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Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species?

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Abstract. The ecological impact stemming from a biological invasion is the most poorly understood aspect of the invasion process. While forecasting methods are generally lacking, a potential means of predicting future impacts is to examine the effects caused by a nonindigenous species (NIS) at previously invaded locations, i.e., its invasion history. However, given the context dependence of impact and the scarcity of data, it is uncertain whether invasion history can in fact be used to forecast the effects of most introduced species. Using a sample of 19 aquatic NIS listed with the IUCN's 100 World's Worst Alien Invasive Species, we reviewed the literature to determine (1) the amount of information currently available concerning their ecological impacts, (2) if the effects reported to be caused by each NIS are consistent across multiple studies, and (3) whether their invasion histories provide sufficient quantitative information to assess and forecast the severity of their impacts on recipient environments. As a case study, we conducted a meta-analysis and developed models that relate the severity of the impacts of a well-documented invader, common carp (*Cyprinus carpio*), to two potential predictor variables: biomass and time since introduction. We then tested whether models developed from one set of observations can predict the severity of impacts reported at other sites. Models incorporating biomass and pre-impact conditions explained 91% of the variation in carp impact severity at new locations (i.e., those not used to build the models). For most other NIS, limited availability of comparable quantitative data currently prevents the development of similar empirical models for predicting the severity of future impact. Nonetheless, invasion history can often be used to develop informative predictions concerning the type and direction of impacts to be expected at novel recipient sites.

Key words: common carp; Cyprinus carpio; *impact; invasive species; meta-analysis; predictive model; risk assessment.*

Introduction

Nonindigenous species (NIS) are often studied at independent stages of the invasion process comprising their transport, establishment, local spread and impacts (Williamson and Fitter 1996, Kolar and Lodge 2001). Empirical analysis of previously documented invasions, combined with theoretical knowledge, has yielded several tools that can be used to predict various aspects of these different stages, particularly the establishment and spread of NIS (e.g., Peterson and Vieglais 2001, Hastings et al. 2005, Lodge et al. 2006). Yet, despite growing recognition of the ecological threats posed by introduced species, relatively few studies have explicitly quantified the effects of NIS on their recipient communities (Parker et al. 1999). Consequently, predictive models of impact are lacking for the majority of even the most widespread and disruptive invaders, and generalizable forecasting methods are almost nonexistent.

Attempts to prioritize limited management resources towards the most disruptive invaders and vulnerable sites would benefit greatly from reliable estimates of potential impacts (Byers et al. 2002), particularly given the growing number of species introduced to new geographic locations each year (Carlton and Geller 1993, Ricciardi 2007). It is generally expected that only a small fraction of these NIS will cause notable damage to their recipient environments (Williamson and Fitter 1996, Ricciardi and Kipp 2008). Some of the factors that may determine whether an introduced species will be detrimental include the absence of natural enemies (Keane and Crawley 2002, deRivera et al. 2005), whether the NIS assumes a novel ecological role in the community (Kats and Ferrer 2003, Ricciardi and Atkinson 2004), and whether the species possesses certain biological traits that predispose it to becoming a nuisance, such as broad environmental tolerances and high reproductive output (Rejmanek and Richardson 1996, Kolar and Lodge 2001, 2002). Yet, attempts to

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generalize such hypotheses across a broad range of invasions have produced mixed results (Lodge 1993, Agrawal and Kotanen 2003, Colautti et al. 2004, 2006). Furthermore, while such criteria can be useful for classifying NIS in terms of the relative risk they pose, they cannot offer insight into the specific types of impacts (e.g., effects on a particular native species or ecosystem process) nor the severity of these effects to be expected at recipient locations—information that is necessary to direct management efforts (Vander Zanden and Olden 2008).

