47, 48, 54, 55, 65, 75, 104, 113, 114, 137, 160
Oxygen demand	19, 47, 53, 104
pH	7, 17, 44, 47, 48, 53, 54, 63, 66, 95, 96, 104, 105, 108, 113, 114, 143
Phosphate/Phosphorous	11, 17, 18, 19, 31, 44, 47, 48, 54, 55, 58, 61, 63, 65, 67, 75, 79, 98, 100, 104, 106, 108, 113, 114, 115, 123, 124, 137, 160
Potassium	17, 48, 58, 75, 105, 113, 115, 123
Sulfate	47, 55, 105, 115
Sulfur bacteria	48
Tannin-Lignin levels	31, 47, 108
Temperature	54, 113
Total nitrogen	5, 17, 18, 48, 58, 63, 100, 108
Total photosynthetic pigments	53
Turbidity	18, 19, 47, 48, 53, 54, 66, 95, 104, 108, 110, 123, 143
Water clarity/Secchi	55, 58, 98, 114, 137

[a]Reference numbers correspond to the number preceding citations in the bibliography listed in the appendix.

for vegetation control, and the procedure for ensuring infertility is tightly regulated by the U.S. Fish and Wildlife Service. Only certified triploid grass carp can be possessed west of the Continental Divide and in the Rio Grande Basin (California Laws: Fish and Game Code, Section 6440-6460). Alaska, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, Oregon, North Dakota, Rhode Island, Vermont, and Wisconsin banned both diploid and triploid grass carp (reviewed in Mitchell and Kelly 2006), while some states allow possession of diploid grass carp for aquaculture purposes, production of triploids, or even vegetation control.

In states where grass carp possession is regulated, a special permit (from the departments of natural resources) is required for stocking grass carp. Often, however, a free permit can be obtained by anyone who demonstrated a need to control aquatic vegetation. Satisfactory guidelines have been developed from the standpoint of limited knowledge about ecological effects of this introduction (Table 6). These guidelines, if followed closely, may help ensure that, if deleterious effects occur after grass carp introduction, such effects are at least contained to small ponds not connected to any natural aquatic systems (also see Cooke et al. 2005, p. 443). The recommended maximum stocking density is sufficiently low to prevent, in most cases, complete vegetation removal, and adequate precautions are taken with respect to rare and endangered species. Also, this publication provides the pond owner with sufficient information on the importance of aquatic vegetation and possible changes in water quality after vegetation control by grass carp. Due to its generalist habits, grass carp is not well-suited for selective control of invasive aquatic plants when some level of native plants is desired.

Other Asian carps, such as black (*Mylopharyngodon piceus* Richardson), silver (*Hypophthalmichthys molitrix* Valenciennes), and bighead (*H. nobilis* Richardson) have become invasive species of special concern (reviewed in Schofield et al. 2005), and there is a high likelihood that asian carp may become invasive as well. Some populations have already naturalized, and it is now critical to study their effects on ecosystems as well as make it unlawful to continue stocking diploid grass carp. The importance of changing regulations in states that still allow possession and stocking of diploids cannot be overemphasized (also see Cooke et al. 2005, p. 437).

Recommendation for future research

More research is needed to investigate both direct and indirect impacts of grass carp, with greater emphasis on indirect impacts. Future investigations need to better quantify these impacts within and across vegetated habitats for a better understanding of community processes. Improved measurement of habitat heterogeneity using new descriptors (e.g., complexity indices, fractal dimension) is essential for an accurate assessment of habitat changes and their effect on community. Additional information is also required to determine how grass carp impact multi-species interactions (e.g., interspecific competition and trophic/predator-prey interactions) and individual behavior (e.g., foraging efficiency, predator avoidance, and habitat use). Future investigations need to address impacts of all life stages of grass carp, especially in systems where reproduction of naturalized populations has been confirmed. It is important to study ecosystem effects of grass carp, such as changes in rates of nutrient cycling, nutrient compartmentalization, and habitat coupling.

