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Reviewing uncertainty in bioenergetics and food web models to project invasion impacts: four major Chinese carps in the Great Lakes

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Abstract

Bioenergetics and food web models are tools available for understanding and projecting the impacts of aquatic species invasions on food web structure and energy allocation of an ecosystem. However, uncertainty is inherent in modeling the impact of invasive species in novel ecosystems, as assumptions must be made about physiological responses to novel environments and interactions with existing (native and non-native) species. Here we use the four major Chinese carps (FMCC) in the Laurentian Great Lakes as a case study to categorize and describe the suite of uncertainties inherent in projecting the impact of invasive species with bioenergetics and food web models. We approach this case study in a decision analytic framework, describing structural uncertainties, environmental variation, partial observability, partial controllability, and linguistic uncertainty. Finally, we review and give suggestions for how the use of methods including adaptive management, scenario planning, sensitivity analyses, and value of information, as well as efforts to ensure clarity in language and model structure, can enable modelers and managers to reduce and account for key uncertainties and make better decisions for the control of invasive species.

Keywords: Asian Carp; Ecopath with Ecosim; invasive species risk assessment; Laurentian Great Lakes; ecological modeling

Introduction

Understanding how ecosystems might change following the establishment of invasive species is a core component of invasive species risk assessment and necessary to decide whether species management (i.e., prevention, eradication, or control) is warranted. The predominant mechanism by which invasive species exert effects on other species appears to be predation and competition for prey resources (Mills et al., 1993; Sturtevant et al., 2019; Zhang et al., 2019). At the extreme, species invasions can drastically change food web structure and function (e.g., Willson et al., 2011). Therefore, methods to identify the ecological impact of invasive species must be capable of determining how species assimilate prey in new environments and the impacts of this consumption on the food web as a whole.

The ecological impacts of invasive species are often evaluated after invasions have occurred, which hinders preventative decision making. Forecasting tools are urgently needed to gauge how the recipient community could change in response to a new invader, which would help to prioritize management responses and resources. Two major approaches to forecasting ecological impacts of invasive species are to: (1) project individual or population level consumption by the invader on existing prey species (Cooke and Hill, 2010; Dick et al., 2014; Jackson et al., 2015) and (2) project direct and indirect effects of the invader on existing species by accounting for predator–prey interactions in the food web (Zhang et al., 2019).

Bioenergetics (Kitchell et al., 1974; Ney, 1993; Winberg, 1956) and food web models (Zhang et al., 2019, 2016) describe the flow of energy (consumption and growth) between species and their environment under different ecological conditions. In particular, bioenergetics models estimate how much somatic growth can be supported by thermal conditions and prey availability and may therefore help determine whether sufficient prey exists to support an invasive species, as well as the consequences of consumption on prey resources (Johnson et al., 2005). Food web models explain how changes in consumption and trophic relationships shift energy flows within a community, allowing the direct and indirect impacts of invasive species to be better understood (Kao et al., 2018, 2016, 2014; Zhang et al., 2019). Using these two tools may therefore provide a comprehensive evaluation of potential invasions. However, both bioenergetics and food web models are complex, leading to considerable uncertainty in parameterization and interpretation.

When dealing with potential invasions, uncertainty can hinder our understanding of the probable effects of species on the ecosystem, as well as our ability to make decisions about how to minimize these effects via prevention or control (Robinson et al., this issue). Most uncertainty is attributed to our limited knowledge about the invasive species and their adaptive potential in new environments. To fundamentally reduce uncertainty, modeling should be carried out with input from and feedback to field studies and invasive species managers. This review will serve as a way for modelers to communicate with biologists and managers by classifying and summarizing uncertainties associated with ecological models.

Efforts to project the potential impacts of the four major Chinese carps (hereafter FMCC; bighead carp [*Hypophthalmichthys nobilis*], silver carp [*H. molitrix*], black carp [*Mylopharyngodon piceus*], and grass carp [*Ctenopharyngodon idella*]) on food webs of the Laurentian Great Lakes illustrate how reducing and accounting for critical uncertainties will increase the utility of the models for understanding potential effects and making informed decisions. The FMCC present high invasion risk to the Great Lakes (Cudmore et al. 2017, 2012; Drake et al., 2020), with grass carp already extant and reproducing in the Lake Erie basin (Embke et al., 2016). FMCC have invaded the Mississippi River system with silver carp becoming a dominant species in many river reaches (see Chapman et al., this issue for a review of the status of each species in North America). Species-specific bioenergetics and food web models have been developed, or are under development, to estimate the ecological dynamics of FMCC in the Great Lakes basin and account for the different trophic positions and feeding strategies (planktivorous, herbivorous, molluscivorous) of each species. While current models have provided significant insight, a more complete treatment of the uncertainty inherent in these models is needed to evaluate model projections and prioritize future research needs. The FMCC are an ideal example to emphasize the generality of uncertainty for any novel invader, as they have similar life histories, but each species will capitalize on different prey resources, and thus, pose different food web impacts. Determining how uncertainties within the models change projections within the recipient community is urgently needed to refine the scope and scale of potential ecological effects.

Model uncertainty is complex and includes numerous components. We first describe a typology of uncertainties that can influence bioenergetics and food web models. This framework, which is rooted in decision analysis, lends structure to delineating uncertainties in terms of reducibility, system understanding, inaccuracies in observation, and incomplete influence of control actions on an invader. We then review and give suggestions for how efforts to evaluate these uncertainties in terms of value of information, scenario planning, and sensitivity analyses can highlight key uncertainties that must be reduced to increase the utility of models for decision support and risk assessments. Throughout, we use projecting the ecological effects of FMCC in the Great Lakes as a case study to demonstrate model uncertainties and how they may be handled; however, these generalities are pertinent for how we handle modeling of new species in new environments.

Typology of Uncertainties in Bioenergetics and Food Web Modeling

There are five components of a decision analytic framework that can be used to categorize uncertainties in bioenergetics and food web modeling. Williams (1997) describes four uncertainties related to information used to model population processes when making harvest management decisions: structural uncertainty, environmental variation, partial observability, and partial controllability. In addition, Regan et al. (2002) included another common and important type of uncertainty: linguistic uncertainty. Categorizing uncertainties in this manner can help to identify general solutions for similar types of uncertainties. Below we describe each of the five categories of uncertainty in bioenergetics and food web modeling for the risk assessment of FMCC in the Great Lakes and discuss whether they can be resolved with more research effort (i.e., epistemic uncertainties) or are unresolvable and can only be accounted for (i.e., aleatory uncertainties). The information we describe is summarized in Table 1.