Estimating the potential impacts of a novel introduced species is a challenging task (Byers et al. 2002). However, knowledge of the effects caused by NIS at previously invaded sites (i.e., invasion history) may be useful for forecasting their impacts in new locations. Indeed, some introduced aquatic species, including the European green crab (*Carcinus maenas*), zebra mussel (*Dreisenna polymorpha*), and grass carp (*Ctenopharyngodon idella*), have been shown to cause categorically similar effects in most areas where they have become established (Grosholz and Ruiz 1996, Ricciardi 2003, Dibble and Kovalenko 2009). Furthermore, several studies have illustrated that, for at least some widespread invaders, information on previous ecological impacts can serve as a basis for generating robust predictions that can inform management decisions (e.g., Branch and Steffani 2004, Vander Zanden et al. 2004, McCarthy et al. 2006, Ward and Ricciardi 2007, Jokela and Ricciardi 2008).

Information on impacts can also be derived through experimental investigation, so we should be able to expand the amount of data available even for NIS that have not yet become widely established. However, despite promising results, studies of invasion history have thus far been relatively rare and quantitative analyses, leading to the development of empirical predictive models, have only been performed for a very small number of species—namely widespread invaders whose impacts have been particularly well documented, such as the zebra mussel (Ward and Ricciardi 2007) and rusty crayfish (*Orconectes rusticus*) (McCarthy et al. 2006). The feasibility of developing predictions for many other NIS therefore remains to be demonstrated.

A number of challenges may impede the use of invasion history as means of forecasting the impacts of most introduced species. First, given the scarcity and heterogeneous quality of information on the impacts resulting from biological invasions (Parker et al. 1999, Byers et al. 2002), it is unknown how much data are available concerning the effects of any particular NIS, whether this information is comparable across previous observations, or amenable to quantitative analysis. Furthermore, introduced species cause multiple distinct types of impacts, and the magnitude or even the direction of any particular effect can vary substantially across space and time (e.g., McIntosh 2000, Ross et al. 2003, Branch and Steffani 2004, Strayer et al. 2006, Ricciardi and Kipp 2008). Given this variability and the constraints of data limitation, it remains to be determined whether invasion history can be generally employed to predict the type, direction and severity of future impacts.

Variations in the severity of impact caused by an invasive species are arguably the result of a multitude of differences in extrinsic conditions between recipient habitats. However, it is also possible that a substantive proportion of this variability can be explained by a relatively small number of predictable factors. In particular, it has been suggested that the magnitude of the impacts caused by an introduced species should be correlated with its abundance across invaded locations (Parker et al. 1999, D'Antonio and Kark 2002). This intuitive relationship has been demonstrated empirically for several aquatic NIS (e.g., Madsen 1998, Ricciardi 2003, Chumchal et al. 2005, Pintor et al. 2009). Therefore, we may be able to explain much of the variation in the severity of impacts caused by particular invaders by accounting for differences in their local densities or the local environmental factors that control their abundances. However, our ability to test such relationships and determine their predictive value will be limited by the amount and quality of information made accessible by other researchers.

The purpose of this study was to compile and examine the invasion histories of multiple NIS and to assess the feasibility of using this information to develop predictions regarding their future impacts. We conducted an extensive literature search to summarize the information that is currently available concerning the invasion histories of 19 aquatic invasive species. We then assessed how the quantity of available data varies across species and invaded systems and examined how information derived from disparate studies can be combined to gain a predictive understanding of the impacts caused by introduced species on their recipient communities.

Specifically, we evaluated whether for a given NIS similar types of impacts are reported across multiple studies and tested if these studies are consistent in their conclusions regarding the direction of the observed impacts. We then examined whether studies reporting categorically similar effects had provided quantitative information that could be combined to statistically assess variation in impact severity. Finally, using a meta-analytical approach, we conducted a case study for common carp (*Cyprinus carpio*) to demonstrate how quantitative data can be used to explain variability in the severity of impacts observed across invaded locations. Specifically, we developed empirical models that relate the magnitude of several impacts to carp biomass and time since introduction, as reported by multiple studies, and tested whether predictions from such models can be extrapolated to new situations.

Table 1. List of 19 marine (MAR) and freshwater (FW) NIS currently among the 100 world's worst alien invasive species, including scientific and common names, a description of the native range, and the total number of impact studies identified for each species.

