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Review

A Review of Grass Carp and Related Species Literature on Diet, Behavior, Toxicology, and Physiology Focused on Informing Development of Controls for Invasive Grass Carp Populations in North America

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Abstract: Grass carp (*Ctenopharyngodon idella*) are globally important in aquaculture and aquatic vegetation control. However, escaped grass carp have established invasive populations. A targeted keyword search was performed on a carp (order: Cypriniformes) literature database maintained by the U.S. Geological Survey to identify literature relevant to grass carp. Additional sources cited in reviewed documents and provided by numerous reviewers were also included. There were three focus areas designed to provide support for invasive grass carp management: (1) diet and behavior; (2) physiological constraints, toxicity, and biology; and (3) gut physiology. Each focus area provides information to guide development of potential pathways for invasive grass carp control. Information from other carp species was used to fill in gaps where grass carp information was lacking and provide additional, potential research directions. Diet-related information included food selection and aquacultural diet formulations. Behavioral information included stimuli and non-physical barriers to attract, repel, or stop movement. Physiological constraints, toxicology, reproductive control, and biological control provide a research review for control options. Gut physiology and related control pathways provide knowledge to improve toxin or pathogen delivery. This review provides a basis for developing approaches and research for controlling invasive grass carp populations, aquaculture, and native population management.

Keywords: carp; *Ctenopharyngodon*; *Hypophthalmichthys*; diet; behavior; toxicology; physiology; gut physiology; control pathways

Key Contribution: This manuscript informs the development of research approaches for controlling grass carp populations and provides management implications. Simultaneously, this review identifies control attempts that were ineffective due to issues with behavior, compound toxicity and/or other impracticalities.

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Citation: Wildhaber, M.L.; West, B.M.; Ditter, K.K.; Moore, A.P.; Peterson, A.S. A Review of Grass Carp and Related Species Literature on Diet, Behavior, Toxicology, and Physiology Focused on Informing Development of Controls for Invasive Grass Carp Populations in North America. *Fishes* **2023**, *8*, 547. https://doi.org/10.3390/fishes8110547

Academic Editors: Siquan Tian and Jie Cao

Received: 18 April 2023
Revised: 30 September 2023
Accepted: 9 October 2023
Published: 10 November 2023

1. Introduction

Depending on context, a single aquatic species can play one of many roles within ecosystems and human-controlled systems, such as aquacultural operations, artificially created bodies of water and dammed river systems. Grass carp (*Ctenopharyngodon idella*) is one such species whose role changes dramatically among aquatic systems. Grass carp are a globally important aquaculture species [1,2], and they are a management priority within their native range in China where dam construction is negatively affecting their populations [3,4]. This species is used as a management tool to control nuisance aquatic vegetation [5,6]. However, non-native populations of grass carp are considered invasive in places such as the United States and Europe, where their ability to reproduce prolifically and eliminate aquatic vegetation can have broad-reaching, negative ecological effects [7–9].

In this review, we consolidate and present information on the biology and management of grass carp, along with applicable information on related fish species where research is limited or non-existent for grass carp. The primary purpose for inclusion of information from related species was to provide direction for additional grass carp research that may have promise, not necessarily directly applicable results. The term 'focal carp' is used in this review to refer to the following members of the family *Xenocyprididae*: grass carp, bighead carp (*Hypophthalmichthys nobilis*), and silver carp (*Hypophthalmichthys molitrix*); we focus on these species because they are invasive in United States waterways. Common carp (*Cyprinus carpio*) are also frequently mentioned because they are a large member of the same order as the focal carp, Cypriniformes, with invasive populations around the world, including the United States. We collectively refer to fish in this order as 'cypriniforms'. This review is intended to support the process of identifying approaches that can be used individually or in concert to help control non-native populations of grass carp. Broad focus areas are (1) diet and behavior; (2) physiological constraints, biology, and toxicology; and (3) gut physiology. Because of the difference in diet among the focal carp, diet and gut physiology components of this review are limited, almost exclusively, to grass carp. Given the nature of research on grass carp, this review contains information usable by more than just invasive species researchers and managers; it could also be useful to aquacultural researchers, managers tasked with controlling aquatic vegetation, and fisheries biologists. For a list of selected research and other reviews covering important aspects of grass carp biology and management, see Table 1.

Table 1. Selected list of review articles and studies that provide key information related to grass carp biology and management. [—, geographic region not defined]. 'Cypriniform' = fish in the same order as grass carp, Cypriniformes.

Citation	Geographic Region(s)	Description of Topics Included
[1]	Russia, including the Amur River Basin; Eastern Europe	Review of Russian language literature on grass carp; topics include geographical distribution; comparison of morphology between introduced and native populations; reproductive biology; growth and size at various ages; and feeding habits
[10]	Yangtze River, China	English translation and context for a comprehensive Chinese study on the early development of grass carp and three other species in the family *Xenocyprididae*
[11]	China and Japan	Includes grass carp and other carps; topics are morphology, classification, geographical distribution in China, feeding habits, growth, reproduction in the wild, artificial propagation, rearing in aquaculture
[12]	Global	Structural adaptations of grass carp associated with feeding on plants, feeding efficiency, and polyculture of grass carp and other herbivorous fish
[13]	Canada	Grass carp feeding habits, reproduction, parasites, predators, ecological effects upon introduction, factors influencing invasive potential
[14]	United States	Aquatic vegetation control using grass carp, feeding habits, digestion, reproduction, growth, potential tradeoffs of their introduction
[15]	Malacca, Malaysia	Grass carp rate of growth, sex differences, age and size at maturity, natural and artificial spawning, pituitary hormones
[16]	Global	Estimating triploid induction in batches of larval fish, including grass carp and other fish species

Table 1. *Cont.*

Citation	Geographic Region(s)	Description of Topics Included
[9]	Canada; North America; global	Physical description of grass carp, native distribution, non-native distribution globally and in North America prior to 2016, predicted future range in North America, growth, physiological tolerances, reproduction, feeding and diet, habitat, predators, behavior, parasites, pathogens, ecological effects upon introduction, human use, and conservation status
[17]	United States	Grass carp history in the United States, growth, factors affecting food consumption, selection of plant foods
[18]	United States	Grass carp size, taxonomy, identification, life history and biology, native and non-native range, status in the United States, effects upon introduction, diseases and parasites
[19]	United States	Grass carp morphology, anatomy, growth rate, feeding habits, macrophyte selection, artificial stocking, effects on water quality, and reproduction
[8]	—	Natural habitat, introductions, environmental consequences of stocking, stocking density
[20]	Global	Grass carp taxonomy, biology, summary of invasiveness, description, global distribution and introductions, food sources, predators, environmental effect, effect on humans
[21]	Montana, United States	Grass carp description, taxonomy, distribution, growth, life cycle, reproduction, habitat, diseases, genetics, food selection, feeding behavior, environmental effects, potential for escape, dispersal, and establishment in Montana
[22]	United States	Includes grass carp and other cypriniform species considered invasive in the United States; topics include description, reproduction, and spawning requirements
[23]	United States	Identification key for grass carp and other cypriniforms considered invasive in the United States
[2]	China	Review of Chinese language literature on grass carp; topics include reproductive physiology, biology, and ecology; endocrinology; native distribution; diet and growth across all life stages; differences among populations; grass carp introductions outside the native range; the effects of river dams; and the effects of environmental pollutants

1.1. Grass Carp as a Non-Native Species

1.1.1. Occurrence and Spawning

The grass carp resides in subtropical to temperate environments in large rivers and lakes in eastern Asia. Its original range contains both coastal and inland waters, and it extends from southern Russia southward to northern Vietnam [24]. Within large rivers in their native range (i.e., the Amur, Yangtze, Yellow, and Min Rivers), grass carp are restricted to the lower and middle reaches (Ref. [25] and cited by [24]). They are benthic herbivores that can grow to a total length of 150 cm, reach a mass of 45 kg [18] and live >30 years [26]. Grass carp exhibit some degree of selectivity when foraging for macrophytes, but they will feed on almost any macrophyte if their preferred macrophytes are unavailable [13,27,28]. In lakes and ponds, they feed on available macrophytes until all accessible aquatic vegetation is eliminated [29–31], then shift to shoreline terrestrial plants when no aquatic macrophytes remain [32]. Grass carp occur in a wide range of aquatic habitats and environmental conditions, tolerating fast-flowing currents and still water, temperatures ranging from 0 to 38 °C, salinities as high as 20 ppt, and dissolved oxygen as low as 0.5 ppm [18].

The spawning of grass carp typically occurs over fast-flowing riverbeds. In the first hour after fertilization, grass carp eggs swell with water and harden, decreasing their density to just slightly above the specific gravity of water, allowing them to stay suspended [33]. In the Illinois Waterway, June is the principal spawning month for invasive populations of focal carps [34]. Total egg drift is positively associated with cumulative June degree-days and higher variability in river discharge with egg drift quadratically associated with adult focal carp density [34]. Counts of larval grass carp indicate that in the Lower Mississippi River, grass carp spawn from May to July with water temperatures between 21 and 28 °C in current velocities between 0.8 and 2.2 m/s (Ref. [35] as cited in [36]). In the Upper Mississippi River, grass carp spawning occurs in May through June between 18 and 30 °C [37]. Others observed spawning occurring at temperatures as low as 17.6 °C (K. Kuronuma, 1958 as cited in [38]). Excessively high water temperature can negatively affect grass carp reproduction; ovulation rates in grass carp at 24 °C are more than three times the rates at 28 °C [39]. Simulated spawning migrations of grass carp found an interaction between water temperature and minimum flow rate is needed for successful migration: at 16 °C, a flow velocity of 0.40 m/s was needed, whereas at 24 °C a flow velocity of 0.30 m/s was needed [40]. As water temperature increased from 16 °C to 24 °C, the concentration of estradiol, a hormone associated with endocrine disruption [41,42] and gonad development [40], increased in females. Aside from isolated incidents within their native range, grass carp do not spawn in ponds unless induced via hormone injection (Ref. [14] as cited by [43], later reported in [14] citing [44–46]). It is believed that areas of high flow, turbulence, and turbidity promote the successful recruitment of grass carp (Refs. [8,38,47]. In the Pearl River, China, larval density is correlated with river discharge [48].

1.1.2. Introduction to North America

Grass carp have been introduced into many countries for aquacultural production and as a means of aquatic plant control. As of 2004, grass carp had been introduced into 49 countries in Europe, 17 of which now have established populations [24]. Grass carp range has expanded beyond areas of intentional introduction in the United States and, as of 2021, they have been documented in 45 states [49]; Alaska, Maine, Montana, Rhode Island, and Vermont are the exceptions. The introduction of grass carp in the United States has been previously reviewed by multiple sources (Table 1) and is presented below.

The first grass carp were imported by the U.S. Fish and Wildlife Service (USFWS) to Arkansas in 1963 to control aquatic vegetation, where they escaped into local rivers in 1966 (Ref. [50] as cited by [51]). They were also intentionally introduced to open waters in Arkansas in 1971 (Ref. [50] as cited by [51]). In Missouri, grass carp were first recorded in commercial fishing records in 1971 from the Missouri River, 1972 in the Lower Mississippi River, and 1973 in the Upper Mississippi and St. Francis Rivers [52]. Grass carp larvae were first collected in the Mississippi River in 1975 [53]. In 1984, strong evidence of grass carp breeding in the Missouri River was found in the form of 78 young-of-the-year grass carp in an overflow pool [54]. Intentional introduction of triploid grass carp, that is, functionally sterile grass carp with an extra set of chromosomes, began in the United States in the 1980s [55]; triploid grass carp are discussed further in 'Section Triploids' within Section 3.2.5.

Intentional and unintentional grass carp introductions in the United States have continued into the 21st century. A 2015 report compiling 10 years of introduction data from the mid-2000s to mid-2010s found that 20 to 25% of reported grass carp introductions were in open aquatic systems, allowing for possible escapes from the originally stocked water bodies [56]. The likely primary sources of continued grass carp escapes into the Missouri River Basin in the 2010s were the aquaculture industry, incidental baitfish relocations, and stocking of grass carp (especially diploid, fertile individuals) for vegetation control [9,57,58].

1.1.3. Observed and Potential Effects

Several authors have reviewed the observed effects of introduced grass carp on water bodies [8,9,59,60]. While the ecological effects of grass carp have been widely studied, fewer studies have addressed effects on habitat and communities [60,61]. The primary effect of introduced grass carp is direct removal of aquatic vegetation via consumption, affecting native fish communities, changing water quality, and causing other subsequent disturbances to ecosystem services.

Effects on Vegetation

Numerous studies document the effect of grass carp on aquatic vegetation; many of these studies have been reviewed by other authors [9,62]. Reduction or elimination of aquatic vegetation in water bodies is well documented, but the extent of vegetation removal varies. To the best of our knowledge, reasons for differences in vegetation removal extent by grass carp have not been thoroughly investigated, but differences in vegetation communities across aquatic systems may explain some of this variation; see grass carp vegetation selectivity in 'Section 3.1.1. In Situ Diet and Selectivity'. Grass carp have negative effects on vegetation in Central European oxbows (Ref. [63] as cited by [64]). Introduced grass carp in lakes throughout Washington State had lake-specific effects on macrophyte communities, including eradication in 39% of lakes, reduced abundance in 18% of lakes, and no significant effects on macrophyte communities in 42% of lakes [31]. In Florida lakes, stocked grass carp eliminated aquatic vegetation within two to three years [65–67]. Grass carp stocking in artificial canals in the Czech Republic resulted in a reduction of aquatic plant water surface coverage from 65 to 70% down to 10% [68]. Aquaculture ponds stocked with grass carp at densities of 200 to 600 per ha resulted in the complete consumption of the plant genera *Cladophora*, *Zygnema*, and *Chara* by the end of the four-month study; the only plant not consumed was *Phragmites australis* [69]. In a water body in the former USSR, 36 of 58 original plant species appeared to have been eradicated two years after stocking grass carp (Ref. [70] as cited by [8]). Grass carp introduced to what was formerly a shallow clearwater, shallow lake in Poland resulted in the near complete elimination of macrophytes [71]. In that lake, meadows of charophytes (for example, *Chara tomentosa* and *C. polyacantha*) were the first macrophyte communities to disappear, as these communities are sensitive to both grazing and increased turbidity. Disagreements exist about the degree to which grass carp prefer members of the *Chara* genus; some authors list charophytes as generally avoided due to odor (Ref. [72] as cited by [71]), while others list them as readily consumed (Ref. [73] as cited by [71]).

Studies tracking effects of grass carp on invasive or nuisance aquatic plants generally follow their being stocked, often involving high stocking densities [28,74,75]. Stocking of grass carp in 0.04-hectare ponds in Louisiana was effective at removing invasive water-hyacinth (*Eichhornia crassipes*) within 30 days [76]. In Florida lakes, grass carp reduced invasive hydrilla (*Hydrilla verticillata*) biomass by 45.7% and primary productivity by 63.0% [74]. Grass carp have been used to control invasive parrotfeather (*Myriophyllum aquaticum*) in North Carolina; however, high stocking densities of grass carp were required due to their low preference for this species [28]. When stocked at high densities, grass carp have effectively eliminated invasive and nuisance plant species, including Brazilian waterweed (*Egeria densa*), blunt pondweed (*Potamogeton ochreatus*), tall spike rush (*Eleocharis sphacelata*), and stonewort (*Nitella hookeri*) in some New Zealand water bodies [77,78].

Introduced grass carp can also affect native plant species. When grass carp were introduced to control invasive hydrilla in Texas, four native plant species, water star-grass (*Heteranthera dubia*), Illinois pondweed (*Potamogeton illinoensis*), squarestem spikerush (*Eleocharis quadrangulata*), and common threesquare (*Schoenoplectus pungens*) were eliminated [79]. Two other native Texas plant species, American eelgrass (*Vallisneria americana*) and softstem bulrush (*Schoenoplectus tabernaemontani*), are susceptible to herbivory but survived high grass carp stocking densities, and four other native species, fragrant water-lily (*Nymphaea odorata*), creeping burhead (*Echinodorus cordifolius*), American water-willow (*Justicia americana*), and pickerelweed (*Pontederia cordata*) were able to establish and spread, even at high grass carp densities [79]. Some New Zealand native plant communities that were negatively affected by grass carp stocking were able to reestablish after fish were removed [78].

In addition to affecting aquatic vegetation, grass carp also consume terrestrial vegetation. Grass carp can rip whole plants out of substrate and destroy vegetation along the fringe of lakes (Ref. [80] as cited by [81]). In ponds devoid of aquatic vegetation, grass carp graze heavily upon shoreline terrestrial plants [32]. This removal of shoreline vegetation can lead to erosion and sediment accumulation (Ref. [82] as cited by [83]). Their selection of various terrestrial plants and aquatic macrophytes is further addressed in 'Section 3.1.1. In Situ Diet and Selectivity'.

Effects on Fish and Other Animals

The extensive removal of aquatic vegetation by grass carp has effects on other aquatic animals. These include: population-level effects, changes in age structure, individual body condition, growth rate, and diet. Much of this research has emphasized species of commercial or recreational importance (for example, [7,84–86] but see also [87,88]. A subset of studies on fish populations experiencing changes after grass carp introduction and subsequent reduction or removal of aquatic vegetation is presented in Table 2.

The effects of introduced herbivores on other species can be extensive. For example, cultivation of herbivorous species, including grass carp, in Russian reservoirs altered commercial catches, resulted in the elimination of pike (*Esox* spp.) and perch (*Perca fluviatilis*), and declines of crucian carp (*Carassius carassius*) and roach (*Rutilus rutilus*; Ref. [70] as cited by [1]). Potential reasons for population declines include competition for food and increased predation due to removal of shelter for small fish [29,87]. Conversely, fish populations may increase following grass carp introductions due to improved water quality, decreased diurnal oxygen depletion, the prevention of noxious phytoplankton blooms, and increased prey abundance following aquatic vegetation removal [7,89]. These rationales for population increases do not apply to all aquatic systems; some studies found decreased water quality and increased algal bloom frequency after grass carp introduction [90,91]. The effects of grass carp on populations of other fish species are not always consistent. For example, population declines are sometimes, but not always, recorded for largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) [7,28,84,89,92].

Grass carp can transmit parasites to native fishes. Transmission of the monogenean parasites *Dactylogyrus* and *Gyrodactylus* from invasive populations of grass carp to native fish species has been recorded in New Zealand (Ref. [93] as cited by [94]). Grass carp are one of the original primary hosts of the tapeworm *Schyzocotyle acheilognathi* (syn. *Bothriocephalus acheilognathi*); this parasite can kill novel hosts, for example, some native North American fish species [95]. In describing parasites of fishes in the Virgin River, Utah, [96] provides a review of the tapeworm introduced into the United States with the introduction of grass carp. It should be noted that grass carp are not the only host of *S. acheilognathi*. This tapeworm can be found on every continent except Antarctica and infects at least 312 fish species; in 2017, 25% of global records of *S. acheilognathi* were from common carp, and 9% were from grass carp [97]. In North America, *S. acheilognathi* is abundant in the Great Lakes independent from grass carp [98], and native fathead minnow (*Pimephales promelas*) serve as a primary host in Colorado [99]. Additional information on this tapeworm and its relationship to grass carp can be found under 'Section Pharmaceuticals, Miscellaneous Toxicants, and Radiation' and 'Section Infectious Disease' within Section 3.2.4. and Section 3.2.6, respectively.

In some aquatic systems, vegetation removal by grass carp is associated with changes in population age structure, individual body condition, growth rate, and diet of other fish species. In both Missouri and Florida, grass carp introduction was followed by changes in the age structure of bluegill populations, skewing toward younger age classes due to increased numbers of juveniles [84,89]. Longear sunfish (*Lepomis megalotis*) experienced a similar demographic shift toward lower age classes in a Texas reservoir [7]. Effective removal of aquatic vegetation by stocked grass carp in Arkansas lakes did not appear to affect fish populations, but it did increase condition of largemouth bass, redear sunfish (*Lepomis microlophus*), and bluegill [92]. Following grass carp introduction to a Texas reservoir, black crappie (*Pomoxis nigromaculatus*) and white crappie (*Pomoxis annularis*) experienced increased growth rates, and the size at which largemouth bass became piscivorous decreased as a result of increased prey availability in littoral zones where vegetation had previously existed [100,101]. For New Zealand smelt (*Retropinna retropinna*) and common bully (*Gobiomorphus cotidianus*) in New Zealand, the loss of aquatic vegetation due to introduced grass carp resulted in a dietary shift from zooplankton to chironomids [87].

In non-fish species, introduced grass carp have led to population declines due to competition for food and some habitat changes. Grass carp have been successfully used as a biological control for two disease-carrying snail species (*Biomphalaria alexandrina* and *Bulinus truncatus*) by removing the snails' food source [30]. By removing aquatic vegetation, grass carp may make disease-carrying aquatic snails (*B. alexandrina* and *Radix natalensis*) more exposed to predators such as molluscivorous black carp (*Mylopharyngodon piceus*; Ref. [102]). The presence of grass carp in Louisiana ponds decreases the harvestable yield of red swamp crayfish (*Procambarus clarkii*) [29]. This decrease could be attributed to competition, as well as potential predation upon the crayfish once the grass carp exhaust vegetative food sources [29]. In Germany, introduced grass carp are considered a good host of the larval stage of the native and declining unionid mussel *Anodonta cygnea* [103]. Grass carp have the potential to deteriorate waterfowl habitat through competition for food [85]. Some waterbird species, including American coot (*Fulica americana*) and ring-necked duck (*Aythya collaris*), feed heavily on some of the same plants fed on by grass carp, including Illinois pondweed, nitella (*Nitella furcata*), and hydrilla [104]. Eurasian coot (*Fulica atra*) and swans (*Cygnus* sp.), both herbivorous waterbird taxa, have been reported to leave ponds stocked with grass carp (T. Krzywosz, W. Krzywosz, and J. Radziej, 1980 as cited in [105]). Following aquatic vegetation reduction from introduced triploid grass carp in a South African lake, there were reports of declines in the herbivorous waterbirds, red-knobbed coot (*Fulica cristata*), Egyptian goose (*Alopochen aegyptiaca*), and yellow-billed duck (*Anas undulata*; Ref. [106]).

Grass carp alter habitat, generally by removing aquatic macrophytes, which can lead to population increases of some taxa [69]. Removal of macrophytes by grass carp in a reservoir in Florida was associated with an increase in total macroinvertebrates [107]. Aquaculture ponds in Turkey stocked with grass carp had higher benthic fauna abundance than ponds without grass carp [69]. Grass carp feces can also provide a food source for some non-fish aquatic species, such as benthic invertebrates [108]. When grass carp are inoculated with larval *A. cygnea* in an experimental setting, the mean number of excysted juvenile *A. cygnea* larva per individual grass carp is 9.1 [103]. Use of high stocking densities of triploid grass carp (i.e., >72 grass carp per vegetated hectare) in small earthen ponds in Texas almost completely removed 'nuisance macrophytes,' including hydrilla, resulting in the creation of available habitat for the establishment of the freshwater clam *Corbicula fluminea*, which is an invasive species in the United States [109]. In the same lake, piscivorous birds, namely reed cormorant (*Microcarbo africanus*) and white-breasted cormorant (*Phalacrocorax lucidus*), increased in numbers following triploid grass carp introduction.

The responses of aquatic animals to introduced grass carp are mixed. However, the diversity and number of taxa that have documented population declines after grass carp introduction seem to outnumber those of the species that benefit (Table 2). Additionally, the combination of population declines and the demographic shift of increased numbers of younger fish may have undesirable effects on angling due to a relative lack of larger individuals being available to catch [105] citing J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 [110]. Despite our understanding of potential effects of carp on ecosystems, there are still many uncertainties related to predicting the ecosystem-level effects of grass carp invasion in any particular area, such as recruitment estimates, adaptability of impacted prey and predator species, trophic interactions, and species-specific bioenergetics parameters [83].

Table 2. Selected studies documenting changes in fish populations or biomass after the introduction of grass carp with subsequent reduction of vegetation.

Family	Species	Location	Status	Change	Reference
Atherinopsidae	brook silverside (*Labidesthes sicculus*)	Texas, USA	Native	Decrease	[7,88]
Atherinopsidae	inland silverside (*Menidia beryllina*)	Texas, USA	Invasive	Increase	[7,88]
Catostomidae	lake chubsucker (*Erimyzon sucetta*)	Florida, USA	Native	Increase	[84]
Centrarchidae	warmouth (*Lepomis gulosus*)	Florida, USA	Native	Decrease	[84]
Centrarchidae	bluegill (*Lepomis macrochirus*)	Texas, USA	Native	Decrease	[7]
		Arkansas, USA	Native	None	[92]
		Missouri, USA	Native	Increase	[89]
		Florida, USA	Native	Increase	[84]
		North Carolina, USA	Native	Increase	[28]
Centrarchidae	redear sunfish (*Lepomis microlophus*)	Arkansas, USA	Native	None	[92]
Centrarchidae	*Lepomis* spp., (6 species)	Texas, USA	Native	Decrease	[7]
Centrarchidae	largemouth bass (*Micropterus salmoides*)	Florida, USA	Native	Decrease	[84]
		Arkansas, USA	Native	None	[92]
Centrarchidae	white crappie (*Pomoxis annularis*)	Texas, USA	Native	Decrease	[7]
Clupeidae	threadfin shad (*Dorosoma petenense*)	Texas, USA	Native	Increase	[7]
Cyprinidae	crucian carp (*Carassius carassius*)	Russia	Native	Decrease	[70] as cited by [1]
Cyprinidae	common carp (*Cyprinus carpio*)	Texas, USA	Invasive	Increase	[7]
Esocidae	pike (*Esox* spp.)	Russia	Native	Decrease	[70] as cited by [1]
Esocidae	northern pike (*Esox lucius*)	Poland	Native	Decrease	J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 as cited in [105]
Fundulidae	*Fundulus* spp. (3 species)	Texas, USA	Native	Decrease	[7]
Ictaluridae	brown bullhead (*Ameiurus nebulosus*)	Texas, USA	Native	Increase	[7]
Ictaluridae	channel catfish (*Ictalurus punctatus*)	Texas, USA	Native	Increase	[7]
Leuciscidae	common bream (*Abramis brama*)	Poland	Native	Decrease	J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 as cited in [105]

Table 2. *Cont.*

Family	Species	Location	Status	Change	Reference
Leuciscidae	white bream (*Blicca bjoerkna*)	Poland	Native	Decrease	J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 as cited in [105]
Leuciscidae	blacktail shiner (*Cyprinella venusta*)	Texas, USA	Native	Increase	[7]
Leuciscidae	fathead minnow (*Pimephales promelas*)	Missouri, USA	Native	Increase	[89]
Moronidae	white bass (*Morone chrysops*)	Texas, USA	Native	Increase	[7]
Moronidae	yellow bass (*Morone mississippiensis*)	Texas, USA	Native	Increase	[7]
Percidae	yellow perch (*Perca flavescens*)	North Carolina, USA	Native	Increase	[28]
Percidae	European perch (*Perca fluviatilis*)	Poland	Native	Decrease	J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 as cited in [105]
		Russia	Native	Decrease	[70] as cited by [1]
Percidae	pikeperch (*Sander lucioperca*)	Poland	Native	Decrease	J. Mastyński, J. Malecki, and M. Iwaszkiewicz, 1987 as cited in [105]
Retropinnidae	New Zealand smelt (*Retropinna retropinna*)	New Zealand	Native	Decrease	[87]
Multiple families	unspecified herbivorous fish species (74 species)	Pakistan	Unknown	Decrease	[86]
Multiple families	various pond-dwelling species (7 species)	Florida, USA	Native	Decrease	[84]

Effects on Plankton, Algae, and Water Quality

The removal of plant material and subsequent conversion by digestion and degradation into waste are associated with changes in plankton communities, algae quantities, and water quality in some aquatic systems. Other reviews describing effects of grass carp stocking related to plankton, algae (measured as chlorophyll *a*), and water quality have found conflicting results [8,9]. Effects of grass carp on plankton vary. In experimental ponds, removal of filamentous macroalgae by grass carp was associated with higher phytoplankton abundance [111]. The presence of grass carp in ponds decreased the number of individual, genera, and orders of plankton present [112], and density [91]. In Turkey, ponds stocked with grass carp had higher abundance of phytoplankton and zooplankton than those without grass carp [69]. Documenting changes in zooplankton communities in four Florida lakes before, during, and after complete removal of macrophytes by stocked grass carp found that effects of macrophyte removal were decreased zooplankton species richness, increased total zooplankton abundance, and a shift from aquatic systems dominated by copepods or copepods and cladocerans (i.e., water fleas) to systems dominated by rotifers and small cladocerans [113]. Other studies have found limited to no effect on the phytoplankton community [67,114]. In addition to secondary effects of vegetation removal, transfer of ′hitchhiker′ plankton species from aquaculture tanks into the environment can occur when any species of fish is moved between locations; introduced grass carp are one source of these plankton. In New Zealand, zooplankton, including the globally invasive, North American calanoid copepod *Skistodiaptomus pallidus*, have been unintentionally introduced during grass carp stocking events [115]. These findings regarding zooplankton have led other authors to hypothesize that other non-native plankton taxa, such as the freshwater diatom *Discostella asterocostata*, could also be unintentionally introduced alongside grass carp [116].

Introduced grass carp may increase algal concentrations in some, but not all, aquatic systems [8]. Vegetation removal by grass carp from a Texas impoundment resulted in increased chlorophyll a levels and decreased clarity due to algal blooms [91]. Removal of water-hyacinth by grass carp from a lake in Indonesia resulted in increases in chlorophyll a [117]. Grass carp were not an effective control measure for cyanobacteria-infested (blue-green algae) waters [118].

Other water quality changes not directly related to plankton or algae have followed grass carp introduction. Removal of macrophytes by grass carp in a Florida reservoir increased particulate organic matter [107]. The presence of grass carp was documented to affect the water quality in a city water-supply reservoir in Texas as a result of invasive plant control [119]. A combination of macrophyte grazing, sediment disturbance, and production of nutrient-containing feces by intentionally introduced grass carp resulted in the conversion of a shallow clearwater lake in Poland, to a turbid system [71]. Turbidity and potassium (K) increased in Indiana ponds stocked with grass carp after the fish had consumed available aquatic vegetation [120]. Increases in turbidity were recorded in four Florida lakes following vegetation removal by stocked grass carp, but only modest increases in nutrient levels [66]. In a pool-based experiment in which hydrilla had been established, removal of vegetation by stocked grass carp resulted in decreased oxygen and pH and increased hardness and nitrogen (N) in the form of nitrate [90]. Removal of water-hyacinth by grass carp from a lake in Indonesia resulted in changes in pH, conductivity, biological oxygen demand, chemical oxygen demand, free carbon dioxide (CO_2), total P, total N/total P ratio, nitrite, and nitrate resulting in a change from a hyper-eutrophic to an oligotrophic system [117]. Aquaculture ponds in Turkey stocked with grass carp resulted in higher nitrite-N, nitrate-N, and total phosphate than control ponds [69]. Removal of vegetation by grass carp may reduce habitat for denitrifying bacteria and may be a causal agent for increases in N associated with introduced grass carp [121] as cited by [122].

Most research on the effects of grass carp on water quality has been conducted in ponds or lakes (for example, [66,69,90,120,123]). However, effects of grass carp on water quality in river systems, that is, habitats where grass carp can effectively reproduce, may differ and have downstream consequences. Introduction of grass carp to a portion of the Po River Basin, a known spawning area for an invasive population of grass carp in Northern Italy, was associated with detrimentally high levels of N in the downstream Goro Lagoon [122]. The changes in N in the Goro Lagoon are not clearly attributable to non-grass carp-related sources, such as change in watershed use or agricultural practices [122]. Though the influences of grass carp on plankton, algae, and water quality are inconsistent, the numerous studies documenting negative water quality changes following grass carp introduction poise this species as a likely threat to water quality in many aquatic systems outside its native range.

1.1.4. Status and Management Concerns

The USFWS has assessed the grass carp as posing a high ecological risk in the contiguous United States due to its history of invasiveness, climate suitability, and its ability to serve as a host for diseases and parasites [124]. A compilation of expert opinion surveys on effects of non-native fish species on the Great Lakes ranked grass carp as one of 13 'high-impact class' species [125]. Workshop proceedings detailing management concerns related to grass carp at the beginning of the 21st century are contained in [126]. A socio-economic risk assessment of potential grass carp effects on the Great Lakes is provided by [127]; it predicts negative effects on native fish fisheries, recreational fishing, and subsistence fishing. Grass carp are also ranked third to goldfish (*Carassius auratus*) and Prussian carp (i.e., gibel carp, *Carassius gibelio*) as having the greatest potential effect on native environments in Europe [128]. Mesocosm experiments show that sediment disturbance by common carp reduces methane production but increases overall greenhouse gas production by oxygenating sediment and increasing aerobic decomposition [129]. These results may apply to grass carp raised or introduced in ponds, as they are also primarily benthic.

Suitable conditions for grass carp survival and reproduction are widespread outside its native range, and this species has a high potential for dispersal within connected waterways. Within North America, a model incorporating the environmental conditions of grass carp native range predicted that almost the entire continental United States, southern Alaska, much of the southern half of Canada, and parts of Mexico are climatically suitable for grass carp [130,131]. Suitable spawning conditions for grass carp are locally prevalent in Europe [8], Lake Erie [47], and downstream of dams in the Mississippi and Arkansas Rivers [38]. A review of the biology of grass carp and other carps in the context of potential invasion of the Columbia River Basin (northwestern continental United States and southwestern Canada) is provided in [132]; information includes spawning conditions, factors important to the survival of all life stages, required climate, and diet of various life stages. Grass carp are seasonally migratory, and individuals could potentially disperse across long distances; in the Mississippi River, grass carp can migrate over 1700 km (Ref. [50] as cited by [131,133].

Grass carp reproduction has been confirmed in multiple United States waterways. Predictions of grass carp spawning in the Arkansas River were confirmed via collections of larvae [47,53]. Grass carp have established populations in the Mississippi River Basin [134,135] and two Lake Erie tributaries [135–137] as cited by [134,135]. Breeding populations have been recorded in the Mississippi, Illinois, and Missouri Rivers and a recent risk assessment concluded that establishment of breeding populations of grass carp in the Great Lakes Basin is also possible [138]. Grass carp have been observed in the Great Lakes since the 1980s [135], but spawning was not confirmed in a Great Lakes tributary until grass carp eggs were found in the Sandusky River in the 2010s [136] as cited by [139]. Recent telemetry studies of grass carp in Lake Erie have since found extensive movement of individual grass carp within the Great Lakes Basin [139]. Eggs resembling those of non-native carps were collected between 2014 and 2019 in the Illinois Waterway and were identified to have originated from silver carp (71.7%), followed by those of grass carp (14.1%) and bighead carp (14.1%); most of the remaining eggs belonged to native silver chub (*Macrhybopsis storeriana*; Ref. [34]).

Lake Erie within the Great Lakes Basin is one water system that has received research attention related to grass carp management; these studies provide frameworks that could be applied in other aquatic systems. Without grass carp population control, population models in the western Lake Erie Basin predict that grass carp densities could reach nearly 40 fish per hectare by the 2040s [140]. However, the same model suggests that removing seasonally concentrated grass carp in high catchability habitats (for example, warm water effluent near power plants in fall) combined with preventing 50% of spawning in the Sandusky River (Ohio) via a moderately efficient barrier could keep grass carp densities within the target of ≤10 fish per hectare [141]. The Ohio Department of Natural Resource's Lake Erie Grass Carp response strategy for 2019 to 2023 includes a combination of preventing new introductions and range expansions of grass carp and limiting the size of existing grass carp populations [142]. Previous work has been carried out to predict where water quality and habitat may be suitable for grass carp establishment in the Great Lakes [143].

2. Methods Summary

This literature review is intended to inform research on the identification of: (1) candidate compounds (for example, amino acids, plant extracts) that could be used to attract grass carp for easier removal; (2) candidate toxins that could be used for removal of grass carp through poisoning; and (3) intestinal pathways within grass carp for increasing effectiveness in delivery methods and effect of candidate toxins. This manuscript provides literature that directly supports the three goals outlined above using three complementary focus areas: (A) diet and behavior; (B) physiological constraints, toxicity, and biology; and (C) gut physiology. Each focus area provides information intended to guide development of potential pathways for invasive grass carp control. Information from other carp species is intended to help fill gaps in grass carp information and provide new, potential research directions. Duane Chapman and Amy George of CERC maintain a comprehensive database of literature continuously updated via periodic literature searches where the focal species are silver, bighead, black, and grass carp; other cypriniforms and some non-cypriniform fish species are represented as well (Database contact, Amy George, USGS). The literature review was conducted by using a variety of terms (Table 3) to search CERC's database between 5 June and 30 July, 2019. To account for additional documents added to the database after the 2019 searches, a follow-up search was conducted in March 2022. 'Introduction' of this manuscript is the first section produced as a result of the literature review. To credit authors reviewing other sources, multiple citations follow '(Author X as cited by Author Y)' or a similar format. Note that not all 'Author X' papers were directly examined; some were inaccessible or in non-English languages. Per U.S. Geological Survey citation requirements, such inaccessible secondary citations are not listed in the literature cited, but authors and years are listed in the text next to the numerical primary citation.

