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Bioenergetics modelling of grass carp: Estimated individual consumption and population impacts in Great Lakes wetlands

Adam S. van der Lee [a,*], Timothy B. Johnson [b], Marten A. Koops [a]

[a] Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867 Lakeshore Rd., Burlington, ON L7S 1A1, Canada
[b] Ontario Ministry of Natural Resources and Forestry, Aquatic Research and Monitoring Section, 41 Hatchery Ln, Picton, ON K0K 2T0, Canada

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ABSTRACT

Grass carp (*Ctenopharyngodon idella*), native to eastern Asia, have established populations throughout the Mississippi River basin and are now reproducing naturally in the Great Lakes basin. As a large herbivorous fish, there is concern that an established grass carp population in the Great Lakes may threaten nearshore vegetated areas and wetlands. We parameterized a bioenergetics model for grass carp from the primary literature to quantify individual consumption levels and estimate the impacts of an established population on macrophytes in representative areas of Lakes Erie and Ontario. Individual life time consumption was estimated under average, cool and warm temperature conditions. Under average temperature conditions, a population of grass carp could consume up to 27.6 kg of vegetation per kg of fish per year, depending on energy density of the vegetation. When consumption was estimated for populations of various grass carp biomass densities, most simulated scenarios resulted in <50% of vegetation remaining in an invaded wetland after one year, with the majority of consumption from pre-adult stages. Direct impacts will likely exceed these effects due to losses to vegetation production potential from grass carp feeding early in the growing season and grass carp foraging activity resulting in plant damage or uprooting.

Introduction

Grass carp (*Ctenopharyngodon idella*) is a large (up to 45 kg; Fishbase, Froese and Pauly, 2005) herbivorous fish native to eastern Asia. First introduced to North America in the 1960s for aquatic vegetation control in aquaculture (Mitchell and Kelly, 2006), grass carp escaped captivity and established breeding populations in multiple states in the Mississippi River basin (Nico et al., 2015). Continued expansion into the Great Lakes is possible because environmental conditions are suitable for colonization (Herborg et al., 2007) and the surrounding tributaries are likely suitable for reproduction (Kocovsky et al., 2012). In the summer of 2015, 31 adult grass carp were captured at various locations in and around Lakes Erie and Ontario (Nico et al., 2015). Nine grass carp were capture on the Canadian side of the Lakes with six identified as diploid adults ranging in age from 8 to 14 years (Cudmore, DFO, 2015, personal communication) suggesting reproduction is possible. Grass carp have been confirmed to be reproducing in the Great Lakes basin (Chapman et al., 2013, Embke et al., 2016) although not in the Great Lakes proper.

As a predominately herbivorous species, grass carp are fairly unique among freshwater fishes. Grass carp have been widely introduced throughout the world for aquatic weed control because they are voracious consumers of plant material (Pipalova, 2006). Grass carp preferentially feed on submerged, rooted macrophytes, followed by filamentous algae, and fibrous, emergent vegetation (Swanson and Bergersen, 1988). Literature reports of prey preference are quite variable (e.g. Wiley et al., 1986, Pine and Anderson, 1991, Cudmore and Mandrak, 2004), but appear to be related to handling time (Dibble and Kovalenko, 2009) and independent of caloric content (Wiley et al., 1986). Preference for specific species may also be related to chemical composition of the plants (Bonar et al., 1990). Consumption rate was found to increase with calcium content, possibly due to palatability or because it is required for growth, and decrease with cellulose content which may increase handling time (Bonar et al., 1990). Grass carp will consume animal matter as part of their diet (Fedorenko and Fraser, 1978), and animal matter may be required for positive growth for young juveniles (Fischer, 1973) although wild grass carp are known to feed almost exclusively on macrophytes from approximately one month after hatching (Cudmore and Mandrak, 2004).

Introduced grass carp have had significant deleterious effects on both water quality and biota (Wittmann et al., 2014), and there is concern that an established, reproducing grass carp population may

* Corresponding author.
E-mail address: adam.vanderlee@dfo-mpo.gc.ca (A.S. van der Lee).

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threaten Great Lakes wetlands. Invasion of grass carp in Vaal River, South Africa may be responsible for the reduction in the quantity and diversity of submerged macrophytes in the river (Weyl and Martin, 2016). There are more than 2000 wetland complexes in the Great Lakes although >50% of those in Lakes Michigan, Erie and Ontario are degraded (Cvetkovic and Chow-Fraser, 2011). Wetlands also face threats from invasive plant species (Tougas-Tellier et al., 2015) and climate change (Short et al., 2016). Wetlands contain over 300 species of vascular plants (Herdendorf, 1992) and provide multiple ecosystem services including providing habitat for fishes (Jude and Pappas, 1992, Trebitz and Hoffman, 2015) and waterfowl (Prince et al., 1992) as well as maintaining water quality (Sierszen et al., 2012). Herbivory in aquatic ecosystems is significant with herbivores on average removing 40–48% of macrophyte biomass annually (Bakker et al., 2016). Establishment of grass carp populations in the Great Lakes are, therefore, expected to further stress Great Lakes wetland environments, potentially compromising their ecological utility.