Species	Common name	Habitat	Native range	Studies
Asterias amurensis	North Pacific seastar	MAR	northwestern Pacific	4
Carcinus maenas	Green Crab	MAR	northwestern Europe	18
Caulerpa taxifolia	Caulerpa	MAR	circum tropical	18
Cercopagis pengoi	Fish hook water flea	FW	Ponto-Capian	6
Clarias batrachus	Walking catfish	FW	southeastern Asia	1
Corbula amurensis	Asian clam	MAR	Japan, China, and Korea	2
Cyprinus carpio	Common carp	FW	central Asia	46
Eichhornia crassipes	Water hyacinth	FW	Amazon basin	4
Eriocheir sinensis	Chinese mitten crab	MAR	China and Korea	4
Gambusia spp.	Mosquito fish	FW	southern United States	24
Lates niloticus	Nile Perch	FW	Nile River	11
Micropterus salmoides	Largemouth bass	FW	eastern Canada and United States	10
Mnemiopsis leidyi	Comb jelly	MAR	North and South American Atlantic coast	7
Mytilus galloprovincialis	Blue mussel	MAR	Mediterranean, Black and Adriatic Seas	15
Oncorhynchus mykiss	Rainbow trout	FW	North-eastern and western pacific coasts	24
Oreochromis mossambicus	Mozambique tilapia	FW	Mozambique and South Africa	3
Pomacea spp.	Golden apple snail	FW	Argentina and Amazon basin	5
Salmo trutta	Brown trout	FW	Europe, northern Africa, and western Asia	29
Undaria pinnatifida	Japanese kelp	MAR	Japan, China and Korea	6

Methods

Literature review

To construct invasion histories for multiple species, we conducted a review of the literature concerning the ecological impacts of each of 19 marine and freshwater NIS (Table 1) currently listed by the International Union for the Conservation of Nature (IUCN) among the 100 World's Worst Alien Invasive Species (Lowe et al. 2004). We chose these NIS because they were expected to have well-documented impacts and thus should represent some of the best examples to illustrate the use of invasion history as a predictive tool.

We restricted our analysis to marine and freshwater NIS featured on the list, as biological invasions are particularly prevalent and damaging in aquatic systems (Carlton and Geller 1993, Ruiz et al. 2000, Ricciardi and Atkinson 2004). One aquatic species on the IUCN's list, the zebra mussel *Dreissena polymorpha*, was excluded from our study because its invasion history has been examined in detail elsewhere (Ricciardi 2003, Ward and Ricciardi 2007). Furthermore, we did not consider species listed as either amphibious or semi-aquatic (e.g., cane toad, *Bufo marinus*; red eared slider turtle, *Trachemys scripta*). Finally, due to similar morphology and impacts that sometimes result in misidentification or taxonomic uncertainty (Komak and Crossland 2000, Rawlings et al. 2007), information on *Gambusia holbrooki* and *Pomacea insularum* was combined with that of their congeners *G. affinis* and *P. canaliculata*, respectively.

We limited our search to peer-reviewed journal articles to ensure the quality of the data used in our analyses and because we assumed the scientific literature to be representative of the quantity of information available concerning the impact of each species. Given the variable nature of the impacts caused by NIS, we set several preliminary criteria for the inclusion of publications in our study. First, for logistical feasibility, we restricted our definition of impact to a reported change in the abundance, distribution, fitness, or behavior of native species, or in the diversity, community composition, or abiotic properties of the recipient system or experimental treatment, that had been attributed to the NIS. We thus excluded studies that documented only socioeconomic impacts. We also explicitly excluded studies that had examined the effects of our sample NIS on other introduced species, or those conducted within their native ranges.

To reduce bias, the literature search was conducted by two researchers and cross-validated by a third researcher (Gates 2002). Relevant publications were located through several online databases including Science Citation Index Expanded (SCI-EXPANDED, 1900–April 2009), BIOSIS previews (1969–April 2009) and Aquatic Sciences and Fisheries Abstracts (ASFA, 1971–April 2009). Initial search terms included (1) *invasive*, *non-indigenous*, *introduced*, *exotic*, or *alien species*, (2) the scientific and common names of each NIS, and (3) *impact*, *effect*, *affect*, and *influence*. Additional studies were located by searching citations from relevant publications. Review articles or studies that analyzed previous research findings were used for locating primary literature but were not included in our analysis. When articles presented the results of two or more distinct approaches (e.g., a lab experiment coupled with a field survey) we considered each as a separate study.