Table 3. Search terms applied to the CERC carp database for the three focal areas of this grass carp literature review.

Grass Carp Diet and Behavior	Carp Control Based on Physiological Constraints, Toxicity, and Biology	Grass Carp Gut Physiology and Related Control Pathways
Aquaculture	Antimycin	Cellulose
Attract	Lethal	Digestion
Avoid	Lethal dose	Food particle size
Bait	Rotenone	Food milling
Commercial diet	Toxic	Gastrointestine
Deter	Toxic dose	Gastrointestine enzyme
Diet	Toxic food	Gastrointestine pH
Food	Toxic plant	Gut
Food selection	Toxicity	Gut enzymes
Foraging	Ziram	Gut pH
Grazing		Intestine
Gut content		Intestine enzyme
Gut content analysis		Intestine pH
Management bait		Toxin processes
Plant morphology		
Plant texture		
PrenFish		
Prentiss		
Raising		
Seasonal behavior		
Wild diet		

Across all focal area searches applied to the database, nearly 4000 PDF (portable document format) file names were identified. Approximately 1600 of the identified PDFs were not considered based on title or text extracted via term searches. Over 900 of the identified documents were cited in this manuscript. Combining the identified documents, secondary citations, and a small number (<20) of documents identified independently from the searches, the reference list for this manuscript includes over 1000 references.

3. Results: Review of Focal Areas

3.1. Diet and Behavior

Understanding grass carp feeding habits, dietary requirements, plant preferences, and behavior has important consequences for vegetation management using grass carp, grass carp aquaculture, and management of invasive populations of grass carp. Feeding rates and dietary preferences are known to vary with life stage, region, season, temperature, and flow [27,144]. Much of the grass carp-specific research related to diet, food preferences, growth, and behavior has been conducted in aquaculture systems (for example, [72,145]), or in locations where grass carp were intentionally introduced, especially in areas dominated by invasive macrophytes (for example, [5,6]). Concerns have been raised that 'food preference' anthropomorphizes the selection of food by grass carp [27]. However, for lack of a one-to-one substitution for the words 'preference' and 'prefer' in some cases, we use these words to describe the relative degree of selection compared to availability of certain foods over others.

3.1.1. In Situ Diet and Selectivity

A great deal of work has been carried out on the diet and dietary selectivity of grass carp at various life stages, and the findings of these studies have been reviewed elsewhere (for example, [13,20,27,28,60,146,147]). We provide a summary of information on food selection in grass carp for animals and microorganisms (Table 4) and plants and algae (Table 5).

While adult carp are primarily herbivorous, fry require a diet high in animal protein and depend primarily on small aquatic invertebrates and phytoplankton [13,27,38,148]. The size of food particles considered suitable for commencement of feeding in larval grass carp is 90 to 150 μm [149]. Yield of grass carp larvae is positively correlated with plankton primary production [150]. By two weeks after hatching, and at sizes of 12 to 17 mm long, grass carp feed on larger prey, such as *Daphnia* (an anomopodan water flea) and insect larvae [13,25].

Across a variety of studies, grass carp transition from primarily animal foods to almost exclusively macrophytes prior to 50 days of age; the exact age varies between studies and environmental conditions [25,151–153]. According to [25], after three weeks, the occurrence of plants in the diet increases with the appearance of filamentous algae and macrophytes, while nearly exclusive macrophyte feeding does not begin until 1 to 1.5 months after hatching. Grass carp fry become herbivorous approximately 3 weeks after hatching (Ref. [24] as cited by [9]). Grass carp fry are described as shifting from primarily animal material in the first week to primarily plant material as early as the second week [153], and by the seventh week grass carp shifted from filamentous algae to macrophytes. Grass carp fry transitioned from feeding exclusively on plankton (taxon Infusoria; orders Rotifera and Crustacea) to primarily algae and macrophytes with some insect larvae and detritus as the fish age into fingerlings (age of 25–30 days after hatching with weight of 8–10 g were considered fingerlings) [154]; a similar pattern was noted by [155]. Developing grass carp in polyculture with silver carp and common carp have been observed eating exclusively zooplankton and small benthos at 14 days of age, before transitioning to a diet consisting of 50% macrophytes at 26 days, 85% macrophytes at 36 days, and 100% macrophytes at around 44 days [151]. The age at which grass carp fry transitioned to 100% macrophytes was temperature dependent; in warmer weather grass carp began to consume only macrophytes at 36 to 40 days when they reached a length of 50 mm, while in colder weather grass carp did not start to consume exclusively macrophytes until 46 days of age (45 to 52 mm length, similar length; Ref. [151] as cited by [1]). Early work in Poland gives similar descriptions of food item selection and foraging rate changes in larval grass carp as they develop [152]. In reference to grass carp of unspecified age, ref. [27] reports that grass carp will not eat zooplankton and aquatic insects even when starving; these fish were likely older due to their consumption of grass on the edge of ponds.

Selectivity of grass carp for vegetation tends to decrease as grass carp grow and age, with younger grass carp selecting almost exclusively soft plant tissues (Ref. [156] citing [157]). Grass carp across a range of ages (0 to 2+ years) showed selection for softer plants in Portuguese canals, but grass carp 2+ years in age tended to be less selective than younger fish and would incorporate more fibrous plant tissue in their diet [156]. Even as large adults, grass carp generally select against fibrous and woody plants [27], but to some extent, larger and older grass carp will feed on tough and fibrous plants (Ref. [156] citing [157]; Ref. [9] citing [158]). Selection for Brazilian waterweed (*Egeria densa*) by grass carp is age dependent; juvenile grass carp avoid this plant, whereas adult grass carp graze upon it heavily [31]. Feeding rates of two size classes of grass carp, ~14 g and ~375 g, over five days are reported by [17] (p. 6), presenting the results of [159]. Both size classes eliminated (i.e., consumed) 100% of *Nitella* (a charophyte green alga), duckweeds (*Lemna* sp.), and Canadian waterweed (*Elodea canadensis*) present in the ponds. The 375 g grass carp also eliminated 100% of pond water-starwort (*Callitriche stagnalis*), paspalum grass (*Paspalum* sp.), watercresses (*Nasturtium* sp.), and curlyleaf pondweed. The 14 g grass carp eliminated less than 50% of those same plant species. Within plant species, grass carp select for different parts of a plant to varying degrees. Grass carp used for vegetation control feed on fresh shoots of recently cut sedges (*Fimbristylis acuminata*, *Scleria poiformis* [syn. *S. poaeformis*], *Fuirena umbellata*, and *Rhynchospora aurea*) where these sedges are otherwise too tough to be consumed [27]. Similarly, grass carp feeding on water-hyacinth will consume roots and leaves but tend to avoid the petioles and older leaves (Refs. [160,161] as cited by [156]).

In addition to fish size, the dietary composition of adult grass carp may be driven by a combination of learned and innate selectivity and is affected by a number of environmental factors such as season and temperature [9,144,162]; hydrology [162]; water chemistry [163]; and food availability [164]. For relationships between feeding rate and water quality factors and temperature, see 'Section 3.2.1. Physiological Tolerances'. Selection of macrophyte species by grass carp in experimental pools with multiple macrophyte species available suggest that the selection hierarchy across macrophyte species parallels handling times (primarily mastication and ingestion due to search and decision times assumed to be relatively low), resulting in maximum ingestion rate [165]. Alternatively, some authors (for example, V. Cure, 1970 as cited in [71]) suggest that vegetation selection of grass carp is driven primarily by availability and secondarily by innate selectivity. For example, while adult grass carp primarily consume aquatic vegetation, they are known to consume terrestrial plants, insects, and small fish when aquatic vegetation is limited [164]. In a report from Malaysia, grass carp acclimated to eating hydrilla and moved to a new pond with multiple types of vegetation will exclusively consume hydrilla until that plant has been eliminated [27]. The same report notes that grass carp acclimated to less selected-for foods, such as *Charales* and *Najas*, will not select for these plants if presented with more palatable options. Feeding rate of grass carp is positively correlated with calcium and cellulose content of plants when comparing consumption rates of the same species of plants from locations with differing water chemistry [163]. Additional support for dependency of feeding rate of grass carp on fish age and size, temperature, oxygen concentration, location, and plant species is provided by [17] citing a variety of sources, including N. S. Stroganov, 1963 and [15,27,157,166–173].

When presented with four different macrophytes, sago pondweed, Eurasian watermilfoil, longleaf pondweed (syn. American pondweed, *Potamogeton nodosus*), and *Cladophora* (a filamentous green algae), triploid grass carp have shown to have differing relative consumption of macrophyte taxa influenced by season and whether the grass carp were in still or flowing water [162]. It was also found that in spring, *Cladophora* is the most common consumed macrophyte by wet mass in still water, and that longleaf pondweed (*Potamogeton nodosus*) is the most common consumed macrophyte by wet mass in flowing water. Similarly, in 1-year old triploid grass carp selection for curlyleaf pondweed, Canadian waterweed and Eurasian watermilfoil varied based on season and flow [144]. Grass carp selected for Eurasian watermilfoil over curlyleaf pondweed in the fall in static water with the opposite selection order in the winter in flowing water [144]. In earthen ponds, plant matter was found to be the main food present in grass carp guts in the summer, with artificial fish food in spring and autumn, and no food in winter [174]. For adult grass carp in Uzbekistan and Turkmenistan it has been reported that detritus consumption increases in fall, and algae consumption increases in spring (M.A. Abdullayev and B. Khakberdiyev, 1989 as cited in [1]). When offered 70 different plant species over a range of temperatures, grass carp in the Moscow area selected for fineleaf pondweed (*Stuckenia filiformis*); sharp-leaved pondweed *Potamogeton acutifolius*; *Elodea*; red clover (*Trifolium pratense*); pea plants (*Pisum sativum*) while blooming, common vetch (*Vicia sativa*), cow vetch (*Vicia cracca*), silverweed cinquefoil (*Potentilla anserina),* leaves of dandelion, leaves of cereal grains, grains and young leaves of oats, and soft leaves of corn at all temperatures, but other plants were not selected for or consumed in all temperature conditions. Contrasting with these studies, the macrophyte selection hierarchy for grass carp in New Zealand varies little over the seasons [175].

Table 4. List of aquatic animals and heterotrophic microorganisms and the degree to which they are consumed by young grass carp (fry/fingerling; all <1 year old unless otherwise noted) according to the referenced literature. A general common name is provided in brackets under the scientific name for each taxa, where applicable. Consumption classes are as follows: "Avoided" = grass carp either did not consume the food item or consumed quantities below the level of detection. "Consumed" = grass carp observed consuming the food, but the quantity of consumption was not noted. "Rarely" = grass carp were observed consuming food, but only reluctantly, in small quantities, and/or in the absence of food that were more readily consumed. "Conditional " = consumption rate dependent on conditions within a study, such as seasonality and grass carp age. "Moderately" = food selected for over some, but not all, foods presented, or it was consumed at an intermediate rate relative to other foods that were available. "Readily" = food selected for over most other foods and/or consumed at a high rate. In the "Consumption" column, the parenthetical number followed by "ref." or "refs." indicates the number of references associated with a consumption class. Parenthetical letters and letter ranges in the "Consumption" and "Reference(s)" columns correspond to each other within a row. All insects listed are aquatic larvae or nymphs unless otherwise noted. * = taxonomic synonym or misspelling used in at least one reference; *Naiadae* = *Naidae*, *Polyphemus* = *Poliphamus*, *Limnephilus* = *Limnophilus*. ** = aquatic insect with unspecified life stage. † = consumed by grass carp >1 year in age in the absence of macrophytes. †† = consumed by grass carp >1 year in age in association with pondweed (genus *Potamogeton*), a plant. ‡ = nauplius or juvenile life stage specified. ‡‡ = rainbow trout fry are consumed; rainbow trout eggs are not. # = review article incorporating many sources.

Taxon	Consumption	Reference(s)
Acanthodiaptomus spp./sp. [copepod]	Consumed (1 ref.)	V.P. Mitrofanov, G.M. Dukravets, and A.F. Sidorova, 1992 as cited in [1]
Aeshna affinis [dragonfly]	Avoided (1 ref.)	[154]
Alonella spp./sp. [water flea]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [1]; (b) M. Linchevskaya, 1966 as cited in [1]
Amphipoda (order) [scud]	Consumed (1 ref.)	[176]
Anax spp./sp. [dragonfly]	Avoided (1 ref.)	[154]
Anisops spp./sp. ** [backswimmer]	Avoided (1 ref.)	[176]
Arcella spp./sp. [amoeba]	Readily (1 ref.)	[25]
Archichauliodes spp./sp. [fishfly]	Consumed (1 ref.)	[176]

Table 4. *Cont.*

Taxon	Consumption	Reference(s)
Baetis spp./sp. [dragonfly]	Readily (1 ref.)	[154]
Berosus spp./sp. [water scavenger beetle]	Rarely † (1 ref.)	A.F. Mukhamedova, 1963 as cited in [1]
Bosmina spp./sp. [water flea]	Consumed (1 ref.)	[153]
Bosmina longirostris [water flea]	Consumed (1 ref.; a), Conditional (1 ref.; b), Readily (3 refs.; c-e)	(a) [152]; (b) [151]; (c) [1] citing [151]; (d) [25] citing [151]; (e) [154]
Brachionus spp./sp. [rotifer]	Consumed (2 refs.; a-b)	(a) [1]; (b) [20]#
Brachionus plicatilis [rotifer]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Brachionus quadridentatus [rotifer]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Ceriodaphnia spp./sp. [water flea]	Avoided (1 ref.; a), Rarely (1 ref.; b)	(a) [25] citing [151]; (b) [1] citing [151]
Ceriodaphnia quadrangula [water flea]	Avoided (1 ref.)	[151]
Chaetogaster spp./sp. [oligochaete worm]	Moderately (1 ref.)	[154]
Chironomidae (family) [midge]	Consumed (3 refs.; a-c), Readily (1 ref.; d)	(a) B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]; (b) [1]; (c) [176]; (d) M. Linchevskaya, 1966 as cited in [1]
Chironomus spp./sp. [midge]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [20]#; (b) [154]
Chydorus spp./sp. [water flea]	Avoided (1 ref.; a), Rarely (1 ref.; b)	(a) [25] citing [151]; (b) [1] citing [151]
Chydorus sphaericus [water flea]	Avoided (1 ref.; a), Readily (1 ref.; b)	(a) [151]; (b) [154]
Cladocera (order) [water flea]	Consumed (2 refs.; a-b)	(a) [152]; (b) [20]#
Cloeon dipterum [mayfly]	Readily (1 ref.)	[154]
Copepoda (order) [copepod]	Consumed (1 ref.; a) ‡, Rarely (1 ref.; b), Readily (1 ref.; c) ‡	(a) [20]#; (b) [1] citing [151]; (c) M. Linchevskaya, 1966 as cited in [1]
Culex spp./sp. [mosquito]	Moderately (1 ref.)	[154]
Cyclops strenuus [copepod]	Avoided (1 ref.)	[151]
Daphnia spp./sp. [water flea]	Consumed (1 ref.)	[152]
Daphnia longispina [water flea]	Moderately (1 ref.; a), Readily (3 refs.; b-d)	(a) [154]; (b) [1] citing [151]; (c) [25] citing [151]; (d) [151]
Deleatidium spp./sp. [mayfly]	Consumed (1 ref.)	[176]

Table 4. *Cont.*

Taxon	Consumption	Reference(s)
Diaphanosoma spp./sp. [water flea]	Consumed (1 ref.)	[1]
Diaphanosoma brachyurum [water flea]	Readily (1 ref.)	[155]
Diaptomus spp./sp. [water flea]	Avoided (2 refs.; a-b)	(a) [151]; (b) [155]
Euplotes patella [ciliate]	Readily (1 ref.)	[154]
Filinia spp./sp. [rotifer]	Consumed (1 ref.)	[177]
Filinia passa [rotifer]	Consumed (1 ref.)	[152]
Gammaridae (family) [river shrimp]	Consumed (1 ref.)	B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]
Gammarus pulex [river shrimp]	Readily (1 ref.)	[178]
Gyrinus spp./sp. [whirligig beetle]	Avoided (1 ref.)	[154]
Hydropsyche spp./sp. [caddisfly]	Consumed (1 ref.)	[176]
Infusoria (unclassified) [aquatic microorganisms]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [179]; (b) [179]
Keratella spp./sp. [rotifer]	Consumed (1 ref.)	[1]
Keratella quadrata [rotifer]	Readily (1 ref.)	[154]
Keratella valga [rotifer]	Readily (1 ref.)	M. D. Rozmanova, 1966 as cited in [25]
Lecane spp./sp. [rotifer]	Consumed (1 ref.)	[153]
Leuctra fusca [stonefly]	Readily (1 ref.)	[154]
Libellula depressa [dragonfly]	Avoided (1 ref.)	[154]
Limnodrilus hoffmeisteri [oligochaete worm]	Consumed (2 refs.; a-b)	(a) [180]; (b) [181]
Limnephilus spp./sp. * [caddisfly]	Consumed (1 ref.) ††	B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]
Mesocyclops spp./sp. [copepod]	Consumed (1 ref.)	[1]
Mesocyclops leukarti [copepod]	Avoided (1 ref.)	[154]
Moina spp./sp. [water flea]	Consumed (1 ref.)	[1]
Moina rectirostris [water flea]	Readily (1 ref.)	M. D. Rozmanova, 1966 as cited in [25]
Monostyla spp./sp. [rotifer]	Consumed (1 ref.)	[153]

Table 4. *Cont.*

Taxon	Consumption	Reference(s)
Naididae (family) * [oligochaete worm]	Consumed (1 ref.)	[152]
Clitellata	Readily (1 ref.)	[176]
Ostracoda (class) [seed shrimp]	Consumed (1 ref.)	[1]
Plecoptera (order) [stonefly]	Moderately (1 ref.)	[176]
Polyarthra vulgaris [rotifer]	Readily (1 ref.)	[154]
Polyphemus pediculus * [onychopod]	Readily (3 refs.; a-c)	(a) [1] citing [151]; (b) [25] citing [151]; (c) [151]
Potamopyrgus antipodum [New Zealand mud snail]	Consumed (1 ref.)	[176]
Potamopyrgus antipodarum [freshwater snail]	Consumed (1 ref.)	[176]
Protozoa (unclassified)	Consumed (2 refs.; a-b)	(a) [27]; (b) [20]#
Rhantus suturalis [supertramp beetle]	Avoided (1 ref.)	[154]
Oncorhynchus mykiss [rainbow trout]	Avoided (1 ref.; a) ‡‡, Consumed (1 ref.; b) ‡‡	(a) [176]; (b) [176]
Scapholeberis mucronata [water flea]	Readily (3 refs.; a-c)	(a) [1] citing [151]; (b) [25] citing [151]; (c) [151]
Simocephalus spp./sp. [water flea]	Consumed (1 ref.; a), Moderately (1 ref.; b)	(a) [152]; (b) [154]
Stylaria lacustris [oligochaete worm]	Moderately (1 ref.)	[154]
Stylonychia mytilus [ciliate]	Readily (1 ref.)	[154]
Telmatogetoninae (subfamily of *Chironimidae*) [midge]	Consumed (1 ref.; a), Rarely † (1 ref.; b)	(a) [152]; (b) A.F. Mukhamedova, 1963 as cited in [1]
Tipula spp./sp. [crane fly]	Readily (1 ref.)	[154]
Trichoptera (order) [caddisfly]	Consumed (1 ref.)	B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]
Zooplankton (unclassified)	Consumed (2 refs.; a-b), Readily (1 ref.; c)	(a) [27]; (b) [164]; (c) B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]

3.1.2. Aquacultural Diet and Associated Production

Because of the economic importance of grass carp in global aquaculture, a great deal of research has been carried out to find economical diet formulas for optimal production of grass carp. This research covers grass carp requirements of macronutrients, amino acids, vitamins, and minerals and the effects of deficiencies in these, as well as the effects of other dietary supplements and feed sources. We also review the effects of other factors on grass carp growth and production. For the effects of nutrient deficiencies on the intestinal tract of grass carp, nutrient requirements specific to intestinal function, and information on the effects of supplemental probiotics, see Section 3.3.4. 'Effects of Dietary Nutrient Levels on Intestines'. Table 6 provides a summary of the optimal levels of various amino acid, vitamins, minerals, and other supplements to diet based on a variety of endpoints.

Table 5. List of terrestrial plants, macrophytes, and non-macrophyte algae and the degree to which they are consumed by grass carp (>1 year old) according to referenced literature. A common name is provided in brackets under the scientific name for each taxa, where applicable. Consumption classes are as follows: "Avoided" = grass carp either did not consume the food item or consumed quantities below the level of detection. "Consumed" = grass carp observed consuming the food, but the degree of consumption was not noted. "Rarely" = grass carp were observed consuming food, but only reluctantly, in small quantities, and/or in the absence of food that were more readily consumed. "Conditional" = consumption rate varied depending on conditions within a study, such as seasonality, grass carp age, macrophyte growth stage. "Moderately" = food selected for over some, but not all, foods presented, or it was consumed at an intermediate rate relative to other foods. "Readily" = food selected for over most other foods that were available and/or consumed at a high rate. In the "Consumption" column, the parenthetical number followed by "ref." or "refs." indicates the number of references associated with a consumption class. Parenthetical letters and letter ranges in the "Consumption" and "Reference(s)" columns correspond to each other within a row. * = taxonomic synonym used in at least one reference; some of these synonyms include *Carex elata* = *C. hudsoniilowei*, *Elodea* = *Anachris*, *Colocasia esculenta* = *C. antiquorum*, *Erythranthe guttatta* = *Mimulus guttatus*, *Hydrocharis morsus-ranae* = *H. morus*, *Ludwigia* = *Jussiaea*, *Myriophyllum aquaticum* = *M. brasiliense*, *Nitella flexilis* = *Chara flexilis*, *Persicaria amphibia* = *Polygonum amphibium*, *Persicaria decipiens* = *Polygonum salicifolium*, *Persicaria hydropiperoides* = *Polygonum hydropiperoides*, *Phragmites australis* = *P. communis*, *Scleria poaeformis* = *S. poiformis*. ** = Diatoms consumed in association with *Potamogeton*. † = Tough stems of *Lagarosiphon* rejected. †† = Consumed while the plant or its shoots are young. ‡ = Plants over 1 meter in height not consumed. ‡‡ = Roots not consumed. # = review article incorporating many sources; some information on "consumed" vs. "avoided" may conflict within these reviews.

Taxon	Consumption	Reference(s)
Acorus calamus [sweet flag]	Consumed (1 ref.)	[20]#
Algae (unclassified)	Readily (1 ref.)	[179]
Alisma spp./sp. [water-plantain]	Consumed (1 ref.)	[20]#
Alisma gramineum [narrowleaf water-plantain]	Readily (1 ref.)	M. Saadati, 1974 as cited in [164]
Alisma plantago-aquatic [common water-plantain]	Consumed (2 refs.; a-b)	(a) [147] citing [182]; (b) [183]
Alternanthera spp./sp. [joyweed]	Avoided (1 ref.)	[60]#
Alternanthera philoxeroides [alligator weed]	Avoided (1 ref.; a), Rarely (1 ref.; b)	(a) [184]; (b) [17] citing [171]
Anabaena spp./sp.	Consumed (1 ref.)	[1]
Aphanizomenon flos-aquae	Consumed (1 ref.)	[169]
Araceae (family) [duckweed]	Readily (1 ref.)	[147] citing [185]
Azolla spp./sp. [mosquito ferns]	Consumed (2 refs.; a-b), Readily (2 refs.; c-d)	(a) [20]#; (b) [164]; (c) [186] citing [187]; (d) [173]
Azolla filiculoides [Pacific mosquitofern]	Avoided (2 refs.; a-b), Readily (1 ref.; c)	(a) [184]; (b) [158]; (c) [156]
Azolla pinnata [feathered mosquitofern]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [147] citing [168]; (b) [185]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Azolla rubra [red Azolla]	Rarely (1 ref.)	[159]
Bacillariophyceae (class) [diatoms]	Consumed ** (1 ref.)	B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]
Bacopa caroliniana [blue water hyssop]	Avoided (1 ref.)	[184]
Beta vulgaris [sugar beet]	Avoided (1 ref.)	[183]
Bidens tripartita [three-lobed beggar-ticks]	Consumed (2 refs.; a-b)	(a) [147] citing [168]; (b) [20]#
Brasenia spp./sp. [watershield]	Avoided (1 ref.)	[60]#
Brasenia schreberi [watershield]	Consumed (1 ref.; a), Rarely (1 ref.; b), Readily (1 ref.; c)	(a) [184]; (b) [188]; (c) [17] citing [171]
Butomus umbellatus [flowering rush]	Consumed (2 refs.; a-b)	(a) [147] citing [168]; (b) [20]#
Cabomba spp./sp. [fanwort]	Avoided (1 ref.)	[60]#
Cabomba caroliniana [Carolina watershield]	Consumed (1 ref.)	[147] citing [189]
Calamagrostis epigejos [bush grass]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Calla palustris [water arum]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Callitriche spp./sp. [water-starworts]	Consumed (1 ref.; a), Readily (2 refs.; b-c)	(a) [17] citing [191]; (b) [183]; (c) [178]
Callitriche stagnalis [pond water-starwort]	Consumed (1 ref.; a), Conditional (1 ref.; b) Readily (1 ref.; c)	(a) [17] citing [191]; (b) [159]; (c) [175]
Callitriche palustris [vernal water-starwort]	Consumed (1 ref.)	[183]
Carex spp./sp. [sedges]	Consumed (2 refs.; a-b)	(a) [183]; (b) [184]
Carex lowei * [tufted sedge]	Avoided (1 ref.; a), Consumed (2 refs.; b-c)	(a) [168]; (b) [147] citing [190], [182]; (c) [20]#
Carex nigra [black sedge]	Consumed (3 refs.; a-c), Rarely (2 refs.; d-e)	(a) [147] citing [190]; (b) [147] citing [182]; (c) [20]#; (d) [192] citing [193], [194], N. S. Stroganov, 1963, and V. Krupauer, 1967 (e) [195]
Carex pseudocyperus [cyperus sedge]	Consumed (2 refs.; a-b), Rarely (2 refs.; c-d)	(a) [147] citing [190], [182]; (b) [20]#; (c) [192] citing [193], [194], N. S. Stroganov, 1963, and V. Krupauer, 1967; (d) [195]
Catagrose aquatica [manna grass]	Consumed (1 ref.)	[183]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Centella asiatica [coinwort]	Consumed (1 ref.)	[184]
Ceratophyllum spp./sp. [hornwort]	Avoided (1 ref.; a) Readily (1 ref.; b)	(a) [60]#; (b) [196]
Ceratophyllum demersum [coontail]	Avoided (3 refs.; a-c), Consumed (4 refs.; d-g), Rarely (5 refs.; h-l), Conditional (1 ref.; m), Moderately (1 ref.; n), Readily (8 refs.; o-v)	(a) [72]; (b) [156] citing [73]; (c) [158]; (d) [17] citing [191]; (e) [147] citing [182]; (f) [184]; (g) [20]#; (h) [159]; (i) [166]; (j) [197]; (k) [198]; (l) [199] (m) [188]; (n) [200]; (o)[185]; (p) [192] citing [193], [194], N. S. Stroganov, 1963, and V. Krupauer, 1967; (q) [195]; (r) [201]; (s) [17] citing [171] (t) [173]; (u) [156]; (v) [202]
Chara spp./sp. [stonewort]	Avoided (1 ref.; a), Consumed (4 refs.; b-e), Rarely (1 ref.; f), Readily (13 refs.; g-s)	(a) [60]#; (b) [17] citing [191]; (c) V.P. Mitrofanov, G.M. Dukravets, Antsiferova et al. 1968, and A.F. Sidorova, 1992 as cited in [1]; (d) [184]; (e) [20]#; (f) [203] (g) [192] citing [193], [194], N. S. Stroganov, 1963, and V. Krupauer, 1967; (h) [195]; (i) M. Saadati, 1974 as cited in [164]; (j) [183]; (k) [204]; (l) [196]; (m) [173]; (n) [165]; (o) [146]; (p) [158]; (q) [71] citing [73]; (r) [177]; (s) [205] citing [173]
Chara globularis [fragile stonewort]	Rarely (1 ref.)	[178]
Chara vulgaris [common stonewort]	Consumed (1 ref.)	[147] citing [190]
Characium spp./sp. [unicellular green algae]	Consumed (1 ref.)	[177]
Charales (order) [stoneworts]	Readily (1 ref.)	[201]
Chlamydomonas spp./sp. [unicellular green algae]	Consumed (1 ref.)	[177]
Cladium spp./sp. [sawgrass]	Avoided (1 ref.; a), Rarely (1 ref.; b)	(a) [60]#; (b) [205] citing [206]
Cladium jamaicense [sawgrass]	Rarely (1 ref.)	[17] citing [171]
Cladophora spp./sp. [filamentous green algae]	Consumed (3 refs.; a-c), Readily (2 refs.; d-e)	(a) [1]; (b) [1]; (c) [20]#; (d) M. Saadati, 1974 as cited in [164]; (e) [146]
Cladophoraceae (family) [filamentous green algae]	Consumed (1 ref.)	[183]
Colocasia esculenta * [elephant ear]	Rarely (1 ref.; a) Consumed (1 ref.; b)	(a) [185] (b) [184]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Commelina virginica [Virginia dayflower]	Consumed (1 ref.)	[184]
Cosmarium spp./sp.	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Echinodorus spp./sp. [burhead]	Avoided (1 ref.)	[60]#
Egeria spp./sp. [waterweed]	Avoided (1 ref.)	[60]#
Egeria densa [Brazilian waterweed]	Avoided (1 ref.; a), Consumed (3 refs.; b-d), Rarely (1 ref.; e), Conditional (1 ref.; f), Readily (3 refs.; g-i)	(a) [159]; (b) [17] citing [191]; (c) [184]; (d) [20]#; (e) [188]; (f)[197]; (g) [173]; (h) [72]; (i) [205] citing [173]
Eichhornia spp./sp. [water-hyacinth]	Avoided (1 ref.)	[60]#
Eichhornia crassipes [water-hyacinth]	Avoided (2 refs.; a-b), Consumed (3 refs.; c-e), Rarely (3 refs.; f-h), Moderately (2 refs.; i-j)	(a) [72]; (b) [146]; (c) [147] citing [190]; (d) [184]; (e) [20]#; (f) [186] citing [185]; (g) [173]; (h) [156] (i) [17] citing [171]; (j) [207]
Eleocharis spp./sp. [spikerushes]	Avoided (1 ref.; a), Moderately (1 ref.; b)	(a) [60]#; (b) [17] citing [171]
Eleocharis acicularis [needle spikerush]	Consumed (1 ref.)	[72]
Eleocharis baldwinii [road grass]	Consumed (1 ref.)	[184]
Eleocharis palustris [creeping spikerush]	Consumed (1 ref.)	[183]
Eleocharis quadrangulata [square rush]	Consumed (1 ref.)	[184]
Elodea spp./sp. * [waterweeds]	Readily (2 refs.; a-b)	(a) [1] citing N. S. Stroganov, 1963 (b) [27]
Elodea canadensis [Canadian waterweed]	Consumed (5 refs.; a-e), Conditional (1 ref.; f), Readily (9 refs.; g-o)	(a) [208]; (b) [147] citing [168]; (c) [17] citing [191]; (d) [183]; (e) [20]#; (f) [144]; (g) [192] citing [193], [194], N. S. Stroganov, 1963, and V. Krupauer, 1967; (h) [195]; (i) [159]; (j) [204]; (k) [201]; (l) [165] (m) [188] (n) [209]; (o) [146]
Elodea nuttallii [western waterweed]	Consumed (1 ref.; a), Rarely (1 ref.; b), Readily (1 ref.; c)	(a) [181]; (b) [178]; (c) [72]
Equisetum spp./sp. [horsetail]	Consumed (2 refs.; a-b)	(a) [147] citing [210]; (b) [20]#
Erthranthe guttatta * [monkeyflower]	Avoided (2 ref.; a-b)	(a) [159]; (b) [159]
Eryngium aquaticum [bitter snakeroot]	Consumed (1 ref.)	[184]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Ficus grossulariodies [fig tree]	Rarely (1 ref.)	[27]
Filamentous algae (unclassified)	Avoided (1 ref.; a), Rarely (1 ref.; b), Readily (2 refs.; c-d)	(a) [201] citing N. S. Stroganov, 1963, R. Tsharyiev and D.S. Aliev 1966; (b) [205] citing [206]; (c) [201] citing [211], W. Prihodko and A. Nosal 1966; (d) [17] citing [171]
Fimbristylis acuminata [pointed fimbristylis]	Conditional †† (1 ref)	[27]
Fontinalis spp./sp. [fountain moss]	Consumed (2 refs.; a-b), Readily (1 ref.; c)	(a) [147] citing [190]; (b) [20]#; (c) [201]
Fontinalis antipyretica [willow moss]	Consumed (1 ref.)	[20]#
Fuirena umbellata [umbrella sedge]	Conditional †† (1 ref.)	[27]
Galium palustre [marsh bedstraw]	Avoided (1 ref.)	[168]
Glyceria fluitans [floating sweet-grass]	Consumed (3 refs.; a-c), Readily (2 refs.; d-e)	(a) [147] citing [182]; (b) [183]; (c) [20]#; (d) [168]; (e) [209]
Gomphonema spp./sp. [diatoms]	Readily (1 ref.)	[155]
Gomphosphaeria lacustris [colonial cyanobacteria]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Groenlandia densa [opposite-leaved pondweed]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [183]; (b) [204]
Halophila gaudichaudii [paddle weed]	Consumed (1 ref.)	[185]
Hippus vulgaris [mare's tail]	Rarely (1 ref.)	[204]
Hottonia palustris [water violet]	Conditional (1 ref.)	[168]
Hydrilla verticillata [hydrilla]	Consumed (5 refs.; a-e), Readily (13 refs.; f-r)	(a) [147] citing [182]; (b) [184]; (c) [60]#; (d) [9]; (e) [20]#; (f) [185]; (g) [27]; (h) [146] citing [212]; (i) [146] citing [17,213]; (j) [17] citing [171]; (k) [196]; (l) [173]; (m) [214]; (n) [72]; (o) [146]; (p) [158]; (q) [205] citing [173]; (r) [215]
Hydrocharis morsus-ranae * [frogbit]	Consumed (2 refs.; a-b), Rarely (2 refs.; c-d)	(a) [147] citing [168]; (b) [20]#; (c) [192] citing [193], [194], and V. Krupauer, 1967; (d) [195]
Hydrocotyle spp./sp. [water pennyworts]	Rarely (1 ref.)	[17] citing [171]
Hydrocotyle umbellata [dollarweed]	Consumed (1 ref.)	[184]
Hydrodictyon reticulatum [water net]	Avoided (1 ref.; a), Consumed (1 ref.; b)	(a) N. S. Stroganov, 1963 as cited in [201]; (b) [183]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Isoetes kirkii [quillwort]	Consumed (1 ref.)	[17] citing [191]
Juncaceae (family) [rushes]	Rarely (1 ref.)	[27]
Juncus spp./sp. [rushes]	Consumed (1 ref.)	[183]
Juncus articulatus [jointed rush]	Consumed (1 ref.)	[20]#
Juncus effusus [common rush]	Consumed (2 refs.; a-b), Rarely (2 refs.; c-d), Conditional (1 ref.; e)	(a) [147] citing [190]; (b) [20]#; (c) [192] citing [193], [194], and V. Krupauer, 1967; (d) [195]; (e) [168]
Juncus filiformis [thread rush]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Lactuca sativa [lettuce]	Consumed (2 refs.; a-b), Readily (1 ref.; c)	(a) [147] citing [182]; (b) [20]#; (c) [168]
Lagarosiphon spp./sp. [waterweed]	Avoided † (1 ref.; a), Readily (1 ref.; b)	(a) [17] citing [191]; (b) [27]
Lagarosiphon major [curly waterweed]	Consumed (1 ref.; a), Conditional (1 ref.; b)	(a) [17] citing [191]; (b) [159]
Landoltia spp./sp. [duckweed]	Readily (1 ref.)	[173]
Leersia hexandra [southern cutgrass]	Consumed (1 ref.)	[184]
Lemna spp./sp. [duckweed]	Avoided (1 ref.; a), Consumed (3 refs.; b-d), Readily (5 refs.; e-i)	(a) [60]#; (b) [17] citing [191]; (c) [183]; (d) [20]#; (e) [201]; (f) [196]; (g) [173]; (h) [156] citing [73], [72]; (i) [200]
Lemna minor [common duckweed]	Avoided (1 ref.; a), Consumed (5 refs.; b-f), Readily (5 refs.; g-k)	(a) [209]; (b) [147] citing [190]; (c) [180]; (d) [181]; (e) [184]; (f) [20]#; (g) [192] citing [193], [194], and V. Krupauer, 1967; (h) [168]; (i) [195]; (j) [159]; (k) [158]
Lemna trisulca [ivy-leaved duckweed]	Readily (3 refs.; a-c)	(a) [185]; (b) [192] citing [193], [194], and V. Krupauer, 1967; (c) [195]
Lilaeopsis lacustris [microsword]	Consumed (1 ref.)	[17] citing [191]
Limnobium spongia [American frogbit]	Consumed (1 ref.)	[184]
Limnophila heterophylla [marshweed]	Consumed (1 ref.)	[186] citing [185]
Limnophila sessiliflora [dwarf ambulia]	Consumed (1 ref.)	[184]
Lolium spp./sp. [ryegrass]	Consumed (1 ref.)	[183]
Ludwigia spp./sp. *	Avoided (1 ref.)	[60]#