Data are needed to determine appropriate levels of abundance and diversity at which aquatic plants should be maintained to prevent a shift to turbid state and negative effects on animal communities. This review shows that aquatic macrophytes are important for habitat heterogeneity and ecological stability; however, it is difficult to achieve optimal habitat heterogeneity and/or only target invasive plants with this non-selective biocontrol agent. Further study of how grass carp feeding preferences across a range of environmental conditions influence spatial attributes of aquatic habitats will help predict community responses to changes in habitat heterogeneity. Meanwhile, innovative research is needed to find suc-

TABLE 6. INFORMATION FROM "GRASS CARP IN NEW YORK PONDS", PUBLICATION OF NEW YORK STATE DEPARTMENT OF ENVIRONMENTAL CONSERVATION, DIVISION OF FISH, WILDLIFE & MARINE RESOURCES.

". . . approve and issue permits for stocking of up to 15 United States Fish and Wildlife Service certified triploid grass carp [from approved suppliers possessing a valid permit to import and sell triploid grass carp in New York State] per surface acre for aquatic plant management purposes in ponds five (5) acres or less in size which lie wholly within the boundaries of lands privately owned or leased by the individual making or authorizing such treatments if:

- aquatic plants targeted for control significantly impair the intended use(s) of the pond;
- the pond harbors no species of wildlife, fish, shellfish or crustacea identified by the Department as being endangered, threatened or special concern; or any species of plant identified as being endangered, threatened or rare;
- the pond is not contiguous to or part of a New York State regulated freshwater wetland.
- is not an impoundment or natural pond on a permanent stream or a source of a permanent stream.
- at least two years have elapsed since the last stocking of triploid grass carp

"Triploid grass carp are extremely potent plant consumers. If overstocked, they are capable of eradicating all plants from a pond for periods exceeding 10 years. Besides the obvious impact such complete plant removal will have on vegetation-dependent fish and wildlife, total devegetation of a pond can also result in the development of severe algae blooms, foul smells and an overall decline in water clarity. To minimize or prevent such adverse impacts, plant populations should be maintained at approximately 20-30% of the pond's surface area.

Due to various factors that impact triploid grass carp feeding, it is impossible to precisely predict the exact number of fish to stock to achieve the 20-30% plant coverage target. The only way to prevent excessive plant control is through use of an incremental approach. This approach involves the stocking of triploid grass carp at the stocking rates suggested below, followed by a two-year waiting period for the fish to achieve maximal control. Then, if needed, more fish are added in small increments at two-year intervals until plant populations are reduced to the 20-30% threshold."

cessful methods to provide more accurate control for different levels of plant growth, abundance, and composition. Detailed evaluation of community responses to differential stocking rates is needed, as are the techniques to control current grass carp populations already released into natural systems.

Understanding ecological impacts is paramount to appropriate management of aquatic communities. Current data are not sufficient to adequately answer important questions about use of grass carp as a biocontrol agent for aquatic plants. The problem of assessing all possible impacts is not unique to grass carp: it has been shown for most introduced biocontrol agents (reviewed in Simberloff and Stiling 1996). The extent to which these approaches are used in future research will determine the amount of knowledge gained relative to understanding the ecological impacts of grass carp on aquatic communities. Until these data are collected, a more conservative approach should be used when developing guidelines for grass carp use.

ACKNOWLEDGMENTS

We appreciate the help provided by J. Cruickshank, E. Forrester, R. Kimbrough, B. LaValley, and J. O'Keefe for their assistance in the retrieval and initial analysis of literature, and S. Harrel and P. Smiley for editorial comments provided on an earlier draft of this manuscript. This manuscript was significantly improved by the suggestions of three anonymous reviewers. The Aquatic Ecosystem Restoration Foundation funded an earlier review of the literature that was incorporated in this manuscript. We thank J. Madsen and the GeoResources Institute at Mississippi State University for support and the U.S.G.S. Invasive Species Science Program for funding this project.

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