Structural Uncertainty

Structural uncertainty, or process uncertainty, refers to uncertainty regarding the biological and ecological processes of the system being modeled (Peterman, 2004; Williams, 1997). Structural uncertainty can be expressed as either functional uncertainty, in which discrete models describe different hypotheses about states of knowledge, or parametric uncertainty, in which there is a large range of potential parameter values. Both of these forms of structural uncertainty are important in bioenergetics and food web models, particularly for invasive species like the FMCC, for which there are limited data to predict their behavior and effects in a new habitat. Functional uncertainties exist with regard to the effects of anthropogenic and environmental drivers in the present and future, such as climate change and land use change, as well as trophic interactions among the FMCC and between the FMCC and existing species. Parametric uncertainties exist in myriad forms for both food web and bioenergetics models, stemming from a lack of information about basic parameters for all species and uncertainty about parameter estimates for invasive species in novel habitats. Below we describe several aspects of these uncertainties for the FMCC in the Great Lakes, focusing on climate change, land use change, trophic interactions, and general parametric uncertainties for the two model types.

Effects of climate change

Climate change is expected to make the Great Lakes' thermal environment more favorable for the survival and establishment of FMCC (Alsip et al., 2020; Coulter et al., 2018). However, the influence of these large lakes on regional climate (Notaro et al., 2013), with their high interannual meteorological variation and complex hydroclimatic linkages (Gronewold et al., 2015; Lenters et al., 2013; Xue et al., 2017), can hinder projection of the effects of climate change at time scales relevant for the ecological modeling of FMCC establishment and impacts. Effects of climate change on Great Lakes aquatic habitats may result in a deeper thermocline, warmer surface waters, a longer period of summer stratification, and milder winters (Brandt et al., 2002; Brooks and Zastrow, 2002; Collingsworth et al., 2017; McCormick and Fahnenstiel, 1999); these changes would provide favorable thermal habitat for the growth of FMCC. To date, several bioenergetics models indicate growth potential, overwinter survival, and consumption rates of bighead, silver, and grass carps will increase under warming scenarios if food is not limiting (Alsip et al., 2020; Coulter et al., 2018; van der Lee et al., 2017). Thus, accounting for and, if possible, reducing the uncertainty in climate warming effects on the thermal environment is important to projecting FMCC growth dynamics for a given year in the near to distant future.

Changes to the thermal environment and precipitation and wind patterns under a projected future climate may change the species composition and productivity of primary and secondary producers across the Great Lakes (Brinker et al., 2018; Mandrak, 1989; Reavie et al., 2017). These projected changes in prey availability may differentially affect consumption and growth of FMCC and should be accounted for in modeling efforts. Bighead and silver carp, together known as the bigheaded carps, primarily feed on both phytoplankton and zooplankton, grass carp feed on benthic macrophytes, and black carp are primarily molluscivorous but also feed on other benthic organisms. Therefore, we expect each FMCC species to respond differently to changes in productivity related to climate change. For example, in oligotrophic areas, increased temperature could increase macrophyte growth, but in more eutrophic areas shading by algae may reduce light penetration and macrophyte growth, leading to site-specific differences in grass carp population dynamics. Similarly, increases in temperature and precipitation may also increase the relative abundance of cyanobacteria biomass and the magnitude and frequency of harmful algal blooms (HABs) in eutrophic areas like Western Lake Erie or Green Bay, Lake Michigan (Michalak et al., 2013; Paerl and Huisman 2008). Increases in cyanobacteria may provide more food for bigheaded carps but would reduce mussel filtration (Vanderploeg et al., 2009), and thus may indirectly affect black carp by reducing dreissenid mussel biomass (Drake et al. 2020). In future modeling efforts, reducing structural uncertainty regarding climate effects on primary and secondary production in different habitats of the Great Lakes and the consequent effects on FMCC energetics will improve understanding of when and where ecological impacts will be greatest, and help prioritize prevention and control efforts.

In addition to the FMCC, other invasive species may be affected by climate change, resulting in greater uncertainty in bioenergetics and food web model outcomes. In the absence of HABs, increases in water temperature will increase filtration rates of dreissenid mussels, which could decrease available biomass of phytoplankton and zooplankton, thereby decreasing potential production of bigheaded carps while providing increased biomass of dreissenid mussels for black carp production. Conversely, filtration by bigheaded carps could reduce plankton biomass before it becomes available to dreissenid mussels. Alsip et al. (2020) used a biophysical model linked to a bioenergetics model to project that climate warming, by extending the stratification period, would reduce the time that dreissenid mussels could access prey throughout the whole water column, increasing the length of the growing season of bigheaded carps in Lake Michigan. Increases in water clarity and light resulting from dreissenid mussel filtration would stimulate the growth of aquatic plants, benefitting grass carp growth in nearshore habitats.

Uncertainty in range expansion of other aquatic invasive species may have unknown or uncertain effects on the establishment of FMCC. For example, in northern areas of the Great Lakes, climate change has the potential to increase the abundance and food consumption of parasitic sea lamprey (*Petromyzon marinus*), as well as thermal habitat overlap between sea lamprey and the FMCC, potentially resulting in greater predation rates on FMCC adults. In southern areas of the Great Lakes, effects of climate change on sea lamprey are less certain, as temperatures may become unfavorable for its reproduction or growth (Lennox et al., 2020). Although future species invasions are difficult to predict, a better understanding of potential interactions among the FMCC and existing invasive species in the Great Lakes, similar to the work of Alsip et al. (2020), will reduce some of this structural uncertainty.

Land use change

Modeling physiological, community, or ecosystem responses to land use change is often obscured by uncertainties about the progression of the rate and type of change, and the resulting effects on the biophysical environment that drive modeled processes. Using information from land use and human population models to inform ecological models can help resolve uncertainties in the aquatic ecosystem response to changes in land use and land management. Understanding how changes in land use will affect the availability of food or alter the thermal environment is necessary to project habitat quality and FMCC bioenergetics into the future. For example, annual US phosphorus loads are forecasted to increase by 3.4–5.8% from 2010 to 2040 without accounting for the effect of climate change on hydrology (LaBeau et al., 2014), which could increase the frequency of large runoff events and thereby increase annual loads even more (Bosch et al., 2014; Michalak et al., 2013). This is particularly important for the planktivorous bigheaded carps for which simulation studies have demonstrated that growth is notably responsive to differences in phosphorus loads under different scenarios for Lakes Michigan (Alsip et al., 2020) and Erie (Zhang et al., 2016). In contrast, increases in large runoff events and urbanization that lead to increased sedimentation and turbidity in nearshore waters might negatively affect the biomass or quality of macrophytes and mussels as food for grass and black carps. Finally, an increase in frequency of runoff events may increase spawning success for all FMCC (Kolar et al., 2007; Kočovský et al. 2012), resulting in increased recruitment and population growth. Therefore, isolating the different effects of land use change (e.g., increased phosphorus loads, sedimentation, changes to water temperature and hydrology) on survival, growth, and establishment of each carp species can improve understanding of how expected changes in land use could influence invasion risk.