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Ludwigia hexapetala [water primrose]	Consumed (1 ref.)	[184]
Ludwigia octovalvis [Mexican primrose-willow]	Rarely (1 ref.)	[17] citing [171]
Ludwigia palustris [water purslane]	Consumed (1 ref.)	[184]
Ludwigia peploides [floating primrose-willow]	Avoided (1 ref.; a), Readily (1 ref.; b)	(a) [216] (b) [72]
Luziola peruviana [Peruvian watergrass]	Consumed (1 ref.)	[217]
Lyngbya wollei [cyanobacteria]	Avoided (1 ref.)	[218]
Lysimachia vulgaris [garden loosestrife]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Manihot esculenta [cassava]	Rarely (1 ref.)	[27]
Merismopedia spp./sp. [colonial cyanobacteria]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Microcystis spp./sp. [colonial cyanobacteria]	Consumed (1 ref.)	[1]
Microspora spp./sp. [filamentous green algae]	Consumed (1 ref.)	[177]
Mougeotia spp./sp. [filamentous green algae]	Avoided (1 ref.)	[27]
Murdannia keisak [marsh dewflower]	Consumed (1 ref.)	[184]
Myriophyllum spp./sp. [watermilfoil]	Avoided (1 refs.; a), Consumed (2 refs.; b-c), Rarely (1 ref.; d), Readily (3 refs.; e-g)	(a) [60]#; (b) [186] citing [185]; (c) [20]#; (d) [165]; (e) [192] citing [193], [194], and V. Krupauer 1967; (f) [195]; (g) [196]
Myriophyllum aquaticum [parrot feather watermilfoil]	Avoided (4 refs.; a-d), Consumed (1 ref.; e), Rarely (2 refs.; f-g)	(a) [17] citing [191]; (b) [156]; (c) [156]; (d) [184]; (e) [72]; (f) [173]; (g) [156]
Myriophyllum quitense [waterwort watermilfoil]	Consumed (1 ref.)	[17] citing [191]
Myriophyllum heterophyllum [broadleaf watermilfoil]	Avoided (1 ref.; a), Consumed (1 ref.; b)	(a) [184]; (b) [218]
Myriophyllum laxum [loose watermilfoil]	Readily (1 ref.)	[17] citing [171]
Myriophyllum pinnatum [cut-leaved watermilfoil]	Consumed (1 ref.)	[184]
Myriophyllum propinquum [spiked watermilfoil]	Consumed (1 ref.; a), Rarely (1 ref.; b)	(a) [17] citing [191]; (b) [159]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Myriophyllum spicatum [Eurasian watermilfoil]	Avoided (2 ref.; a-b), Consumed (7 refs.; c-i), Rarely (9 refs.; j-r), Conditional (2 refs.; s-t), Readily (3 refs.; u-w)	(a) [183]; (b) [158]; (c) [147] citing [190], [182]; (d) [183]; (e) [162]; (f) [72]; (g) Pavlov and others, 1994 as cited in [1]; (h) [219]; (i) [20]#; (j) [204]; (k) [17] citing [171]; (l) [173]; (m) [203]; (n) [205] citing [206]; (o) [178]; (p) [202]; (q) [215]; (r) [199]; (s) [188]; (t) [144]; (u) [201]; (v) [197]; (w) [156]
Najas spp./sp. [water naiad]	Avoided (1 ref.; a), Readily (2 refs.; b-c)	(a) [60]#; (b) [196]; (c) [214]
Najas flexilis [Slender naiad]	Readily (1 ref.)	[165]
Najas fovelata	Consumed (1 ref.)	[20]#
Najas graminea [ricefield water-nymph]	Rarely (1 ref.; a), Readily (1 ref.; b)	(a) [27]; (b) [146] citing [213]
Najas guadalupensis [southern naiad]	Consumed (1 ref.; a), Readily (3 refs.; b-d)	(a) [20]#; (b) [173]; (c) [158]; (d) [205] citing [173]
Najas gracillima	Readily (1 ref.)	
Najas minor [brittle naiad]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [184]; (b) [165]
Nasturtium spp./sp. [watercress]	Rarely (1 ref.)	[173]
Nasturtium officinale [watercress]	Consumed (1 ref.; a), Rarely (2 refs.; b-c), Moderately (2 refs.; d-e)	(a) [20]#; (b) [192] citing [193], [194], and V. Krupauer 1967; (c) [195]; (d) [159]; Ref. [175]
Nechamandra alternifolia [nechamandra]	Avoided (1 ref.; a), Consumed (1 ref.; b)	(a) [185]; (b) [186] citing [185]
Nelumbo spp./sp. [lotus]	Avoided (1 ref.)	[60]#
Nelumbo lutea [American lotus]	Avoided (1 ref.)	[184]
Nitella spp./sp. [stoneworts]	Avoided (1 ref.; a), Consumed (3 refs.; b-d)	(a) [146]; (b) [185]; (c) [17] citing [191]; (d) [20]#
Nitella flexilis * [smooth stonewort]	Consumed (1 ref.; a), Rarely (1 ref.; b)	(a) [72]; (b) [27]
Nitella hookeri [stonewort]	Readily (1 ref.)	[159]
Nuphar spp./sp. [water-lilies]	Avoided (1 ref.; a), Rarely (1 red; b), Consumed (1 ref.; c)	(a) [60]#; (b) [205] citing [206]; (c) [20]#
Nuphar lutea [yellow water-lily]	Consumed (1 ref.; a), Rarely (1 ref.; b)	(a) [20]#; (b) [173]
Nymphaea spp./sp. [water-lilies]	Avoided (1 ref.; a), Consumed (1 ref.; b), Rarely (2 refs.; c-d)	(a) [60]#; (b) [20]#; (c) [186] citing [185]; (d) [173]
Nymphaea odorata [fragrant water-lily	Consumed (1 ref.; a), Rarely (2 refs.; b-c)	(a) [184]; (b) [17] citing [171] (c) [205] citing [206]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Nymphoides spp./sp. [floating heart]	Rarely (1 ref.)	[186] citing [185]
Nymphoides aquatica [floating heart]	Consumed (1 ref.)	[184]
Oedogonium spp./sp. [filamentous green algae]	Rarely (1 ref.; a), Readily (1 ref.; b)	(a) [177]; (b) [155]
Orontium spp./sp. [golden club]	Avoided (1 ref.)	[60]#
Oscillatoria spp./sp. [filamentous cyanobacteria]	Consumed (1 ref.)	[1]
Ottelia spp./sp. [duck lettuce]	Consumed (1 ref.)	[186] citing [185]
Panicum hemitomon [maidencane]	Consumed (1 ref.; a), Moderately (1 ref.; b)	(a) [184]; (b) [17] citing [171]
[guinea grass]	Rarely (1 ref.)	[27]
Panicum repens [torpedograss]	Consumed (2 refs.; a-b), Moderately (1 ref.; c), Readily (1 ref.; d)	(a) [184]; (b) [20]#; (c) [17] citing [171]; (d) [173]
Paspalum spp./sp. [paspalum]	Moderately (1 ref.)	[159]
Paspalum repens [water paspalum]	Consumed (1 ref.)	[184]
Pediastrum spp./sp. [colonial green algae]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Pediastrum simplex [colonial green algae]	Readily (1 ref.)	[154]
Peltandra virginica [green arrow-arum]	Consumed (1 ref.)	[184]
Persicaria amphibia * [water knotweed]	Conditional (1 ref.)	[188]
Persicaria decipiens * [slender knotweed]	Avoided (2 refs.; a-b)	(a) [159]; (b) [175]
Persicaria hydropoperoides * [swamp smartweed]	Avoided (1 ref.)	[184]
Phacotus lenticularis [unicellular green algae]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]
Phalaris arundinancea [reed canary grass]	Consumed (1 ref.)	[183]
Phragmites spp./sp. [reed grasses]	Avoided (1 ref.; a), Consumed (1 refs.; b)	(a) [60]#; (b) [183]
Phragmites australis * [common reed]	Avoided ‡ (1 ref.; a), Consumed (2 refs.; b-h), Rarely (2 refs.; i-j)	(a) [201] (b) [1]; (c) Pavlov and others, 1994 as cited in [1]; (d) [201] citing [220]; (e) [201] citing [193]; (f) [147] citing [168]; (g) [183]; (h) [20]#; (i) [192] citing [193], [194], and V. Krupauer 1967; (j) [195]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Phytoplankton (unclassified)	Consumed (1 ref.; a), Readily (2 refs.; b-c)	(a) [20]#; (b) B.G. Burdiyan and D.A. Razmashkin, 1972 as cited in [1]; (c) [201]
Pistia spp./sp.	Avoided (1 ref.)	[60]#
Pistia stratiotes [water lettuce]	Consumed (2 refs.; a-b), Rarely (2 refs.; c-d), Moderately (1 ref.; e)	(a) [184]; (b) [20]#; (c) [186] citing [185]; (d) [173]; (e) [207]
Pisum sativum [garden pea]	Readily (1 ref.)	[1]
Pithophora spp./sp. [filamentous green algae]	Consumed (1 ref.), Readily (1 ref.)	(a) [185]; (b) [27]
Pluchea camphorata [camphorweed]	Consumed (1 ref.)	[184]
Poa palustris [fowl bluegrass]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Polygonum spp./sp.	Avoided (1 ref.; a), Rarely (1 ref.; b)	(a) [60]#; (b) [27]
Pontederia cordata [pickerelweed]	Consumed (1 ref.; a), Moderately (1 ref.; b)	(a) [184]; (b) [17] citing [171]
Potamogeton spp./sp. [pondweed]	Avoided (1 ref.; a), Consumed (4 refs.; b-e), Readily (6 refs.; f-k)	(a) [60]#; (b) [1]; (b) [147] citing [190]; (d) [60]#; (e) [9]; (f) [17] citing [171]; (g) [196]; (h) [173]; (i) [214]; (j) [205] citing [173]; (k) [164]
Potamogeton acutifolius [sharp-leaved pondweed]	Readily (1 ref.)	[1]
Potamogeton amplifolius [big-leaved pondweed]	Consumed (1 ref.)	[20]#
Potamogeton pusillus [small pondweed]	Readily (1 ref.)	[204]
Potamogeton cheesemanii [floating pondweed]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [17] citing [191]; (b) [175]
Potamogeton crispus [curlyleaf pondweed]	Avoided (1 ref.; a), Consumed (4 refs.; b-e), Rarely (1 ref.; f), Conditional (1 ref.; g), Moderately (1 ref.; h), Readily (2 refs.; i-j)	(a) [158]; (b) [159]; (c) [183]; (d) [216]; (e) [20]#; (f) [165]; (g) [144]; (h) [159]; (i) [188]; (j) [72]
Potamogeton foliosus [leafy pondweed]	Readily (1 ref.)	[165]
Potamogeton illinoensis [Illinois pondweed]	Consumed (2 refs.; a-b), Readily (1 ref.; c)	(a) [184]; (b) [20]#; (c) [17] citing
Potamogeton lucens [shining pondweed]	Consumed (2 refs.; a-b), Rarely (2 refs.; c-d) Conditional (1 ref; e)	(a) [183]; (b) [20]#; (c) [192] citing [193], [194], and V. Krupauer, 1967; (d) [195]; (e) [209]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Potamogeton natans [broad-leaved pondweed]	Avoided (1 ref.; a), Consumed (2 refs.; b-c), Rarely (2 refs.; d-e), Conditional (1 ref.; f), Readily (2 refs.; g-h)	(a) [183]; (b) [183]; (c) [20]#; (d) [204]; (e) [188]; (f) [168]; (g) [192] citing [193], [194]; (h) [195]
Potamogeton nodosus [longleaf pondweed]	Consumed (1 ref.; a), Conditional (1 ref.; b), Readily (1 ref.; c)	(a) [184]; (b) [162]; (c) [72]
Potamogeton obtusifolius [blunt-leaved pondweed]	Consumed (1 ref.)	[20]#
Potamogeton perfoliatus [clasping-leaved pondweed]	Avoided (1 ref.; a), Consumed (1 ref.; b)	(a) [158]; (b) [20]#
Potamogeton praelongus [whitestem pondweed]	Consumed (1 ref.)	[20]#
Potamogeton pusilllus [lesser pondweed]	Consumed (1 ref.)	[184]
Potamogeton zosteriformis [flat-stem pondweed]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [20]#; (b) [188]
Potentilla anserina [common silverweed]	Readily (1 ref.)	[1]
Ranunculus spp./sp. [buttercups]	Avoided (3 refs.; a-c)	(a) [183]; (b) [219]; (c) [60]#
Ranunculus aquatilis [white water crowfoot]	Consumed †† (1 ref.)	[20]#
Ranunculus aquatilis var. *diffusus* [threadleaf crowfoot]	Avoided (1 ref.; a) Rarely (1 ref.; b) Readily (1 ref.; c)	(a) [216]; (b) [204]; (c) [183]
Ranunculus fluitans [river water crowfoot]	Consumed (2 refs.; a-b)	(a) [183]; (b) [20]#
Sagittaria spp./sp. [arrowhead]	Avoided (1 ref.)	[60]#
Sagittaria lancifolia [bulltongue arrowhead]	Moderately (1 ref.)	[17] citing [171]
Sagittaria sagittifolia [arrowhead]	Consumed (2 refs.; a-b)	(a) [183]; (b) [20]#
Salvinia spp./sp. [watermoss]	Avoided (1 ref.; a), Readily (1 ref.; b)	(a) [60]#; (b) [186] citing [187]
Salvinia auriculata [eared watermoss]	Readily (1 ref.)	[207]
Salvinia cucullata [Asian watermoss]	Consumed (1 ref.)	[185]
Salvinia biloba [giant salvinia]	Consumed (1 ref.)	[17] citing [191]
Salvinia minima [common salvinia]	Consumed (1 ref.; a), Moderately (1 ref.; b)	(a) [184]; (b) [17] citing [171]
Scenedesmus spp./sp. [colonial green algae]	Readily (1 ref.)	M. Linchevskaya, 1966 as cited in [1]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Scenedesmus bijugatus [colonial green algae]	Readily (1 ref.)	[154]
Scenedesmus quadricauda [colonial green algae]	Readily (1 ref.)	[154]
Schoenoplectus lacustris [lakeshore bulrush]	Consumed (2 refs.; a-b)	(a) [183]; (b) [201]
Scirpus spp./sp. [clubrushes]	Avoided (1 ref.; a), Consumed (2 refs.; b-c)	(a) [60]#; (b) [147] citing [182]; (c) [20]#
Scirpus sylvaticus [wood clubrush]	Consumed (1 ref.)	[20]#
Scleria poiformis *	Conditional †† (1 ref.)	[27]
Solanum tuberosum [potato]	Avoided (1 ref.)	[183]
Sphagnum spp./sp. [peat mosses]	Consumed (2 refs.; a-b), Conditional (1 ref; c)	(a) [147] citing [190]; (b) [20]#; (c) [168]
Spirodela spp./sp. [duckweed]	Consumed (1 ref.; a), Readily (2 refs.; b-c)	(a) [17] citing [191]; (b) [196]; (c) [173]
Spirodela polyrrhiza [greater duckweed]	Consumed (3 refs.; a-c), Readily (1 ref.; d)	(a) [147] citing [168]; (b) [216]; (c) [20]#; (d) [185]
Spirogyra spp./sp. [water silk]	Avoided (1 ref.; a), Consumed (2 refs.; b-c), Rarely (1 refs.; d), Readily (1 ref.; e)	(a) [27]; (b) [185]; (c) [20]#; (d) [216]; (e) [146]
Stachys palustris [marsh woundwort]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Stratiotes aloides [wateraloe]	Consumed (1 ref.; a), Rarely (1 ref.; b)	(a) [20]#; (b) [173]
Stuckenia filiormis [slender-leaved pondweed]	Consumed (1 ref.; a), Readily (1 ref.; b)	(a) [20]#; (b) [1]
Stuckenia pectinata [sago pondweed]	Avoided (1 ref.; a), Consumed (3 refs.; b-d), Conditional (1 ref.; e), Readily (11 refs.; f-p)	(a) [158]; (b) [185]; (c) [72]; (d) [20]#; (e) [162]; (f) [192] citing [193], [194]; (g) [195], and V. Krupauer, 1967; (h) [183]; (i) [204]; (j) [201]; (k) [165]; (l) [188]; (m) [203]; (n) [156] citing [73]; (o) [200]; (p) [178]
Tamarix spp./sp. [salt cedar]	Consumed (1 ref.)	Pavlov and others, 1994 as cited in [1]
Trapa spp./sp. [waterchestnut]	Consumed (1 ref.)	[186] citing [185]
Trapa natans [waterchestnut]	Consumed (3 refs.; a-c)	(a) [147] citing [190]; (b) [183]; (c) [20]#
Trifolium spp./sp. [clover]	Consumed (1 ref.)	[1]
Trifolium pratense [red clover]	Readily (1 ref.)	[1]
Trifolium repens [white clover]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Triglochin striata [streaked arrow grass]	Consumed (1 ref.)	[17] citing [191]
Typha spp./sp. [cattails]	Avoided (3 refs.; a-c), Consumed (3 refs.; d-f), Rarely (2 refs.; g-h), Moderately (1 ref.; i)	(a) [201]; (b) [146]; (c) [60]#; (d) [201] citing [220], [173]; (e) [183]; (f) [20]; (g) [173]; (h) [205] citing [206]; (i) [17] citing [171]
Typha domingensis [southern cattail]	Consumed (1 ref.)	[20]#
Typha angustifolia [narrow-leaved cattail]	Avoided (1 ref.; a), Consumed (3 refs.; b-d)	(a) [17] citing; (b) [147] citing [182]; (c) [183]; (d) [20]#
Typha latifolia [broadleaf cattail]	Avoided (1 ref.; a), Consumed (3 refs.; b-d), Rarely (3 refs.; e-g)	(a) [168]; (b) [147] citing [190]; (c) [183]; (d) [20]#; (e) [192] citing [193], [194], and V. Krupauer, 1967; (f) [195]; (g) [209]
Utricularia spp./sp. [bladderworts]	Readily (1 ref.)	[17] citing [171]
Utricularia aurea [golden bladderwort]	Consumed (2 refs.; a-b)	(a) [147] citing [221], [222]; (b) [147] citing [221]
Utricularia foliosa [leafy bladderwort]	Consumed (2 refs.; a-b)	(a) [147] 2 citing [221], [222]; (b) [147] citing [221]
Utricularia stellaris	Consumed (1 ref.)	[186] citing [185]
Utricularia vulgaris [common bladderwort]	Consumed (2 refs.; a-b), Conditional (1 ref.; c)	(a) [184]; (b) [20]#; (c) [188]
Vallisneria spp./sp. [eel grass]	Avoided ‡‡ (2 ref.; a-b), Consumed (1 ref.; c), Readily (2 refs.; d-e)	(a) [17] citing [191]; (b) [60]#; (c) [20]#; (d) [196]; (e) [214]
Vallisneria americana [American eel grass]	Consumed (1 ref.; a), Rarely (2 refs.; b-c), Readily (2 refs.; d-e)	(a) [184]; (b) [17] citing [171]; (c) [173]; (d) [188]; (e) [197]
Vallisneria natans [eel grass]	Consumed (1 ref; a.), Readily (1 ref.; b)	(a) [17] citing [191]; (b) [215]
Vallisneria spinulosa [eel grass]	Readily (1 ref.)	[202]
Vallisneria spiralis [eel grass]	Consumed (2 refs.; a-b), Readily (1 ref.; c)	(a) [186] citing [185]; (b) [147] citing [168]; (c) [199]
Vicia cracca [tufted vetch]	Readily (1 ref.)	[1]
Vicia sativa [common vetch]	Readily (1 ref.)	[1]
Wolffia spp./sp. [watermeal]	Readily (3 refs.; a-c)	(a) [185]; (b) [196]; (c) [173]
Wolffia arrhizal [spotless watermeal]	Consumed (2 refs.; a-b)	(a) [147] citing [190]; (b) [20]#
Wolfiella gladiata [sword-like bog-mat]	Consumed (1 ref.)	[184]

Table 5. *Cont.*

Taxon	Consumption	Reference(s)
Zizania latifolia [Manchurian wild rice]	Consumed (2 refs.; a-b)	(a) [147] citing [182]; (b) [20]#
Zygnema spp./sp. [filamentous green algae]	Readily (1 ref.)	[209]

Macronutrients

The proper balance of macronutrients and their individual effects have been assessed in grass carp at various developmental stages. Dietary carbohydrate content and the ratio of carbohydrates to other macronutrients is one area of research. In 90-day trials of grass carp diets containing differing levels of protein and carbohydrates, compared to a control diet that was 25% carbohydrate and 40% protein by mass, an increased carbohydrate diet (42%) with the same level of protein as the control (40%) resulted in decreased growth [223]. In the same set of trials, an increased carbohydrate diet (40%) with lower protein (25%) resulted in a higher growth rate than either of the diets containing 40% protein. Grass carp showed a strong potential to adapt to a high (50%) carbohydrate diet compared to other fish species through increased glycolysis, glycogen accumulation, and glucose-induced lipogenesis [224]. Feeding grass carp a high (60%) carbohydrate diet increased their ability to clear a glucose load [225]. Grass carp fed with a carbohydrate to lipid ratio of 7.5 resulted in greater weight gain, specific growth rate, feed conversion ratio, protein efficiency ratio, and protein production value compared to carbohydrate to lipid ratios of 1.7 and 202.5 [226]. Excessive dietary carbohydrates (45.45 g 100 g^{-1}) increase total bodily lipid content in grass carp relative to a diet with sufficient dietary carbohydrates (21.81 g 100 g^{-1}), resulting in appetite suppression and depressed growth [227].

Dietary lipid content and the ratio of lipids to other macronutrients is another area of research. A high lipid diet results in decreased food intake compared to diets with lower lipid levels [228]. Low or excess lipids in the diet of young grass carp induce mRNA changes suggesting decreased immune function of the head kidney, spleen, and skin, increased oxidative damage and apoptosis, and impairment of the antioxidant system; dietary lipid levels of 52.1 g/kg maximize levels of immunoglobulin M antibodies, an indicator of immune function [229]. Phospholipid diet supplementation improved immunity, antioxidant status, and the tight junction barrier in young grass carp gills [230]. Low or excessive dietary lipid content (compared to the optimal 5.02%) impaired immune function and led to increased gill rot morbidity from *Flavobacterium columnare* [231]. Excessive dietary lipids can damage the intestines and cause inflammation; a diet formulated with 8.1% crude lipids in the form of soybean oil and fish oil causes these effects in grass carp [232].

Dietary protein content and the ratio of protein to other macronutrients is another area of research. Dietary protein content of 41 to 43% maximizes weight gain percentage in grass carp fry (Ref. [233] as cited by [234]). This is supported by another finding of a similar protein level of 40% being optimal for grass carp fry [235]. Fingerling grass carp fed periphyton had a 71% protein digestibility, higher than hybrid red tilapia (*Oreochromis mossambicus* × *O. niloticus*) and five cypriniform species [236]. A suitable diet for juvenile grass carp for growth and nutrient utilization is 33% digestible protein, 6% lipid, and 10.7 kJ/g digestible energy [237]. To maximize growth rate in grass carp exiting overwinter starvation, the optimal dietary protein and lipid levels are 31% and 8%, respectively [238]. Faster-growing individual grass carp have a lower protein degradation rate and higher protein retention compared to slower-growing grass carp [239]. Compared to a control diet with 29% crude protein and 5% crude lipid, diet with lower protein and higher lipids (26% crude protein, 6% crude lipid) leads to a lower growth rate and decreased intestinal immunity [240]. It appears that grass carp can grow effectively with dietary protein levels of 25% to 43%; however, the levels of other macronutrients influence the realized growth rate.

Many researchers have compared the effects of different protein sources, such as fishmeal, soy, and other plant proteins, on grass carp in aquacultural settings. Reduction of protein levels in grass carp feed from 28% to 26% increases morbidity from *A. hydrophila* infection; protein sources in diets included fishmeal, dehulled soybean meal, cottonseed meal, and rapeseed meal [241]. A reformulation of the 26% protein diet where some of the protein was replaced with enzyme-treated soy protein to offset low dietary protein-associated morbidity from *A. hydrophila* infection; estimated optimal levels of enzyme-treated soy protein for this effect are 1.03% of the total diet [241]. Replacement of fishmeal with chicken intestine meal that contained equivalent proportions of macronutrients and energy content, resulted in increased grass carp growth rate [242]. With fishmeal and soy products, after a 5-week acclimating period, grass carp (initial mass = 153 g) fed the diet with soy protein had a higher food consumption rate than grass carp (initial mass = 153 g) fed the fishmeal-containing diet [243]. After a 7-week trial, the soy protein group had a higher weight gain rate than fishmeal group, despite slower weight gain in the soy protein group prior to the 5-week mark [243]. Partial replacement of the soybean meal, wheat meal, and soybean oil in a commercial grass carp diet with 5% seed meal derived from the grass *Cenchrus flaccidus* increased growth in juvenile grass carp over 8 weeks [244]. Grass carp recovered from stress symptoms that arose from overconsumption of soybean meal when the diet consisted of 40% soybean meal, rather than 100% [245]. Replacement of fishmeal with soybeans as the source of protein in fry grass carp diet results in decreased weight gain, feed efficiency, and protein retention efficiency [246]. Replacing soybean meal with fava bean meal in the commercial diet for grass carp at levels greater than 420.3 g/kg had negative effects on growth [247]. Replacing more than 16.64% of soybean meal in grass carp feed with cottonseed meal decreased weight gain and percent efficiency ratio while increasing food conversion ratio [248]. For juvenile grass carp, cottonseed meal and sunflower meal could be substituted for soybean meal without adverse effects on six metrics comprising weight gain, specific growth rate, feed conversion rate, protein efficiency ratio, apparent digestibility coefficients of protein, and sum of amino acids [249]. Corn meal substitution resulted in decreases for five of the six values with an increase in feed conversion rate [249]. Replacement of up to 60% of fishmeal in the diet with cottonseed meal had no negative effects on growth [250]. Grass carp fed a diet with soybean or rapeseed as a source of plant protein exhibited reduced growth compared to grass carp fed a fishmeal diet [251]. However, rapeseed meal led to higher expression of ghrelin, which induces appetite, compared to fishmeal as a dietary protein source for juvenile grass carp [252]. Changing the aquacultural diet of grass carp by completely replacing fishmeal with soybean meal to create equivalent macronutrient profiles causes enteritis and reduces weight gain [253]. Growth rate of grass carp has been observed to not be affected by partial or complete replacement of soybean meal with larvae of black soldier fly (*Hermetia illucens*) as a protein source [254]. The growth rate of grass carp decreased as the percentage of rapeseed meal increased in the food they were being fed [173]. Altering the aquacultural diet of grass carp by completely replacing rapeseed meal (28% of control diet) with maize distiller's dried grain with solubles (30.9% of experimental diet) increases specific growth rate [255]. Juvenile grass carp fed a commercial diet where 40% and 100% of fishmeal was replaced with detoxified castor bean meal had decreased specific growth rate, feed conversion efficiency, protein efficiency ratio, and feed intake [256]. Grass carp can utilize a variety of food sources, with high protein food such as soybeans or fishmeal allowing fish to grow quickly. However, a diet with a paucity of variety can also reduce fish growth, indicating that it is likely that a diet which provides a blend of nutrients allows for maximum growth.

Dietary Amino Acids

In addition to research on protein in grass carp diets, there has also been research on supplementation of individual amino acids in their diet. The addition of lysine to grass carp feed improved weight gain, protein and amino acid retention, and feed efficiency [257,258]. A diet with 2.44% lysine resulted in the highest final body weight of 1.95 g, weight gain rate of 441.8% and specific growth rate of 3.02%/day [259] and increased survival and upregulated genes associated with greater immune function and antioxidant capacity [260]. Compared to lower-than-optimal dietary lysine levels of 13 and 15 g/kg diet, grass carp fed optimal dietary lysine levels of 17 g/kg diet have a higher weight gain rate [261]. However, optimal dietary lysine does not offset lower weight gain caused by low oxygen conditions [261]. Dietary arginine supplementation improved growth in young grass carp [262]. Additionally, supplementation of 0.7% arginine improves immune function and reduces mortality in another cypiniform, mrigal carp (*Cirrhinus mrigala*), exposed to *A. hydrophila* [263]. The addition of alanine and glycine to a soybean meal diet improved growth of grass carp [264]. N-acetyl cysteine supplement to the diet of grass carp increased weight gain and specific growth while N-acetyl cysteine with glycine increased feed efficiency [265]. Optimal leucine supplementation improved grass carp growth and antioxidant capacity [266]. Betaine supplementation of 3.2 g/kg diet to a basal diet low in methionine for 60 days resulted in similar results in growth as supplementing synthetic DL-methionine, while greater concentrations resulted in increased growth as indicated as final body weight and percent weight gain [267]. Dietary supplementation with taurine increased growth, feed efficiency, and protein efficiency ratio in grass carp [268]. Deficient or excessive tryptophan increased reactive oxygen species content and caused severe oxidative damage in gills of grass carp. A 0.75% dietary supplementation of alpha-ketoglutarate, an amino acid precursor, promotes growth and enhances antioxidant capacity and immunity in fingerling grass carp [269].

Vitamins and Minerals

The dietary vitamin requirements and effects of deficiencies for grass carp have been important areas of research conducted in support of grass carp aquaculture. Vitamin E deficiency decreased growth, impaired immune function; disturbed structural integrity of the head kidney, spleen, and skin in grass carp; and impaired gill immunity and antioxidant capacity [270,271]. Dietary vitamin C deficiency decreases growth and head kidney and spleen immunity and structural integrity in young grass carp [272]. Vitamin C applied to grass carp kidney cells at a concentration of 140 µM can partially alleviate the effects of a 25 µM lead solution by counteracting lead-induced reduced cell viability and oxidative stress [273]. Dietary pyridoxine (vitamin B6) levels of 4.85, 4.78 and 4.77 mg/kg diet are needed for grass carp to have reduced *F. columnare*-caused gill rot morbidity, induce optimal lysozyme activity, and increase malonaldehyde content, respectively [274]. Feed supplemented with 5000 IU/kg food of vitamin D3 increases growth in grass carp compared to non-supplemented feed [275]. Feed acidified with 2% formic acid increases growth in fingerling grass carp compared to non-supplemented feed; a combination of 2% formic acid and 5000 IU/kg food of vitamin D3 increases growth even more than formic acid or vitamin D3 supplementation alone [275]. Using parameters related to antioxidant status and immunity, a biotin-deficient diet reduces antioxidant enzyme levels [276]. Folic acid deficiency impairs gill function in young grass carp [277].

The effects of dietary levels of minerals for grass carp is another aspect of diet that has garnered significant research. Deficient or excessive dietary iron (Fe) in grass carp exposed to the pathogenic bacterium *A. hydrophila* cause decreased growth performance and impaired immune function and structural integrity [278] and increased enteritis morbidity in grass carp infected with *A. hydrophila* [279]. For information on the effects of excessive aqueous exposure of copper (Cu) on grass carp and related species, see 'Section 3.2.3. Metals'. (Dietary phosphorous (P), up to 10 g/kg diet, improved growth in grass carp while dietary starch of 350 g/kg diet decreased it [280]. Dietary P deficiency can lead to decreased growth and immune function, and it can affect head kidney, spleen, and skin structural integrity in young grass carp [281]. Fingerling grass carp supplemental dietary chromium (Cr) levels of 0.8 mg Cr/kg diet increases growth and feeding efficiency [282]. Symptoms of selenium (Se) deficiency in grass carp are decreased growth and impaired immune function in the head kidney, spleen, and skin [283]. Grass carp fed a diet supplemented with 2 mg/kg Se nanoparticles and 2 g/kg garlic extract had higher growth performance and lower serum cortisol than those whose diet was only supplemented with 1 mg/kg Se nanoparticles and 1 g/kg garlic extract [284]. Selenium nanoparticle supplement of 0.3 to 0.6 mg/kg in a high fat grass carp diet increases survival and relieves hepatopancreas injury [285]. Grass carp given greater than 34 mg/kg diet of zinc (Zn) had increased final body weight, weight gain, and specific growth [286]. Alkaline phosphatase purified from grass carp is not affected by the cationic forms of lithium (Li^+), sodium (Na^+), or potassium (K^+); is activated by magnesium (Mg^{2+}), manganese (Mn^{2+}), and cobalt (Co^{2+}); and is inhibited by Zn^{2+}, indicating that Mg^{2+}, Mn^{2+}, or Co^{2+} may be essential to the function of this enzyme3 [287]. The addition of dietary K to grass carp diets increased growth and feed efficiency [288]. The addition of azomite, a nonessential mineral, to grass carp diet at a rate of 0.2% increased growth [289].

Other Dietary Supplements

Multiple studies have assessed the effects of various levels of fatty acids in the diet of grass carp. Juvenile grass carp fed an experimental diet enriched with eicosapentaenoic acid showed better growth performance than groups without eicosapentaenoic acid or groups fed a diet enriched with arachidonic acid [290]. Dietary supplementation of 0.30% arachidonic acid suppressed lipid accumulation and improves the health status in juvenile grass carp [291]. A diet containing 3% conjugated linoleic acid in grass carp feed resulted in reduced feeding rate and growth, and diets varying from 1.5 to 3% conjugated linoleic acid decreased lipid content in the liver, intraperitoneal fat, and muscle [292]. Dietary supplementation with alpha-lipoic acid, a fatty acid and antioxidant, to a standard commercial diet decreased final body weight, weight gain rate, and food intake in grass carp compared to diets without lipoic acid supplementation [228].

A variety of miscellaneous organic compounds have been tested as food additives for grass carp. Supplementation of the enzyme cellulase to a diet containing shredded common duckweed (*Lemna minor*) and wheat flour increases growth rate of grass carp and increases the intestinal activities of cellulase, protease, and amylase [293]. Dietary choline, an essential nutrient, improves gill antibacterial properties and decreases inflammatory status in the gills of grass carp [294] and improves growth [295]. Dietary choline of 407 mg/kg of diet or greater, led to increased final body weight, percent weight gain, and specific growth rate of grass carp after 70 days of feeding, though the gains diminished at concentrations greater than 1216 mg/kg [296]. Choline is also known to affect cell apoptosis in the intestine [297]. The addition of glutathione, an antioxidant, to the diet of grass carp fed rapeseed meal neutralized the negative effects of rapeseed oil [298]. The addition of the reduced form of glutathione to grass carp diet resulted in increased growth, survival, and immunity to infection in juvenile grass carp [299]. Feeding grass carp a diet supplemented with 3 mg/kg diphenyl diselenide for the 30 days prior to, as well as during, a 96-h exposure to 15 µg/L methylmercury chloride (CH_3HgCl), can reduce or completely alleviate CH_3HgCl-caused disruptions to cellular respiration in the gills and liver [300], and alleviated behavioral effects [301]. Dietary supplementation of antimicrobial peptides (AMPs), small organic molecules that degrade more quickly than traditional antibiotics, at 400 to 800 mg AMPs/kg diet increases growth rate in grass carp [302]. The addition of the steroids adrenosterone and 11-ketotestosterone to feed of juvenile common carp increased food conversion efficiency [303].

Several studies have demonstrated that supplementation of (2-Carboxyethyl) dimethylsulfonium Bromide (Br-DMPT) to a non-fishmeal diet results in positive effects on fish growth and health. Dietary supplementation of Br-DMPT at 260.0 mg/kg diet increased percent weight gain in grass carp beyond both a standard fishmeal-containing diet and a 100% plant-based diet without Br-DMPT supplementation [304]. Dietary supplementation of Br-DMPT to a non-fishmeal diet at 260.0 and 390.0 mg/kg diet for grass carp resulted in a lack of obvious pathological symptoms when exposed to *A. hydrophila* [305]. Additionally, control fishmeal-containing diet fish showed no pathological symptoms, but grass carp fed non-fishmeal diets with Br-DMPT levels of 0.0, 130.0, and 520.0 mg/kg diet had lesions and hemorrhaging caused by *A. hydrophila*. Dietary supplementation of Br-DMPT at 260.0 mg/kg diet promoted immune organ structural integrity and increased immune function in grass carp challenged with a non-lethal strain of *A. hydrophila* [306].