Data summary and analysis

Articles meeting our criteria were reviewed by two researchers and summarized according to the following categories: the type of research conducted (either experimental [e.g., lab or field] or observational [e.g., correlative, before–after control–impact (BACI) designs]); the specific location where the research was carried out; the impacted variables under investigation (a particular indigenous species, a certain functional group, an abiotic parameter, etc.); the direction of the effect (positive, negative, or a nondirectional change); the proposed mechanism by which the effect occurred (e.g., predation, habitat modification) and other relevant information, such as the number of countries where each NIS was reported to have become established.

We defined a positive or negative effect in terms of the direction of the change, i.e., as either an increase (positive effect) or reduction (negative effect) in the variable being measured (e.g., benthic invertebrate diversity, macrophyte density, reproductive output of a particular native species, total phosphorus concentrations), that was attributed to the NIS. Nondirectional changes included impacts such as shifts in community composition or modifications in the diet of a native species, but where no positive or negative direction could be assigned based on the information presented in the article.

The resulting database was used to quantify the amount of information available concerning the invasion history of each NIS and to determine whether this information could be used to gain a predictive understanding of their impacts. First, to assess whether certain NIS are likely to possess more detailed invasion histories than others, we tested whether the number of studies reporting impacts varied between marine and freshwater taxa or between vertebrate and invertebrate invaders. Owing to unequal variances between groups and skewed distributions, we used Welch's t test and restricted our comparisons to two-tailed tests (Ruxton 2006). Using least-squares regression, we also examined whether the number of studies reporting the impacts of each NIS was dependent upon the extent of its invaded range, estimated by the number of countries in which a species has become established. Both variables were log-transformed prior to analysis to achieve normality. For these and subsequent tests, results were considered significant at $P \leq 0.05$.

Data for each NIS were then grouped according to affected taxon, abiotic parameter, functional group, or other biologically relevant impact categories. This was done to determine the quantity of information available for any particular type of impact and to test whether the direction of the various effects attributed to each species were consistent across multiple studies, with the greatest degree of resolution possible. To assess consistency within each impact category we used a G test to determine if the number of observed positive and negative effects differed from that expected by chance. Impacts categorized as nondirectional changes, which made up less than 5% of all records, were not considered. We also restricted our tests to impact categories where the number of cases expected under the null hypothesis for each outcome was no less than 3 (Sokal and Rohlf 1995).

Finally, to examine whether invasion history could be used to derive quantitative information suitable for assessing the severity of impacts, we first identified the most commonly documented impact category for each NIS. When five or more published studies were located, we revisited relevant articles to determine if sufficient information (i.e., raw data, statistics, graphical information) was available to quantify impact severity and if these estimates were directly comparable across studies. For each impact category examined, we then determined the maximum number of studies that could be combined using meta-analysis or other statistical techniques. We also identified the main impediments to combining quantitative information from multiple publications.

The results derived from these analyses were then used to rank each NIS according to the relative degree of utility of invasion history for generating impact predictions. Based on the most commonly cited impact category for each species, the 19 NIS were ordered hierarchically according to the following criteria: (1) the number studies, providing comparable quantitative data regarding the severity of the reported impacts; (2) the level of agreement among studies concerning the direction of the effect (either significantly different from random, not significantly different or insufficient data); and (3) the total number of studies reporting the particular ecological impact.

Meta-analysis of common carp effects

Of the species examined in our literature review, common carp (*Cyprinus carpio*) had by far the greatest number of publications reporting its ecological impacts, so this NIS was used as a case study to examine whether the severity of impact could be predicted from invasion history. The majority of studies reporting quantitative information on the impacts of carp were experimental (e.g., in situ enclosure or exclosure experiments, mesocosm studies, introductions to experimental ponds) and many had reported that several types of impacts (including those on rooted macrophytes and various water quality parameters) vary linearly as a function of carp biomass (e.g., Robel 1961, Crivelli 1983, Breukelaar et al. 1994, Lougheed et al. 1998, Chumchal et al. 2005). We therefore conducted a meta-analysis to test the generality of these relationships and to examine whether the severity of the impacts caused by common carp could be predicted from its local density.