Trophic interactions

Uncertainty about the diet of invaders in novel environments also presents a challenge for improving model projections. Planktivorous bigheaded carps are capable of surviving on diets dominated by detritus or cyanobacteria, including *Microcystis* (Anderson et al., 2016; Vörös et al., 1997; Zhang et al., 2016), making them highly adaptable to new environments. Accounting for this dietary breadth in modeling efforts demonstrated a > 4-fold increase in the volume of suitable habitat available for bigheaded carps compared to when they were restricted to feeding on phytoplankton alone (Alsip et al., 2019). Food items previously incorporated into models for bigheaded carps include detritus/dreissenid biodeposits, *Microcystis*, green algae, and macrozooplankton (Alsip et al., 2019; Anderson et al. 2017, 2015; Cooke and Hill, 2010). Future models of bigheaded carps should also include microzooplankton (e.g., rotifers, copepod nauplii, and dreissenid veligers) in carp diets as they made up about 74% of total zooplankton biomass in Lake Michigan (Thomas et al., 2017).

There is general uncertainty about whether or how black and grass carps will show preference for prey based on the quantity and quality of food items in the Great Lakes. For bioenergetics model simulations, reliable prey abundance estimates are necessary to develop credible projections of carp biomass and impact. Although estimates for benthos biomass are available for the Great Lakes, macrophyte biomass and species composition are poorly sampled, which could ultimately affect decisions for the control of these species (Robinson et al., this issue). In addition, uncertainty about black carp prey preferences has implications for the response of the food web components that are consumed (Smyth et al., 2020).

Whether the FMCC consume fish larvae also is highly uncertain. Although there are no field observations of the FMCC eating fish eggs or larvae, these invasive carps would occupy areas that are spawning and nursery habitats for many native fishes. Moreover, black carp have been observed to consume larval fishes in controlled laboratory experiments, although there is no conclusive evidence they will consume larval fishes in natural environments (Hung et al., 2014). Alewife (*Alosa pseudoharengus*) serve as an example of the potential for invasive species to have unanticipated effects on larval fishes. Alewife were not reported to consume larval fishes in their native habitat, but in the Great Lakes, their consumption of larval fishes can significantly decrease the recruitment of many fish species (Mason and Brandt, 1996; Dettmers et al., 2012; Kao et al., 2014; Madenjian et al., 2008). Incorporating potentially novel foods, such as larval fishes (e.g., Zhang et al., 2016), into future models is needed to evaluate the implications of these uncertainties on the establishment and impact of FMCC in the Great Lakes.

In addition to consumption of existing prey species by non-native species, the adaptation of existing predators to new prey resources also affects the potential abundance of non-native species. Uncertainty in this adaptation, however, obscures projections related to the probability and rate of proliferation of a new invader. Existing predators first must recognize the new species as prey, which creates a time lag between invader establishment and the onset of predation by existing species. The length of this time lag depends on the behavior of the new species, its abundance relative to existing prey, and detection by the predator (Abrams and Matsuda, 2004).

Moreover, predators switching their diet to the FMCC may facilitate co-existence of some competing species, such as bigheaded carps and existing planktivores (Abrams and Matsuda, 2004; Murdoch, 1969; Murdoch et al., 1975).

Uncertainty in occurrence and strength of these trophic interactions is most important for models that attempt to project FMCC population growth, asymptotic population size, and effects on Great Lakes food webs. For example, many piscivores in Lake Erie are generalists and opportunists (Johnson et al., 2005). The reproducing population of grass carp in western Lake Erie (Embke et al., 2016) may constitute a new prey source for these predators, as has been observed for round goby (*Neogobius melanostomus;* Foley et al., 2017). However, the rapid growth in body size of FMCC juveniles creates uncertainty in the potential for similar changes in Great Lakes piscivore diets (see Cudmore et al., 2017, 2012; Drake et al., 2020). In addition, some predators are known to feed on bigheaded carps in their introduced range of the Illinois and Upper Mississippi Rivers. Mesocosm studies indicate largemouth bass (*Micropterus salmoides*) preferred bighead carp over silver carp or native prey fishes (Sanft et al., 2018), while additional predator diet studies and mesocosm experiments suggest silver carp is less preferred than native prey fishes (Wolf and Phelps, 2017). Adult bigheaded carps have been found in stomachs of large blue catfish (*Ictalurus fircatus*; Locher, 2018), whereas several smaller native predators such as white bass (*Morone chrysops*), shortnose gar (*Lepisosteus platostomus*), and flathead catfish (*Pylodictis olivaris*) will readily consume juvenile silver carp when they are abundant (Anderson, 2016). Reducing uncertainty associated with predation on FMCC by Great Lakes species would improve our understanding of the degree to which predation affects establishment probability and the levels of achievable FMCC biomass.

Modeling bioenergetics of invasive species and their impacts on food webs requires accounting for indirect trophic interactions and cascading effects in a large, complex ecosystem, which leads to highly uncertain outcomes. Managers must account for these uncertainties when considering methods to control and mitigate the effects of these species. For example, grass carp will consume aquatic macrophytes that provide spawning or nursery habitat for native species like centrarchids, esocids, percids, and numerous imperiled species (Cudmore et al., 2017; van der Lee et al., 2017). These effects would be most severe in wetland habitats such as Lake St. Clair and other large, shallow embayments that currently support macrophytes and wetland fishes. Dead benthic macrophytes are an important source of detritus for benthic invertebrates in nearshore habitat, so grass carp expansion could lead to bottom-up control on the production of benthos that may serve as prey for benthivores.

If bigheaded carps are introduced to the Great Lakes, their consumption could reduce the biomass and size of zooplankton prey for planktivorous larval, juvenile, and adult fishes (e.g., alewife), thereby reducing their growth and recruitment (Minder and Pyron, 2018; Sampson et al., 2009). A decrease in alewife would negatively affect biomass of Chinook salmon (*Oncorhynchus tshawytscha*), which rely on alewife for prey (Dettmers et al., 2012; Kao et al., 2016, 2018). Alewife also prey on fish early life stages (Mason and Brandt, 1996) and cause thiamine deficiency syndrome, which leads to early life mortality in lake trout (*Salvelinus namaycush*; Czesny et al., 2009). If competition for plankton by bigheaded carps causes a decline in alewife populations, recruitment of some predator species, such as lake trout and walleye (*Sander vitreus*), could increase. However, bigheaded carps had only minor negative effects on native age-0 fish in the Illinois River, perhaps because abundant age-0 bigheaded carps might release age-0 native fish from predation pressure (DeBoer et al., 2018).