Multiple plant-, algae-, and yeast-based derivatives have been tested as dietary additives for grass carp. Supplementation of thymol, an herbal food additive, to the diet of fingerling grass carp at 100 mg/kg diet increased growth rate and increased liver energy metabolism and antioxidant status [307]. Cinnamaldehyde supplementation at 144 mg/kg of diet increased percent weight gain and specific growth rate over the course of a 60-day study [308]. Supplementation of silymarin, a flavonolignan found in milk thistle (*Silybum marianum*), in the diets of grass carp elevated dietary lipid levels, promoted growth and protein efficiency, suppressed lipid accumulation, and improved health [309]. Addition of berberine, an alkaloid found in plants, to grass carp cell cultures alleviated cellular lipid metabolic disorder [310]; stimulating fish liver cells safe concentrations were 25 to 50 µmol/L with concentrations greater than 50 µmol/L being toxic and affecting cell function in normal growth cells [311]. The addition of chitosan, a carbohydrate, to the diet of grass carp promotes growth and protects against the effects of starvation [312]. In a comparison of anti-inflammatory dietary additives, 0.1 g/kg diet emodin increased weight gain in grass carp; neither 1 g/kg diet β-glucan nor 1 g/kg diet inulin had a significant effect on weight gain [313]. Mannan oligosaccharide supplementation at 400 mg/kg diet reduces grass carp reovirus-induced skin lesion morbidity [314]. Dietary supplementation of xylo-oligosaccharides, indigestible carbohydrates that serve as prebiotics, at 0.1% of the diet increases weight gain and reduces mortality rate of juvenile grass carp infected with *A. hydrophila* [315]. Dietary supplementation of alginate oligosaccharides, depolymerized products of alginate (a compound found in brown algae), at 10 g/kg diet increases weight gain rate in grass carp [316]. Dietary supplementation with 393.67 mg/kg diet curcumin, the primary pigment in turmeric (*Curcuma longa*) rhizomes, increases weight gain and reduces *A. hydrophila* mortality in juvenile grass carp (mean mass = 5.3 g; Ref. [317]). Green tea waste supplementation to a commercial diet improved certain biomarkers of health without affecting growth of grass carp [318]. Dietary hardy rubber tree (*Eucommia ulmoides*) leaf extract supplemented to a basal diet of 300 g/kg crude protein at 4 g/kg increased weight gain in grass carp by 4% and decreased the feed conversion ratio by 4% [319]. Addition of sacred lotus (*Nelumbo nucifera*) leaf extract at 0.14% of pelleted grass carp feed can improve growth, antioxidant status, and immune response of juvenile grass carp [320]. Extract of Japanese honeysuckle (*Lonicera japonica*) added to commercial diet at 10 to 40 g/kg diet does not affect growth rate of grass carp [321]. Addition of purslane (*Portulaca oleracea*) extract at 0.5% of pelleted grass carp feed can improve growth, lipase activity, the antioxidant status, and immune response of fingerling grass carp [322]. The dietary supplementation of goji berry (*Lycium barbarum*) improved the growth of grass carp [323]. Dietary *Porphyra yezoensis* (a marine red macroalgae) improved growth and immunity in grass carp; the optimal dose of dietary *P. yezoensis* was 3 g/kg diet [324]. Replacing 10% to 20% of a commercial grass carp diet with paper mulberry (*Broussonetia papyrifera*) leaves results in a decreased growth rate compared to the grass carp fed a pure commercial diet; replacement of 5% of the commercial diet with paper mulberry leaves does not affect the growth rate [325]. A yeast protein concentrate obtained from a bio-ethanol process using wheat, added to feed of grass carp improves growth, the optimal level is 15% and 20% of the diet [326]. Supplementation of a plant protein-based diet with 5 g/kg diet polyphenols from apple (*Malus domestica*) improves antioxidant capacity, suppresses inflammatory responses, and enhances intestinal barrier function of grass carp, but it does not affect growth rate [327]. Sutchuenoside A isolated from the thick-stemmed wood fern (*Dryopteris crassirhizoma*) stimulates immune response in grass carp [328].

Table 6. A summary of the optimal levels of dietary supplements including amino acids, vitamins, and minerals for grass carp based on a variety of endpoints reported in referenced literature. Average size refers to the reported length or weight of grass carp tested. * Except where other units are specified.

Supplement	Average Size	Optimal Diet (g/kg Diet) *	Endpoint	Reference(s)
AMINO ACIDS				
arginine	278.8 g	13.45	Growth	[262]
arginine	6 g	15.3	Growth	[329]
glutamine	7.16 g	3–6	Growth	[330]
histidine	3.68 g	12.1	Growth	[331]
leucine	295.85 g	13.0	Growth Biochemistry	[266]
lysine	3.15 g	20.6	Growth	[332]
lysine	460 g	9.53–10.6	Biochemistry	[257]
lysine	165 g	13.51 13.58	Morbidity Growth	[333]
methionine	178–626 g	9.56	Growth	[334]
methionine (methionine hydroxy analogue)	259.70 g	5.21 5.76 5.68–6.85	Growth Morbidity Biochemistry	[335]
taurine	38.1–38.9 g 125–130 mm	0.6	Growth/Feed efficiency	[268]
threonine	441.9 g	11.6	Growth/Feed Efficiency	[336]
tryptophan	287 g	3.97–4.14	Gill Health	[337]
VITAMINS				
biotin	117.11 g	0.000245–0.000354	Biochemistry, gene expression	[276]
biotin (B7)	117- 534 g	0.00021 0.00023 0.00024–0.00025	Growth Morbidity Biochemistry	[338]
E	266.39 g	0.116–0.140	Morbidity	[271]
C	264.37 g	0.123 0.130–0.138	Morbidity Biochemistry	[272]
folic acid	267.69 g	0.00106 0.00207–0.00208	Growth Biochemistry	[277]
MINERALS				
Ca	4.52 g	10.4	Growth	[339]
Cu	282.0 g	0.00478 0.00470–0.00495	Growth Biochemistry	[340]
Fe	292.0 g	0.0735 0.0690–0.728	Growth Biochemistry	[341]
Fe	242.32 g	0.0757 0.0870 0.0789–0.0832	Growth Morbidity Biochemistry	[278]
Fe	242.0 g	0.0834 0.0854–0.0867	Morbidity Biochemistry	[279]
K	4.8 g	4.65 5.98–7.27	Growth Biochemistry	[288]

Table 6. *Cont.*

Supplement	Average Size	Optimal Diet (g/kg Diet) *	Endpoint	Reference(s)
Mg	5.56 g	0.687	Growth	[342]
Se	11.2 g	0.00083	Growth	[343]
Se	226.48 g	0.000546 0.000575 0.000598–0.000604	Growth Morbidity Biochemistry	[283]
Se	71.57–73.21 g	0.000562	Growth	[344]
Zn	244.14 g	0.0612 0.0614 0.0692–0.0695	Growth Morbidity Biochemistry	[345]
NUTRIENTS				
choline	266.5–787.1 g	1.137 1.211 1.191–1.555	Growth Meat Quality Biochemistry	[294,295]
choline	9.28–108.97 g	1.548	Morbidity	[346]
choline	9.29 g	1.331 1.283	Growth Feed Efficiency	[296]
choline	9.28–108.97 g	1.364–1.574	Immune function	
choline	142.2 g	1.162–1.781	Biochemistry	[297]
SUPPLEMENTS				
Br-DMPT	216.49 g	0.291–0.312	Morbidity Immune function	[347]
exogenous nucleotides	200.0 g	0.526–0.640	Gill health	[348]
glutathione	5.10 g	0.381	Growth	[299]
isalo scorpion cytotoxic peptide	136.88 g	1.52 2.00	Growth Morbidity	[349]
mannan oligosaccharides	215.85 g	0.429 0.499 0.536–0.562	Growth Morbidity Biochemistry	[350]
silymarin	24.2 g	0.0576 0.0575	Growth Physiology	[351]
xylooligo-saccharides	167.46 g	0.0518 0.0554–0.0579	Growth Biochemistry	[352]

Alternative Aquacultural Diets

In addition to research specifically related to protein sources, comparison of various alternative diet compositions is a large area of research for grass carp. Many of these studies involve plant-based diets, often comparing these diets to commercial diets. Comparison of two isonitrogenous grass carp commercial diets (~321 g crude protein/kg diet) containing either 100% animal protein sources or animal protein sources from +80 g of purified β-conglycinin, the most abundant protein in soy, found that grass carp fed the β-conglycinin diet gain weight at a slower rate than the 100% animal protein group [353]. Juvenile grass carp (approximately 15 g) grew best and had the highest survival rate when fed alfalfa (also called lucerne, *Medicago sativa*), and they had the lowest survival rate when fed a low protein formulated diet with 25% protein [145]. Grass carp fed alfalfa grew faster than grass carp fed leaves from the horseradish tree (also called drumstick, *Moringa oliefera* syn. *M. pterygosperma*), with a better feed conversion ratio for the latter [354].

Grass carp fed Eurasian watermilfoil or common duckweed grew better than grass carp fed hornwort (*Ceratophyllum demersum*), water fern, Bermuda grass (*Cynodon dactylon*), alfalfa, or the combination of all six plant species [355]. Grass carp fed duckweed showed 65% digestibility based on dry matter [182]. Grass carp with initial mass of ~176 g have shown increased growth associated with increased consumption of hydrilla (*Hydrilla verticillata*; Ref. [356]); the same trend has been observed in grass carp 6 to 12 months of age [27]. Elephant grass (also called Napier grass, *Cenchrus purpureus*) has potential use in polyculture with grass carp [357]. Digestibility of elephant grass for grass carp was 19.7% on a dry matter basis [358]. Juvenile grass carp grew better on teosinte grass combined with a daily feed ration (soy, wheat, milo, meat-and-bone meal, vitamins and minerals) compared to fish on either alone [359]. Grass carp grew faster and had a better feed conversion ratio when fed cabbage (*Brassica* sp.) compared to kikuyu grass (*Cenchrus clandestinus*; Ref. [360]). Grass carp fed grasses (*Lolium perenne*, *Euphrasia nemorosa*, and *Sorghum X drummondii*) grew slower, had denser muscles, and lower fat accumulation than grass carp fed a commercial feed containing 28% crude protein, 7.06% crude fat, 8.75% moisture, 15% crude fiber, and 15.63% ash [361]. Grass carp raised in coastal, tidally inundated, brackish (1.0 ppt salinity) wetlands in Bangladesh had higher growth rate when feeding upon planted *Hygroryza aristata* (a floating grass) than when fed a commercial diet [362]. Diets with intermediate survival rates included duckweed (*Lemna* sp.), water fern (also called Pacific mosquitofern; *Azolla filiculoides*), and a formulated diets with 35% protein [362].

The use of fava beans (also called broad beans or faba beans, *Vicia faba*) as feed for grass carp has been widely researched, as it is thought to improve the flesh texture of grass carp to produce ‘crisp grass carp,’ which has high economic value and is protected as a China Geographical Indication Product (Ref. [363] as cited by [364]). Several studies have shown that the use of fava bean diets (whole or residues) decreases weight gain compared to commercial or other common diets [364–367]. Alternatively, diets utilizing fava bean extracts as a component tend to increase weight gain while promoting flesh qualities similar to Crisp Grass Carp [364,367,368]. Flesh changes induced by fava beans include increased muscle compactness and greater lipid accumulation [365].

Aquacultural grass carp diets based on aquatic animals have received some attention. For larvae, there is evidence that grass carp grow better on fresh rotifers compared to nematodes, brine shrimp, and two commercial dry diets [369]. Grass carp larvae raised on a diet of egg yolk also consume protozoa and zooplankton present in their environment [27]. In a comparison of two food sources in laboratory setting, benthic detritus worms of the family *Naididae* (formerly *Tubificidae*) and lettuce (*Lactuca sativa*), year-old fingerling grass carp had a higher growth rate when fed detritus worms than lettuce [370]. Grass carp grew faster when fed a diet of detritus worms than when fed duckweed, likely due to absorption rate differences between food types [180]. Grass carp (~300 g body mass) fed exclusively lettuce lost, on average, 2.2% of their initial body mass over 10 days, whereas ~300 g grass carp fed exclusively detritus worms gained, on average, 3.9% of their initial body mass over 10 days [190].

As a potential way of reducing aquacultural production cost, food waste diets for grass carp have been studied. A cereal-based food waste diet supplemented with 1% enzymes (bromelain and papain) improved growth and immunity compared to grass carp fed a control commercial diet or food waste diet alone [371]. However, a second food waste diet which contained higher quantities of corn starch and lipids performed poorly regardless of enzyme supplementation [371]. In an assessment of dietary prebiotic fibers as an additive to a food waste-based diet, supplementation of 0.2% inulin, 2% inulin, and 2% mannan oligosaccharides increased specific growth rate compared to the food waste diet control [323,372]. The addition of a mixture of brewer’s yeast (*Saccharomyces cerevisiae*) and two protein-digesting enzymes (bromelain and papain) at 25 g/kg diet to a 75% food waste grass carp diet resulted in relative weight gain that was greater than the control diet (i.e., a non-food waste diet) and equivalent to the control diet supplemented with 50 g/kg brewer’s yeast [373]. No differences were found in growth among grass carp fed food waste feeds, elephant grass, mixed food waste and elephant grass, and a commercial diet [374].

Starches and cereals have also been researched as potential components of grass carp aquacultural diets. Increasing corn starch in diets fed to grass carp did not affect specific growth rate, feed efficiency, or protein retention efficiency [375]. Grass carp that were provided feed with dietary wheat starch greater than 33% had decreased weight gain, feed efficiency, and protein efficiency ratio [376]. The effects of overfeeding cereals to common carp and grass carp can include increased disease susceptibility; adequate amounts of green vegetation are necessary to counteract this effect [377]. In an aquacultural setting, adding 200 g/kg of rice bran treated with phytase to commercial grass carp feed increases the nutritional availability of P from the rice bran and may eliminate the need for mineral P supplementation from dicalcium phosphate [378].

The effects of indirectly increasing food supply of grass carp by fertilizing water with additives has also been assessed. Grass carp had higher survival and produced greater yield of daily weight gain and total harvested fish weight per hectare in a pond treated with cow manure slurry compared to a pond without the slurry [379]. Addition of organic and inorganic fertilizer to the ponds where they were held increased growth rate of grass carp [380].

Other Factors Related to Growth Rate

A variety of other research has been carried out on factors that could influence individual growth of grass carp. Research in support of grass carp aquaculture has focused on energy budgets. In research informing an energy budget for young grass carp, growth rate was linearly correlated with ration size, and feeding metabolism accounted for 30.7% of food energy at all ration levels [381]. Increased ration levels increased feeding rate and weight gain in grass carp, while restricted food resulted in decreased body lipid and energy content [382]. The optimum feeding rate for juvenile grass carp was 1.98% of body weight per day [383]. It has been estimated that 80% of the apparent satiation level (i.e., feeding level at which a group of fish stopped feeding) is the optimal level of feed for grass carp based on nutrient utilization and that grass carp grow better on the same feed type (i.e., soybean meal, rapeseed meal, or cottonseed meal) in extruded compared to pelleted form [384]. Grass carp stocked in six Florida lakes containing hydrilla exhibited linear growth over time [385]. The amount of duckweed needed for grass carp to gain 1 g/day in weight ranges from 16 to 79 g/day [386]. Goldfish growth is greater under white light than red light while goldfish growth under either light frequency is not affected by music [387]; these findings have not been confirmed with grass carp or non-goldfish carp species to our knowledge. In a test of exercise measured in body lengths/sec, ranging from 0 to 1.5, grass carp growth rate was found to increase with increased exercise [388].

Multiple studies have demonstrated that individual growth rate is also related to population density. It has been demonstrated in a laboratory setting that as density of grass carp larvae increased, growth, survival, and water quality decreased [389]. Likewise, in production ponds stocked with 6 species of fish, including grass carp, increased density decreased growth rate; however, higher densities resulted in higher feed conversion ratios, measured as grams of food needed to produce a net gram of fish per pond [390,391]. Similarly, grass carp raised at lower stock densities may have greater growth and faster protein turnover; the latter effect was predicted by measuring the response of the ubiquitin proteasome system [215]. One potential unintended response of reducing grass carp population sizes is the potential for density-dependent release of growth rate for those that remain [389,391]. For additional factors affecting growth rate related to water quality and temperature, see 'Section 3.2.1. Physiological Tolerances'.

3.1.3. Control through Behavior

Due to the invasive nature of grass carp outside its native range and its negative impacts on ecosystems, there is much interest in leveraging existing knowledge on the behavior of this species to enhance population control and removal efforts [392]. Of particular interest is determining a means of attracting or aggregating grass carp in one area to increase the efficiency of removal attempts or the selection of deterrents or barriers that may be leveraged to prevent range expansion. In the following sections the known behavioral responses of grass carp to a variety of stimuli that may aid in management efforts are discussed. Research on related species is included where relevant to address data gaps and identify areas of research needs for grass carp.

Daily and Seasonal Behavioral Patterns

Daily and seasonal behavioral patterns of grass carp provide insight into potential factors that may allow for more targeted capturing methods. Aggregation in some carp species can be affected by environmental conditions, particularly water temperature (Ref. [393] citing [394]). Due to a tendency for grass carp to overwinter at low densities in debris-laden shallow water in a Missouri reservoir, attempting to locate groups of grass carp using a subset of tagged grass carp and subsequently using nets to capture them in this environment has been deemed inefficient [395]. Additionally, the effectiveness of these methods may be affected by diurnal behaviors. Grass carp stocked in an irrigation canal showed strong diurnal differences in feeding behavior and habitat selection, with feeding and movement occurring primarily during the day [396]. At night, grass carp stayed close to tiled groundwater inputs.

Control and Exploitation of Feeding Response

Some research has been carried out into the potential control of the feeding response of the focal carp species (grass carp, bighead carp, and silver carp). Stimuli can be classified as ′incitants′ that induce food capture, ′suppressants′ that decrease food grasping rate, ′stimulants′ that promote high ingestion rate, ′deterrents′ as substances causing food abandonment and rejection, and ′enhancers′ as substances that increase food ingestion (Ref. [397] citing [398–401]). Increased levels of the phytochemicals rutin, quercetin, and kaempferol are tied to avoidance of coontail and Eurasian watermilfoil by grass carp, which is assumed to be the reason for these plant species being selected against, as grass carp ate more macrophytes that had higher protein contents and fewer macrophytes with high flavonoids [198]. Some studies have looked at manipulation of physiological signaling pathways to control feeding behavior in carp. For example, injection of the neurotransmitter neuropeptide Y into the brain of grass carp increased food uptake, suggesting that further understanding of this compound may help in finding effective methods for enhancing grass carp feeding efficiency [293]. Similarly, injection of the gastrointestinal peptide ghrelin induced higher food intake in 70% of grass carp tested, and this effect was partially blocked by intraperitoneal injection of obestatin-like anorexigenic peptide4 [402]. Excessive dietary carbohydrates increased total lipid contents in grass carp, resulting in depressed food intake and growth [227]. In filter-feeding bighead and silver carp, respiratory buccal-pharyngeal pumping behavior has been used to demonstrate that a spirulina algae (*Arthrospira* spp.), a cyanobacterium, produces a significant response and that a mixture of 18 L-amino acids alone produced less of a response than this algae [403]. Additionally, this buccal-pharyngeal pumping behavior in response to food is significantly reduced in fish with occlusion of the nares. These results suggest there are important components in the algae food source other than just L-amino acids and that the olfactory sense is a major mediator of the feeding behavior [403]. Time since feeding affects oxygen consumption efficiency in swimming grass carp; times listed from highest to lowest efficiency are 2 days > 6 h > 2 weeks [404]. For additional factors affecting feeding response related to water quality and temperature, see 'Section 3.2.1. Physiological Tolerances'.

The response of focal carps to baits in the context of trapping and fishing, generally quantified via capture rate or efficacy, has been studied. Baiting cages, traps, and areas with hydrilla and duckweed are potentially effective ways of attracting and removing grass carp from irrigation canals [405]. However, baiting an area to attract groups of grass carp for removal is considered more effective than using plant-baited traps (Ref. [406] citing [5]). Fishing for grass carp using hook-and-line and similar methods is generally ineffective. After 427 hours of fishing in seven ponds stocked with grass carp, only nine grass carp were hooked with only two landed using earthworms as bait; no grass carp were landed using artificial minnows, spinners, or aquatic and terrestrial vegetation [407]. One source notes that, in the absence of consumable vegetation, grass carp may be caught using worms and other suspended baits (Ref. [112] as cited by [148]). A comparison of gauze-covered, wheat flour-based bait balls containing possible chemo-attractants found that bait balls formulated with L-glycine, L-glutamic, and L-arginine at 10^{-2} M and dimethylthetin at 10^{-1} M induced higher bite rates than bait balls without additional possible chemo-attractants [408]. A survey of commercial fishers in Missouri found that a few grass carp were caught on trot lines baited with green sunfish (*Lepomis cyanellus*) or small common carp [52]. Herding fish and removing them using gill nets or seines is the most effective method for removing grass carp when compared to various capture techniques (angling, pop-nets, lift nets, traps) in baited areas and angling in non-baited areas [409].

Chemosensory Stimuli

A variety of research has been carried out on physiological and behavioral responses to chemical stimuli; some of this research could be applied to identify potential compounds to attract or deter focal carp and other fish species. Such compounds could be used to aggregate invasive populations of focal carp for easier removal. Olfactory (i.e., related to stimulus detection) and gustatory (i.e., related to consumption) processes in fish related to chemical stimuli, such as amino acids, have been previously reviewed (for example, [397,410]). Some studies (for example, [410–412]) focus primarily on physiological responses with the understanding that these responses may be linked to behavioral responses. Other studies (for example, [397,413]) directly test behavioral responses. Ontogeny and anatomy of the olfactory organ in grass carp has also been studied [414]. They note that the number of olfactory sensory neurons in the olfactory organ is approximately 51,000 cells/mm^2.

Some behavioral and physiological work has been conducted specifically on grass carp and related species regarding food-related cues, such as amino acids. Much of this work involves electro-olfactography (EOG), a technique that quantifies the change in electrical potential produced by the olfactory cells of the fish, to measure physiological olfactory responses to compounds [397,410,412]. Electro-olfactory response in common carp have been evaluated in L-glutamine, L-lysine, and L-methionine (Ref. [415]; as cited by [397]); betaine hydrochloride (Ref. [415] as cited by [397]); and L-arginine and L-alanine (Ref. [416] as cited by [397]). Amino acids that elicit EOG responses in grass carp, ranked from highest to lowest relative response, are cysteine, arginine, methionine, alanine, glutamic acid, glycine, threonine, phenylalanine, aspartic acid, and proline [411]; however, ref. [412] found no significant differences in initial response of grass carp to L-alanine, L-arginine, L-aspartic acid, L-asparagine, L-glutamine, or L-glutamic acid. In grass carp, L-alanine, L-histidine, and L-cysteine are stimulants at 20 °C; while L-histidine and L-valine are stimulants at 13 °C (Z. Adámek, K. Fašaić, and L. Debeljak, 1990 as cited in [397]); Ref. [412] found that EOG response increased with increased temperature in grass carp. Overall response to the six amino acids studied by [412] was greater for the herbivorous grass carp compared to bighead and silver carp. For juvenile bighead carp, EOG response increase with increased mass [412]. Among several cereals, that is, maize, sorghum, wheat, rye, and triticale, koi (*Cyprinus rubrofuscus*) select for maize over sorghum, wheat, and rye after 10 min of exposure, but they show no other significant differences in selection between cereals after 30 min [397]. For koi, addition of L-alanine to a 3:1 maize:sorghum food mixture increases selection more so than additions L-arginine, L-lysine, and L-methionine after 30 min of exposure, and addition of betaine increases selection of that food mixture compared to the mixture alone [397]. Identifying compounds such as these which may increase the selection of particular baits by grass carp has the potential to help managers select appropriate baits for removal and control of the species.

Behavioral response of focal carp to the odor of predators, alarm compounds, pheromones, and other compounds is another area of research; related research on other fish taxa may provide insight into future research directions for grass carp. The concentration of a water extract of alarm cue compounds from adult grass carp skin needed to elicit a response decreases rapidly as grass carp increase in size (A. Kasumyan and V.Y. Ponomarev, 1986 as cited in [417]). Juvenile silver carp do not innately avoid odors of North American predator fish such as largemouth bass, smallmouth bass, and longnose gar, and they are not able to recognize the odor of smallmouth bass as a predator after learning the odor of the congeneric largemouth bass [418]; grass carp likely have similar naïveté. In research on responses to alarm cue compounds produced by silver carp, bighead carp, and two North American fishes, golden shiner (*Notemigonus crysoleucas*) and fathead minnow, silver carp only responded to conspecific alarm compounds, and bighead carp responded to both conspecific and silver carp cues [419]. Silver carp respond to alarm cue compounds by increasing distance between individuals, and bighead carp form clusters of multiple individuals. As part of a management and control plan for invasive populations of focal carp, [420] discusses the use of pheromones to evoke behavioral responses in fish. Various sources note the potential use of pheromones for controlling common carp and aggregating non-native populations of focal carp for removal using attractants or baits [421–424]. Pheromones from alarmed common carp serve as a deterrent for common carp (Ref. [423] as cited by [425]). In a study involving stimulating ovulation in silver carp through injection of carp pituitary powder, review of several studies of behavioral response of various non-cypriniform fish taxa to pheromones was provided; it suggested these responses may be observable in silver carp [426]. Arctic char (*Salvelinus alpinus*) males release Prostaglandin F2α to attract females and stimulate spawning (Ref. [427] presenting unpublished data by; as cited by [426]; see [428] for published data); other pheromones have similar functions in other fish species (Ref. [429]; as cited by [426]). Pheromones released by male fish in some species may also serve to facilitate coordination of reproductive behavior of males (Ref. [430]; as cited by [426]); to the best of our knowledge, this process has not been studied in grass carp specifically. Silver carp avoid chemical plant effluents containing dye, dyeing wastewater, petrochemical, or organic compounds and other organic toxicants such as nitronaphthalonc, m-Nitroaniline, m-dinitrabenzene, and tributlyphoshate [413].

Learning

Some research has been conducted on learning in grass carp and common carp, especially the use of sound as an attractant via learned behavior involving food reinforcement. For grass carp conditioned to be attracted to sound using food, a conditioned attraction to sound in the absence of food is retained for at least four months [431]. A pair of studies tested recapture of mango tilapia (*Sarotherodon galilaeus*); gray and red tilapia (*Oreochromis* sp.); and common carp after food-reinforced acoustic conditioning that began in a laboratory and continued after the fish were introduced into a reservoir in Israel [432,433]. In those studies, grass carp and common carp already present in the reservoir before and during the study were caught in an acoustic fish trap after incidentally becoming acoustically conditioned during the in-reservoir training trials for the marked fish. Additionally, they found that this conditioning behavior seemed to be transferred to resident common carp individuals based on a capture rate of 154% that of the number of conditioned common carp individuals introduced into the system. Grass carp have been trained, using food reinforcement, to be attracted by low frequency sound (600 to 1000 Hz), with 600 Hz and 800 Hz having the greatest percent return rate of trained grass carp [434]. As the basis of their frequency selection, [434] cite [435] indicating the common carp hearing range is 50 to 3000 Hz. Though learning was observed in grass carp, retention time for this learned behavior was not assessed [434]. At least one type of pesticide affects the ability of common carp to learn. Exposure of common carp to sublethal levels of the pyrethroid deltamethrin affects their nervous system and their ability to learn [436].

Non-Physical Barriers and Related Deterrents

Many non-physical barrier and deterrent types, including electrical, visual, acoustic, chemical, and hydrological, are used to elicit avoidance behavior or cause mortality in a variety of fish taxa (reviewed by [425]; Ref. [437] including Appendix C). Some of these barrier types have been employed or considered to prevent invasive populations of focal carp from moving into new waterbodies. A report from 2004 discussing strategies to limit infiltration44 of invasive populations of focal carp into the Upper Mississippi River Basin assessed the application and potential degree of success of several barrier types, including electrical field, acoustic, bubble curtain, and hybrid methods [438]. From the report and interpretation of the report by [406], ref. [438] suggests there is little to no support for use of strobe lights, support for use of bubble curtains in combination with other deterrence methods such as strobes lights or sound, support for flow velocities greater than the swimming capabilities of the target fish species, and good support for the use of sound. Stocked grass carp seemed to avoid areas where water velocities were higher than 80 cm/s [396].

The use of non-physical barriers to prevent movement of invasive populations of focal carp in the Great Lakes is one area of research and discussion. Discussion of the use of electrical, sound, and CO_2 barriers to keep invasive fish out of the Great Lakes at the Brandon Road Lock and Dam near Joliet, Illinois can be found in a report by the U.S. Army Corps of Engineers regarding the Great Lakes and Mississippi River Interbasin Study (see [439] including Appendices H.1 and H.2). Extensive research on the various potential operational protocols (for example, fish size and behavior, water conductivity and temperature, and current type and field size, etc.,) that might be used for the Chicago Sanitary and Shipping Canal (CSSC) was conducted by [440]. Grass carp population models for the western Lake Erie basin predict that a barrier preventing 50% of grass carp from migrating to spawning areas in the Sandusky River (Ohio) will be one critical component in keeping grass carp populations below the target $\leq$10 fish per hectare in that area by the mid-21st century [140]. As an alternative or supplement to non-physical barriers, machine learning-based image recognition systems that open a physical barrier for fish species native to the Laurentian Great Lakes area, but close the barrier for invasive fishes, including grass carp, are being researched [441].

The electrical barrier at the CSSC, which is designed to keep invasive fish out of the Great Lakes, has been extensively studied as a barrier for multiple fish species, including focal carps. The application of electrical barriers in the CSSC to keep silver carp and bighead carp from entering the Great Lakes is described by [420] (cited by [425]). The history, design, application, and general effectiveness of the CSSC electrical barrier as a non-native focal carp deterrent is presented by [442]. Gizzard shad have been used as a surrogate for focal carps on the effects of operating parameters, seasonality, and boat hull composition on the effectiveness of the electric barrier at the Chicago Sanitary and Ship Channel [443]. Increase in electrical field strength from 0.79 V/cm to 0.91 V/cm was needed to raise incapacitation from 97% to 100%; they also determined that summer is the season where fish could move the furthest distance upstream of the barrier [443]. The amount of electricity needed to kill early life history stages of bighead carp is considered impractical given the estimated need of electricity is 16 times the amount that is currently used for the CSSC fish barrier [444]. One weakness of electrical barriers is that the passage of large vessels (for example, barges) made from conductive metals can temporarily negate electrical barriers; arrays of multiple barriers can be used to offset this issue [440,443,445]. Except for one fish moving upstream with a tow, the CSSC electrical barrier was effective at keeping common carp from moving upstream in the canal [446]. During the summer and fall, fish congregated near the peak voltage of the CSSC electrical barrier, challenging the barrier [447].

In addition to CSSC electrical barrier studies, other research has been conducted specifically on focal carp and common carp regarding their responses to electricity. Single, narrow high voltage electrical barriers are not considered effective because they can induce panic responses that can allow fish to breach a barrier (Ref. [448] as cited by [443]). A low-voltage electric guidance system was successful at directing common carp into mock traps for increased effectiveness of removal [449]. The effectiveness of an electric barrier in the laboratory to inhibit movement of common carp using a relatively weak voltage gradient of 0.2 to 0.4 V/cm has been demonstrated by [450]. A V-shaped barrier fitted with an electrical deterrent was able to almost completely confine grass carp to a reservoir embayment [451]. For a comparison of different levels of voltage as a means of sedation of grass carp, see [452]. Research using electrofishing to immobilize juvenile grass carp found that a low water temperature (12 °C) and low frequency (10 Hz) reduced the voltage gradient needed to immobilize fish, and that necessary field intensity (V/cm) decreased with increasing fish length [453]. Eliciting avoidance behaviors using a boat simultaneously equipped with an acoustic deterrent (broadband sound speakers) and an electrical deterrent (pulsed DC sphere anode array) was more effective at herding silver carp than either method alone, and that the effectiveness of using an acoustic or electric deterrent alone is not significantly more effective than the control treatment of boat noise alone4 [454].

A variety of research has been carried out to determine the effectiveness of light and/or bubble curtains as potential non-physical barriers to focal carp movement. The potential roles of bubble curtains in preventing movement of focal carp are reviewed by [455]. As of December 2021, experiments using bubble curtains as a means of blocking downstream movement of grass carp eggs and larvae were ongoing [455]. The effects of a 300-lux light and flow rate on the distribution of juvenile grass carp within a recirculating channel was tested by4 [456]. Juvenile grass carp had minimal response to the light in still water and water flow fast enough to induce swimming against the current (0.2 m/s), but that the fish distanced themselves slightly from the light source at an intermediate flow velocity (0.1 m/s). The ability for strobe lights and bubble curtains to deter grass carp decreases with increased turbidity [406]. A sound-bubble-strobe light barrier was 95% effective at deterring upstream movement of grass carp [457,458]. In trials assessing the effect of five different light colors on the efficacy of a fish capture system for juvenile grass carp, capture rate is highest for blue light, second highest for natural light, third highest for green light, fourth highest for white light, and lowest for red light [459]. The successful use of WaterMark Quadrafoil (Jackson, Mississippi) larval fish light traps set overnight to collect grass carp larvae was documented by [460]. Silver and bighead carp visual sensitivity is temporarily depressed by strobe lights, making optical barriers less effective for deterring these fishes [461]. Strobe lights also worked as a deterrent for common carp [457]. For a description on how high-powered lights are used in inland fisheries to attract small fish for harvesting see [462].

Barriers based on CO_2 can elicit avoidance behavior and cause mortality in fish and other aquatic organisms. Dissolved CO_2 was registered as the pesticide Carbon Dioxide-Carp by the USEPA in 2019 (Ref. [463] as cited by [455]). USEPA-prescribed levels for evoking avoidance behavior in focal carp are 100 to 150 mg/L CO_2; for use as an under-ice, lethal control method, the prescribed concentration is 200 mg/L CO_2 for $\geq$96 h. Bighead carp avoid CO_2 in flowing water at concentrations of approximately 16 to 40 mg/L [464]. Some fish species avoid areas with elevated CO_2 in water with limited flow (Ref. [464] citing [465–467]. Elevated CO_2 exposure does not inhibit a behavioral response of silver carp exposed to a conspecific skin extract (alarm cues) compared to the fathead minnow, which exhibited impaired inhibition [468]. The CO_2 concentration thresholds for avoidance response and narcosis in silver and bighead carp decrease with decreasing water temperature [469]. Carbon dioxide barriers in field and pond trials deter silver and bighead carp and other fish species, but they are not 100% effective at deterring all individuals [467,470]. Potential unintended effects of dissolved CO_2 use in management context, including changes in water chemistry, changes in organismal biochemistry, and the toxicity of CO_2 to invertebrates, are reviewed by [471].

A more recent review of research conducted prior to 2020 relevant to the use of CO_2 to create non-physical barriers to deter fish, with silver and bighead carp as focal species, is provided by [472] and includes additional insights to the research discussed previously. Some key points from this review follow: CO_2 may be a more effective non-physical barrier than electric barriers for small fish, such as juvenile focal carp (Ref. [472] citing [473]). Tracking fish using acoustic telemetry found that CO_2 injected into the water column is effective at reducing the movement of grass and bighead carp across a U-shaped pond by 58% at 121 mg/L CO_2 and by 78% at 213 mg/L CO_2 compared to baseline movements before injection of CO_2 [474]. The CO_2 concentration threshold needed to elicit avoidance behavior in silver carp and bighead carp is generally 60 to 100 mg/L (Ref. [472] citing [464,466,467,475]). There is large inter-individual variability in CO_2 concentration thresholds; for juvenile bighead carp and silver carp, the threshold needed for avoidance behavior for individuals ranges from ~60 to 300 mg/L CO_2 (Ref. [472] citing [476]). Information about potential ways to engineer a non-physical barrier using water infused with a deterrent and/or toxicant (for example, CO_2, ozone) for aquatic invasive species management is provided by [477]. There is a positive relationship between water temperature and the concentration of CO_2 needed to deter bighead carp and silver carp (Ref. [472] citing [469]). Fish under stress may require higher CO_2 levels as a deterrent; largemouth bass with artificially elevated cortisol (stress hormone) required higher levels than unstressed fish (Ref. [472] citing [478]). For additional information on the effects of CO_2 on focal carps, see 'Section Water Quality Constraints and Effects' within Section 3.2.1.

Both ozone and induced hypoxic conditions have been discussed as means of controlling the movement of invasive fishes. A review of what was known about the use of ozone to control the spread of invasive aquatic species at the time of writing is provided by [479]. Prior to the invasion of the Great Lakes by round goby (*Neogobius melanostomus*), it was suggested that the CSSC, which is seasonally hypoxic due to anthropogenic discharge, could be converted to a perennially hypoxic zone to keep this species from entering the Great Lakes (Ref. [480]; as cited by [425]). However, note that not all fish species respond similarly to hypoxia and that hypoxic waters may not deter grass carp; see 'Section Water Quality Constraints and Effects' within Section 3.2.1. for discussion and references related to hypoxia tolerance of grass carp.