Rather than using the more conventional approach of converting the statistics reported in each publication to standardized effect sizes (Hedges 1992), we opted to employ a meta-analysis procedure based on linear mixed-effect models (LMEM). LMEM provide an appropriate framework in which to analyze data with an inherently grouped and thus nonindependent structure, such as those derived from the same study or experiment (Pinheiro and Bates 2004). By incorporating both fixed (i.e., across-study) parameters and random (i.e., within-study) effects, this approach allowed us to

TABLE 2. Descriptions and abbreviations for the eight biotic and abiotic impact categories examined in the carp meta-analysis. The number of studies and total number of observations (indicated in parentheses) used to fit the models and validate model predictions are given.

Impact category	Abbreviation	Unit	Number of studies	
			Fitting	Validation
Biotic				
Macrophyte density	MAC	g/m^2	6 (49)	2 (2)
Benthic invertebrate density	BI	g/m^2	3 (10)	0
Phytoplankton biomass	PHYT	chlorophyll *a* (μg/L)	8 (37)	5 (6)
Abiotic				
Total phosphorus	TP	μg/L	8 (46)	5 (6)
Total nitrogen	TN	μg/L	6 (34)	2 (3)
Turbidity	TUR	nephelometric turbidity units (NTU)	13 (81)	3 (4)
Total suspended solids	TSS	mg/L	5 (30)	1 (1)
Inorganic suspended solids	ISS	mg/L	4 (21)	1 (1)

use multiple observations from a wide range of published studies to examine the relationship between various impact categories and carp biomass, while accounting for intrinsic variations among studies.

Raw data were first compiled from the text, tables or figures (i.e., by digitizing graphs) presented in each article. For each observation of impact, we recorded the corresponding biomass density (kg/ha) of carp as reported nearest the time when the impact was measured, most often at the conclusion of the experiment. When density was not reported directly, it was calculated from the reported carp biomass and the enclosure or water body size, where possible. Given that the impacts of carp might also vary with the amount of time since they have become established in the recipient system, we also recorded experimental duration, i.e., the number of days between the introduction of carp and the measurement of impact.

We were able to investigate eight impact categories, including the effects of carp on rooted macrophytes, benthic macroinvertebrates, phytoplankton, turbidity, total nitrogen, total phosphorus, total suspended solids, and inorganic suspended solids (Table 2). Observations within each category were converted to the most commonly reported unit of measurement, where possible, or were otherwise discarded from the analysis. Although several studies reported the impacts of carp on zooplankton, the reported metrics varied greatly, sometimes involving density (individuals/L), biomass (g/L), species richness, or diversity (e.g., Shannon-Weaver index) of the zooplankton community. As a result, these data could not be confidently standardized and this impact category was not examined in the meta-analysis. For each impact category, studies with fewer than three observations were retained for validation of the fitted models.

Model development

For each impact category we then developed a series of models to examine (1) the variability in the severity of carp impacts across different studies, (2) the relationship between impact severity and carp biomass, and (3) the effect of experimental duration. Depending on the distribution of the data, variables were transformed to fit the assumption of normality, generally by applying a logarithmic transformation. For each category, we began by fitting fixed-effect null models where the expected severity of impact (Y_j) was estimated by a single across-study mean impact term (β_0; Eq. 1). We then included a flexible intercept term (U_{0k}) to account for variations in the mean impact severity observed among different studies, where the magnitude of carp impact (Y_{jk}) for observation j from study k was estimated by Eq. 2:

$$Y_j = \beta_0 + E_j \quad (1)$$

$$Y_{jk} = \beta_0 + U_{0k} + E_j. \quad (2)$$

To determine the amount of variation that could be explained by carp biomass and experimental duration, the next set of models included all previous terms and a fixed estimate for a common across-study slope (β_1) between carp biomass (C) and impact severity (Eq. 3), as well as a fixed slope (β_2) for experimental duration (D; Eq. 4):