The FMCC have complementary diets, and in China, are raised together in aquaculture ponds where they feed on different prey types, at different depths, and thus avoid competition (Lin, 1982). However, interactions among these species in introduced habitats present potential uncertainties. The bigheaded carps feed on plankton, but finer gill raker spacing of silver carp relative to bighead carp allow it to access smaller particles (Kolar et al., 2007). In North American rivers, silver carp appear to be in better condition and more abundant than bighead carp where the two co-occur in high densities, implying that silver carp are a superior competitor for plankton in mesotrophic and eutrophic riverine ecosystems (DeBoer et al., 2019). However, silver carp's higher energy density requires them to consume more energy than bighead carp to achieve similar growth. This implies that, all else being equal, silver carp need to consume more per gram body weight to grow than do bighead carp (Alsip et al., 2019). In food-rich environments, this would be a successful strategy as prey abundance would not limit silver carp growth. However, in the food-limited habitats of the Great Lakes, fishes that can survive on less food would likely be more successful. Furthermore, typical species-specific differences in gill raker morphology among the bigheaded carps may change when bighead x silver carp hybrids are produced in the wild. Resulting hybrids can exhibit significant differences in gill raker morphology (Mozsár et al., 2017) that could affect foraging efficiency and, thus, add an additional layer of uncertainty.

The interactions between black carp and other FMCC could be affected by the ability of black carp to consume dreissenid mussels (reviewed in Nico et al. 2005). Black carp consumption of large numbers of dreissenid mussels could increase the availability of primary production, which is now sequestered by the mussels, to zooplankton and would benefit bigheaded carps. Such consumption by black carp is unlikely to occur at a lake-wide scale because of cold bottom temperatures in some lakes, but it could occur in isolated patches of warmer preferred temperatures (Drake et al., 2020; Smyth et al., 2020). On the other hand, reduced dreissenid filtration could result in decreased light availability for benthic macrophytes, which would limit food availability to grass carp. Potential interactions between grass and black carps may be weaker when benthic macrophytes are abundant, but then may intensify after benthic macrophytes are greatly reduced and grass carp begin to consume an increasing proportion of the benthos. These uncertainties should be accounted for in bioenergetics modeling efforts, as these potential interspecific interactions could affect FMCC performance in new environments.

Parametric uncertainty in food web models

A food web model can potentially include hundreds of parameters. As such, the largest source of uncertainty in these models involves estimating parameters such as biomass, consumption rate, and diet composition (e.g., Christensen and Walters, 2004). For example, uncertainties in fish biomass estimates could include estimating abundance from catch-per-unit-effort data, converting fish abundance into biomass with averaged individual weight, spatial and temporal averages, and fishing gear catchability. Sensitivity analyses could be conducted to determine the effect of parametric uncertainty on model outputs and to understand where efforts are best placed to reduce parametric uncertainty.

Recently, Rutherford et al. (in press) used Ecopath with Ecosim (EwE) food web models (Christensen and Walters, 2004; Heymans et al., 2016) to investigate potential food web effects of bigheaded carps across habitats in Lakes Michigan, Huron, and Erie. The simulated effects of bigheaded carps were highly sensitive to the values set for prey vulnerability, a parameter in the EwE model which integrates many characteristics of the recipient ecosystem that may affect prey consumption by predators. These characteristics include restrictions of predator or prey spatiotemporal distributions through predation avoidance, habitat limitations, agonistic behavior, and physical transport (Ahrens et al., 2012). Prey vulnerability is difficult to measure in the field and tends to be a calibrated parameter. Rutherford et al. (in press) borrowed values of plankton prey vulnerability from reference planktivorous fishes in the model ecosystem, which likely underestimated prey availability to bigheaded carps because invasive species tend to have better feeding efficiency (Cuthbert et al., 2019). Thus, studies that compare feeding efficiency between the FMCC and their food competitors in the same environment would improve estimation of vulnerability and, consequently, biomass and food web impact of the FMCC.

Parametric uncertainty in bioenergetics models

In bioenergetics models, parametric uncertainty has largely resulted from a lack of species-specific parameters and physiological functions. Compared with well-established bioenergetics models (e.g., lake trout; Stewart et al., 1983), current bioenergetics models of bigheaded carps lack species-specific parameters for egestion, excretion, and specific dynamic action (Alsip et al., 2019; Anderson et al., 2017, 2015). Parameter borrowing is a common approach when species-specific information is not available, but finding bioenergetics model parameters of a surrogate fish can be difficult (Ney, 1993). For example, allometric relationships of egestion and excretion for bioenergetics models of bigheaded carps were borrowed from brown trout (*Salmo trutta*; Elliot, 1976), which can be problematic as bigheaded carps do not have true stomachs like brown trout (Kolar et al., 2007). For the grass carp bioenergetics model that includes more species-specific parameters, van der Lee et al. (2017) used a Monte Carlo approach to investigate effects of parametric uncertainty and found that consumption estimates were particularly sensitive to variation in parameters associated with respiration and egestion.

Further investigation of respiration parameters is warranted to reduce uncertainty in FMCC bioenergetics models, as respiration accounts for a species' greatest energetic loss, and consumption requirements for bigheaded carps, and likely other FMCC, are quite sensitive to adjustments in respiration parameters (Cooke and Hill, 2010). While there are numerous reports on grass carp oxygen consumption and derived allometric relationships for respiration (reviewed in van der Lee et al., 2017), there is only one set of reported respiration parameters and allometric relationships for each of bighead and silver (Hogue and Pegg 2009), and black carps (Lv et al. 2018; Smyth et al. 2020). Comparing respiration parameters for FMCC between studies can help resolve uncertainties in metabolism. Further, reducing uncertainty in activity costs could refine understanding of the ability of FMCC to maintain weight while moving through colder and less productive regions in the Great Lakes.