Water flow is also a means for controlling the movement of focal carp; much of this research has been conducted in the context of facilitating focal carp migration within their native range in China. Flows of 0.3 m/s produced the highest percentage of successful upstream migration of grass carp [481]. Juvenile grass carp (5.70–15.00 cm in length) critical and burst swimming speeds increased with increasing body length, meaning smaller fish are less capable of swimming upstream at higher water velocities [481]. Tests of the success rate of juvenile grass carp passing through a vertical slot fishway find the configuration with the highest success rate is a baffle lead angle of 45° and upstream flow velocity of 0.01 to 0.45 m/s, and that juvenile grass carp generally avoid water with turbulent kinetic energy higher than $0.012\ m^2\ s^{-2}$ [482]. Laboratory work on the effects of turbulence on swimming behavior, grass carp larvae avoid areas with turbulent kinetic energy of $>0.05\ m^2\ s^{-2}$ [483]. Adult grass carp which are about to spawn appear to be attracted to turbulence [38] (as cited by [484]). The results of a fishway study support a velocity preference of bighead carp ranging from 0.15 to 0.45 m/s [485]. The construction of the Three Gorges Reservoir on the Yangtze River in China, a major disruption to water flow, resulted in a 14-day delay, 10 fewer annual days, a 2-day shortening, and disappearance of a peak in spawning of black, grass, silver, and bighead carp [4]. In an invasive population management context, water flow of 1.1 to 1.5 m/s would be effective at containing subadult and younger bighead carp and silver carp [486].

Sound may be useful as a repellent for some species of focal carps. Within schools of grass carp larvae, individuals do not consistently respond to tones ranging in frequency from 100 to 1000 Hz (18% to 33% response rate), and there is no relationship between tone frequency and individual response rate [487]. Grass carp respond to broadband sound frequencies of 0.2 to 4.0 kHz; maximum sensitivity is for frequencies from 0.3 to 0.4 kHz based on having those frequencies having the lowest sound pressure level [488]. An in situ experimental acoustic barrier designed to deter upstream non-native carp movement was installed during March 2021 downstream of Lock 19 on the Mississippi River near Keokuk, Iowa; as of December 2021, studies on the efficacy of this system are ongoing at the time of writing (reviewed by [455]). Laboratory elliptical flume tests of cyclic broadband sound combined with an air curtain, termed a proprietary ensonified bubble curtain (EBC), have found that groups of 10 grass carp (mean length = 133 cm) had mean individual crossings per 6-min exposure period of 3 when exposed to an EBC, 46 when exposed to cyclic broadband sound alone, and 57 when exposed to the control treatment of no experimental stimulus [489]. The authors translate the crossing values to mean blockage efficiencies of 95% for the EBC and 21% for the cyclic broadband sound only, indicating that sound-only barriers are unlikely to deter grass carp. One EBC, the BioAcoustic Fish Fence (BAFF; Fish Guidance Systems Ltd., Fareham, UK), is, at the time of writing, being field-tested as a deterrent for upstream movement of non-native carp at the Barkley Lock and Dam on the Cumberland River near Grand Rivers, Kentucky [455]. Common carp show little response to broadband sounds when compared to silver and bighead carp under identical conditions [490,491]. Silver carp response in the field to broadband sound is demonstrated by [492]. The hearing frequency thresholds of silver and bighead carp are given by [492]. Use of broadband acoustic signal based on a motorboat as a deterrent is demonstrated for silver and bighead carp [493]. Playback of a 100-horsepower boat motor acoustic stimulus to deter passage of silver carp through culverts in Illinois found that passage of neither silver carp nor native centrarchid fishes is reduced by the acoustic stimulus [494].

3.2. *Control Based on Physiological Constraints, Toxicity, and Biology*

Understanding the physiological tolerances of grass carp to environmental conditions, the effects of pesticides and toxicants, and biological measures of control may yield insights on improving management of invasive populations of grass carp. Here, we review the research that has been conducted on the water quality and temperature constraints of grass carp, the major pesticides that have been examined for carp population control, and additional compounds that are toxic to grass carp. Additionally, we look at research on the feasibility and effectiveness of biological controls on reproduction, such as induced triploidy, functionally sterile hybrids, and other genetic controls on reproduction. Finally, we examine the known predators and diseases of grass carp.

3.2.1. Physiological Tolerances

Understanding the environmental conditions (e.g., abiotic factors) of grass carp tolerance is particularly important for predicting where populations may invade and become established. The information can also be used to alter environments to limit grass carp spread.

Water Quality Constraints and Effects

Research has been carried out on the effects of various aspects of water quality on survival, development, reproduction, feeding response, and sublethal effects on individual health of focal carp (grass carp, bighead carp, and silver carp). Water quality components that have been assessed include supersaturation of dissolved gasses, pH, ammonia, dissolved oxygen, carbon dioxide, salinity, and nitrite.

Water supersaturated with total dissolved gasses (TDGs), a state which can be caused by flood outflow from dams, can cause a pathology termed ’gas bubble disease‘ which can be lethal to carp and other fishes [495,496]. Several studies have been conducted on the effects of TDG supersaturation on various carp species, including grass carp, due to the presence of large dams and declining populations in their native range (Ref. [3] as cited by [2]). Grass carp continuously exposed to water with total dissolved gas supersaturation (TDGS) of 120% to 135% have temporarily decreased swimming performance compared to fish at 100% TDGS [497]. The grass carp studied in swimming trials with supersaturated TDG water almost completely recovered their swimming ability within two hours. The in situ effects of TDGS on grass carp (mean fork length = 13 cm, mean weight = 45 g) downstream of a hydroelectric dam in the Yangtze River, China found that 100% of caged individuals at ≤1 m depth died within a few hours when exposed to TDGSs of ~130% [498]. Individuals between 1 m and 2 m depth survived longer than the fish at ≤1 m, but that the mortality rate is still 100% after 275 h of exposure to TDGSs fluctuating between ~115% and 130%. In grass carp, smaller juveniles (mean fork length = 2.53 cm, mean weight = 0.17 g) have higher TDGS tolerance than larger juveniles (mean fork length = 5.17 cm, mean weight 1.64 g) [499]. The median lethal times for smaller juvenile individuals are 88.13 h at 130% TDGS, 61.49 h at 135% TDGS, and 35.88 h at 140% TDGS. For larger juvenile individuals they are 36.55 h, 21.75 h, and 6.37 h, respectively [499]. No mortality was recorded among juvenile grass carp exposed to water with 115% saturation of TDG for 96 h [499].

Effects of extreme pH on early life stages of grass carp has been studied. Development of grass carp embryos is possible at pH = 5.5 and pH = 9.5, with 26% and 23% of larva surviving and hatching normally, respectively [500]. At pH values at or below 5.5, embryo mortality increased as pH decreased, and for pH values at or above 9.5, embryo mortality increased with pH [500].

The effects of ammonia have also been studied in multiple carp species. Tests on the effects of 48-h acute ammonia exposures on grass carp at 1.7 mg/L total ammonia nitrogen (TAN) and 50 mg/L TAN found no mortality [501]. However, these acute ammonia exposure tests found that the 50 mg/L TAN group of grass carp had digestive tract disruption, including swollen intestinal villi and decreased intestinal amylase activity. An assessment of the effects of different concentrations of TAN on juvenile grass carp found that ≤2 mg/L TAN does not reduce specific growth rate of juvenile grass carp [502], while 4.5 to 18.0 mg/L TAN leads to decreasing specific growth rate with increasing TAN concentration. Exposure to this range of TAN concentrations continues to suppress growth for over a month after exposure. Additionally, ≥9.0 mg/L TAN causes organ dysfunction to the gills, liver, and muscle tissue, generally from oxidative damage, both during exposure and for over a month after exposure [502]. Increased ammonia can also retard development of grass carp embryos [503]. Grass carp larvae/juveniles become less sensitive to ammonia as they grow (Ref. [504] citing [505]). It is important to note ammonia is less toxic to silver and bighead carp in the wild than in the laboratory [504]. Pre-acclimation of common carp to low levels of ammonia results in increased survival time when they are exposed to high ammonia levels [506]. Additionally, administering taurine via injection appears to mitigate the effects of ammonia acute toxicity in grass carp [507].

The effects of oxygen levels on various physiological functions and behaviors have been assessed in grass carp and other cypriniforms. Grass carp have high tolerance of low concentrations of dissolved oxygen (Ref. [508]; as cited by [17]). The lethally low dissolved oxygen concentration for grass carp fry is approximately 0.5 mg/L according to [509] (as cited by [19]). The dissolved oxygen lethal concentration for juvenile grass carp is 0.44 mg/L [510]. Similarly, lethal dissolved oxygen concentrations for grass carp of unspecified age are between 0.3 mg/L and 0.4 mg/L (Ref. [508]; as cited by [17]). The asphyxiation point of grass carp was recorded as 0.30 to 0.51 mg/L O_2 (S. Chen, W. Chen, and Z. Fan, 2004 as cited in [511]). In mrigal, hypoxia (0.50 mg/L dissolved oxygen) depressed the immune response to *A. hydrophila* and increased mortality when exposed to the pathogen [263]. In artificially induced spawning female grass carp, moderate dissolved oxygen concentration (4.5 mg/L) resulted in greater egg production and egg weight index percentage compared to high (7.0 mg/L) and low (0 mg/L) oxygen concentrations [512]. Daily grass carp consumption rate of duckweed decreased under low dissolved oxygen concentrations [513]. Dissolved oxygen levels below 4 mg/L have decreased grass carp food consumption by 40% (Ref. [148]; as cited by [17]).

Carbon dioxide tolerance of various cypriniform species has been described by multiple studies. In water with 365 mg/L CO_2, 30% of common carp died within 1.5 h, and 70% died within 10 h (Ref. [514]; as cited by [471]). Carbon dioxide decreases in toxicity to larvae of three Indian cypriniform species (catla, *Labeo catla*; rohu, *Labeo rohita*; and mrigal) as O_2 concentration increases [515]. Stationary common carp exposed to moderate levels of increased CO_2 only temporarily depressed oxygen utilization; swimming common carp exhibited an increased respiration rate and decreased oxygen consumption and utilization [516]. The effectiveness of reducing bighead and silver carp population size by increasing CO_2 under ice via application of dry ice was demonstrated by [517]. In ponds experimentally treated with CO_2, both common carp and grass carp have survived CO_2 levels (mean ± SEM: 46.8 ± 12.1 mg/L CO_2, 35,510 ± 7308 μatm) that are lethal to bighead carp and silver carp (Ref. [470] as cited by [517]). Acute hypercapnia exposure (i.e., exposure to elevated CO_2 levels) affects silver carp gene tissue specific expression [476]. CO_2 levels have been shown to have both lethal and sub-lethal effects on grass carp and similar species. Since CO_2 can be used as a barrier to prevent grass carp from entering new systems, it is important for managers to understand the necessary levels of CO_2 required to deter grass carp, so they can compare this to the tolerances of native species to make appropriate decisions.

Various research studies have been conducted on the effects of salinity, also referred to as chloride concentration or dissolved solid concentration, on survival and physiology across life stages of grass carp and other cypriniforms. For cypriniform eggs, hatching success of bighead carp was not affected over a total dissolved solids range of 48 to 395 mg/L [518]. However, grass carp eggs and embryos experienced 100% mortality at salinities of 6.3 g salt/kg water (‰) and 11.5‰ salinity in water from the Black Sea and Caspian Sea, respectively (T. I. Rykova, 1964 as cited in [1]). Introduction of grass carp larvae to a stagnant pond with a dissolved mineral concentration that increased to 9766 mg/L over time resulted in 100% mortality within 7 days (E. N. Gannokha, 1972 as cited in [1]). In grass carp fry, salinity tolerance can vary based on the source of the saline water. Estimated maximum salinity tolerance of grass carp fry is estimated at 9‰ to 10‰ salinity for water from the Azov Sea; this tolerance is estimated at 13‰ to 14‰ salinity for water from the Aral Sea (S. Doroshev, 1963 as cited in [1]). At the fingerling life stage, the 96-h LC_{50} for salinity for grass carp is 15.1‰ [519]. At least in juvenile grass carp, acclimation can play a role in survival under various salinity conditions. Time-to-death for ~145 grass carp exposed to elevated salinity lengthened with increased salinity acclimation prior to testing; individuals acclimated to 9‰ salinity had an upper 24-h tolerance limit of approximately 16‰ [520]. For the ~145 grass carp acclimated to 9‰ salinity, no mortalities were recorded after 24 h exposure to 15‰ salinity, but 100% mortality was recorded at 17‰ salinity with a median time to death of 17 h [520]. Grass carp can survive in sodium chloride solutions from 9 to 18 g/L [19,521]. In terms of physiological and sublethal effects of salinity, fingerling grass carp can acclimate to brackish water, but they cannot tolerate salinities of more than 9‰ and experience decreased growth and food consumption at this salinity [522]. Daily food intake of grass carp decreased by one third when salinity was increased from 500 to 2000 mg chloride ions per liter (Ref. [523] as cited by [524]). Increased salinity increases oxygen consumption and, at high concentrations, causes loss of control of plasma electrolyte concentrations in grass carp [522]. In 0.17 to 0.75 g grass carp, increasing chloride concentration increases oxygen consumption and reduces mortality at lethal concentrations of nitrite (1.71 mg N-NO_2/L) [525,526].

Water hardness can affect hatching success of cypriniforms under certain conditions. At the time of writing, this research has centered on focal carp other than grass carp. Hardness (mg $CaCO_3$ mg /L, measured by titration) does not appear to be linked to hatching success in bighead carp [518]. Across hardness values ranging from 50 to 250 mg/L of $CaCO_3$, hatching success of silver carp eggs is higher at 50 mg/L than at ≥100 mg/L if eggs are exposed during the swelling phase (within one hour of fertilization), but there is no evidence of water hardness affecting hatching success if eggs are exposed to different degrees of water hardness after the swelling phase [527].

Nitrite can have both lethal and sublethal effects on grass carp and other cypriniforms. A 96-hour LC_{50} of 1.71 mg nitrite as $N\text{-}NO_2/L$ was reported for 0.17 to 0.75 g grass carp [525]. The 96-h LC_{50} for nitrite was 3.50 mg/L for grass carp; it was 30.93, 20.38, and 19.91 for common, bighead, and silver carp, respectively [528]. For sublethal effects on grass carp, nitrite concentrations of 0.5 to 1.0 mg $N\text{-}NO_2/L$ depressed oxygen consumption in 0.17 to 0.75 g grass carp but did not cause mortality over 96 h [526]. Acute nitrite exposure of 0.5 to 16 mg/L may lead to hypothyroidism in juvenile grass carp via disturbance of the homeostasis of thyroid hormone metabolism [529]. Increased levels of nitrite decrease the scope for growth of grass carp [530].

Limited research has been conducted on the effects of turbidity and sediment on cypriniforms. Turbidities between 80,000 and 250,000 ppm cause mortality in common carp [531]. Grass carp eggs are normally suspended in the water column; when they are partially or fully buried in sediment, they show decreased survival and an increase in deformities upon hatching [532].

Temperature Constraints and Effects

Research has been carried out on the effects of water temperature as it relates to optimal temperatures, survival, development, reproduction, feeding response, and sublethal negative effects on individual health of grass carp. Topics covered in previous reviews providing information related to grass carp biology and temperatures include conditions within the native range of the grass carp [24], thermal biology [533,534], and effects of temperature conditions on feeding (Ref. [17] pp. 5–6; Ref. [8] p. 4).

Both the critical thermal minimum temperature and upper incipient lethal temperature (TL_{50}) of grass carp have been quantified for multiple life stages. The critical thermal minimum temperature for adult grass carp is 0.5 °C (Ref. [535]; as cited by [533,534]). Larval and juvenile grass carp have a similar minimum temperature for survival of approximately 0 °C [536]. The critical thermal maximum (the temperature above which a fish loses its ability to maintain an upright posture in the water column) is estimated at 39.3 °C in two studies (Ref. [534] citing [537,538]). At 15 days old, grass carp larvae can survive temperature changes as extreme as a decrease from 31 °C to 14 °C and an increase from 14 °C to 31 °C (E. L. Zubareva and others, 1980 as cited in [1]). For embryonic grass carp, 28 °C was the TL_{50} for prolonged exposure to heat; a range of 30 °C to 32 °C is TL_{50} for embryos exposed to brief heat shock [539]. Multiple studies have found TL_{50} for grass carp to be between 39 °C and 42 °C [539–541]. Some authors have found lower TL_{50} values. One of these studies lists a TL_{50} of 36.5 °C [542]; as cited by [533], and another lists a TL_{50} of 37.7 °C for grass carp acclimated to 34 °C [543]. The TL_{50} increases with increasing acclimation temperature in grass carp, from as low as 25.8 °C for an acclimation temperature of 5 °C, to as high as 37.7 °C for an acclimation temperature of 34 °C [543]. Heat shock proteins likely contribute to these thermal tolerance thresholds; genetic insertion of a grass carp heat shock protein 90 gene (CiHsp90) into *E. coli* and mouse myeloma cells increase survival rates when these cells were subjected to cold and heat shocks of 4 °C and 42 °C, respectively [544].

Optimal and preferred temperatures have been quantified in grass carp. An older extended abstract lists the optimal temperature for embryogenesis is 22 °C to 25.5 °C with threshold temperatures of 17 and 30 °C [536]. More recent research applied updated methods to measure embryogenesis and disputed past claims that optimal embryogenesis temperatures for grass carp are between 21 to 26 °C [545]. These authors proposed an updated optimal embryogenesis temperature of 32 °C. Optimal temperature for larvae and juveniles, based on the highest survival rate, occurs between 24 °C and 32 °C [536]. The optimal growth temperature of grass carp (starting mass = 40 to 50 g) is between 32 and 34 °C; growth ceases and fish begin to lose weight at 36 °C [539]. Other studies have found the optimal growth temperature to be between 18.3 and 30 °C (Ref. [534]

citing [24,542]). The optimal temperature for grass carp spawning is estimated to be between 22 and 30 °C (Ref. [534] citing [538,546]). Similarly, the optimal temperature for egg development is estimated to be between 22 and 32 °C (Ref. [534] citing [545,547,548]). Thermal optimums for grass carp also depend on the climatic zone where the fish is raised; for example, grass carp raised in Russia grow faster between 15 and 25 °C than those raised in warmer environments such as Iran and Cuba (A. K. Bogeruk, 1984 as cited in [1]). Thermal preference of grass carp was 35 °C [540]. Several studies found final temperature preferences between 25.3 and 30.2 °C (Ref. [534] citing [537,549]). Other research on grass carp avoidance of different temperatures indicated a slightly lower preferred temperature: the fish avoided temperatures at or above 35 °C, but they did not avoid temperatures between 28 °C and 33 °C [541]. Preferred temperature increases with increasing acclimation temperature in silver, bighead, common, and grass carp [543]. One attempt to exploit the preferred temperature of grass carp using heated water as an attractant was less successful than herding fish and removing them using gill nets or seines [409].

Several physiological changes related to temperature have been recorded in grass carp. Grass carp embryonic and larval heart rates increase with increasing temperature [550]. Five swimming performance metrics (critical swimming speed, oxygen consumption, maximum linear velocity, maximum linear acceleration, and escape distance) are all higher at 25 °C than at 15 °C for grass carp [551]. In response to a cold shock of 15 °C, the subsequent increase in plasma glucose content correlates with glucose-6-dehydrogenase and lactate dehydrogenase activities in grass carp [552]. Juvenile grass carp held at 30 °C for between two and three weeks have a lower critical oxygen tension than those held at 10 °C, 15 °C, or 20 °C; this difference indicates that grass carp have higher hypoxia tolerance at 30 °C than at 10 to 20 °C [553]. Grass carp are able to undergo gill remodeling as part of the temperature acclimation process [553]. Temperature also influences starvation rate. Lethal starvation time at 18.0 °C to 23.0 °C is 7.3 to 12.0 days for grass carp fry and 15 to 271 days for grass carp fingerlings; lethal starvation time was inversely proportional to water temperature [554].

A variety of research has been carried out on the effects of temperature on grass carp feeding rate, behavior, and growth rate; findings vary between studies, but general patterns are evident across studies. Within this review, sources pertaining to the relationship between temperature and feeding that were found via citation by [17] (pp. 5–6) include [159,555], and those directly noted below. Below a certain temperature, grass carp cease to feed, though this temperature seems to vary between study populations. This feeding cessation temperature has been reported as 11 °C (Ref. [166] as cited by [17]) and 16 °C in another (Ref. [546] as cited by [17]). In contrast, grass carp fed intermittently at 3 °C to 9 °C and steadily at 10 °C to 16 °C (N. S. Stroganov, 1963 as cited in [17]). Studies have identified temperature gradients across which grass carp foraging rate increases. A nearly fivefold difference in food consumption is found between grass carp held at 12.8 °C (mean = 4.1 kg food/fish/year^{-}) and those held at 18.3 °C (mean = 18.3 kg food/fish/year; Ref. [555]). Across a range of mean monthly temperatures (6 to 21 °C) in New Zealand, feeding rate of grass carp increased and plant species selectiveness decreased with increasing mean monthly temperature [159]. Across a gradient of three temperatures (14.4, 18.8, and 24.4 °C), researchers found an increase in feeding rate with each incremental increase in temperature; growth rate increased with increasing feeding rate [556]. Grass carp feeding and growth rate increase across a temperature gradient ranging from 17 to 25 °C [557]. In young grass carp, food selectivity decreases with temperature, demonstrated via an increase in the number of plant species consumed (Ref. [1] citing N. S. Stroganov, 1963). Temperatures where grass carp feed intensively (i.e., more than just steady feeding) and optimally (i.e., highest rate of feeding) have also been identified. Intensive feeding in grass carp occurs at temperatures as low as 16 °C (N. S. Stroganov, 1963 as cited in [17]); others documented intensive feeding between 20 °C and 23 °C (Ref. [17] citing [157,159]). Multiple studies report optimal foraging temperatures between 20 °C and 30 °C for grass carp (Ref. [17] citing N. S. Stroganov, 1963; Ref. [157]; and [558]). Similarly high annual food consumption is found at 18.3 °C, 23.9 °C, and 29.4 °C [555]. Feeding in grass carp declines above thresholds of 30 °C (Ref. [558]; as cited by [17]) and 33 °C [27].

Multiple authors have described tolerance and observed preference of grass carp toward various climatic conditions. Within their native range, grass carp inhabit a broad range of climatic conditions with mean annual air temperatures ranging from 25 °C in the southernmost part of its range to −6 °C in the northernmost part (ref. [24] Figures 3 and 4 on pp. 37–38). The distribution of mean annual air temperatures within its range is bimodal, with one mode centered on 0 °C and the other at 16 °C (ref. [24] Figure 4 on p. 38). In the Czech Republic, only 10% of grass carp survived winter in ponds where mean water temperatures are 4.2 °C, dropping to as low as 0.9 °C, compared to 97.8% for grass carp held in recirculating systems with average temperatures of 20.8 ± 0.4 °C (mean ± SD; Ref. [559]). Grass carp survival has been recorded in ice-covered ponds and in water temperatures as high as 35.6 °C [17,90,560].

3.2.2. Pesticides

A variety of pesticides have potential to serve as means of control for invasive fish populations, including grass carp. Some of these pesticides and other biocides used for aquatic nuisance species control are reviewed in a report by [437], including Appendix B. We discuss several of these in the following sections, including their toxicity to grass carp, their potential applications and limitations, as well as delivery systems. A recent review of chemical controls and pest management includes general discussion of pesticides such as rotenone, the lampricides 3-trifluoromethyl-4-nitrophenol (TFM), niclosamide, and antimycin A along with various delivery systems such as the use of microparticles [561].

Rotenone

Rotenone is a naturally occurring toxin found in some plants in the legume family (*Fabaceae*; Ref. [562]). Rotenone has been tested throughout the world, including the United States [439] and New Zealand [563] as a method for controlling invasive fish populations. A pesticide information profile for rotenone that describes its naming convention, makeup, and some review of the categories of organisms, excluding focal carp, to which it is toxic was provided by [564] as part of their 'Extension Toxicology Network'. Applications of rotenone for controlling non-native fishes, such as common carp in Australia, are generally best applied in scenarios with relatively small and unconnected bodies of water and are further reviewed by [565].

In experimental ponds, 2 mg/L of rotenone (formulation: Noxfish) resulted in 50% grass carp mortality in 4 days and 100% mortality within 18 days at temperatures of 0 to 4 °C. The 24-h LC_{50} for grass carp in lake water (Lake Baldwin, FL) at 30.8 °C is 94 μg/L; total mortality occurred within 24 h at concentrations of 150 μg/L and higher [5]. The 96-h LC_{50} at 12 °C for common carp exposed to Noxfish (5% rotenone) was 50 μg/L [566], while the toxic concentrations for a variety of other freshwater species range from 21.5 (Atlantic salmon, *Salmo salar*) to 497 (goldfish, *Carassius auratus*) μg/L. The dose resulting in a 50% mortality (LD_{50}) for common carp force-fed rotenone-laced food is 8.1 mg rotenone/kg food with an extrapolated 99% mortality estimate of 11.6 mg/kg food [567]. Rotenone can have adverse effects on aquatic organisms other than grass carp. Exposure of non-target aquatic organisms, including amphibians, macroinvertebrates, and zooplankton, to rotenone levels ranging from 12.5 to 100 μg/L produces a combination of behavioral and mortality effects [568].

In addition to being toxic, rotenone also elicits avoidance response in grass carp. However, at least one attempt to use the deterrent properties of rotenone in conjunction with the attractive potential of potassium permanganate ($KMnO_4$, a compound that neutralizes rotenone) to herd grass carp into a fyke net was unsuccessful [405]. These researchers observed a general pattern of avoidance of rotenone and attraction to $KMnO_4$, but the fish recovered from rotenone too quickly to be captured. It was suggested that fine-tuning the ratios and placement of the compounds may allow for greater success, but that toxic effects of these compounds on other organisms would need to be mitigated [405]. A review of observed toxic concentrations of rotenone to a variety of aquatic invertebrates and vertebrates up to the date of publication is provided by [569]. The long-term effects of rotenone application to aquatic invertebrates is presented by [570].

Antimycin A

A variety of research has also gone into development and testing of antimycin A for the purpose of removing invasive aquatic species through poisoning. Antimycin A is a fungicide used as a general fish toxicant (Refs. [571–573]; reviewed by [562]). Multiple studies have assessed the toxicity and palatability of antimycin A to cypriniforms, including grass carp. Grass carp along with other carp species showed intermediate sensitivity to the piscicide and exhibited the same amino acids at the antimycin A binding site [574]. A review of previous applications of antimycin, in a formulation referred to at the time as Fintrol 5, 15, and 30, for fish removal up to the time of publication describes the concentrations of antimycin that killed various species of fish in Canada, Guatemala, and the United States when added directly to a water body, including common carp, noting that common carp did not try to avoid antimycin [575]. In common carp erythrocytes (red blood cells) incubated with antimycin A, oxidative phosphorylation is inhibited, resulting in degradation of glucose [576]. Research with common carp found that microparticle encapsulated antimycin A levels > 4 mg/kg in a corn-based diet could be effective at controlling common carp while not significantly affecting percid or centrarchid fishes [577]. The 96-h LD_{50} for oral gavage-administered antimycin A in ethanol is 0.66 mg/kg wet mass of grass carp; for antimycin A in corn oil it is 0.99 mg/kg [578]. Extensive testing of antimycin A toxicity under various water quality conditions and for various life stages were conducted for 31 species of fish, including common carp and goldfish, by [579]. Research from the Fish Farming Experiment Station in Stuttgart, Arkansas found 3 ppb of antimycin A killed grass carp (Meyer, F.P., pers. comm. in [579]).

Due to interest in the use of antimycin A as a pesticide for fish species, the stability of antimycin A under various field and laboratory conditions has been assessed. Environmental conditions, such as pH, sunlight, and temperature, can alter the effectiveness of antimycin A over time. Research into the stability and effectiveness of antimycin A found its concentration half-life to be seven hours to six minutes for pHs ranging from 4.5 to 11.0, respectively [580]; alkalinity and hardness or suspended solids did not have a significant effect on antimycin A half-life. They also found that the half-life of antimycin A is less than 10 min in sunlight and fish mortality rate increased by a factor of three for 24 °C compared to 4 °C. Biological activity half-life of antimycin A ranged from 310 h at pH of 6 to 6.5 down to a half-life of 1.5 h at pH of 10 [581]. The methods developed to test the half-life of antimycin A are presented by [582].

Comparison among Pesticides

There are several pesticides that have been used to control invasive fishes, and many studies compare different pesticide treatments. Due to the large number of studies on both rotenone and antimycin A as control measures for grass carp, other focal carps, and common carp, these compounds are commonly compared [583]. A review by [584] concludes antimycin A and rotenone are effective at eradication of target non-native fish in 89% and 75% of studies reviewed, respectively. The review and comparison of rotenone and antimycin A as pesticides is discussed by [562]. Unlike rotenone, fish do not display avoidance behavior in the presence of antimycin A (Ref. [562] citing [572,585]. Based on [572], [562] note that antimycin A is more toxic than rotenone to fish. Acute 12-h toxicity studies comparing antimycin A and rotenone (Prenfish) cannot be used to predict mortality in bighead and silver carp because apparently moribund fish can recover from rotenone exposure, and antimycin A is slower-acting than rotenone [586]. To induce 100% mortality of common carp and white suckers (*Catostomus commersonii*) in a flowing-water system, 6 h of exposure to 5 ppb of antimycin A are required compared to 18 to 24 h at 50 ppb of rotenone [587]. Temperature is more important than concentration in necessary exposure time for both compounds, with longer contact times required in colder water [587]. Effects are often reversible after 4 to 5 h for rotenone but irreversible for antimycin A after first signs of distress [587]. Sampling of fish using rotenone and antimycin A is discussed by [588]. Higher sensitivity to rotenone than Fintrol (an antimycin A formulation) has been suggested for silver and bighead carp by [589]. However, there was later concern that the antimycin A in the Fintrol used [589] was degraded (Duane C. Chapman, USGS, Written, 22 September, 2022), limiting true comparison. A difference in molecular response to oxidative stress after exposure to rotenone between the very sensitive silver carp and the less sensitive bighead carp has been demonstrated and may explain the differences in sensitivity between these species [590]. In general, these studies show that rotenone is less selective, requires a higher concentration to induce toxicity, is more likely to deter grass carp, and fish are more likely to recover from short-term exposures than with antimycin A.

The work of [591] related to the application of rotenone as well as antimycin A, salicylanilide I, and GD-174 (2-[digeranylamino]-ethanol) in the Chicago Sanitary and Shipping Canal (CSSC) to control invasive populations of carps and is discussed by [425]. The 96-h LC_{50}s ranged from 0.570 to 1.00 ppb for antimycin A, 1.5 to 9.35 ppb for saclicylanilide I, 50 to 80 ppb for Noxfish (5% rotenone), and 50 to 550 ppb for GD-174 for grass, silver, bighead, and common carp as a group [592]. Earlier research by [593] found the 96-h LC_{50} for grass carp is 0.255 ppb for antimycin A (Fintrol), 8.59 ppb for salicylanilide I, 44.5 ppb for juglone, 63 ppb for rotenone (Noxfish), and 141 ppb for niclosamide (Bayluscide).

A comparison of the effects of commonly used pond treatments malachite green, $KMnO_4$, formalin, copper sulfate, and rotenone on silver and bighead carp was carried out by ref. [594]. In these species, 100% mortality occurs at 0.4 ppm malachite green within 48 h in silver carp and within 72 h in bighead carp; 100% mortality occurs at 5.0 ppm $KMnO_4$ within 20 h in silver carp and 4.0 ppm $KMnO_4$ within 20 h in bighead carp, and 90 ppm formalin at 36 h in silver carp. Formalin induces 12% mortality or lower in bighead carp exposed to up to 90 ppm for up to 96 h and concentration (up to 90 ppm) tested. Copper sulfate at 2.0 ppm caused 100% mortality in both species within 24 h. Rotenone at 0.005 ppm caused 100% mortality in silver carp in 24 h, while 0.01 ppm caused 100% mortality in both species in 6 h [594]. For fathead minnows, the activities of permethrin and pydrin are affected by the presence of Canadian waterweed, but the activities of rotenone and antimycin A are not affected [595]. The activities of rotenone, antimycin A, permethrin, pydrin, and salicylanilide are severely inhibited by the presence of bentonite clay; for example, 27 times more pydrin is needed to maintain activity in the presence of 1 g/L of bentonite [595].

Effects of Pesticides on Non-Target Organisms

The largest drawback of both rotenone and antimycin A is that they are both non-selective pesticides that can affect non-target fish, though some carp species may be more sensitive than other non-cypriniform species. Antimycin A is more toxic to bighead and silver carp when delivered as microparticles of a size similar to those targeted by those species during feeding [561] than to native fish species, including bluegill and largemouth bass [561], with toxicity being greater in warmer water [596]. Rainbow trout (*Oncorhynchus mykiss*), a salmonid fish species with invasive populations outside its native range in western North America, required longer exposure to kill using antimycin A compared to rotenone when exposed to concentrations typically used for eradication [597]. A significant positive relationship was found between rainbow trout size and time of death for both compounds; however, this relationship was limited in its ability to predict death based on size. Antimycin A (Fintrol) ranging in concentrations from 6 to 12 μg/L killed all grass carp and the great majority of green sunfish while not killing any channel catfish while 2 mg/L of rotenone (Noxfish) essentially killed all fish present [598]. Aqueous, low-dose antimycin A (1 to 2 ppb), used use to decrease stunting in bluegill populations via decreased density of small individuals, is only effective in the first year when used alone [599]. Including stocking of walleye (*Sander vitreus*) as predators or catch and release of large bluegill and their predators along with the antimycin A treatment is effective at reducing stunting, with antimycin A alone stunting persisted [599]. A dose of 8 ug/L of antimycin A added to high-gradient streams for 8 h was effective at killing brook trout and rainbow trout [600]. The uptake rate, distribution, and elimination of antimycin A in brown bullhead (*Ameiurus nebulosus*) is described by [601]. Macroinvertebrate density in a Wisconsin stream was drastically reduced 2 days after exposure to 17 to 44 ug/L of antimycin A [602]; one year after exposure, the macroinvertebrate community was restored. A risk assessment of the use of antimycin A for the State of Washington provides an extensive review of what is known about antimycin, at the time of publication, and its toxicity to aquatic and terrestrial organisms and an environmental risk assessment [603]; focal carp were not included. Much of the information cited by [603] associated with fishes came from the U.S. Environmental Protection Agency [604–606], and the USEPA ECOTOX database which include tables of 96-h LC_{50}s for numerous recreation and bait fishes, invertebrates, amphibians, and birds.

There are many studies documenting the relative toxicity and use of multiple pesticides between fish species. These studies do not necessarily focus solely on antimycin A and rotenone, but many studies include those compounds in assays of several compounds. The advantages and disadvantages of using rotenone, endosulfan, antimycin A, and acrolein to control invasive fishes is described by [607]. In Minnesota, ruffe (*Gymnocephalus cernuus*) exhibited similar sensitivity to antimycin A and rotenone as brown trout and are more sensitive to antimycin A and rotenone than yellow perch. Ruffe are also much more sensitive to TFM than both brown trout and yellow perch [608]. For four potentially invasive species in North Dakota, gizzard shad (*Dorosoma cepedianum*), rainbow smelt (*Osmerus mordax*), common carp, and Utah chub (*Gila atrarla*), eggs are generally more resilient than larvae when exposed to different potentially toxic compounds, including rotenone, $KMnO_4$, chlorine, acrolein, cyanide, fluoride, ammonia, and nitrite [609]. Of those compounds, the most toxic to eggs and larvae, listed from highest to lowest toxicity, are rotenone, chlorine, and $KMnO_4$ [609].

The effects of various biocides on macrobenthos have been assessed. Antimycin A concentrations from 20 to 40 mg/L or rotenone concentrations from 0.5 mg/L to 2.0 mg/L have no effect on pond macrobenthos [610]. The 96-h LC_{50}s for the Asiatic clam (*Corbicula manilensis*) exposed to six pesticides (99% antimycin A or Fintrol, 5% rotenone or Noxfish, GD-174, Sal 1, Juglone, and sodium nitrite), two lampricides (Bayer 73 and TFM), one collecting aid (isobornyl thiocyanoacetate or Thanite), three therapeutants (formalin or 37% formaldehyde, malachite green oxalate, and nifurpirinol or Furanace), two disinfectants (HTH and betadine solution), and one oxidizing agent ($KMnO_4$) is provided by [611]. They found antimycin A, with a 96-h LC_{50} of 0.065 mg/L, is the most toxic to the Asiatic clam among the pesticides and lampricides tested while nifurpirinol, with an LC_{50} of 7.6 mg/L, is most toxic among the therapeutants and disinfectants tested. At the rate recommended for usage on the target animals these compounds were designed to control, none of these compounds were harmful to the Asiatic clam.

Pesticide Delivery Systems

Due to the risk of affecting non-target organisms with aqueous pesticide exposures, development of alternative, more selective pesticide delivery systems is an area of high research interest. For information on aqueous exposures to pesticides, see 'Section Rotenone,' 'Section Antimycin A,' and 'Section Comparison Among Pesticides', all within Section 3.2.2. Some food-based technologies have been specifically targeted at invasive fish populations. Other technologies that have been developed for intentionally introduced individuals and aquaculture (for example, bio-erodible pellets, vaccines) have components that could be further developed for application to established invasive populations of carps.

Use of food as a pesticide delivery system, especially the use of pellets containing rotenone and antimycin A, has been utilized to target grass carp and common carp.