$$Y_{jk} = \beta_0 + C\beta_1 + U_{0k} + E_j \quad (3)$$

$$Y_{jk} = \beta_0 + C\beta_1 + D\beta_2 + U_{0k} + E_j. \quad (4)$$

Finally, to examine whether the relationship between impact severity and carp biomass varied considerably among studies (i.e., could be characterized by different slopes), we examined models that included a flexible slope term for carp biomass (U_{1k}):

$$Y_{jk} = \beta_0 + C\beta_1 + CU_{1k} + U_{0k} + E_j \quad (5)$$

$$Y_{jk} = \beta_0 + C\beta_1 + D\beta_2 + CU_{1k} + U_{0k} + E_j. \quad (6)$$

The optimal model for each impact category was selected by comparing the residual variance, Akaike's information criterion (AIC) and Bayesian information criterion (BIC) associated with each model described

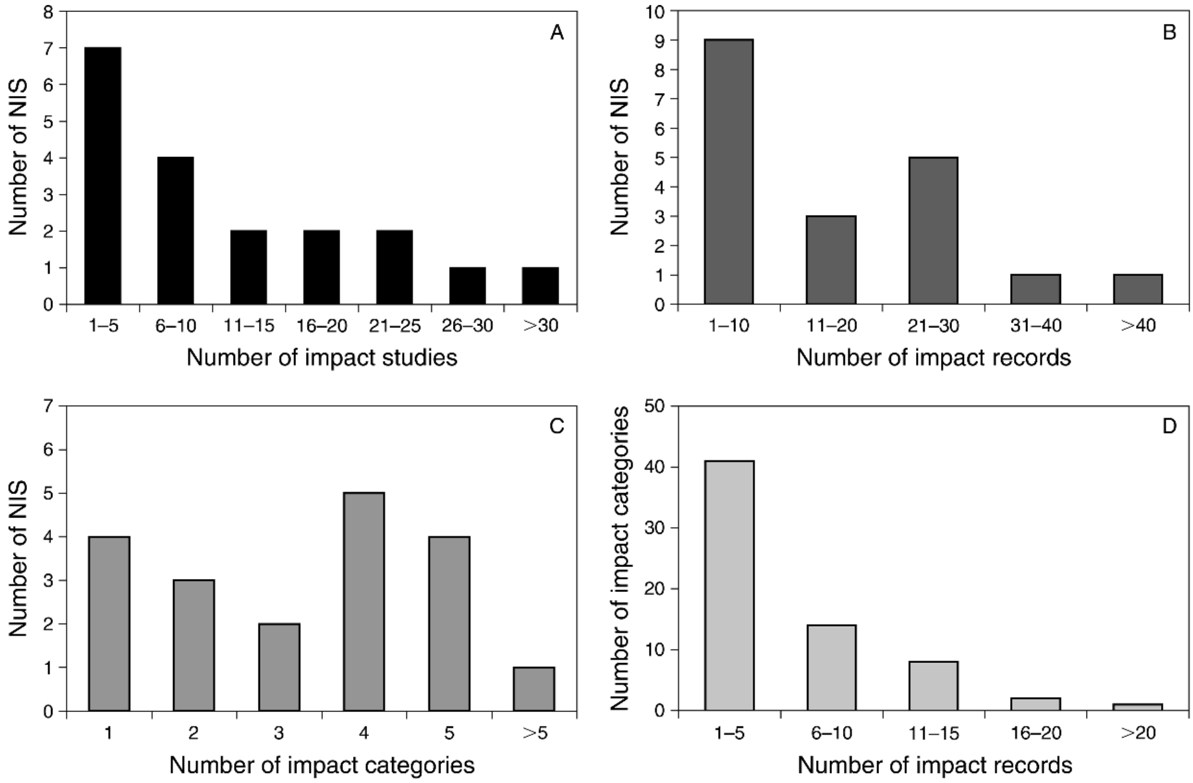

FIG. 1. Frequency of (A) the number of impact studies, (B) the number of impact records, (C) the number of impact categories identified across the 19 nonindigenous species (NIS) examined, and (D) the number of records per impact category.

above. Both AIC and BIC measure the compromise between the fit given by a particular model and its complexity, i.e., the number of parameters included (Johnson and Omland 2004). Although BIC penalizes more heavily than AIC for each additional parameter, models with the lowest values for both criteria were considered to be the most informative. All analyses were conducted using R statistical software (R Development Core Team 2008) and packages lme4 and nlme (Bates 2005).