There also is great uncertainty in the parameters describing foraging and filtration efficiency for FMCC in the Great Lakes. For example, parameters in the model currently used to approximate bighead and silver carp filtration rate as a function of fish weight were derived from juvenile bigheaded carps (Smith, 1989). Recent bioenergetics models have extrapolated this relationship to project growth potential of adult bigheaded carps (4.35–5.48 kg) in Great Lakes habitats (Alsip et al., 2020, 2019; Anderson et al., 2017, 2015; Cooke and Hill, 2010). Additionally, prey- and size-specific foraging rates and filtration efficiencies have not been incorporated into bighead and silver carp bioenergetics models, but experimental work that estimates retention efficiencies, like that of Smith (1989), could be useful. Measuring filtration and retention efficiencies, along with evaluating the effect of size-specific foraging rates on growth potential, should be included in future bioenergetics modeling efforts for bigheaded carps. This is particularly important for reducing uncertainties in growth potential in open water habitats of the Great Lakes where bigheaded carps will be more food limited.

The large geographic ranges of the FMCC lead to wide ranges of parameter values reflecting their broad physiological tolerances and plasticity, as well as the various methods and motivations that were behind the research reporting these values (Cooke, 2016). With increasingly wide ranges for parameter values, parameter estimation becomes more uncertain. To address this, Cooke (2016) stated that researchers should account for genotypic variation and phenotypic plasticity among geographically distinct populations. For example, bighead and silver carp spawning patterns in the Wabash River, Indiana, differed from other parts of the world (Coulter et al., 2013). Recent evidence also suggests that genetic variation and differential gene expression can occur at even finer spatial scales (Jeffrey et al., 2019; Stepien et al., 2019). Therefore, the improvement of future models of the FMCC used for Great Lakes risk assessments is dependent on parameter refinement that focuses on deriving physiological parameters from North American populations.

Environmental Variation

Environmental variation, also described as natural variation (Peterman, 2004), includes variation in any abiotic and biotic component and/or ecosystem process that is external to FMCC modeling but can theoretically influence model outcomes. Variations in the abiotic environment, including episodic changes in weather (e.g., random variation in climate, in contrast to long-term climate change) and heterogeneity in the aquatic habitat (e.g., lake bottom features or water temperature), may influence variation in the biotic environment, and both can directly influence FMCC modeling. For example, episodic changes in temperature can directly influence FMCC physiological processes, whereas the heterogeneity of light penetration may indirectly affect FMCC model outcomes by altering the distribution and abundance of prey. Although this type of uncertainty cannot be reduced, it must be accounted for in modeling efforts (Williams, 1997).

Environmental variation involves temporal or spatial differences in ecosystem components (e.g., distribution of animals and water temperatures) or processes (e.g., predation and consumption; nutrient and energy cycles) and depends on the spatial and temporal scale of observation. Most ecosystem components and processes underlying bioenergetics and food web models exhibit some form of environmental variation, including temperature, primary production, prey availability and energy density, consumption, and trophic transfer efficiency (e.g., Smyth et al., 2020; van der Lee et al., 2017). Therefore, the ability of bioenergetics and food web models to reflect current conditions and project future conditions depends on the degree of environmental variation within an ecosystem, the extent to which models can account for such variation, and whether future conditions will exhibit the same type of variation.

Several authors have shown that the projected establishment and impact of the FMCC in the Great Lakes are influenced by environmental variation. The temperatures experienced by the FMCC will differ based on the location of an introduced population, the behavioral thermoregulation of each species, as well as randomness in thermal regime, all of which will drive the timing and intensity of life history processes. Among-year and spatial climate variability will influence temperature-dependent processes in grass and black carps, including the onset of spawning; young-of-year recruitment, growth, and overwinter survival; and, the length of the cold-water period over which grass and black carps limit consumption (Jones et al., 2017; Smyth et al., 2020). Therefore, accounting for temporal and spatial variation in realized thermal use, and other temperature-dependent processes, could be an important source of uncertainty when projecting FMCC impacts in the Great Lakes (e.g., van der Lee et al., 2017).

Environmental variation can also manifest as spatial and temporal differences in the availability of prey, with implications for the consumption and impact of FMCC in different habitat areas. For example, the area of food availability provided to bigheaded carps by cyanobacteria blooms in Lake Erie could encompass several hundred to several thousand kilometers, depending on the year of observation (Anderson et al., 2015). These differences, combined with increasing phytoplankton availability during the study period, suggested that a small adult bighead carp could attain 20–81% of body weight in a year based on consumption in open waters of the western basin (Anderson et al., 2015). Phytoplankton availability also has been shown to differ between open waters and coastal embayments in Lake Michigan, raising uncertainty about the ability of bighead carp to maintain weight in the open waters of Lake Michigan (Anderson et al., 2017). The potential for bighead carp to exhibit positive growth in open-water areas of the Great Lakes will differ among lake basins, with positive growth expected in some, but not all, open water environments of the Great Lakes (Anderson et al., 2017, 2015). However, these analyses considered phytoplankton or *Microcystis* as the sole prey resource (Anderson et al., 2017); the availability and use of other planktonic food items, such as dreissenid veligers or detritus (e.g. Alsip et al., 2019) could bolster prey availability.

Not all forms of environmental variation can be effectively considered within bioenergetics and food web models. Often, assumptions are made that homogenize model inputs or models are built at such coarse scales that such variability becomes less important (e.g., Mason and Brandt, 1996). However, to address the critical role of environmental variation (chiefly temperature and food availability) on model outcomes, many authors have favored a simulation approach, whereby the key sources of environmental variation are tested within the modeling effort (e.g., temperature effects in van der Lee et al., 2017; prey utilization in Zhang et al., 2016). As with any modeling effort, it is necessary to communicate the forms of environmental variation being considered and their implications on system dynamics. Effectively accounting for environmental variation within bioenergetics and food web models requires that the temporal and spatial variability of relevant environmental components and processes be well understood before decisions are made regarding model development.

Partial Observability

Partial observability (or observation error; Peterman, 2004) results from an imperfect ability to observe true system dynamics (Williams, 1997). There are three aspects that contribute to this uncertainty related to invasive species. First is uncertainty about the ecosystem into which the species will arrive. This can result from monitoring programs that are not adequately designed to detect the information needed to consider invasive species effects, or from a lack of precision in the actual tools and methods used for observation. Second is uncertainty about the invasive species. This is related to parametric uncertainty (see above) and the fact that predictions about ecological impacts will frequently involve extrapolation to new or projected environmental conditions and borrowing parameter values from related species. Finally, there is uncertainty about how a species will interact with a novel ecosystem. Cooke and Hill (2010) were the first to develop a bioenergetics model to assess whether bigheaded carps could survive and grow in the Great Lakes. While some of their model parameters were informed by both existing and new research, they needed to use parameter values from other species (partial observability from extrapolation) and a sample of offshore sites to represent ecosystem conditions (partial observability from existing monitoring programs). They concluded that bigheaded carps could only survive in restricted eutrophic areas of the Great Lakes (e.g., western Lake Erie or Green Bay, Lake Michigan). Anderson et al. (2015) built upon the Cooke and Hill (2010) model by updating it with some species-specific parameter values and used satellite imagery of chlorophyll-*a* to broaden the coverage of ecosystem conditions. Reducing these observation uncertainties resulted in an expanded area of suitable habitat projected for bigheaded carps. Focusing on Lake Michigan, Alsip et al. (2019) evaluated surface and subsurface biomass inputs for three different types of prey (phytoplankton, zooplankton, and detritus), and projected a much larger area of suitable habitat than was projected by Anderson et al. (2017). Contrary to the expectation that uncertainty will expand the possible outcomes from models making them less useful, this example demonstrates that partial observability can underestimate invasion risk.