Pesticide-containing food pellets are often called fish management baits (FMBs). Many fishes must be pre-conditioned to consume the food pellets before consuming FMB [392]. While both rotenone and antimycin A FMBs may be useful for grass carp control, available evidence suggests antimycin A pellets are more effective. This pattern may be due to the lower palatability of rotenone pellets (Ref. [583] as cited by [578]) and the higher toxicity of antimycin A, as discussed in 'Section Comparison Among Pesticides' within Section 3.2.2. Grass carp have much higher consumption and mortality rates with antimycin A pellets compared to rotenone pellets; these factors mean that rotenone pellets sometimes induce 0% mortality in grass carp [612]. Prentox Prenfish™ Grass Carp Management Bait is a patented, commercially available rotenone FMB for grass carp [583,613] Research leading up to this patent found that grass carp did not consume non-toxic training bait (FMB-T) containing fishmeal, chicken-byproduct meal, and brewer's yeast, but that they would consume FMB-T formulated with alfalfa [583]. The use of alfalfa, based FMB-T to attract and condition grass carp and then feeding toxic rotenone FMB pellets, such as Prentox Prenfish™ Grass Carp Management Bait, to kill them is highly effective [583]. Other researchers have also noted reductions in grass carp numbers when rotenone baits are used (Ref. [614] as cited by [612]). However, pelleted rotenone bait is not palatable to grass carp under some conditions, even after being able to attract and train them to feed on non-toxic training bait [615]. Bait labelled Prentox or FBM is up to 79% effective at removing triploid grass carp (Ref. [616] as cited by [617]). During 120 trials with FMB at two Florida lakes, only 18 non-target fish were found dead, while more than 400 grass carp were successfully removed [617]. Given it is mostly selective to attracting grass carp, this rotenone FMB could be effective if the feeders consistently attract most of the naïve grass carp. Rotenone FMB was more effective at removing grass carp in a new area than removing grass carp during retrials in the same area [617]. Common carp reject rotenone-laced food pellets [618,619], but when force fed the pellets, the food is toxic [618].

Delayed release, bio-erodible capsules containing lethal toxins have been tested in grass carp introduced for plant management to prevent establishment of these introduced individuals. The potential use of bio-erodible capsules that would release rotenone to euthanize the grass carp at a given time in the future has been studied by [620]. They tested stainless steel dowel pin retention (i.e., capsule surrogate) over 8 months at various locations in the body of grass carp, finding 90% retention rate for pins implanted perpendicular to the body axis in the throat region. They also describe four possible polymers that could be used to make the bioerodible capsules or plugs for a stainless-steel capsule: poly[bis(p-carboxyphenoxy) propane anhydride], poly[bis(p-carboxyphenoxy) hexane anhydride], poly-l-lactide, and poly(ε-caprolactone). These four polymers are biocompatible and hydrophobic, with no or low toxicity, but only poly-l-lactide did not exhibit surface erosion [620]. Another potential form of bio-erodible capsule described as an 'implant and forget' device is outlined in a United States patent application [621]. Though these studies have focused on controlling intentionally introduced populations, depending on timing of dissolution, this technology could also be deployed to conceal toxins long enough for fish to ingest the capsules allowing them to degrade in the gut and induce mortality.

Other potential methods for delivering toxins to invasive populations of carps could be derived from technologies used to deliver vaccines and micro-particles. Potential vaccines [329,622–627] have been examined for controlling grass carp reovirus which causes severe hemorrhagic disease. *Bacillus subtilis* spores genetically modified to not germinate and to contain up to two grass carp reovirus (GCRV) antigens on their surfaces are the basis of an oral GCRV vaccine that is not degraded in the intestine [628]. An immersion-administered vaccine against grass carp reovirus (GCRV) using copies of the GCRV gene vp4 conjugated with single-walled carbon nanotubes (SWCNTs) elicits a stronger immune response than naked copies of *vp4* [629]. Additionally, copies of a specific subsection of *vp4* conjugated with SWCNTs provide greater protection against mortality from GRCV than copies of the entire *vp4* gene conjugated with SWCNTs. A test of various vaccination regimes based on a lysate made from whole-cell *A. hydrophila* found that the following factors made the vaccine more effective: injection instead of immersion, addition of SWCNT to link the lysate, and 10 mg lysate/L instead of 5 mg/L [630]. This test found that immersion in 10 mg lysate/L with SWCNT resulted in 30% relative percent survival, and injection with 10 mg lysate/L with SWCNT resulted in 80% relative percent survival. The optimal procedure for administering the GCRV *vp4* subsection + SWCNT vaccine developed by [629] is a 12-h immersion, 10 mg antigen/L, and a fish density of 15 fish/L [631]. This vaccination procedure reduces mortality from 100% (control) to 21.67% during exposure to GCRV-JX02. For common carp, an immersion-administered, antiviral vaccine that is absorbed through the skin has been developed by filling single-walled carbon nanotubes with an antigenic protein [632]. Potential vaccine delivery through *Bacillus subtilis* spores [633], silkworm pupae [624], and carbon nanotubes as a carrier molecule [634] have been examined for these grass carp reovirus vaccines. Microparticle encapsulated antimycin A added to a corn-based diet has been tested for controlling common carp [577]. Both silver and bighead carp remove small (50 to 100 micrometer) and large (150 to 200 micrometer) micro-particles with silver carp removing more small than large particles [635]; this follows food particle size selection historically found in these two species [636]. Optimal food particle sizes for common carp are 125 to 300 um, 300 to 500 um, 300 to 790 um, and 500 to 1000 um carp fry weighing 15 to 23 mg (TL 13 to 18), 46 to 97 mg (TL 17 to 22), 105 to 209 mg (TL 20 to 25), and 210 to 466 mg (TL 24 to 31), respectively [637]. Evacuation rates of 42.7 um and 1086 um microplastic particles in common carp are 7.3 h and 4.6 h, in the range of food particles and suggesting passive excretion [638]. Fluorescent latex microspheres have been used to assess onset of feeding in larval silver carp [639]. These studies on micro-particles could be applied in future research using pesticides-containing micro-particles designed to target invasive populations of carps, especially filter-feeding species. For example, the potential toxicity of quantum dot semiconductors (nanoparticles that fluoresce), to crucian carp has been assessed as a potential drug delivery system [640].

3.2.3. Metals

Numerous studies have been conducted on the toxicity of a variety of metals, especially heavy metals, and metal salts to carp species. Table 7 summarizes the 96-h LC_{50}s for various metals in grass carp that were reported in the papers reviewed.

Cadmium

Several studies have looked at the toxicity of cadmium (Cd) to grass carp and other carps. The 24-h LC_{50} of $CdCl_2$ is 30.58 mg/L $CdCl_2$. A number of sublethal effects have also been reported. Concentrations as low as 50 ug/L Cd, levels considered safe to humans, resulted in reduced growth in grass carp [641]. Exposure of Cd at 1.0 mg/L reduced hatching rate of grass carp eggs by 25% (Ref. [2] citing [642]). Grass carp eggs exposed to 100–300 ppm Cd starting 6 h post fertilization altered isoenzyme expression and development [643]. Grass carp exposed to 0.2 mg/L Cd during embryonic development and hatching exhibited increased heart rate during that process [550]. Histopathology revealed sublethal effects of Cd including gill ray hyperplasia, proliferation and focal loss of lamellar epithelium, subepithelial edema, and vacuolation of cytoplasm of lining epithelium in the gills, accumulation, necrosis, and congestion in the liver, hydropic swelling and necrosis in the kidneys, and inflammation and necrosis in the muscular tissue [644]. Exposing grass carp to 1 mg/L duckweed (*Lemna gibba*) and 5 mg/L of dried *Spirulina platensis* concurrently with 5 mg/L $CdCl_2$ significantly reduced Cd bioaccumulation in the liver and muscles and had fewer histopathological alterations after a 15-day exposure than those exposed to Cd alone [644]. These findings were in agreement with other research suggesting that compounds that could chelate with Cd would reduce metal uptake (Ref. [644] citing [645]). Cd levels that are a tenth of the LC_{50} can alter grass carp ventilatory responses [646]. Vitamin E provides limited protection from Cd toxicity with metallothionein providing moderate protection [647]. Allograft inflammatory factor-1 appears to be involved in Cd-induced stress in grass carp [648]. Alterations in antioxidant responses and neurological parameters are induced by 2.97 mg/L Cd, but the biocide tributyltin reduces these effects [649].

There is additional toxicity data available for other carp species. The safe concentration of Cd in common carp was estimated to be 0.25 mg/L [650]. Concentrations as low as 0.01 mg/L Cd have resulted in stress response and impaired gas exchange in silver carp [651]. In Prussian carp, exposure to waterborne Cd at 500 µg/L for four weeks severely damages the intestinal lining, likely reducing the digestive and immune function of the intestine [652]. Prussian carp eggs are resistant to waterborne Cd, with concentrations up to 1 mg/L Cd having no effect on development or hatching [653]. However, 10 mg/L Cd did result in a significant increase in deformed larvae. Common carp larvae exposed to Cd at 0.2 mg/L Cd (as $CdCl_2$) starting at 1 day post hatch had anterior and posterior swim bladder chambers that are 20% smaller than unexposed controls, and about 20% of fish did not experience inflation of the anterior swim bladder chamber [654]. Exposure to Cd during development is also known to cause egg swelling (K. Lugowska, 2005 as cited in [655]), acceleration of hatching (K. Lugowska, 2005 as cited in [655]), physical malformations [655], and decreased hatching success (Ref. [655] citing J. Sikorska and K. Lugowska, 2005) in common carp.

Copper

Copper (Cu) is also known to have lethal and sublethal effects. Cu exposure at 0.16 mg/L reduced hatching rate of grass carp eggs by 10% (Ref. [2] citing [642]). Short copper exposures (<96 h) resulted in hematological changes in 8.5 g grass carp [656]. Exposure to 1 mg/L copper for 96 h resulted in decreased hemoglobin, red blood cells, and monocytes, and increased lymphocytes [656]. Grass carp 1-h ventilation frequency and amplitude increased with exposure to Cu^{2+} [657]. Copper at 100 µM decreased viability of grass carp hepatocytes in vitro by inducing changes in lipid metabolism, but concurrent supplementation of 5 µM Se protected against these effects [658]. Increasing the Se concentration to 10 µM no longer afforded protection against reduced cell viability. Increased hardness decreased toxicity of Cu to grass and silver carp and loach fry (*Misgurnus mizolepis*) [659]. The combination of oxytetracycline and Cu in solution compared to either alone resulted in reduced growth and feed utilization along with numerous negative physiological effects [660].

There is additional toxicity data available for other carp species. Copper sulfate at 0.15 mg/L or greater is toxic to larval silver carp [661]. Common carp larvae exposed to Cu at 0.2 mg/L Cu (as copper sulfate, $CuSO_4$) starting at 1 day post hatching had anterior and posterior swim bladder chambers that were 30% smaller than unexposed controls and about 24% of fish did not experience inflation of the anterior swim bladder chamber [654]. Exposure to Cu during development is also known to cause egg swelling (Ref. [655] citing [662]), retardation of development and hatching (Ref. [655] citing [663] and K. Lugowska, 2005), physical malformations [655], decreased hatching success (Ref. [655] citing [662–664]), and increased mortality during development (I. Słomińska, 1998 as cited in [655]) in common carp. Exposure to Cu also alters the oxidative stress response in common carp at 65 ug/L which is 10% of the 96-h LC_{50} for this species [665]. The hormone and ion regulation of common carp in response to this same concentration (65 ug/L) after exposures lasting up to one month are described by [666]. The safe concentration of Cu in common carp was estimated to be 0.02 mg/L [650]. In common carp, copper oxide nanoparticles and ionic $CuSO_4$ are similarly toxic when consumed at 100 and 1000 mg Cu/kg diet [667].

Lead

Lead (Pb) is a heavy metal known to have lethal and sublethal effects on grass carp. Grass carp eggs exposed to 100 to 300 ppm Pb starting 6 h post fertilization altered isoenzyme expression and development [643]. Exposure to Pb at 1 mg/L reduced hatching success of grass carp eggs by 10% (Ref. [2] citing [642]). Grass carp exposed to 3.0 and 4.0 mg/L

Pb during embryonic development and hatching exhibited increased heart rate during that process [550]. Short exposures (<96 h) to Pb resulted in hematological changes [668]. Exposure to 216 mg/L Pb for 96 h resulted in decreased hemoglobin, red blood cells, and monocytes [656]. Concentrations as low as 5.0 ug/L Pb, levels considered safe to humans, resulted in reduced growth in grass carp [641]. Exposure to 1 mg/L of Pb for 42 days caused damage to the intestinal lining of grass carp [669]. Glucose regulated protein of the endoplasmic reticulum of grass carp cells helps protect the cells from exposure to Pb and thermal stress [670,671]. Lead-exposed grass carp given dietary garlic (*Allium sativum*) and Fu-ling (*Wolfiporia cocos*), alone or in conjunction, had lower muscle and liver lead levels after 48 h compared to carp without dietary supplementation [672].

Some additional toxicity data are available for other carp species. In common carp, Pb is also known to cause egg swelling (I. Słomińska, 1998 as cited in [655]), retardation of development (Ref. [655] citing [663] and K. Lugowska, 2005), physical malformations [655], decreased hatching success (Ref. [655] citing [663]), and increased mortality during development (I. Słomińska, 1998 as cited in [655]). Injection of $CeCl_3$ ameliorates the effects of Pb exposure in crucian carp [673].

Mercury

Mercury appears to be highly toxic to grass carp. Exposure to Hg at 0.1 mg/L reduced hatching success of grass carp eggs by 80% (Ref. [2] citing [642]). Grass carp 1-h ventilation frequency and amplitude increased with exposure to Hg^{2+} [657]. Finally, a 96-h exposure of juvenile grass carp to 15 µg/L CH_3HgCl disrupted cellular respiration in the gills and liver [300].

Other Metals and Mixtures

There are some toxicity data available for other metals including zinc (Zn), nickel (Ni), chromium (Cr), silver (Ag), aluminum, and titanium. A Zn exposure of 10 mg/L reduced grass carp egg hatching rate by 10% (Ref. [2] citing [642]). Grass carp 1-h ventilation frequency and amplitude decreased with exposure to Zn^{2+} [657]. The 96-h LC_{50} for juvenile silver carp is 68 mg/L for zinc sulphate [674].

The safe concentration of Zn in common carp was estimated to be 0.7 mg/L [650]. In developing common carp, as nickel increased, percentage of eggs that hatched decreased and percent abnormal larvae increased [675].

Short Cr exposures (<96 h) resulted in hematological changes in grass carp [668]. Exposure to 18 mg/L Cr for 96 h resulted in decreased hemoglobin, red blood cells, and monocytes in grass carp [656]. Exposure to Cr at 60.24 mg/L reduced hatching rate of grass carp eggs by 5% (Ref. [2] citing [642]. Replacing 25% of grass carp aquarium water with Cr-containing, untreated industrial leather tanning effluent caused 100% mortality within 96 h [676].

Silver (Ag) is particularly toxic to grass carp eggs causing a 45% reduction in hatching rate at 0.01 mg/L Ag. Titanium dioxide nanoparticles enhanced the toxicity of Ag nanoparticles along with decreasing weight gain in common carp [677]. Exposure of grass carp to 0.1 mg/L of aluminum, the concentration noted as considered protective of aquatic life, resulted in oxidative stress and neurotoxicity [678]. Acute toxicity tests of titanium dioxide nanoparticles on juvenile common carp did not produce lethal effects but did result in physiological changes, such as liver hyperplasia and gill and skin hypertrophy [679]. Magnetite (Fe-based) nanoparticles produced negative phycological and genotoxic effects in Prussian carp [680]. The effects of metal mixtures have also been assessed. Exposure of juvenile common carp to an environmentally relevant mixture of metals containing Cu (4.8 µg/L), Cd (2.9 µg/L), and Zn (206.8 µg/L) only had minimal, sublethal effects on the gills and metabolism at a water temperature of 20 °C; there are no discernable negative effects of the metals mixture at 10 °C [681].

Table 7. A summary of the grass carp 96-h LC_{50}s for various metals reported in studies included in this literature review. Size refers to the reported size/age of carp tested. * Converted to active ingredient concentration.

Metal	Form	Size	Species	Concentration (mg/L Active Ingredient)	Citation
Cadmium	$CdCl_2$	6–8 g	Grass	12.3 *	[644]
Cadmium	$Cd(NO_3)$	1.84 g	Grass	18.47	[657]
Cadmium	$CdCl_2$	0.4 g	Common	2.51	[650]
Copper	$CuSO_4$	600 g	Grass	1.2–1.7	[682]
Copper	$CuSO_4$	Juvenile	Grass	0.09	[657]
Copper	$CuSO_4$	0.4 g	Common	0.2	[650]
Lead	-	Juvenile	Grass	576	[683]
Mercury	$HgCl_2$	1.84 g	Grass	0.23	[657]
Mercury	-	Fry	Grass	0.362	[683]
Mercury	$HgCl_2$	45.37 g	Grass	0.39	[684]
Mercury	$HgCl_2$	20 g	Grass	0.62	[685] citing [686]
Nickel	$NiCl_2$	6.0 g	Silver	57	[674]
Silver	polyvinylpyrrolidone-coated nanoparticles	11.6 g	Common	0.31	[687]
Zinc	$ZnCl_2$	1.84 g	Grass	31.37	[657]
Zinc	$ZnCl_2$	20 g	Grass	11.46	[685] citing [686]
Zinc	$ZnSO_4$	0.4 g	Common	7.05	[650]
Zinc	$ZnSO_4$	6.0 g	Silver	68	[674]

3.2.4. Other Toxicants

Biotoxins

Research has been conducted on mycotoxins (toxins produced by fungi) on carps; some of these compounds are food related. The effects of mycotoxins on fish growth and health have been reviewed by [688]. The discussion of aflatoxins (AFB1; secondary metabolites of *Aspergillus flavus* and *Aspergillus parasiticus* fungi) and their negative effect on animals was carried out by [689,690]. The findings provide support for effects of different levels of exposure to AFB1 on growth and development of deformities in juvenile grass carp. Smaller juvenile grass carp (initial mass ≈ 3 g) fed up to 4979.2 µg/kg diet AFB1 suffered no obvious ill effects and exhibited growth rates equivalent to control group fish [691]. No mortality was found for grass carp fed diets containing up to 100 ppb AFB1 for seven days [692]. However, when grass carp consumed diets with 75 to 100 ppb AFB1 for seven days, lesions formed on the liver, kidney, intestine and gills, and weight gain decreased compared to control fish [692]. For Prussian carp, 2000 µg/kg diet of AFB1 did not affect growth or liver function but did decrease fecundity [693]. Support for effects of different levels of exposure to deoxynivalenol, a common animal feed mycotoxin, on development of deformities and intestinal alterations in grass carp has been documented [694]. Based on enteritis morbidity the reasonable dose of deoxynivalenol for grass carp was 251.66 µg/kg diet [691]. Grass carp fed diets containing zearalenone, a mycotoxin and common feed contaminant, have increased susceptibility to *hydrophila a*-caused enteritis morbidity at dietary zearalenone levels of 1000 to 2500 µg/kg diet [695]. Even in the absence of *A. hydrophila*, dietary zearalenone can cause intestinal damage in the form of lesions, oxidative damage, and tight junction breaches in juvenile grass carp at levels of 1000 to 2500 µg zearalenone/kg diet [696]. Dietary exposure to the mycotoxin Ochratoxin A, starting at concentrations of 1209 ug/kg diet, depressed weight gain and growth rate and induced oxidative damage in the intestines of juvenile grass carp, disrupting intestinal integrity and increasing intestinal permeability [697].

The effects of cyanotoxins (toxins produced by cyanobacteria), especially microcystins, have also been assessed in various cypriniform species. Blooms of cyanobacterial species such as *Microcystis* spp. can kill grass carp and other fish species in aquaculture systems [698]. Increased kaironomes, released by active predators, increased microcystin production in *Microcystis aeruginosa* [699]. The LC_{50} for common carp exposed to *Microcystis* was 7.3 mln algal units/dm^3 [700]. Microcystins produced by cyanobacteria were hepatotoxic and immunotoxic to silver carp [701] and caused dissociation of organ cells, necrosis, and hemorrhage [702]. They also cause apoptosis and necrosis in bighead carp [703]. A 96-h exposure of grass carp larvae to a combination of 100 µg/L purified microcystin-LR and 0.264 mg/L ammonia nitrogen induces gene expression changes consistent with oxidative stress, but it does not result in mortality [704]. The LD_{50} of microcystins to silver carp is 270 ug/kg body weight [705]. Extracts of the cyanobacteria genus *Anabaena* containing 83 to 333 µg/L of anatoxin-a reduce hatching success of common carp eggs; however, pure anatoxin-a at the same concentrations has no effect on hatching success [706]. Common carp larval growth is less when fed *Artemia nauplii* cultured on *Microcystis aeruginosa* compared to control larvae [707]. Grass carp force-fed the toxic cyanobacteria *Nostoc muscorum* exhibited detrimental effects on gill filaments, intestine, liver, and kidney [708]. Grass carp are susceptible to avian vacuolar myelinopathy, a waterbird neurological syndrome caused by a cyanotoxin [709]. Exposure to both the aquatic bloom-causing actinobacterium *Streptomyces griseus* and isolate of an exotoxin it produces, streptomycin, causes deformities in the gills of common carp fry [710].

Work has been carried out on the assessment of the effects of phytotoxins (toxins produced by plants) on carp species and their potential as mechanisms for control of non-native carps (Table 8). Tea tree oil is an effective anesthetic for common carp at the lowest concentration of 0.5 mL/L with mortality occurring in exposures longer than 30 min [711]. Likewise, clove oil is an effective anesthetic for common carp at 30 mg/L [712]; Ref. [713] found a similar anesthetic concentration of 30 to 50 mg/L. Medicinal plant extracts from *Piper betle* and *Psidium guajava* are effective at killing common carp at 0.4 and 0.3 mg/L, respectively, resulting in 75% and 83% mortality within 20 min [714]. Alkaloids extracted from the rhizomes of the aquatic plant *Nuphar lutea* produced an LC_{100} of 4.0 mg/L and higher for larval common and grass carp [715]. Grass carp orally dosed with a water extract of water buttercup (*Ranunculus aquatilis* var. *diffusus*) develop intestinal lesions; the toxin believed to cause these effects is ranunculin [216]. Research of detoxification of *Jatropha curcas* kernel meal as a food source for common carp production, [716], referring to [717,718], describes the high level of antinutrients such as trypsin inhibitor, lectin, phytate, and the presence of toxic phorbol esters, which make this food source toxic to carp.

Some common plant-based food sources used in commercial grass carp production naturally contain antinutrients; the effects of these compounds on grass carp have been studied due to their potential implications for aquacultural production. Phytic acid is an antinutrient that naturally occurs in some plants, including soy. Experimental dietary supplementation of phytic acid decreases weight gain, feed intake, feed utilization, and digestive enzyme activities of grass carp [719]. To prevent reduced weight gain and avoid additional enteritis morbidity during *A. hydrophila* infection, the maximum allowable dietary levels of phytic acid are 2.17% and 1.68%, respectively [720]. The maximum allowable level of dietary phytic acid for grass carp to avoid additional head kidney lesion morbidity during *A. hydrophila* infection is estimated at 1.79% of the diet [721]. Glycinin, a different component of soybean, supplemented to a basal data at 8%, decreases the growth performance of grass carp by inducing intestinal damage and decreasing amino acid absorption capacity, but much of this effect is mitigated by simultaneously supplementing with 1.2% glutamine [722]. The same trial found that glycinin impaired immune function by reducing intestinal immune components and caused inflammation mediated through PKC-ζ/NF-κb and mTORC1 signaling [723]. Finally, this trial found that glycinin induced DNA fragmentation and other apoptosis indices in the mid and hindgut and disrupted the intestinal structural integrity, but co-administration of glutamine mitigated these effects [724].

Erucic acid, an antinutrient found in rapeseed (*Brassica napus*) meal, can lead to increased *hydrophila a*–caused enteritis morbidity if present in grass carp diet at levels > 0.53% [725]. Dietary erucic acid levels of > 0.64% can reduce growth rate in grass carp [726].

Table 8. A summary of the 96-h LC_{50}s of various phytotoxins to grass carp. Size refers to the reported size or age of grass carp tested.

Source	Average Size	Carp Species	Concentration (mg/L)	Citation
Babchi bark (*Cullen corylifolia*)	101 mm	Grass	9.4	[727]
Bai Wei (*Vincetoxicum atratum*)	101 mm	Grass	39.5	[727]
Clove oil	Eggs, larvae	Common	18.10	[712]
Morus alba bark	22.2 g	Grass	38.0	[728]
Morus alba bark	22.2 g	Grass	26.9	[728]

Herbicides, Fungicides, and Pesticides

The effects of a variety of herbicides on cypriniforms, including grass carp, have been studied. Table 9 provides a summary of the 96-h LC_{50}s for various herbicides, fungicides, and pesticides. Application of herbicides used in support of rice production, butachlor thobencarb at 1.5 kg/ha and oxyfluorfen at 0.25 kg/ha, to rice fields stocked with grass carp found various effects on the gills, muscle tissue, and liver of the stocked grass carp [729]. The common carp 36-day LC_{50} for the symmetrical triazine aquatic herbicide terbutryn is 3.06 mg/L [730]. Bighead carp exposed to 500 ug/L of the herbicide Acetochlor exhibited decreased growth compared to control fish [731]. For common carp embryos and larvae, the 31-day LC_{50} for terbuthylazine-desethyl is 441.6 ug/L [732] and the no-effects-concentration (NOEC) is 160 ug/L for terbuthylazine [733]. The herbicide atrazine causes apoptosis in a grass carp cell line [734]. A three-week exposure of common carp to atrazine at 3000 µg/L caused behavior abnormalities and is associated with increased occurrence and severity of infection by the parasites *Trichodina epizootica*, *Ichthyophthirius multifilis*, and *Dactylogyrus extensus* [735], and atrazine at 1000 µg/L is consistently associated with increased occurrence and severity of infection by *T. epizootica*, *I. multifilis*, and *D. extensus* in common carp across a 12-week trial; on some weeks of the 12-week trial, there was increased occurrence and severity of infection with the parasites *T. epizootica* and *D. extensus.*

Some research has been conducted on the effects of fungicides on carps; see also 'Section Antimycin' within Section 3.2.2. The toxic effects of thiram, a fungicide, at concentrations ranging from 1.12 to 28.98 ppm based on metabolic profiles in bighead and silver carp cell lines is provided by [736]. For the fungicides pyribencarb, kresoxime-methyl, and andazoxystrobin, the concentrations where succinate-cytochrome c reductase activity in common carp hepatopancreatic cells is 50% inhibited are 5.100 µM, 0.220 µM, and 0.770 µM, respectively [737]. At real-world, application-level concentrations of 30, 38, and 50 mg/L, fosetyl-Al and fenamidone based fungicide histological effects occur in bighead carp [738]. Ziram is used to treat a variety of plant diseases and results in cytotoxic effects in rat hippocampal astrocytes [739]. The fungicide Ziram (zinc dimethyldithiocarbamate) was not toxic to grass carp of up to a concentration of 250 mg/kg through gavage or direct delivery to the gut of the fish, but was toxic at 150 mg/kg via intraperitoneal injection [740].

The effects of a variety of pesticides on carps and other fish species have also been studied. It appears that 60 uL/L of the biopesticide azadirachtin disrupts common carp metabolism [741]. The pesticide 'Triology,' which contains neem oil extracted from the neem tree (*Azadirachta indica*), has a LC_{50} (time not given) of 112 mg/L [742]. The grass carp 48-h LC_{50} for the pesticide isothiazolinone is 0.53 and 0.41 mg/L at 15 and 25 °C, respectively [743]. The 35-day LC_{50} of the pesticide prometryne for young common carp is 2314 µg/L [744]. The pesticide glyphosate reduces embryo survival and egg hatching success in common carp at concentrations as low as 0.1 mg/L [745]. The pesticide dichlorvos affects behavior and causes mortality and deformities in zebrafish embryos [746]. The 24-h LC_{50} for common carp is 20 mg/L dichlorvos (Ref. [747] as cited by [746]). A commercial formulation of the synthetic pyrethroid fenpropathrin, Danitol, produced a 48-h LC_{50} of

3.589 ug/L in grass carp [748]. Grass carp challenged by *A. hydrophila* infection after exposure to the pesticide cypermethrin at 0.651 µg/L for 42 days had significantly higher 48-hr mortality rates compared to the control group infected with *A. hydrophila* without exposure to potentially toxic compounds [749]. Exposure to a combination of 0.651 µg/L cypermethrin and 0.3 µg/L of the antibiotic sulfamethoxazole (SMZ) for 42 days followed by *A. hydrophila* infection resulted in an even higher 48-h mortality rate than the cypermethrin-only group [749]; similar strength of response pattern to SMZ and cypermethrin was observed for increased inflammatory response in the gills of grass carp [750]. Using a similar exposure scheme these treatments caused neurological damage to the cerebellum accompanied by behavioral changes such as slowed movement, side-swimming and sinking to the bottom [751]. The pesticide fenitrothion decreases the activity of 3-beta HSD enzyme in the gonads of common carp [752]. A myriad of detrimental effects of Deltamethrin, a synthetic pyrethroid, have been documented in silver carp [753]. Negative hematological, morphological, and behavioral effects of the insecticide methyl parathion have also been documented in silver carp [754]. At real-world, application-level concentrations of 6.6, 10, and 20 mg/L, histological effects occur in bighead carp exposed to a thiamethoxam based insecticide [738]. As part of their work, they describe the work of [755] on grass carp as not showing anatomical or morphometric changes from exposure to the pesticide endosulfan. Endosulfan is highly toxic to grass carp and exposed fish exhibited fusion and disruption in the gills and severe congestion in high dosed fish [755]. The synthetic pyrethroid pesticide fenvalerate sublethal aqueous exposure (1.2 to 2 µg/L) damages red blood cells and causes gill lesions in grass carp [756]. Endosulfan at concentrations as low as 0.75 ppb/day causes DNA damage in grass carp blood cells within 7 days [757]. In a series of binary and tertiary mixtures of chlorpyrifos, endosulfan, and bifenthrin, all mixtures containing endosulfan were more toxic than the chlorpyrifos + bifenthrin mixture to grass carp fingerlings [758]. Across all treatment groups, however, grass carp are less sensitive to the pesticide mixtures than common carp. Trichlorofon, an organophosphate pesticide also used an antiparasitic treatment in aquaculture, can also affect grass carp. One effect of trichlorofon is reduced weight gain; in an experiment that added 0.25 mg/L tricholofon to an aquaculture tank once per week for five consecutive weeks, grass carp exposed to tricholofon had an average weight increase of 17.18%; control group fish had an average weight gain of 53.26% [759]. Exposure to trichlorofon pesticide spraying of the concrete ponds in which they were being held resulted in decreased egg production and egg weight index percentage during spawning in artificially induced female grass carp, with no spawning if water levels were dropped to 50 cm from 1 m [512]. The organophosphorus pesticide malathion, induces apoptosis in grass carp, resulting in cytotoxic effects [760]. As noted in 'Section Learning' within Section 3.2.4., exposure of common carp to sublethal levels of the pyrethroid deltamethrin affects their nervous system and their ability to learn [436].

Table 9. A summary of the 96-h LC_{50}s of various herbicides, fungicides, and pesticides to grass carp. Size refers to the reported size/age of grass carp tested.

Source	Type	Average Size	Carp Species	Concentration (mg/L)	Citation
dimoxystrobin	fungicide	40–50 g 180–200 mm	Common	0.039	[761]
pyraclostrobin	fungicide	40–50 g 180–200 mm	Common	0.042	[761]
trifloxystrobin	fungicide	40–50 g 180–200 mm	Common	0.090	[761]
atrazine	herbicide	33.63 g 141 mm	Grass	80	[762]
pretilachlor	herbicide	1–2 g	Grass	1.43	[763]

Table 9. *Cont.*

Source	Type	Average Size	Carp Species	Concentration (mg/L)	Citation
azadirachtin (NeemAzal)	pesticide	7.2 g 71 mm	Grass	0.73	[764]
chlorpyrifos	pesticide	8.2 g 98 cm	Grass	0.00724	[765]
cypermethrin	pesticide	7–7.5 g 60–70 mm	Mrigal	0.00423	[766]
diafuran	pesticide	11.7 g 104 mm	Grass	2.71	[767]
dicofol	pesticide	unknown	Grass	0.292	[768]
endosulfan	pesticide	2.7–3.1 g 6.3–7.1 mm	Grass	0.001711–0.00591	[769]
fenvalerate	pesticide	19.05 g 130.1 mm	Grass	0.0050–0.00625	[756]
malathion	pesticide	30 g	Grass	2.138	[770]
Nuvan	pesticide	3–4 g 50–60 mm	Grass	6.5	[771]
pesticide mixture with endosulfan	pesticide	fingerling	Grass	0.00216–0.00749	[758]
quinalphos	pesticide	4 g 45 mm	Common	0.00275	[772]

Pharmaceuticals, Miscellaneous Toxicants, and Radiation

Largely due to their importance as aquacultural species, there have been many studies of the effects of various drugs and pharmaceuticals on carp. Table 10 provides a summary of the 96-h LC_{50}s for various pharmaceuticals and miscellaneous toxicants. Due to the aquacultural focus, some of this research focuses on safe concentrations as opposed to lethal concentrations. A concentration of 0.7 mL/L of 2-phenoxyethanol is an effective anesthetic for silver carp [773]. In studying the use of praziquantel to treat for the tapeworm *Schyzocotyle acheilognathi* (syn. *Bothriocephalus acheilognathi*) in grass carp the 24-h and 96-h LC_{50}s are 63.4 and 60.6 mg/L and the highest non-lethal concentrations (LC_0s) are 60.0 and 60.6 mg/L, respectively [774]. The anthelmintic drugs niclosamide and mebendazole were somewhat toxic to grass carp at concentrations of 150 and 50 mg/kg body mass, respectively, in work carried out exploring their usefulness as a treatment for *S. acheilognathi* [775]. Grass carp challenged by *A. hydrophila* infection after exposure to the antibiotic SMZ at 0.3 µg/L for 42 days did not have significantly different 48-hr mortality rates compared to the control group infected with *A. hydrophila* without exposure to potentially toxic compounds [749]. However, exposure to a combination of 0.3 µg/L SMZ and 0.651 µg/L of the pesticide cypermethrin for 42 days followed by *A. hydrophila* infection resulted in significantly higher 48-h mortality rate than both the control group and groups exposed to each compound alone. Using a similar exposure scheme, these treatments caused neurological damage to the cerebellum accompanied by the behavioral changes such as slowed movement; the combination group also exhibited side-swimming and sinking to the bottom [751]. Carbamazepine, a human pharmaceutical, increases reactive oxygen species stress in common carp [776]. The anti-depressants fluvoxamine and fluoxetine are the strongest inhibitors of C17,20-lyase and CYP11b enzymes, with 50% maximal inhibitory concentration in the range of 321–335 lM and 244–550 lM, respectively, when compared to interference of fibrate (gemfibrozil, clofibrate, clofibric acid) and anti-inflammatory (ibuprofen, diclofenac) drugs [777]. Exposure of grass carp to ibuprofen at a level consistent with environmental contamination, 48.0 ng/L, produces molecular and cellular responses consistent with altered immune status [778]. Sertraline, a selective serotonin reuptake inhibitor (SSRI) antidepressant, at three concentrations (4.36, 21.3, and 116 µg/L) induced increased swimming activity, decreasing shoaling behavior, decreased foraging rate, and decreased food consumption compared to the control in crucian carp [779]; 48-h LC_{50} of the SSRI in fathead minnow fry is 205 µg/L (Ref. [780] as cited by [779]). Diphenhydramine, an antihistamine, increases shoaling and decreases swimming and feeding in crucian carp at or above 21.7 mg/L [781]. The lowest effective concentration of the analgesic tramadol hydrochloride for affecting early ontogeny is 10 ug/L in common carp [782]. The cytotoxic effect of enrofloxacin at 200 ug/mL on grass carp hepatic cells results in cell death (i.e., apoptosis) via effects on the mitochondria of the cells [783]. In grass carp ovarian cells, bisphenol A (BPA) at a concentration of 30 µM reduces cell viability compared to a control; lower BPA concentrations (0.3 µM and 3 µM) did not affect cell viability [784]. At concentrations of 1000 µg/L and 1500 µg/L, BPA exposure in bighead carp is sublethal, but it is associated with clinical and behavioral abnormalities such as gill cover movement, erratic swimming, surface breathing, lying on the bottom, and fin tremors [785]. Pollutants occurred in higher concentrations upstream of the stalled range expansion boundary for silver and bighead carp ranges within Illinois Waterway in 2015 (River Mile 278; Ref. [786]). The authors suggest a shortlist of possible pollutants that might prevent range expansion of invasive populations of carps: four pesticides (2,4-D, acetochlor, carbendazim, metolachlor, and terbuthylazine), five specific pharmaceuticals (diphenhydramine, fexofenadine, metformin, sulfamethoxazole, and tramadol), antidepressants, four wastewater indicator chemicals (4-nonylphenol, 4-tert-octylphenol, BPA, and galaxolide), esterone (a hormone), 4-nonylphenolmonoethoxycarboxylate (a carboxylic acid), and 1,4-dioxane (a volatile organic compound), boron, and lead.