Bioenergetics models provide a quantifiable means, through estimates of consumption, to assess the trophic impact of a species on a resident ecosystem (Hanson et al., 1997). Bioenergetics models are based on energy mass balance where energy consumed is balanced by the costs of metabolism, growth and waste (Hanson et al., 1997). Previously, bioenergetics models have been used to assess the potential for other fish invasive to the Great Lakes to establish populations given available prey resources, and the impacts of those species were they to become established. Cooke and Hill (2010) compared energy requirements of silver (*Hypophthalmichthys molitrix*) and bighead carps (*H. nobilis*) to the availability of phytoplankton and zooplankton and concluded that under specific temperature and activity regimes these species may struggle to survive in many open water areas in the Great Lakes. Anderson et al. (2015) provided an update, which included improved estimates of algal concentrations, and concluded that these carps will not be food limited in Lake Erie. Lee and Johnson (2005) developed a bioenergetics model for round goby which invaded the Great Lakes in the early 1990s (Charlebois et al., 1997), and the model has been applied to understand energy (Johnson et al., 2005), nutrient (Bunnell et al., 2005), and contaminant fluxes (Wallace and Blersch, 2015) in Lake Erie and elsewhere. Our objectives were to 1) parameterize a bioenergetics model for grass carp, 2) quantify consumption for individual grass carp under alternative temperature scenarios, and 3) estimate potential impacts on macrophyte communities in representative areas of Lakes Erie and Ontario.

Methods

Model

We modelled grass carp bioenergetics using the principles of the Wisconsin model (Hanson et al., 1997) where annual growth, ΔB (g_{fish}/y), is:

$$\Delta B = \sum_{d=1}^{365}\left([C_d-(R_d+S_d+F_d+U_d)]\frac{E_{prey}}{E_{fish}}W_d\right)-GW_s. \quad (1)$$

where d is day of year, C is the daily per gram consumption of food, R is respiration or the per gram cost of metabolism, S represents the per gram cost of specific dynamic action, F is the per gram losses to egestion and U is excretion or the per gram losses as nitrogenous waste. Variables are expressed in units of $g_{prey}/g_{fish}/d$ and must be converted to units of $g_{fish}/g_{fish}/d$ through the ratio of energy densities of the prey, E_{prey}, and grass carp, E_{fish}. W_d is the weight (g) of the fish on day d and G represents gonad production, which is incorporated as a proportion of body weight the day of spawning, s. Values related to variable estimates are listed in Table 1.

Daily consumption rate ($g_{prey}/g_{fish}/d$) is a function of body size and temperature:

$$C = p \cdot a_C W^{-b_C} f_C(T), \quad (2)$$

where $f_C(T)$ is the temperature-dependence function with temperature, T, in °C, a_C and b_C are the intercept and slope of the allometric function (Table 1), and p which scales from 0 to 1 and represents the proportion of maximum feeding rate required to produce the observed growth; any reference to p throughout the remainder of this manuscript is referring to the proportion of maximum consumption.

Temperature-dependence is modelled using Eq. (3) described in the Wisconsin model (Thornton and Lessem, 1978, Hanson et al., 1997). This form is appropriate for cool and cold water species and is the

Table 1
Summary of parameter values used in the grass carp bioenergetics model.

Symbol	Description	Value	Source
a_C	Intercept of allometric consumption function	1293.5/E_{prey}	Fischer (1973)
b_C	Exponent of allometric consumption function	Table 2	Filtered
te_1	Temperature for xk_1 (°C)	8	Cudmore and Mandrak (2004)
te_2	Temperature for xk_2 (°C)	22	Fedorenko and Fraser (1978)
te_3	Temperature for xk_3 (°C)	30	Kilambi and Robison (1979)
te_4	Temperature for xk_4 (°C)	35	Wiley and Wike (1986)
xk_1	Proportion of C_{max} at te_1	0.15	This analysis
xk_2	Proportion of C_{max} at te_2	0.98	This analysis
xk_3	Proportion of C_{max} at te_3	0.98	This analysis
xk_4	Proportion of C_{max} at te_4	0.05	This analysis
a_R	Intercept of allometric respiration function	0.0017	Cui et al. (1994)
b_R	Exponent of allometric respiration function	Table 2	Filtered
c_R	Temperature coefficient for respiration	0.048	Wiley and Wike (1986)
ACT	Activity level	2.0 if $T \geq te_1$ 1.5 if $T < te_1$	This analysis
a_S	Coefficient for specific dynamic action	0.07	Carter and Brafield (1992); Wiley and Wike (1986)
a_F	Proportion of consumed food egested	Table 2	Filtered
a_U	Proportion of assimilated energy excreted	0.076	Cui et al. (1992)
$DD15$	Spawning required of degree days above 15 °C	633	Kocovsky et al., 2012
E_{fish}	Energy density of grass carp	4874	Scott and Orr (1970); Hadjinikolova et al. (2008)
E_{prey}	Approximate energy density of prey source	900 (duckweed); 1500 (Hornwort); 2250 (*Elodea*);	Fischer (1968); Wiley and Wike (1986);