Partial Controllability

Partial controllability (or implementation uncertainty; Peterman, 2004) results from the differences between intended and realized outcomes of management actions (Williams, 1997). Any action for prevention and control can vary in its effectiveness based on unexpected events, catchability of the species, potential errors in predicting the effectiveness of actions, human error, or lack of human willingness to follow management regulations. Some aspects of invasive species management should be under greater control than is faced by natural resource management because more of the actions are carried out by the management agencies. For example, unlike sport or commercial fishing regulations (e.g., catch limits) that rely on stakeholder compliance, invasive species removal efforts are largely enacted by agency staff, leading to less uncertainty related to predicted versus realized effects of the removal action. This should reduce partial controllability associated with a willingness to follow regulations (human nature). However, prevention is also targeted with public outreach and changes in human behavior designed to reduce the risk of moving invasive species (e.g., bait releases, cleaning boats, etc.), which rely on human willingness to apply these actions and would be associated with greater implementation error (Drake et al., 2015). To date, partial controllability has not yet been considered when planning management strategies for FMCC.

Linguistic Uncertainty

Linguistic uncertainty, which is a hindrance to biological understanding, includes categories such as vagueness, context dependence, ambiguity, indeterminacy of theoretical terms, and underspecificity (Regan et al., 2002). Many of the efforts at modeling bioenergetics and food web effects of the FMCC on the Great Lakes require diverse teams of researchers. In any team setting, these categories of linguistic uncertainty must be guarded against, such that all members of the research team have complete clarity about model structure, parameter values and descriptions, and other aspects of the model, like spatial and temporal scale. Even in the development of this manuscript, substantial effort was spent by the authors to arrive at a common set of terms. In addition, communication of modeling outcomes to managers and stakeholders requires ensuring that terms are fully understood and agreed upon. Many of these linguistic uncertainties are also related to risk assessment, including discussions around terms such as the "impact" of an invasive species (e.g., ecological impact of grass carp; Cudmore et al., 2017), or how to best define establishment of an invasive species (Kočovský et al., 2018b). In addition, changes in the ecosystem related to invasion risk should be discussed in terms of values and objectives, as modelers and managers may have different perspectives on the effects of different magnitudes of change in a system. For example, a change in fish biomass within the large bounds of uncertainty in a food web model may seem insignificant to a modeler but may be quite concerning to a manager. Finally, the terminology related to FMCC can be confusing for stakeholders and the general public, which can lead to misunderstandings related to model outputs and risk assessments. Kočovský et al. (2018a) described myriad linguistic uncertainties with using the term "Asian carp", including confusion among the public and professionals about which species are being discussed, confusion in translation to Chinese and other languages, and miscommunication among cultures. Although linguistic uncertainty is not quantified in bioenergetics and food web models, the related confusion can have lasting effects on development of these models and communication of results.

Accounting for Important Uncertainty

We have used a decision analytic framework to describe and categorize the uncertainties inherent in modeling the bioenergetic and food web effects of the FMCC on the Great Lakes ecosystem. The list of uncertainties is long, but we argue that there are approaches that can be used to account for and, when possible, reduce these uncertainties. We describe methods for determining how to allocate research effort to most benefit risk assessments and management decisions, as well as approaches to account for irreducible uncertainties in modeling efforts. In all cases, we provide guidance and suggestions (see Table 1 for synthesis) but acknowledge that at times the way to account for these uncertainties is less clear.

Structural Uncertainty

Research efforts to reduce or resolve structural uncertainties, such as adaptive management, will likely be part of FMCC control plans in the Great Lakes moving forward (see Robinson et al., this issue and Herbst et al., this issue for an example with grass carp). However, as is the case with most aspects of invasive species control, we have described many sources of structural uncertainty that could be reduced. We suggest that these structural uncertainties could be considered in terms of their ultimate effects on decisions. Those uncertainties that affect a control and prevention decision, and that can be reduced ("important uncertainties"), could then be prioritized for further research and adaptive management efforts (Runge et al., 2011).

Determining the value of gathering information about a particular uncertainty can aid biologists and managers in ascertaining the important uncertainties for invasive species impacts, and related aspects of control and prevention. A suite of calculations, known as expected value of information, provides a method for elucidating these important uncertainties (Runge et al., 2011). This method describes the value of gathering new information in terms of the difference between enacting a management or control action after gathering new information and enacting the action without the new information (Raiffa and Schlaifer, 1961; Runge et al., 2011). By calculating the value of new information in terms of gains in outcomes from management actions, research and monitoring efforts can be directed at those uncertainties that have the greatest value of information.

Three value of information measures are relevant for bioenergetics and food web modeling of FMCC: expected value of perfect information (EVPI), partial expected value of information (EVPXI), and expected value of sample information (EVSI). Each of these measures provide an understanding of how resolving structural uncertainty, such as what we describe for

FMCC, might lead to better overall management and control responses. Expected value of perfect information describes how important a gain in information is to improving the performance of the control or management action (Runge et al., 2011). In cases like FMCC in the Great Lakes, EVPXI highlights how reductions in various components of uncertainty, like particular effects of climate change, can improve management actions, whereas EVSI can indicate how gathering a sample of information, rather than completely resolving an uncertainty, can improve management outcomes (Runge et al., 2011). Each of these measures can be used to inform bioenergetics and food web modeling for FMCC, but they will require the elucidation of specific objectives for control decisions, description of formal models of system uncertainties, and a set of control actions designed to achieve the objectives (Runge et al., 2011).

In addition to value of information, scenario planning (Peterson et al., 2003) can be useful for understanding the effects of uncertainties related to climate or land use change on FMCC and their effects on the Great Lakes. By creating plausible scenarios of future climate or land use, researchers can evaluate the relative differences in model outputs under different scenarios. For example, recent work on scenarios of phosphorus loading in Lake Michigan indicated that the growth potential of bigheaded carps is especially responsive to this variable (Alsip et al., 2020). Describing multiple future scenarios and related predictions for ecosystem change is also known as predictive control (Allen and Gunderson, 2011; Game et al., 2014).