A variety of additional compounds not mentioned in the previous sections are toxic to cypriniforms. Tests on the blood of one-year-old grass carp indicate that ozone at concentrations of 0.118 mg/L and 0.278 mg/L causes a physiological response with an exposure of 90 min, with increases in malondialdehyde content; decreases in glutathione content; and concentration- and exposure time-dependent changes in the activity of glutathione peroxidases (GPX; Ref. [787]). The 48-h LC_{50} value for larval grass carp exposed to ozone is 31 µg/L [788]. Silicon-based quantum dots (nanoparticles that fluoresce) damage the kidneys of crucian carp, but the renal cells can regenerate and repair the damage [640]. Bighead carp larvae appear to be effective at eliminating spherical microplastics (5 µm diameter) [789]. A delayed decrease in growth was observed for common carp exposed to microplastics [790]. Polyvinyl chloride microplastic inhibits growth in common carp [791]. Exposure to spherical microplastics (32–40 µm diameter) at 1000 µg/L leads to lower weight gain in grass carp compared to unexposed individuals [306]. Grass carp exposed to 0.04 ng/L microplastic particles (0.03 µm mean particle size) for 20 days show decreased avoidance of simulated predatory stimulus (vibration) and impaired shoaling ability when exposed to an individual arapaima (*Arapaima gigas*), a neotropical predatory fish [792]. Fluoride induces apoptosis in the kidney of common carp [793]. Incubation of common carp erythrocytes (i.e., red blood cells) using gaseous N, potassium cyanide, and methylene blue lead to oxidative phosphorylation inhibition resulting in degradation of glucose [576]. The acute oral toxicity of 1496 chemicals force-fed to the common carp are reported by [794]. Polybrominated diphenyl ethers, a class of environmental contaminants, are thyroid endocrine disruptors and cause DNA damage in crucian carp [795]. Dibutyl phthalate, a plasticizer and environmental contaminant, induces stress responses in the liver, kidneys, and gills of grass carp at concentration of 10 to 1000 µg/L [796]. Tributyltin, an antifouling agent, appears to be neurotoxic to fish based on work with common carp [797]. Exposure of grass carp to detergents decreased growth rate and superior lethal temperature and increased final preferred temperature [526]. Phenol is an endocrine disrupter and causes oxidative stress in common carp [798]. Polycyclic aromatic hydrocarbons disrupt synthesis of androgens and estrogens in the gonads of common carp [799]. The beta and gamma radiation LD_{50} for common carp are 500.5 and 601.3 rads, respectively [800]. Bioaccumulation of hexabromocyclododecane diastereoisomers (HBCDDs), a class of water-insoluble flame retardants that generally accumulates in sediment, has been studied in mirror carp, a domestic variety of common carp. Sediment disruption by pond loach (*Misgurnus anguillicaudatus*) in microcosms increases bioaccumulation of HBCDDs in mirror carp [801]. No toxic effects of HBCDDs on mirror carp were observed; mean accumulation of microcosm with pond loach is approximately 760 ng total HBCDDs/g mirror carp dry mass [801]. In addition to detection of higher pollutant concentrations upstream of the silver and bighead carp invasion front in the Illinois Waterway, there is evidence that silver carp are being affected by those pollutants. Near the Illinois Waterway invasion front, silver carp transcriptome signatures are consistent with physiological stress associated with exposure to pollutants [802].

Table 10. A summary of the 96-h LC_{50}s for various pharmaceuticals and miscellaneous toxicants reported in studies included in this literature review. Size refers to the reported size/age of carp tested. * Converted to active ingredient concentration.

Source	Type	Average Size	Carp Species	Concentration * (mg/L)	Citation
acetaminophen	Pharmaceutical	eggs	Common	0.00129	[803]
arsenate		10.5 g 82 mm	Catla	43.78	[804]
bleaching power	Fishery drug	2.18 g 56 mm	Grass	2.75	[805]
chlorine dioxide	Fishery drug	2.18 g 56 mm	Grass	6.34	[805]
mix copper sulfate and iron sulfate	Fishery drug	2.18 g 56 mm	Grass	0.11	[805]
dibromo dimethyl hydantoin	Fishery drug	2.18 g 56 mm	Grass	14.1	[805]
monochoramine	Disinfectant	5.07–8.06 g 72–85 mm	Common	1.0 to 1.5	[806]
praziquantel	Pharmaceutical	9.1 g	Grass	60.6	[774]
trichlorfon	Fishery drug	2.18 g 56 mm	Grass	8.48	[805]
triclosan	Pharmaceutical	14 g 73 mm	Rohu	0.39	[807]

3.2.5. Reproductive and Genetic Controls

In addition to the many compounds and toxins discussed so far there are also potential biological means of controlling grass carp populations. These include methods of preventing or limiting reproduction, such as production of functionally sterile triploid grass carp, hybridization, genetic modification, and physical sterilization.

Triploids

Induced triploidy increases the number of chromosomes an organism possesses. It has been used to prevent reproduction of grass carp stocked for vegetation control since the early 1980s [55], as triploid grass carp are functionally sterile [808–810]. In 1985, the U.S. Fish and Wildlife Service released an opinion stating that triploid grass carp were environmentally safe; from 1985 to 2004, triploid carp certified by the U.S. Fish and Wildlife Service (see [811] for more information of carp ploidy and applicable rules) were shipped to 30 states in the United States [51]. After the original importation of grass carp into North America, more than 7 million triploid grass carp, considered non-reproductive, were distributed in the United States from 1985 to 2005 [51]. Regulations on importing triploid and diploid grass carp vary among states, with some states allowing both diploids and triploids, some triploids only, and some neither [51,56–58,811].

Similar to diploid grass carp, intentional introduction of triploid grass carp is used for aquatic vegetation control. In commercial water-lily (*Nymphaea* spp.) ponds in Texas, triploid grass carp were effective for controlling several invasive and undesired plant species, including Eurasian watermilfoil (*Myriophyllum spicatum*), coontail (*Ceratophyllum demersum*), bladderwort (*Utricularia*), southern naiad (*Najas guadalupensis*), curlyleaf pondweed (*Potamogeton crispus*), and hydrilla [75]. Triploid grass carp have been used to successfully control sago pondweed (*Stukenia pectinata*) and *Lagarosiphon* spp. in a South African lake, reducing the combined wet biomass density of these taxa from 193.11 g m^{-2} to 33.89 g m^{-2} [106].

Despite their generally accepted inability to reproduce, introduced triploid grass carp can also have unintended consequences. A list of trade-offs between allowing and prohibiting use of triploid grass carp can be found in [56]. Triploid grass carp in Devil's Lake, Oregon have a recorded lifespan of at least 30 years [812], meaning that even when grass carp cannot reproduce, they can persist in an ecosystem and have effects for decades. Like diploid grass carp, triploid grass carp can also escape outside their intended introduction location; triploid grass carp have been present in the Great Lakes since 2011 despite not being introduced there [135,813].

A risk analysis of stocking triploid grass carp for biological control of aquatic plants in Florida can be found in [406], and multiple risk assessments have been carried out specifically for Canada [24,814]. A general guide for the use of triploid grass carp for aquatic plant control is provided by [809]. In their review on triploid grass carp, [815] describes the induction process used to produce triploid grass carp and the extreme unlikelihood of successful spawning or reversion to diploidy in the wild.

Because triploid grass carp cannot be distinguished morphologically from diploids, and because induction of triploidy is not always complete for all the embryos subjected to the induction treatment, it is necessary to individually test each fish, usually via a blood test or testing of an extracted eyeball, if accidental introduction of some diploid grass carp along with the triploids is to be avoided [815–817]. A comparison of different methods of triploidy validation including DNA staining and fluorescence quantification with a flow cytometer, erythrocyte nuclear volume with a Coulter counter, silver staining of nucleolar organizer regions, and cytological karyotyping is provided by [818], but the Coulter counter method has become the standard in aquaculture [810] because the method may be easily performed at the aquaculture facility. Use of the more sensitive flow cytometry method found an error rate of 0.25% for the Coulter counter method; specifically 3 non-triploid fish were found among 1200 grass and black carp previously identified as triploid by the Coulter counter method [810]. Because of the potential for human error in identifying triploid grass carp and incentive to sell diploid grass carp as high-priced 'counterfeit' triploids, the U.S. Congress in 1995 directed the U.S. Fish and Wildlife Service to institute a system of certification of triploidy in grass carp. In 2015, an evaluation of this certification process was performed [56,141], including an examination of the potential for diploid grass carp to enter the sale of triploid grass carp post-certification.

Research into altering ploidy of grass carp beyond just triploids has also been conducted. A review of ploidy research carried out in Israel on development of various methods for altering ploidy in fish, including grass carp, is given by [819]. Variable success was demonstrated in using pressure and temperature heat shock to produce tetraploid grass carp larvae; however, no produced larvae survived beyond 50 days [808,820].

Hybrids

The introduction of hybrid and genetically modified individuals has also been utilized to control invasive fish species, primarily as means of preventing the establishment of introduced individuals [821–823]. Use of grass carp hybrids was an early approach in the attempts to mitigate risk of invasion while using grass carp for vegetation control [824]. Grass carp × bighead carp hybrids were much less effective at controlling aquatic vegetation [200,825,826], grew slower, and had smaller gut capacity than grass carp [825]. Research with this hybrid carp estimated that it would require more than double density of hybrids to obtain the same level of vegetation control as grass carp [827]. Morphological and developmental comparisons between this hybrid and grass carp have been published [73,828]. Research has documented that underyearling hybrid grass carp × bighead carp preferred coontail, *Chara* sp. and southern naiad; while only feeding on hydrilla, dwarf hygrophila (*Hygrophila polysperma*), cut-leaved watermilfoil and leafy bladderwort a minor to moderate extent [189]. The researchers found there was no feeding damage to Brazilian waterweed, Illinois pondweed, and Carolina mosquitofern; duckweeds and Columbian watermeal (*Wolffia columbiana*) were readily consumed with water spangles (*Salvinia minima* syn. *S. rotundifolia*) not preferred in their presence; only minor damage to submersed roots of water-hyacinth and water lettuce (*Pistia stratiotes*) was observed. Grass carp × bighead carp hybrids preferred Canadian waterweed, curlyleaf pondweed, and southern naiad, while Eurasian watermilfoil and sago pondweed were the least preferred [829]. Intermediately preferred plants were longleaf pondweed (syn. American pondweed) and hydrilla [829]. Grass carp consumed nuisance plants in greater amounts than triploid grass carp × bighead carp hybrids, which brings into question the value of this hybrid grass carp for plant control [830]. The hybrid cross between grass carp and common carp demonstrated similar utilization of many nuisance plants to non-hybrid grass carp, but some species, particularly water-hyacinth, a significant aquatic weed in Louisiana, and *Elodea* sp., were poorly utilized by the hybrid [831]. Overall, it seems that hybrid carp are not as effective at controlling aquatic vegetation, limiting their utility.

Other Genetic Reproductive Controls

Control of the reproduction of invasive populations of cypriniforms outside of induced triploidy and hybridization has also been researched. A simulated eradication study of the potential effectiveness of release of 'Trojan Y' chromosome (YY) on common carp, one means of ensuring daughterless offspring, is provided by [832]. These simulations predict high eradication probabilities for common carp when population densities are low and other control methods (for example, pesticides, manual removal) are applied in tandem. Corresponding field tests of YY common carp introduction had not been published at the time of writing. Conducting model simulations on the introduction of sex reversed grass carp with two Y chromosomes (YY) into a normal fish population determined that with continuous introduction of small proportions of (YY) females in relation to the normal population leads to the extinction of the invasive species over time. This YY eradication model also indicates that this method could be theoretically practiced in a riverine system, but technical limitations still limit the practical use of this method of eradicating grass carp [833]. Gynogenesis, or ovum development using fertilization with a spermatozoan without paternal genome, has been assessed as an impractical method for production of monosex grass carp [834].

Genetic modification, in the sense of altering or adding to an organism's genome, has been discussed for common carp and invasive species in general. An assessment of the status of genetic engineering for controlling invasive species, in general, is provided by [835]. In a discussion of the environmental risk analysis methodologies for genetically modified organisms, [821,823,836,837] presents the example of introducing daughterless common carp, which are genetically modified to cause all offspring to develop as males, regardless of genetic sex, as a risk analysis exercise. They outline potential hazards that are unique to the use of genetically modified organisms, especially in aquatic settings.

Physical Sterilization

Some work has been carried out on the use of sterilization methods for controlling grass carp. There is particular interest in developing functionally sterile fish which will behave like unsterile fish to identify locations of feral fish [838,839]. Ligation and division of the ductus deferens, a duct used for sperm transport, in bighead and grass carp did not provide permanent means of sterilization of males [839]. Grass carp males and females that had been given a bilateral gonadectomy regenerated viable testes and ovaries, indicating they had regained the potential to reproduce [840]. Surgical and chemical methods of sterilization were assessed in common carp by [838] for long-term sterilization. A GnRH agonist is not able to completely repress sperm production in all individual common carp, despite being highly successful in mammals. Surgical excision of a tubular section of the testes is only 73% successful at 10 months post-surgery. A third method, a non-surgical Essure technique, originally developed as a female contraceptive in humans, is infeasible for common carp and was discontinued during implementation of the study [838]. Thus far, successful methods of permanent surgical sterilization, which retain the behavior of unsterilized fish, have not been identified, but means of chemical sterilization mostly remain untested [839].

3.2.6. Biological Control

Predators

A small amount of research has been conducted on the potential for using native North American predators to control grass carp populations. Several predators of grass carp at various life stages on a global scale are listed by [20]. Most predators on this list consume larvae and fry, and they include birds, several fish species, amphibians, and several aquatic invertebrate taxa. In samples from a Florida lake grass carp were found in the stomach contents of largemouth bass (*Micropterus salmoides*) [841]. In efforts to increase the survival rate of stocked grass carp in Florida water bodies, ref. [842] found that stocked grass carp had to be greater than 450 mm in size to ensure they were not eliminated via largemouth bass predation. In Texoma Reservoir (Oklahoma and Texas, USA), grass carp occurred in 33.3% to 38.7% of the stomach content samples of juveniles of four gar species: alligator gar (*Atractosteus spatula*), longnose gar (*Lepisosteus osseus*), shortnose gar (*Lepisosteus platostomus*), and spotted gar (*Lepisosteus oculatus*) [843]. The size of the grass carp consumed by gar in this study are not directly reported, but the grass carp sampled from the Texoma Reservoir for additional gar diet analyses had 42 to 98 mm total length, whereas the mean lengths of the gar species sampled ranged from 135 mm (shortnose gar) to 194 mm (longnose gar) total length, suggesting that only small juvenile grass carp are susceptible to predation by juvenile gar.

Depredation and responses to predators of other focal carp and common carp in North America may inform predator effects on grass carp. In the Illinois River, bighead carp were found in the stomach contents of several native predators and were preferred by white bass, black crappie, and shortnose gar [844], and pool studies conducted at the Kaskaskia Biological Station in Illinois found that bighead carp and silver carp were similar to native species in their vulnerability to predation by largemouth bass [845]. However, a separate laboratory study showed avoidance of silver carp by largemouth bass [846]. Bluegill may be an effective control for common carp populations [847]; this method would be most effective if bluegills were stocked at high density and had limited competitive food options. The use of predators to control common carp was deemed ineffective (Ref. [848]; as cited by [584]). Naïve bighead carp do not respond to the olfactory cues indicating presence of largemouth bass, but they can learn antipredator behaviors by mimicking the responses of both conspecifics and other prey species [849]. As one example of anti-predator behavior, in laboratory experiments black carp maintained a greater distance from snakehead (*Channa* argus), a potential predator, than other carp. They also spent less time moving and moved less total distance in treatments where a potential predator was present [850].

Infectious Disease

A number of viruses, bacteria, and parasites are known to cause disease in grass carp, resulting in adverse effects on health and survival. Few, if any, of these disease organisms are specific to grass carp, and introduction of any known grass carp pathogen could pose a risk to non-target species. As with much of the research carried out on grass carp, the work on infectious disease has been focused on controlling these diseases in aquacultural settings to improve the growth and survival of grass carp to enhance production. However, this research provides many insights into possible directions for decreasing survival and growth of grass carp via the potential for direct introduction of these diseases to invasive grass carp populations. Alteration of conditions in which those grass carp populations exist may also increase their susceptibility to those diseases. Invasive grass carp populations have lower parasite diversity than native populations of grass carp; possible explanations for this loss of parasites include bottlenecking and lack of intermediate hosts (Ref. [93] as cited by [94]). In Hungary, comparing parasite diversity in centuries-old introduced common carp populations and newly introduced, non-native carp (including grass carp) found that both groups had equivalently low parasite species richness compared to native populations (Ref. [851] as cited by [94]).

The susceptibility of fish to disease can be affected by density, habitat quality, stress, and environmental factors such as water temperature. Long-term crowding stress in grass carp decreased immune response effectiveness and increased susceptibility to pathogens [852]. A major fish kill of grass carp was attributed to multiple diseases primarily caused by bacterial agents resulting from poor water quality, low oxygen, poor food quality, and pesticides dissolved in water or present in feed (Ref. [853] citing [854] and J. Pucher and others, 2012). Between 2011 and 2017, a 'jelly-like gonad condition' that ultimately resulted in sterility was observed in 487 of a total of 2631 male common carp sampled in Tasmania; however, this condition has not been recorded in other common carp populations or in grass carp, and it is unclear whether the condition is caused by genetics, environmental conditions, or a pathogen [855]. In black carp aquaculture ponds, temperature is the main driver of seasonal changes in bacterial communities in the water column [856]. That study found *Chryseobacterium*, *Acinetobacter*, *Rheinheimera*, and *Janthinobacterium* abundances are positively associated with temperature; *Polynucleobacter* and *Prochlorococcus* abundances are negatively associated with temperature; the authors also note that many of these genera can be pathogenic (U. Masayoshi and M. Kiyokuni, 1974 as cited in [856]). Many viruses that infect fishes are only infectious and pathogenic within certain water temperature ranges; the spring viremia of carp virus is one such temperature-sensitive virus (Ref. [857] as cited by [858]). Attempts to infect grass carp in a laboratory setting with a 30-day lymphocystis disease (LCD) virus challenge did not induce disease, suggesting that this LCD virus may need specific environmental conditions to cause infection [859].

Grass carp reovirus (GCRV), a form of aquareovirus, and the resulting hemorrhagic disease have been the subjects of much focus in grass carp research. A description of the hemorrhagic disease caused by GCRV, its status, diagnosis, and research up to the date of publication can be found in [860]. There are three primary genotypes of GCRV identified from China, named genotypes I, II, and III [861]. Representative strains from each genotype include GCRV-873 (genotype I), GCRV-HZ08 (genotype II), and GCRV-104 (genotype III, [862] as cited by [863]). The dominant genotype that causes widespread epidemics of hemorrhagic disease in Chinese grass carp aquaculture is genotype II (Ref. [864] as cited by [861,863]). Even within genotypes, different GCRV strains vary in terms of virulence. The genotype II strain GCRV-HZ08 generally causes 30% mortality in infected grass carp populations (C. Zhang and others, 2010 as cited in [863]). The genotype II strain GCRV-HuNan1307 causes 95% mortality (Ref. [625] as cited by [863]). The GCRV genotype II strain GCRV-JX02 can cause 100% mortality in juvenile grass carp (mean mass = 1.0 g; Ref. [629]). Other highly lethal GCRV strains include GCRV-109 and GCRV-GD108, which cause ~80% and ~100% mortality, respectively (Refs. [865,866] as cited by [863]. GCRV strains with little to no virulence also exist. GCRV-GD1108 is considered nearly avirulent, as it produces low viral loads and does not cause symptoms or mortality [863]. The strain GCRV-GZ1208 primarily causes enteritis with little to no hemorrhaging and has a mortality rate of <10% [867]. Another virulent strain of gentotype II GCRV, HA741, had a mean cumulative mortality rate of 74% over the course of two weeks after exposure [628]. Due to the economic importance of grass carp aquaculture, research is underway to develop treatments and vaccines to increase survival in aquaculture settings. The development of virus-like particles resulted in 83% relative percent survival of grass carp challenged with GCRV genotype II [868].

Due to the threat it poses to grass carp aquaculture, both age-dependent susceptibility of grass carp to GCRV and various genetic and immunological components related to GCRV infection have been studied. The comparison of 5-month-old and 3-year-old grass carp ($n \approx 300$ per group) found 86% mortality in 5-month-old grass carp exposed to reovirus, but no mortality in 3-year-old grass carp [869]. The fact that 3-year-old grass carp are not affected by GCRV as greatly as 1-year-old grass carp is thought to be the result of a faster and more efficient response of the immune system [870]. An experiment involving pre-treating grass carp kidney cells with different compounds prior to reovirus infection found that rapamycin, a cellular autophagy inducer, reduced viral replication compared to the control; 3-methyladenine, an autophagy inhibitor, increased viral replication [871]. Grass carp Junctional Adhesion Molecule-A (JAM-A) is a receptor of GCRV [872], and later research indicated that JAM-A is necessary for GCRV infection [873]. T-cell factor/lymphoid enhancer-binding factor (TCF/LEF) genes participate in the GCRV-related immune response in infected grass carp [320]. Research on molecular cloning of complimentary DNA of coagulation factor VIII and plasminogen provides data that appear to show their importance in the immune response of grass carp to GCRV infection as well [874]. Histidine-aspartic domain-containing protein innate immunity restriction factor found in grass carp appears to suppress GCRV but induces apoptosis with overexpression [498]. Galactose-binding, mannose-binding [875], C-type 1 and 2 [876] lectins, toll-like receptors 1, 2, and 18 [877,878], T-bet gene [879], dicer gene [880], toll-interacting protein and interlukin-1 receptor-associated kinase 1 [881], myeloid factor 88 [882], interferon-beta promoter stimulator 1 [883], tumor necrosis factor-like weak inducer of apoptosis and a proliferation-inducing ligand [884], and interleukin-12 [885] of grass carp are up-regulated after exposure to GCRV. Overexpression of the *SR-B2a* and *SR-B2b* genes in grass carp kidney cells leads to increased replication of GCRV [886]. While GCRV is highly lethal to naïve and susceptible grass carp, populations of grass carp can become immune to GCRV [887], and GCRV can infect many species of fish [888], which would render it a risky option for use as a control in North America.

Other viruses also negatively affect carps. In German ponds primarily containing either koi or farmed common carp with high prevalence and high viral loads of carp edema virus (CEV), grass carp sampled in the same ponds had low prevalence of CEV (1 of 11 sampled; 9.1%) and low viral load where the virus was present (4 copies of CEV-specific DNA per 250 ng DNA; Ref. [889]). The CY1 strain of *Acinetobacter lwoffii* found in the intestines of grass carp causes hemorrhages on the fins and body and resulted in 75% mortality when grass carp were exposed to it [890]. Though the sample size for grass carp in this study was low, it suggests that grass carp have low susceptibility to CEV. Seasonal occurrence of external tumors in farm-raised grass carp in India had been linked to the LCD virus [859]. Most grass carp recover from viral LCD before reaching advanced stages, but cumulative mortality from advanced stages of LCD, chiefly caused by related secondary infections, is estimated to be around 10–15% [859]. In development of methods to control common carp, Australia has also been investigating the use of a different virus, *cyprinid herpesvirus 3* [891,892]. Symptomatic infection of *cyprinid herpesvirus 3* is restricted almost entirely to koi, common carp, and related hybrids and does not induce clinical symptoms in grass carp (Refs. [892,893] as cited by [894]); a disease with a similar single-genus pathogenicity has not yet been reported for grass carp.

There are a number of bacterial infections that have been discovered in grass carp, some of which can lead to septicemia and death. Among these, *A. hydrophila* has received significant attention. *A. hydrophila* is present in nearly a third of grass carp sampled in South China [895]. Investigation into a widespread outbreak of ulcerative disease in grass carp in China from February 2019 to April 2019 found that four bacteria in the *Aeromonas* genus are the causative pathogens: *A. salmonicida*, *A. sobria*, *A. veronii*, and *A. hydrophila* [896]. Follow-up testing of the lethality of these *Aeromonas* species used fifteen (15) ~23 cm-long grass carp per pathogen species and found mortality rates of 100% for *A. salmonicida*, 100% for *A. sobria*, 66.7% for *A. veronii*, and 53.3% for *A. hydrophila*. Use of the bacterial strain *Bacillus licheniformis* FA6 as a dietary probiotic supplement over the course of 56 days resulted in increased weight gain rate, lengthening of villi in the intestine, and decreased mortality rate from the *A. hydrophila* strain AH-1 [897]. A different species of *Aeromonas*, *A. veronii*, can also be pathogenic toward grass carp. The GC9612 strain of *A. veronii* can cause 75% mortality in grass carp [898]. Injection of *A. hydrophila* and *A. sobria* can cause the lethal ulcerative 'red spot disease' in grass carp; 3 of 20 (15%) grass carp injected with the former and 10 of 20 (50%) injected with the latter bacterium developed red spot disease and died [899]. The same research revealed that none of *Staphylococcus epidermidis*, *Vibrio alginolyticus*, *Pseudomonas putida*, *P. fluorescens*, *P. luteola*, and *Citrobacter freundii* caused morbidity or mortality after intramuscular injection. One of the primary symptoms of *A. hydrophila* infection is enteritis (Ref. [288]; as cited by [900]). Due to the intestinal nature of *A. hydrophila* infection and the presence of *Aeromonas* sp. in the gut microbiome of grass carp [901,902], *A. hydrophila* and the *Aeromonas* genus are also discussed in 'Section 3.3.3. Intestinal Microbiome,' 'Section 3.3.4. Effects of Dietary Nutrient Levels on Intestines,' 'Section 3.3.5. Effects of Dietary Additives, Vaccines, and Toxins on Intestines'. Because *A. hydrophila* poses a threat to aquacultural production of grass carp, much of the research on *A. hydrophila* has focused on immune response, treatments, and prevention. The lysosomal aspartic proteinase Cathepsin D gene [903] and C7 complement component [904] increased expression, and factor B catalytic subunit complement C2A gene is up-regulated [905] after grass carp are exposed to *A. hydrophila*. It appears that Interleukin-12 receptor β2 is involved in the regulation of inflammation of the intestine in grass carp as a result of exposure to *A. hydrophila* [906]. The optimal dietary protein level for grass carp for improved disease resistance, immune function and structural integrity in the head kidney, spleen, and skin after exposure to *A. hydrophila* is from 241.45 to 307.84 g/kg diet [907]. Intraperitoneal injection of formalin-killed whole cell *A. hydrophila* vaccine in rohu appeared to increase immunity to *A. hydrophila* [908]. An *A. hydrophila* vaccine, introduced to the intestines of grass carp using single-walled carbon nanotube, is effective at improving the immune response of grass carp intestines to the bacterium [909]. Lipopolysaccharide and outer membrane protein from *A. hydrophila* are potential sources of vaccines against *A. hydrophila* in grass carp [910]. Plant extracts from basil (*Ocimum basilicum*), cinnamon (*Cinnamomum zeylanicum*), common walnut (*Juglans regia*), and peppermint (*Mentha piperita*) improve immune response to *A. hydrophila* in grass carp [911]. Following exposure to *A. hydrophila*, introducing *Bacillus subtilis* to the grass carp digestive tract reduced the effect on intestinal mucosal barrier function damage and inflammation [912].

Other bacteria of interest for grass carp include *Flavobacterium* and *Vibrio* species. *Flavobacterium columnare* is the causal agent of columnaris disease (Ref. [913] as cited by [914]). This disease affects many fish taxa; symptoms can include rotten gills, surface ulcers, and bleeding; and it is considered a threat to aquaculture due to situationally high mortality rates (Ref. [915] as cited by [914]). In China, three genotypes of *F. columnare* were isolated from grass carp; genomovar I represented 82% of samples [914]. In grass carp exposed to inactive *F. columnare*, the ninth member of complement components of the membrane attach complex in grass carp is up-regulated in the head kidney, spleen, and hepatopancreas and down-regulated in the intestine [916]. The optimal dietary protein level for grass carp gills is 286.65 to 296.25 g/kg for disease resistance, immunity, and physical barrier function when exposed to *F. columnare* [917]. Dietary supplementation of hepcidin, a hormone that regulates iron transport, alters iron metabolism and distribution in grass carp and increases the survival rate of grass carp infected with *F. colmnare* [918]; it also protects against *F. columnare* infection [919]. Optimal levels of dietary pyridoxine, 4.85 mg/kg diet, reduce *F. columnare*-caused gill rot morbidity in grass carp [274]. A vaccine for *F. johnsoniae* infection, which causes gill rot in grass carp, is described by [920]. *Vibrio vulnificus* infection, which causes severe, life-threatening disease in humans, is found in grass carp [921]. *Vibrio mimicus* is also known to cause high mortality in fish and induce food poisoning in humans who consume undercooked meat from infected species. The potential effectiveness of *V. mimicus* bacterial ghosts, empty but intact bacterial envelopes, as a vaccine for the bacterial pathogen in grass carp is demonstrated by [922].

Various studies describe some of the parasites found in grass carp, as well as their resulting disease and control. Prominent parasites in grass carp include the tapeworm *Schyzocotyle acheilognathi* (syn. *Bothriocephalus acheilognathi*) and 'Ich' (*Ichthyophthirius multifilis).* Heavy infestations of *S. acheilognathi* can cause reduced growth rates and death in grass carp [775]. However, outside of heavy infestations, *S. acheilognathi* is considered minimally harmful to its native host carp species, such as grass carp, bighead carp, silver carp, and black carp [95]. Of the anthelmintics niclosamide, mebendazole, and praziquantel, only praziquantel is effective at eliminating *S. acheilognathi* from infected grass carp [775]. The annual population dynamics of *S. acheilognathi* in South China are described by [923]. In an experimental setting, inoculation with the parasitic larval stage of the Eurasian unionid mussel *A. cygnea* results in a mortal rate of 6% for grass carp under one year of age [103]. A list of parasites recorded in grass carp less than one year of age in the Amur River between 1962 and 1964 is provided by [924].

Ichthyophthirius multifilis causes white spot disease, which results in high fish mortality. Tumor necrosis factor receptor-associated factor 6 and transforming growth factor-beta-activated kinase 1 are up-regulated in grass carp after exposure to the parasite *I. multifilis* suggesting a role in defense against the parasite [925]. Flavonoids kuwanons G and O extracted from the bark of *Morus alba* are 100% effective at killing *I. multifilis* at 2 mg/L [728]. Sanguinarine from *Macleaya cordata* leaves is an effective control for *I. multifilis* in grass carp at 0.7 mg/L with a 4-h exposure [926]. The monogenean parasitic flatworm *Dactylogyrus* has been recorded on the gills of grass carp in fish farm conditions in Romania [927]. The *Dactylogyrus* species *Dactylogyrus ctenopharyngodonis* and *D. lamellatus* was recorded on grass carp transported from the Amur River to European Russia, along with *I. multifiliis*, *Trichodina* spp. (a protist), and *Sinergasilus major* (syn. *Pseudergasilus major*, a copepod; V.N. Abrosov and O.N. Bauer, 1955 as cited in [1]). More commonly associated with silver carp, the *Dactylogyrus* species *D. hypophthalmichthys* has also been reported in grass carp in Jiangxi Province, China (W. J. Yao, 2000 as cited in [928]). Grass carp that survived infection with the ectoparasite *Dactylogyrus ctenopharyngodonid* are completely resistant to reinfection and partially resistant to infection by *I. multifilis* [225]. Species of coccidia parasites (*Eimeriidae*) found in grass carp are given in [929]. Initially parasite-free grass carp introduced to a southern Siberian lake became infected with *Tripartiella bulbosa* and *Diplostomum spathaceum* at rates of 100% and 93% of individuals sampled, respectively [1]. Fingerling grass carp are susceptible to the parasitic copepod *Lernaea cyprinacea*. In a sample of 20 fingerling grass carp, 40% became infected at a dose of 70 *Lernaea* larvae per fish; there was 0% mortality in the grass carp [930]. In the same study, common carp appeared to be immune to *Lernaea* infection, and 20 fingerling silver carp had an 80% mortality rate when exposed to a dose of 70 *Lernaea* larvae per fish. Alternately, it was found that infection with *Lernaea cyprinacea* does not affect weight gain or survival of grass carp [931].

The presence of the parasite *Argulus foliaceus* in grass carp decreases growth rate and increases mortality [932]. The parasites found in grass carp in the Philippines are described by [933]. A variety of herb extracts have been identified as potential treatments for controlling *Saprolegnia australis* infection in Prussian carp eggs [934]. Sodium chloride at

35,000 mg/L and formalin at 400 mg/L are effective in controlling *Saprolegnia* sp. on grass carp eggs. Of these, Radix Sanguisorbae (root of *Sanguisorba* spp.) extract, a well-known herbal medicine in China, increases survival of infected eggs by 22% (256 mg/L) to 37% (1280 mg/L).

The immunological responses and genetics of grass carp have been studied to better understand how infectious disease can best be treated and managed. Grass carp innate immune response to *A. hydrophila* appeared to be centered around the liver [935]. Induction of cellular autophagy in grass carp plays a role in fish immunity and is involved in control of pro-inflammatory cytokine release [936]. Mitogen-activated protein kinase kinases (MKK) are involved in the intestinal immune response of grass carp to bacterial muramyl dipeptide challenge [937]. The innate immunity of common carp changes seasonally with 11-ketotestosterone, resulting in immune suppression in the spring [938]. Signal transducer and activator of transcription 6 (STAT6) appears to be important to innate immunity and anti-apoptosis in grass carp [939]. The interferon regulatory factor-1 gene in grass carp is up-regulated in the presence of type 1 interferons [940]. It appears multiple variants of the polymeric immunoglobulin receptor gene are involved in antibacterial immunity in grass carp [941]. The tripartite motif 23 (TRIM23) gene provides innate immune regulation in grass carp [942].

3.3. Gut Physiology and Related Control Pathways

To help identify effective types and means for delivering poisons into the body of grass carp for effective control, the third aspect of this review was on their intestinal tract including its structure, physiology, and microbiome to help identify potential directions for improving population control. Most studies reviewed here focus on improvement of aquaculture production of grass carp via improvement of their survival and growth. From the perspective of controlling grass carp populations, this aquaculture-focused research provides many insights into possible directions for exploiting the grass carp's digestive system and related body systems to decrease their survival and growth.

3.3.1. Digestive Tract Structure and Function

The anatomy and structure of the grass carp digestive system and how they relate to carp's diet of plant material have been described by many authors. See [943–945] for images and diagrams of the grass carp digestive system. The physical and histological characteristics of the grass carp intestine have been described by [943,944]. Like other cypriniforms, grass carp do not have a stomach, but rather an intestinal bulb, a dilated area at the anterior region of the intestine [243,946,947]. The digestive tract of the grass carp is simple, consisting of a long intestinal tube connected directly to the esophagus, and ending with an anus [944,945,948]. Additionally, there are no valves or caeca throughout the intestine [944]. A relatively long gut with high surface area allows grass carp to process low-energy plant material quickly and efficiently [949]. While grass carp possess a relatively long gut compared to carnivorous fishes, compared to other herbivorous fishes, the grass carp gut is considered very short (Refs. [167,182,192,945]; as reviewed by [17]). The intestinal quotient (intestine length/total body length) for grass carp ranges from 0.8 to 2.78 and increases as the fish increase in length and as vegetable matter in gut contents increase [950–952].

Based on histology, the grass carp intestine has three 'segments'; each performs different digestion and absorption processes: the anterior intestine contains mucosal folds in the intestine and is the primary site of lipid absorption and resynthesis, while the posterior intestine is the primary site of protein absorption; both of the first two segments have hairlike projections called microvilli to aid in absorption. The third section the rectum has fewer microvilli and specializes in ion transport [945,950]. In cypriniforms, mechanical digestion is performed by the pharyngeal teeth, and most chemical digestion occurs in the intestinal bulb [947]. Grass carp possess specialized pharyngeal teeth which are effective at grinding up vegetation, allowing for 60 to

70% digestion of plant material (Refs. [167,182,192,953], and N.S. Stroganov, 1963; as reviewed by [17]). Once in the intestinal bulb, additional digestion occurs via enzymes secreted by the pancreas and the action of the intestinal microbiome, as discussed below in 'Section 3.3.2. Digestive Enzymes' and 'Section 3.3.3. Intestinal microbiome'. The intestinal bulb and rostral section of proper intestine make up the first segment described by [945]; most digestion and absorption occurs in this segment. The second segment is characterized by enterocytes with numerous pinocytotic vesicles [950]. The suggestion that ion transport is the primary function of the third section of the intestine is carried out by [945] citing [954] (see [945] for illustration).

Multiple studies have documented structures and cells comprising the intestinal walls and how they contribute to digestion for grass carp and similar species. According to [945], the gut surface has mucosal folds which decrease in height from the first section to the third section of the intestine. The innermost layer of the mucosa is a columnar epithelium primarily made up of absorptive cells (enterocytes) possessing microvilli and goblet cells (see [945] images) along with some enteroendocrine cells [950]. In the first section of the intestine, the absorptive cells take up amino acids and lipids. Protein digestion is efficient despite the lack of a stomach and acid digestion [947,950]. The activity of alkaline phosphatase is high in the first segment and decreases through the intestine [955]; this supports the determination that a majority of active absorption occurs in the first gut segment [950]. The second segment is characterized by high pincocytotic activity with cells capable of absorbing macromolecules such as undigested protein and ferritin [950]. The amount of protein absorbed in the second gut segment does not seem to be quantitatively relevant and is not related to the lack of peptic activity in the intestinal bulb, as many had hypothesized [950,956]. Grass carp gut endocrine cell types are immunoreactive to the compounds gastrin, gastric inhibitory peptide, glucagon, glucagon-like immunoreactants, bovine pancreatic polypeptide, leucine-enkephalin, and substance P [957]. The researchers found that many of these immunoreactive endocrine cells are open-type; that is, they have microvilli which connect to the interior of the gastrointestinal tract and can react to chemical stimuli present; this cell structure suggests that the gut contents may act on the apical part of the cell to stimulate or inhibit peptide release from the basal part of the cell [957].

Some studies have quantified functions of grass carp intestine, including gut growth (weight and length), digestibility of different foods, digestion time, absorption of amino acids, and functionality under starvation conditions. Grass carp fed duckweed had higher gut growth rates compared to those being fed chironomid larvae [958]. At 28°C, grass carp required 12 h to process two different formulated diets, compared to typical times of more than 24 h for other fish species [949]. The total absorption ratio of leucine in the intestine of grass carp is 12.83%, 18.85%, and 16.45% with perfusion concentrations of leucine at 1.0, 5.0, and 10.0 mmol/L for 40 min, respectively [959]. For tyrosine these values are 22.18%, 23.68%, and 27.49%, with perfusion concentrations of tyrosine at 0.5, 1.5, and 2.5 mmol/L for 40 min, respectively. Protein synthesis in the liver is reduced via starvation with synthesized protein content in the intestines being 70% lower in starved grass carp than the non-starved control group [960]. The grass carp intestine is able to utilize the fish's plant-based diet to obtain the macronutrients needed for growth and survival. Understanding grass carp digestion and the effects of nutrients, chemicals, and environmental factors on the processes of digestion could allow managers to select baits and times for baiting to attract grass carp to best effect.

3.3.2. Digestive Enzymes

Enzymes within the digestive system play an important role in the ability of grass carp to process their diet and convert it into biologically usable energy sources (see [961] for a table of enzyme functions). Addition of some enzymes to the diet of grass carp can also have effects on growth, intestinal function, and survival. This is especially relevant in aquaculture, where alternative food sources are utilized. A summary of previous research on digestive enzyme activity of fishes (including grass carp, silver carp, and bighead carp), crustaceans, echinoderms, and mollusks paired with influencing factors such as feeding habitat, food composition, and development stage is provided by [961].

As with other teleosts, the pancreas of grass carp produces trypsin, chymotrypsin, and carboxypeptidases to aid digestion in the intestinal bulb [947,950]. Additional enzymatic activity is supplied by the microflora of the intestine. Grass carp gut enzyme makeup includes bacterial cellulase along with high amylase and protease activity; enzyme levels are dependent on diet [962]. Additional information on bacterial enzymes and their role in digestion is discussed in the next section, 'Section 3.3.3. Intestinal Microbiome'. Intestinal protease, lipase, and amylase activities in grass carp are higher than those of crucian carp and lower than those of Mandarin fish (*Siniperca chuatsi*), black carp, common carp, and silver carp [963], with protease activity increasing gradually along the length of the intestine from proximal to distal [963]. Exogenous supplementation of lipase provided juvenile grass carp with improved growth performance, intestinal growth and function, intestinal immune response, intestinal physical barrier, elevated intestinal antioxidant capacity, and the balance of intestinal microflora [964]. Dietary supplementation of 500 U/kg of neutral phytase alongside a diet with 0.5% to 1.0% monocalcium phosphate (MCP, a source of dietary P) increased amylase activity in the foregut and decreased lipase activity in the hindgut (see [945] for gut diagram) of grass carp [965]. A diet of 500 U/kg of neutral phytase alongside a diet with 0.5% to 1.5% MCP resulted in slightly higher serum P than a diet with 2.0% MCP and no phytase supplementation [646]. Research found that AHL-lactonase from *Bacillus* sp. is effective at decreasing and delaying mortality in common carp [966]. Acidic proteinase activity in the intestines of grass carp is highest at pH 2.5 to 3.0 while alkaline proteinase activity is highest at pH 10.0, the activity of the former decreased from esophagus to anus [948]. In the same study, the alkaline proteinases in the grass carp intestine are characterized as trypsin and a non-serine proteinase that is either an elastase or metalloproteinase. Ozone decreases proteinase and amylase activity in the intestines of grass carp [967]. A description of the exogenous proteolytic activity in grass carp fry on different food sources can be found in [233]. Proteolytic and transaminasic activity in the middle section of the intestine of grass carp is suggested as resulting from the absence of a stomach with alanine-aminotransferase trypsin pronounced activity [968].

3.3.3. Intestinal Microbiome

Interest in understanding the grass carp digestive system has extended to describing their microbiome. A review of the intestinal microbiome of grass carp, current up to the time of publication, is provided by [969]. Contained in this review is information on intestinal structure; how grass carp gain the bacteria in their intestinal microbiome from their environment; the composition and function of the intestinal microbiome; and the effects of probiotics (live microbes that are ingested to positively affect intestinal microbiome balance; Ref. [970]), prebiotics (a non-digestible dietary supplement that benefits select microbes in the host; Ref. [971]), and synbiotics (dietary supplements containing both probiotics and prebiotics; Ref. [972]) on grass carp. A general review on the microbiome of carps, including grass carp, is provided by [973].

Many microbial taxa have been identified in the intestines of grass carp; see [969] for a list of species. The intestinal aerobic and facultative anaerobic bacterial community in the grass carp gut contains many taxa common to other freshwater fish; it also contains less ubiquitous taxa such as *Pasteurella*, *Proteus*, *Salmonella enterica* subsp. *arizonae* (syn. *S. arizonae*), *Streptococcus*, and *Yersinia enterocolitic* (Ref. [974]; citing [975,976]). The microbial communities of the grass carp intestines are dominated by the phyla Fusobacteria, Firmicutes, Proteobacteria and Bacteroidetes [902,977–981], but composition varies in different sections of the intestine [981]. In a review of carp microbiomes, the authors concluded that amylolytic bacteria, primarily *Bacillus spp.*, are predominant in the carp digestive tract [973,982,983]. Bacterial taxa identified from the gut microbiome of larval grass carp include α-Proteobacteria, β-Proteobacteria, γ-Proteobacteria, and Actinobacteria [684]. Six anaerobic bacterial genera (*Actinomyces*, *Bacteroides*, *Clostridium*, *Eubacterium*, *Fusobacterium*, and *Peptostreptococcus*), as well as some Gram-negative rods and Gram-positive cocci undescribed at the time of publication, were found in the gut of grass carp (Ref. [975] as cited by [974]). A list of aerobic and facultative anaerobic bacterial taxa can be found in [975]. A table listing 76 phylotypes (as paraphrased from [984], phylotypes are DNA sequences that share particular gene markers) of bacteria they found in the gut of grass carp based on 16S rDNA sequencing is provided by [985]. In describing the microbiome of the grass carp gut, [986] found 1228 phylotypes. The abundance of *A. hydrophila*, *Micrococcus*, *Bacillus*, and *Bacteriodes* type A in the intestines of cultured juvenile grass carp is quantified by [901]. Of these, *A. hydrophila* had the highest count and the highest occurrence (100%, n = 5), while *Bacillus* was only present in one of five grass carp examined [901]. The B8 strain of *Bacillus amyloliquefaciens* was isolated from the intestinal microbiome of grass carp; this *B. amyloliquefaciens* strain shows antibiotic activity against several pathogenic bacteria, including *A. hydrophila*, *A. veronii*, *Edwardsiella tarda*, *Escherichia coli*, *Vibrio mimicus*, and *V. parahaemolyticus* [898]. Seven genera of bacteria were found in the gut of grass carp (*Vibrio, Acinetobacter, Providencia, Yersinia, Pseudomonas, Morganella, Aeromonas*), with *Aeromonas* as the dominant genus [987]. Homoacetogenic bacteria and *Aeromonas* were found in the intestines of grass carp by [988]. *Paracoccus luteus* is a species of aerobic, non-motile, Gram-negative bacterium that was first isolated from grass carp intestines in Henan Province, China and described as new species in 2020 [989]. The aerobic, non-fermentative Gram-negative bacillus *Acinetobacter lwoffii* is found in the intestine of grass carp [890].

Many studies describe the role of the grass carp intestinal microbiome in digestion, especially as it relates to digestive enzymes produced by bacteria. The most abundant bacteria in the grass carp gut are generally those that aid in digestion [977]. For a table of bacteria found in grass carp intestines and their function see [977]. Due to their plant-based diet, various microbial sources of the cellulose-digesting enzyme cellulase are particularly prominent and important for grass carp. Six bacterial strains which were found in the intestines of grass carp and that showed cellulase enzymatic activity were studied by [990]. In a comparison of the microbial communities of the foregut, midgut, and hindgut of four-year-old grass carp, the midgut had higher diversity than the other two sections [991]. That comparison also found that the hindgut contained greater abundance of cellulose-processing genera, including *Bacteroides* and *Spirochaeta.* Four strains of microbes with high cellulase activity found in grass carp intestines are *Bacillus subtilis* (three strains) and *Enterobacter asburiae* (one strain; Ref. [992]). The grass carp intestine microbiota included numerous cellulose-decomposing bacteria genera, such as *Anoxybacillus*, *Leuconostoc*, *Clostridium, Actinomyces*, and *Citrobacter* [977]. The earlier work of [993] documented low cellulytic activity in grass carp with the cellulolytic bacteria population continuously observed at low amounts of $\approx$ 10 cellulasic units. *Bacillus circulans* and *Bacillus megaterium* were identified as the two bacterial species in grass carp guts that exhibited the greatest cellulytic activity; both of these bacteria tolerated temperatures between 15 and 42 °C and pH ranging from 5 to 11 [982].

Comparison of the intestinal microbiomes of low-weight gain and high-weight gain groups of grass carp found that the low-weight gain group's microbiome had higher alpha diversity indices, a higher ratio of Bacteroidetes to Firmicutes, and lower abundance of Order Clostridiales [994]. Some potentially pathogenic bacteria can also contribute to enzymatic digestion in healthy grass carp. For example, *Citrobacter,* noted by [977], is regarded as an opportunistic pathogen and a source of cellulase; three strains of *Citrobacter* were also documented by [995]. Likewise, several studies found that *Aeromonas* was among the predominant genera and hypothesized that it is a significant source of cellulase [902,987,988]. The genus *Aeromonas* contains several facultatively pathogenic strains that can result in enteritis, as discussed in 'Section Infectious Disease' within Section 3.2.6., but bacteria of this genus also seem to normally reside in the grass carp gut and play an important role in digestion. It has been found that of 10 teleost fishes examined, grass carp had the greatest phytase-producing strains of bacteria that are necessary for the release of phosphorus phytic acid and phytate [996]. Tannase, an enzyme which processes tannins found in plants, has been found to be produced by microbiota that were isolated from the gastrointestinal tract of grass carp [997]. Chitinase-producing bacterial strains have been identified in the gut of grass carp [998]. Amylase and protease activities are performed by *Bacillus circulans* rather than *Bacillus megaterium* [982].

The gut microbiome can differ significantly among individual adult grass carp, and environmental conditions may drive some of these differences. Intestines of grass carp collected from a pond contained *Cetobacterium* more frequently than those of grass carp from a lake [999]. In terms of the bacterial makeup of the intestinal mucosa of grass carp, the bacteria in the gut of grass carp differed among fish in different environments [978]. Research found that much of the bacterial community is shared between the microbiome of grass carp and the microbe communities in their environment [977]. Others have found stronger connections to diet than to water or sediment [986]. Grass carp exposed to 1 mg/L of Pb for 42 days exhibited altered intestinal microbiomes; overall abundance and bacterial diversity declined following Pb exposure, and the phyla Fusobacteria and Bacteroidetes had higher relative abundance in the intestines of Pb-exposed grass carp [669]. The intestinal microbiomes of five diploid indigenous grass carp and five pure-line tetraploid grass carp engineered for fast growth are described by [1000], and it was found that while the gut microbiome of both were made up of more than 75% Fusobacteria and Proteobacteria, there were significant differences between the microbiomes of the indigenous and engineered fish. Other research found that Shannon diversity of the intestinal microbiomes did not differ among diploid grass carp and tetraploid grass carp; explicit, pairwise statistical comparisons of individual bacterial taxa were not conducted in this study, but the authors note higher abundance of the bacterial family *Erysipelotrichaceae* (Phylum: Firmicutes) in the tetraploid grass carp. Grass carp, silver carp, bighead carp, and Wuchang bream (*Megalobrama amblycephala)* larvae significantly differed in bacterial components of their microbiomes [684].

The intestinal microbiome of grass carp changes in response to infection with grass carp reovirus; infected grass carp microbiomes contain increased abundance of Fusobacteria, *Cetobacterium*, and lower alpha diversity [1001]. There is significant intra-species variation between the gut microbiomes of grass carp, bighead carp, common carp, and silver carp, even if they are reared under the same environmental conditions, indicating that gut microbiota are not only affected by their environment, but potentially also diet, morphology, trophic level, and phylogeny [902,977]. The changes in the intestinal microbiome of grass carp experiencing bacterial enteritis caused by a non-lethal strain of *A. hydrophila*, recorded from 12 h to 15 days post-infection onset, is provided by [1002]. In summary, like in many species, infection by a pathogen can alter the grass carp microbiome, potentially affecting biologic processes of individuals.

Both varying diet and starvation can cause differences in microbiome composition between individual grass carp and other carp species. Gut microbiome composition differs among grass carp fed commercial feed, those fed ryegrass, and wild feeding grass carp [986]. A comparison of the intestinal microbiomes of grass carp fed a commercial diet, grass, or untreated, antibiotic-containing chicken feces found that the grass carp provided a grass diet had fewer bacterial phyla than the other groups, that Firmicutes was the dominant phylum across diets, and that chicken feces diet had increased the number of potential pathogens and antibiotic-resistant bacteria [1003]. The bacteria of grass carp fed a higher fiber content Sudan grass diet had a higher diversity of cellulolytic bacteria than grass carp fed on artificial feed with lower fiber content [1004]. The bacterial community of the intestines of grass carp fed high-protein, low-fiber formula feed and fed low-protein, high-fiber Sudan grass diets was richer and more diverse in the midgut than the hindgut [1005]; within gut segments, both community parameters were greater in the former diet. Supplementing a standard diet with up to 15% fermented *Broussonetia* *papyrifera* increased the abundance of intestinal *Firmicutes* and *Fusobacteria*, while decreasing the abundance of *Actinobacteria* and *Cyanobacteria* [1006]. When compared to grass carp fed hybrid giant napiergrass (*Cenchrus flaccidus*) or a formula feed, grass carp fed fava beans showed higher relative abundances of Gram-negative and flagellated bacteria [1007]. This fava bean diet and associated microbiome change was associated with damage to the microvilli and increased TNF-α (a compound involved in inflammatory response). Replacement of 50% to 100% of the soybean meal in a grass carp aquacultural diet with larvae of black soldier fly causes intestinal levels of the bacterial genera *Aeromonas* and *Shewanella* to decrease [254]. In common carp, dietary supplementation with phytonutrient-rich waste from the processing of sour cherry and sweet red pepper increased intestinal *Clostridium* and *Lactobacillus*, while decreasing the abundances of potentially pathogenic bacteria [1008]. During periods of starvation, grass carp had a higher abundance of *Vibrio* and a lower abundance of *Bacteroides, Fusobacterium*, *Coprococcus* and *Citrobacter* genera in their intestines, as reported in [1009]. The authors note that starvation in grass carp alters structure and function of microbial communities, influences the intestinal immune system, and stimulates inflammatory responses.

Some studies have found that probiotics can affect the intestinal microbiome of grass carp and intestinal functions such as digestion and immunity. These findings may have application in controlling the microbiome of invasive populations of carps. The common use of prebiotics and probiotics in carp aquaculture was reviewed by [1010]. A particularly prominent probiotic used in grass carp is *Bacillus subtilis,* along with other *Bacillus* species. As mentioned in 'Section Infectious Disease' within Section 3.2.6., oral introduction of *Bacillus subtilis* to grass carp exposed to *A. hydrophila* reduced the effect on intestinal mucosal barrier function damage and inflammation [912]. Eleven *B. subtilis* isolates found in the intestinal tract of grass carp as to their probiotic value were related to water quality control, growth, and immunity in aquaculture [1011]. *B. subtilis* H2 used as a probiotic significantly altered the grass carp microbiome, increasing the relative abundances of *Proteobacteria* and *Bacteroidetes* [1012]. Using *B. subtilis* as a probiotic food supplement improved weight gain rate in grass carp and reduced liver damage caused by *A. hydrophila* infection [1013]. Optimal *Bacillus subtilis* Ch9 levels promote digestion and absorption of nutrients and growth [1014]. *Bacillus subtilis* as a probiotic supplement triggers the dendritic cell mediated immune response in grass carp; this response indicates that *B. subtilis* could be used to improve the balance and tolerance of the immune response [1015]. Feed-based spores of *Bacillus subtilis* for delivery of cysteine protease of *Clonorchis sinensis* trigger mucosal and humoral immunity to *C. sinesis* in grass carp [1016]. The addition of *Bacillus natto* to grass carp diet improved their growth [1017]. The addition of *Bacillus* to the diet of grass carp appeared to promote immunity and antioxidant function [1018]. Adding cultures of bacteria found in the guts of grass carp improved their ability to resist disease [1019]. Use of the bacterial strain *Bacillus licheniformis* FA6 as a dietary probiotic supplement over the course of 56 days resulted in increased weight gain rate, lengthening of villi in the intestine, and decreased mortality rate from *A. hydrophila* strain AH-1 [897]. Adding a multi-strain probiotic of *Bacillus* spp. + *Lactobacillus* to the diet of grass carp at 1.68 g viable bacterial cells/kg diet can increase growth, antioxidant status, and intestinal villi length; supplementation rates of 3.36 to 6.72 g/kg diet of the same probiotic improves hypoxia recovery based on a blood respiration metric [1020]. Dietary supplementation with 10,000,000 colony-forming units/g diet of *B. amyloliquefaciens* for grass carp exposed for 7 days to *A. veronii* resulted in a survival rate of 53%, compared to a 25% survival rate in the control group [898].

In addition to *Bacillus* spp., other probiotics and dietary supplements can also influence the health and microbiome of grass carp. *Lactobacillus acidophilus*, used as a probiotic, increased weight gain in grass carp (Ref. [973] citing [1021]). Probiotics help prevent septicemia (blood poisoning) by *Aeromonas* in grass carp [1022]. A recombinant strain of *Escherichia coli*, engineered for increased lead adsorption, used as a probiotic food additive in grass carp decreased Pb accumulation in the tissues of Pb-exposed fish [1023].

Dietary supplementation with the SL001 strain of the soil microbe *Pediococcus pentosaceus* increased growth rates of grass carp and altered the intestinal microbiome, reducing abundance of potentially pathogenic taxa (for example, *Aeromonas* and *Vibrio*) and increasing abundance of potentially probiotic taxa (for example, *Pediococcus*, *Lactobacillaceae*, *Lactobacillales*; Ref. [1024]). The same study on *P. pentosaceus* SL001 supplementation found that cumulative mortality from *Ahydrophila*, in grass carp fed *P. pentosaceus* is 51%, significantly lower than the control group mortality rate of 90%. Isonitrogenous and isoenergetic diets (i.e., different diets with equal levels of dietary nitrogen and calories, respectively) containing fava bean extracts increased intestinal microbiota diversity in grass carp [368]. Use of exogenous bile acid as a dietary supplement affects the grass carp intestinal microbiome by increasing abundance of *Lactobacillus* and *Bifidobacterium* two beneficial bacterial genera, and decreased abundance of potentially pathogenic *Aeromonas* and *E. coli* [240]. The addition of berberine, an isoquinoline alkaloid, to the diet of grass carp resulted in a more diverse gut microbiota that paralleled decreased serum glucose levels [1025]. The addition of xylo-oligosaccharides at a rate 0.4% to the diet of grass carp improves the intestinal microflora [315]. Waterborne Cd was found to alter the intestinal microbiota composition in the gibel carp [1026]. The addition of lithocholic acid to grass carp diet altered the intestinal microbiome by increasing the proportion of Proteobacteria and Firmicutes while decreasing the proportion of Fusobacteria [1027]. As demonstrated previously, probiotic bacteria play an important role in the digestion and overall health of an organism. Given this relationship, it is no surprise that diet can alter the microbiome. Understanding these interactions could help managers understand differing bait responses, and aquaculturalists and those using carp for weed control to select foods to promote fish health.

Additionally, pharmaceuticals, such as antibiotics and vaccines, can influence the microbiome of grass carp. Research aimed at developing a reliable method of disrupting the intestinal microbiome of grass carp found that a 28-day treatment high-concentration cocktail of four orally administered antibiotics, vancomycin (1 mg/fish/day), enrofloxacin (2 mg/fish/day), florfenicol (2 mg/fish/day), and metronidazole (2 mg/fish/day), was needed to disrupt both the luminal and mucosal microbiota [1028]. During this antibiotic treatment, Proteobacteria expanded, and Fusobacteria were suppressed; no adverse effects on the health or growth of the grass carp were found. Administration of an oral DNA vaccine for *Vibrio mimicus* to grass carp is associated with changes to the gut microbiome in multiple sections of the gut; some documented changes include increases in the relative abundance of *Bacteroides* and *Cetobacterium* in the midgut and hindgut and increases in the relative abundance of *Aeromonas* in the foregut and the midgut [1029].

3.3.4. Effects of Dietary Nutrient Levels on Intestines

A wide variety of research has contributed to understanding how nutrient deficiencies and diet additives can affect the grass carp intestine, leading to effects on production, health, and survival. Many studies also quantified dietary requirements for normal digestive tract function. For other effects of nutrient deficiencies and for dietary requirements of grass carp based on the study of other organ systems, see ‘Section 3.1.2. Aquacultural Diet and Associated Production’.

Dietary protein and amino acids play important roles in intestinal function of grass carp, and deficiencies can disrupt intestinal function. Suggested dietary protein levels for growth and resistance to enteritis are from 286.82 to 292.1 g/kg diet; these levels may enhance intestinal immune function and intestinal physical barrier functions [1030]. Amounts of dietary threonine found to improve intestinal immunity and decrease inflammation was from 14.53 to 15.17 g/kg diet [1031]. Threonine deficiency resulted in decreased growth, feed intake, and body protein synthesis, and altered anterior intestinal development and integrity [1032]. The addition of leucine to the diet of grass carp improved intestinal immune status [1033]. Methionine deficiency caused poor growth and decreased digestive and absorptive function and antioxidant capacity in the grass carp intestine; dietary methionine requirements to restore these functions in sub-adult grass carp is 5.42 to 6.99 g/kg diet in the presence of 1.50 g cysteine/kg diet [1034]. Dietary DL-methionyl-DL-methionine (a source of methionine) improves growth and intestinal immunity in grass carp [1035]. Valine deficiency decreases fish growth and intestinal immune status, the dietary valine requirement of young grass carp ranged from 14.00 to 14.47 g/kg diet [1036]. Phenylalanine diet supplements improved growth, digestive and absorptive ability, and antioxidant capacity of juvenile grass carp; the required phenylalanine, based on percent weight gained, is 10.4 g/kg diet [1037]. Histidine at 3.7 to 12.2 g/kg diet could block copper-induced oxidative damage in grass carp intestines [682]. Dietary histidine deficiency limited juvenile grass carp digestive enzyme activities in intestines [331]. Adding glutamate to the diet of grass carp increased intestinal absorption in the digestive tract and increased fish growth [1038]; they also demonstrated increased digestive enzyme activity and intestinal quotient after 56 days of glutamate supplementation. Dietary tryptophan improved juvenile grass carp growth, intestinal immune response, barrier function, and antioxidant status [1039]. Substitution of fishmeal with soybeans as the protein source disrupts the intestinal epithelium of grass carp [1040].

Several vitamins are important to the intestinal function of grass carp; deficiencies in these vitamins lead to reduced function and, in some cases, structural damage to the intestines. Folic acid deficiency impaired grass carp immunity, antioxidant capacity, and tight junctions in the intestine; the dietary folic acid requirement to minimize oxidative stress in the intestine is 1.80 mg/kg diet [1041]. Niacin deficiency decreased intestinal mucosal immune and physical function and gill immunity in young grass carp [1042,1043]. The estimated niacin requirement for young grass carp based on intestinal lysozyme activity is 39.80 mg/kg diet [1042]. Thiamin deficiency decreased young grass carp growth and immunity of the intestine, head kidney, spleen, and liver [1044]. The dietary thiamin requirement of young grass carp ranged from 0.90 to 1.15 mg/kg diet. Riboflavin deficiency decreased immunity and structural integrity of grass carp intestine; the optimum riboflavin level for intestinal acid phosphatase activity was 6.65 mg/kg diet [1045]. Vitamin A deficiency and excess levels impaired physical barrier functions in grass carp intestines; the optimal level of dietary vitamin A estimated for protecting grass carp from protein oxidation is 2622 IU/kg diet [1046]. Additionally, vitamin A deficiency negatively affected the histomorphology and structural integrity of the head kidney and spleen, impaired antibacterial activity, and increased inflammation; minimum dietary vitamin A requirements using these endpoints were estimated to be 2016 IU/kg [1047].

Various minerals are critical to grass carp intestinal functions, but both deficiencies and excesses can cause disruptions. Phosphorus deficiency decreased the ability of grass carp to combat enteritis due to increased exposure to *A. hydrophila*, suggesting this is related to impairment of intestinal immune barrier and physical barrier function [900]. This same research estimated 4.68 g/kg diet of available P is required for grass carp to help prevent enteritis. Zinc deficiency in young grass carp reduced growth as well as inhibited intestinal immune and barrier function [345]. Magnesium deficiency decreased intestinal growth (intestinal length index, intestinal weight/intestinal length) and overall body growth (percent weight gain) of grass carp, the same effect occurred at extreme levels of Mg [1048]. Manganese deficiency or excess Mn depressed intestinal immunity along with inflammation and dysfunction of intestinal physical barrier [1049].

Levels of other nutrients affect the intestinal functions of grass carp. Pyridoxine deficiency has led to decreases in growth, potential intestinal immunity, and intestinal physical barrier function in grass carp [1050,1051]. Based on intestinal indicators, the dietary pyridoxine requirement for young grass carp is 4.85 to 5.02 mg/kg [1050]. Dietary myo-inositol deficiency decreased immune function, caused inflammation, and has the potential to damage physical barrier function in the intestines of young grass carp when infected with *A. hydrophila* [1052,1053]. The optimal dietary myo-inositol for young grass carp was found to be 296.9 mg/kg diet for lysosome activity and 415.1 mg/kg diet for acid phosphatase activity [1053].

3.3.5. Effects of Dietary Additives, Vaccines, and Toxins on Intestines

Some experimental diet additives showed positive effects on grass carp intestinal functions, especially immunity. Dietary supplements of conjugated linoleic acid of 1.5 to 2.0% in grass carp feed appear to have anti-inflammatory therapeutic potential in grass carp intestines [1054]. Optimal dietary alpha-linolenic acid/linoleic acid ratio improved intestinal immune response and ameliorated the intestinal antioxidant status of juvenile grass carp; the optimal ratio ranged from 1.12 to 1.13 [1055]. Dietary choline of 407 mg/kg of diet or greater, led to increased intestinal somatic index and intestinal length index. Choline deficiency resulted in decreased free amino acids throughout the gut [296]. One study concluded that increased Ghrelin, achieved through injection or dietary choices, likely promoted intestinal cell proliferation and affected the expression of genes related to intestinal peptide absorption and metabolism [252].

Cinnamaldehyde supplementation, up to 108 mg/kg of diet, to a basal diet increased intestinal length, weight, and somatic index, as well as fold heights in the mid and distal intestine [308]. This same study found that cinnamaldehyde elevated the activity of various digestive enzymes including amylase, lipase, chymotrypsin, alkaline phosphatase, and creatine kinase in the intestine and trypsin, lipase, and amylase in the hepatopancreas.

The optimal dietary sodium butyrate supplement for maximizing the effectiveness of the physical barrier function in grass carp intestines was found to be 338.8 mg/kg diet [245]. The optimal amount of dietary sodium butyrate for improved intestinal immune function (i.e., protect against enteritis morbidity and lysozyme activity) was found to be 160.8 to 316.2 mg/kg diet [1056]. Replacement of 75% to 100% of the soybean meal in a grass carp aquacultural diet with larvae of black soldier fly caused intestinal damage, including shortened villi length and thinning of the intestinal wall [254]. Dietary *Eucommia ulmoides* leaf extract supplemented to a basal diet of 300 g/kg crude protein at 4 g/kg increased protease and amylase activity in the grass carp intestine which translated to increased digestibility of dry matter and crude protein [319].

Due to its prevalence in grass carp, various diet additives and vaccine sources have been tested for their utility in combatting *A. hydrophila*; much of this information is also presented in 'Section Infectious Disease' within Section 3.2.6. Plant extracts from basil (*Ocimum basilicum*), cinnamon (*Cinnamomum verum*), English walnut (*Juglans regia*), and peppermint (*Mentha* X *piperita*) improved immune responses to *A. hydrophila* in grass carp [911]. The optimal level of the organic acid methionine hydroxy analogue, ranging from 5.59 to 6.07 g/kg diet, was found to improve young grass carp intestinal immunological and physical barrier function after exposure to *A. hydrophila* [270]. As previously noted in 'Section Infectious Disease' within Section 3.2.6., *A. hydrophila* vaccine improved the immune response of grass carp intestines to the bacterium [909]. Lipopolysaccharide and outer membrane proteins from *A. hydrophila* are potential sources of vaccines against *A. hydrophila* in grass carp [910]. Oil-based inactivated vaccine was found to be effective against *A. hydrophila* in grass carp [1057]. One trial found that 72 mg/kg dietary cinnamaldehyde reduced enteritis in *A. hydrophila*-infected grass carp and increased activity of lysozyme and acid phosphatase along with increased levels complement C3, complement C4, and immunoglobulin M, [1058], which are associated with enhanced immune function [1058]. A nucleotide mixture supplemented into a basal diet at 600 mg/kg for 2 weeks similarly reduced enteritis morbidity in *hydrophila a*-challenged grass carp and increased several indicators of immune function, such as lysosome and acid phosphatase activity, and complement C3, complement C4, immunoglobulin M levels in the intestine [1059]. Betaine supplementation reduced the enteritis morbidity, increased markers of intestinal immune function, and reduced markers of intestinal inflammation in *A. hydrophila*-challenged grass carp compared to fish given no betaine or DL-methionine instead [267]. Grass carp fed a diet supplemented with 1 g/kg *Astralagus* polysaccharides had greater antioxidant and digestive enzyme activity [1060]. The authors also found reduced bacterial loads after *A. hydrophila* challenge in fish fed supplemental *Astralagus* polysaccharides compared to those given only the basal diet. A basal diet supplemented with an optimum level of xylooligosaccharides (40 mg/kg diet) for four weeks resulted in increased intestinal weight, length, and somatic index [352]. Additionally, xylooligosaccharides were reported to decrease indicators of apoptosis during *A. hydrophila* challenge suggesting that they promoted intestinal structural integrity [352].

Some compounds and diet additives have negative effects on grass carp intestines; they can either reduce function of grass carp intestines or cause intestinal damage though toxic effects. As previously mentioned in ' Section 3.1.2. Aquacultural Diet and Associated Production,' fishmeal with soybeans as the protein source for grass carp disrupts the intestinal epithelium [1040]. As previously noted in 'Section Macronutrients' within Section 3.1.2., a 40% soybean meal grass carp diet resulted in recovery from enteritis caused by overconsumption of soybeans [245]. One component of soybean protein, β-conglycinin, is a causal agent associated with soybean-induced intestinal damage and disruption [1061,1062]. β-conglycinin is not fully digestible, and ingestion at 80 g/kg diet can cause amino acid imbalance in the intestine [1061] and inflammation, oxidative damage, and cell apoptosis in the mid and lower intestine [353,1062]. Consumption of cereals in aquacultural settings is linked to enteritis, but adequate amounts of green vegetation can be used to combat this negative effect [377]. Dietary gossypol reduced intestinal amino acid absorption capacity [1063]. Dietary gossypol levels greater than or equal to 103.42 mg/kg diet reduced intestinal immunity and aggravated inflammation in grass carp [1064]. Grass carp exposed to endosulfan exhibited general atrophy, atrophy of villi, and increase goblet cells in intestines [755]. The presence of nanoplastics increased the negative effects of the antibiotic tetracycline on grass carp intestines [1065]. As noted earlier in 'Section Biotoxins' within Section 3.2.4., exposure to the mycotoxin deoxynivalenol results in deformity development and intestinal alterations in grass carp [694] and the cyanobacteria *Nostoc muscorum* produced detrimental effects on the intestine [1066]. As previously noted in 'Section Infectious Disease' within Section 3.2.6., the intestinal immune response of grass carp to bacterial muramyl dipeptide challenge involves MKK [1067].

4. Summary

Based on a targeted search of a relatively comprehensive literature database that focused on grass carp, this manuscript provides a review of literature on topics including biology, diet, behavior, physiological tolerances, toxicology, pathogens, and gut physiology. Where information is currently lacking regarding grass carp, the review supplements information from other members of the order Cypriniformes. This review provides basic background on the history, biology, effects, and management concerns associated with grass carp in North America; and lists of sources for more in-depth information on these topics. The diet component of this review provides information about grass carp diet as it relates to selection of aquatic plant foods, differences in diet across life stages, and research into diet formulations and additives that have been studied in the context of aquacultural production. The behavioral component reviews control of grass carp movement through use of sound and chemical stimuli and methods of controlling their feeding behavior. Also reviewed is avoidance and attraction behavior of grass carp as it relates to the use of non-physical barrier methods such as electrical fields, light, bubbles, CO_2, and water flow. The physiological constraints, toxicology, and biological control components provide a review of the literature on grass carp and related species in support of developing means of eradicating or reducing grass carp populations in natural systems. That section provides basic information that can inform toxic compounds. Lastly, the gut physiology component provides a review of what is currently known about the gut physiology of grass carp to improve the effectiveness of toxic compounds for use in grass carp eradication.

The review focuses on information relevant to current and potential means of controlling non-native grass carp populations. However, components of this review draw extensively from information on grass carp aquaculture, their use as biological control for nuisance aquatic vegetation, and their biology within their native range. This inclusion broadens the utility of this manuscript beyond non-native fish species management. For example, this review could be used by fisheries managers within the native range of the grass carp in Asia, or aquacultural researchers to help conserve populations and increase productivity, respectively.

The synthesized information presented in this review could be considered for use to develop new approaches and areas of research for controlling grass carp populations. This review also helps to identify behavioral, taxological, and physiological areas of research likely to prove unproductive due to limited effects or prohibitive cost. Examples of new approaches that could be tested as a control grass carp population include using toxin- or pathogen-carrying food pellets made of plant materials most selected for by grass carp (for example, waterweed, duckweed, hydrilla) enhanced with attractant compounds that enhance feeding response (for example, amino acids). An inner, delayed release capsule in such a pellet could deliver a pathogen, for example, GCRV, or toxins, for example, phytotoxins or praziquantel at a high dose along with other compounds that may improve gut absorption of those delivered to negatively affect grass carp. Examples of research on other carp species that could be applied to grass carp are various chemical and physical stimuli to alter behavior and pharmaceuticals that may be toxic. The hope is that the information in this review will provide a centralized source for information, and to inspire future research into management of invasive carp.

Author Contributions: M.L.W. conceptualized this study. M.L.W., B.M.W., K.K.D. and A.S.P. developed methodology. M.L.W., B.M.W., K.K.D. and A.S.P. collected data. M.L.W., B.M.W. and A.S.P. developed computer code for data processing. M.L.W., B.M.W., and A.S.P. conducted data analyses. M.L.W., B.M.W., K.K.D. and A.P.M. prepared the original manuscript draft. M.L.W., B.M.W., K.K.D. and A.P.M. conducted manuscript review and/or editing. M.L.W., B.M.W. and A.P.M. visualized data. M.L.W. provided project administration and supervision. All authors have read and agreed to the published version of the manuscript.

Funding: This project was funded by the U.S. Geological Survey, Ecosystems Mission Area Invasive Species Program and the Columbia Environmental Research Center.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: We would like to thank the team of researchers from U.S. Geological Survey, Columbia Environmental Research Center (CERC) and Upper Midwest Environmental Science Center who helped identify the direction and focus terms for this literature review: Robin Calfee, Nile Kemble, Patrick Kroboth, James Larson, Jeff Steevens, David Walters, and Ning Wang. We would like to thank numerous CERC staff that helped with preparation of the document: Keith Grabner, Christina Mackey, Erinn Scott, Zachary Beaman, Jack May, Kendell Bennett, and David Whites. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest: The authors declare no conflict of interest.

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