Although tools like value of information and scenario planning are helpful for elucidating important uncertainties, accounting for all parametric uncertainty in bioenergetics and food web models can be onerous. Sensitivity analyses for these models are difficult to perform and can be resource intensive, but we suggest it is paramount to understand how parameters affect the results of the models. As an example, the Pedigree routine in Ecopath documents the confidence levels of input data based on their origin (Christensen et al., 2008). The uncertainty related to these parameter estimates in Ecopath was evaluated using a Monte Carlo algorithm in the Ecoranger module in earlier model versions (Stewart and Sprules, 2011; Currie et al., 2012). Although the Ecoranger module could provide a heuristic uncertainty analysis for Ecopath input parameters, it was rarely used in published studies owing to a very data intensive task to describe the probabilistic distributions for all input parameters (Christensen et al., 2008). This module was removed in more recent versions of the model but is proposed to be included in future versions. The probabilistic distributions of model parameters associated with FMCC could be identified by a structured expert judgment process, which weights and aggregates expert knowledge on key uncertainties of invasion risk and quantifies uncertainty in a stochastic manner (Wittman et al. 2015; Zhang et al. 2016). Concerted efforts to evaluate sensitivity to parametric uncertainty, similar to these examples, will enable researchers to begin to focus on uncertainty reduction. Furthermore, innovative adaptions of tools like structured expert judgement that are common in other disciplines should be explored as a means of addressing uncertainties in FMCC risk assessments.

Environmental Variation

Environmental variation can be accounted for at the data gathering and modeling stages. Environmental monitoring can provide modelers with better information about the range of anticipated variation in a system (Williams, 1997), which can enable better control responses for invasive species like the FMCC. For example, when considering the variation in spatial and temporal availability of prey items, monitoring programs can be implemented to identify how prey density varies within the ecosystem. Accounting for this uncertainty in model inputs can ensure that the range of possible outcomes is projected (Nichols et al., 2011). This can be accomplished implicitly, by incorporating the range of potential values for environmental state variables, or explicitly, by linking environmental variables with vital rates through functional relationships, such as a relationship between temperature and survival (Nichols et al., 2011).

Earlier we acknowledged structural uncertainty related to climate change and defined environmental variation as any naturally occurring variation unrelated to climate change. Environmental variation includes random variation in climate, which typically occurs at temporal or spatial scales that are finer than those needed to evaluate climate change signals. However, these two sources of uncertainty become more difficult to dissociate when confronting how climate change is presumed to affect environmental variation. Data collected for deriving inputs of ecological models are often assumed to represent stationary processes, but a changing climate will lead to mischaracterization of future environmental variation when using historical data (Johnson et al., 2015; Milly et al., 2008; Nichols et al., 2011). In the face of climate change, Nichols et al. (2011) suggested that models for making management decisions should be developed to incorporate changing probabilistic distributions of environmental variables over time. In addition, models that update probabilistic distributions of environmental variables by more heavily weighting recent monitoring data can begin to account for the future effects of climate change on environmental variability (Johnson et al., 2015). Accounting for projected future changes in environmental variation through evolving probabilistic distributions of external inputs of forcing, or changing the weighting schemes for monitoring data, could be incorporated into bioenergetics and food web models, allowing for shifts in ranges of environmental variables and their ecological effects.

Partial Observability

Uncertainty related to partial observability is reducible through increased monitoring efforts and incorporating a diversity of habitats and long-term assessments that can lead to more precise estimates of variables and better information about habitat (Williams, 1997). This is particularly salient when projecting the ecological impacts of invasive species like the FMCC in a novel ecosystem. As with many uncertainties, collecting more data can help to reduce partial observability. For example, the studies described above of increasing habitat information, such as chlorophyll-*a* coverage (Anderson et al., 2015) and depth (Alsip et al., 2019), show how inclusion of more and better data can provide a more accurate projection of habitat suitability for bigheaded carps. If more data can be collected to reduce observation error in parameters that affect the projection of ecological impacts and the decision-making process for control or prevention, then we believe this is the best option available. However, identifying the key uncertainties related to partial observability will often require a value-of-information analysis to first understand where to allocate efforts to reduce these uncertainties. Therefore, it is paramount to account for these uncertainties in predictive models, especially when working with invasive species. When applying a modeling exercise, partial observability can be included by (1) considering alternative model structures, (2) considering the full range of possible states and implications for the assessment of risk or management actions, and (3) fully considering the tails of parameter distributions and the potential for surprises (e.g., Hilborn, 1987). These considerations will enable researchers and managers to understand where to direct efforts for increased monitoring to reduce partial observability, which requires iterative interactions among researchers, managers, and modelers.

Partial Controllability

Quantifying uncertainty is a common best practice, and applies to partial controllability. Both the expectation (mean) and distribution of the uncertainty should be specified and could be improved by including covariates that affect the uncertainty. For example, the willingness of individuals to apply control actions may be affected by local conditions. The full range of compliance may span from low to high, but if it is dependent on local conditions, the probabilistic distribution may actually be bimodal. Ultimately, a true understanding should consider the constraints or limitations of management or control actions, as well as policies.

By incorporating bioenergetics and food web modeling into a larger decision analysis framework (e.g., structured decision making or adaptive management), ecologists can work with social scientists, decision makers, and managers to understand the full set of management actions and their implementation capacity when building predictive models of ecological impacts. Although predicting human behaviors related to management actions is difficult, including a suite of experts and stakeholders can reduce the uncertainty surrounding the implementation of control actions (Robinson et al., 2019). Models then can be used to evaluate how management strategies are affected by partial controllability. This can be accomplished by building scenarios (e.g., Lauber et al., 2016) that consider the range of events and implementation of management actions, assessing how robust management actions are to implementation uncertainty, and evaluating if managers need multiple tools to manage the consequences of partial controllability (e.g., Coulter et al., 2018).

Linguistic uncertainty

Regan et al. (2002) described five sources of linguistic uncertainty and potential means to reduce it. In general, these methods include specifying the context of discussions, clarifying meanings of ambiguous words, narrowing the bounds as much as possible for underspecified data, and using tools for defining borderline cases for vague terms. Linguistic uncertainty causes difficulties in all aspects of decision making and risk assessment, in part because of the range of expertise required for invasive species management, including ecologists, statisticians, managers, stakeholders, and social scientists. The bioenergetics and food web models that project ecological impacts of invasive species provide needed clarity to the decision-making process and can serve as a tool for reduction of linguistic uncertainty (Irwin et al., 2011). By assigning numerical ranges to model parameters and state variables, terms related to the ecological impacts of invasion are clearly defined. Overall, groups involved in assessing risk and making decisions for the control of invasive species like the FMCC must be aware of the potential effects of linguistic uncertainty and make every effort to account for these effects.

Conclusions

Multiple types of uncertainty exist when projecting the ecological effects of invasive species in novel habitats like the FMCC in the Great Lakes (Table 1). In this review, we identify uncertainties within bioenergetics and food web models, classify these into an existing typology (Peterman, 2004; Regan et al., 2002; Williams, 1997), and provide tools to account for and reduce key uncertainties. Together, we hope this review will spur continued development and application of broad solutions for these types of uncertainties, thereby improving an understanding of the ecological impacts of FMCC in the Great Lakes basin. Although the scope of this paper was applied to the FMCC and their projected effects on the Great Lakes ecosystem, the typology of uncertainties described herein, and the methods and tools suggested, can be applied to invasive species in almost any aquatic ecosystem (e.g., grass carp in the Colorado River [Brandenburg et al., 2019] or snakehead species in North America [Herborg et al., 2008]).

Despite the seemingly overwhelming uncertainties, the models used to make these projections are necessary tools for helping managers and decision makers understand the potential establishment and ecological impacts of invasive species following their introduction because of their ecological realism and ability to account for several aspects of species assimilation within the ecosystem. They also inform a range of critical management questions, such as how reducing abundance of an invasive species can prevent various food web changes. For example, the results of bioenergetics (van der Lee et al., 2017) and population (DuFour et al., this issue) models for grass carp in Lake Erie informed a subsequent decision analysis to determine optimal actions for grass carp control and key uncertainties for implementation of adaptive management (Robinson et al., this issue).

Targeted approaches to reducing identified uncertainties exist and have been reviewed extensively in this paper (Table 1). We do not advocate for a different set of tools to address establishment and impact questions, but rather a refinement of current tools using existing solutions. It is our hope that the synthesis presented here will clarify the range of uncertainties that exist and motivate future research effort towards addressing the unanswered questions related to survival, establishment, and impact of not only the FMCC in the Great Lakes, but aquatic invasive species in general.

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Table 1. Summary of the five types of uncertainty covered in this paper including their definitions, relevance to models of the four major Chinese carps (FMCC), techniques for addressing, research needs for reducing, and examples of relevant references.

Type of Uncertainty	Description	Relevance to FMCC modeling	Techniques for addressing uncertainties	Research needs to reduce or account for uncertainty	Examples of relevant references
Structural	An epistemic uncertainty related to biological and ecological processes of the modeled system; classified as either functional or parametric.	• Effects of environmental drivers and trophic interactions on FMCC (Functional) • Lack of information on certain bioenergetics or food web model parameters (Parametric)	• Sensitivity analysis to identify priority parameters where efforts to reduce parametric uncertainty would be best focused • Monte Carlo analysis to quantify parametric uncertainty • Institute measures of value of information • Scenario planning • Structured expert judgement • Adaptive management	• Resolving uncertainty related to climate change effects on prey biomass and trophic interactions • Narrowed estimates of recruitment for FMCC • Reliable prey biomass estimates and evaluation of potentially novel foods • Predator adaptability to FMCC as prey • Interactions among FMCC • Species-specific bioenergetics parameters • Foraging efficiency of adult FMCC	Alsip et al. (2020) Coulter et al. (2018) Ivan et al. (2020) Robinson et al. (this issue) Wittman et al. (2015) Zhang et al. (2016)
Environmental variation	An aleatory uncertainty dependent on scale of observation; includes random variation in weather and	• Affects all stages of model development, parameterization, validation, and forecasting • Underlying processes and ecosystem	• Model probabilistic distributions of potential values for environmental state variables • Account for predicted future changes in environmental	• Establishment of long-term monitoring programs can provide better information about the anticipated variation in a system	Alsip et al. (2020) Jones et al. (2017) Smyth et al. (2020) van der Lee et al. (2017)

	spatiotemporal heterogeneity in aquatic systems.	components in models are affected by variation in temperature and aquatic habitat, which influences primary production, prey availability, energetic quality of prey, consumption and trophic transfer efficiency	variation (rather than assuming stationarity in environmental processes) through evolving probabilistic distributions, allowing for shifts in ranges of environmental variables • Link environmental variables with vital rates through functional relationships, such as a relationship between temperature and survival		
Partial observability	An epistemic uncertainty resulting from our imperfect ability to observe true system dynamics	• Lack of adequate monitoring programs tracking recipient ecosystem components • Lack of data on FMCC ecology and physiology leads to extrapolating from other species • No information on how FMCC interact with a given novel environment	• Consider alternative model structures • Consider the full range of possible states and implications for risk assessment or management actions • Consider the tails of parameter distributions and the potential for surprises	• Implementation of a value of information analysis to identify where and how best to allocate monitoring efforts • Establishment of monitoring programs tracking relevant ecosystem components	Alsip et al. (2019) Anderson et al. (2017, 2015) Cooke and Hill (2010)
Partial controllability	Uncertainty resulting from differences in intended and	• The realized effects of management decisions informed by models may	• Specify the expectation and probabilistic distribution of the uncertainty	• Increased understanding of the range of possible	Coulter et al. (2018) Drake et al. (2015)

	realized outcomes	differ from the predicted efficacy on prevention and control strategies due to human behavior, unexpected events, catchability of a species, prediction error, or human error	• Identify important covariates that affect uncertainty • Consider constraints of management or control actions • Incorporate modeling into larger decision analytic framework	events and management actions • Assessment of the effect of robust management actions on implementation uncertainty	Lauber et al. (2016) Robinson et al. (2019)
Linguistic	Limitation of biological understanding due to vagueness, context dependence, ambiguity, indeterminacy of theoretical terms, and underspecificity	• “Asian Carp(s)” is a term used to describe four ecologically distinct species • What constitutes an ecosystem impact? • How do we define establishment? • How do managers and modelers value projected model outputs?	• Specify context of discussions, clarify meanings of ambiguous words, and use tools for defining borderline cases for vague terms • Clarify model parameters related to ecological consequences in an intelligible manner for managers and stakeholders • When not collectively referring to all FMCC, specify the distinct species in scientific publications and all communications	• Identification, review, and synthesis of potentially problematic terms • Diverse input to modeling exercises	Kočovský et al. (2018a) Kočovosky et al. (2018b)