As noted above, results from studies reporting fewer than three observations for any impact category were not used in the model development process. Fitted models were further validated by estimating the expected severity of impact for these observations, based on parameter estimates derived from the optimal model for each category. As the number of validation studies for each impact type was low (i.e., $n \leq 5$), we evaluated the predictive power of our models based on regression analysis between observed and predicted impacts across all categories.

RESULTS

Literature review

Of the studies identified during our literature search, only a fraction (~35%) had actually documented the ecological impacts of any of the 19 NIS examined. As such, we were able to identify only 218 published articles that met our criteria. Several of these articles reported the results of multiple approaches (e.g., a lab experiment and a field study) or the impacts of more than one of our sample NIS, yielding what we considered as 237 (103 observational and 134 experimental) case studies. The number of studies reporting the effects of each NIS ranged between 1 for walking catfish and 46 for common carp (Fig. 1A). We found no significant difference between the number of studies reporting the impacts of freshwater vs. marine taxa ($t = 1.14$, df = 15, $P = 0.27$), or between vertebrate and invertebrate invaders ($t = 1.90$, df = 9, $P = 0.09$). Furthermore, although the number of studies for each species tended to increase with the number of invaded countries, the trend was not statistically significant ($R^2 = 0.16$, $F_{1,17} = 3.25$, $P = 0.089$).

Many articles had reported the effects of their focal NIS on multiple factors (e.g., different taxa, several abiotic parameters, and so on), thus we were able to extract a total of 353 different records for impact, ranging from 1 to 113 for each invader (Fig. 1B). The most commonly cited mechanisms by which NIS affected their recipient communities were direct predation ($n = 143$), competition with native species (73), and indirect effects resulting from either trophic cascades (35) or habitat modification (138). Several studies had stated that more than one mechanism was likely

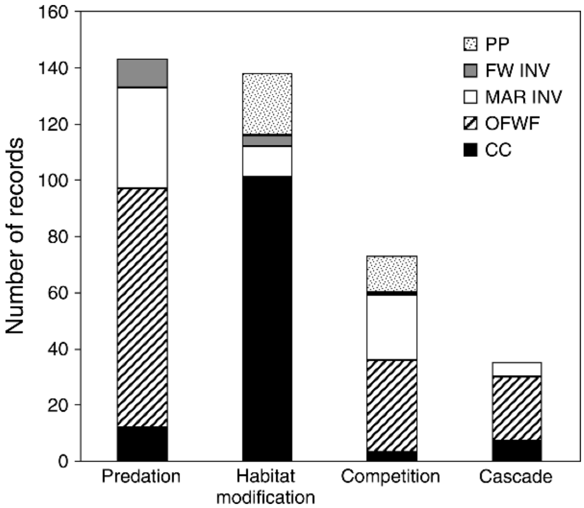

FIG. 2. Contributions of common carp (CC), other freshwater fish species (OFWF), marine invertebrates (MAR INV), freshwater invertebrates (FW INV), and primary producers (PP) to the four most commonly cited impact mechanisms.

responsible for the observed impact; however, carp accounted for more than 70% of the documented effects associated with habitat modification (Fig. 2). By categorizing the impact records for each NIS into groupings of similar effects, we identified 66 unique impact categories, which varied from 1 (for several species) up to 10 (for carp; Fig. 1C), whereas the number of records within each individual impact category ranged between 1 and 22 (Fig. 1D). A full summary of the compiled impact data and source publications is provided in the Appendix.

Direction and severity of impacts

Over one-quarter of the impact categories identified had but a single record, i.e., only one study had documented the particular ecological impact, and only 23 categories had sufficient information to be assessed using the *G* test. For all but two of these categories, the number of positive or negative effects was significantly greater that that expected by chance ($P \leq 0.05$). Thus, with the exception of the effects of *Mytilus galloprovincialis* on gastropod species ($P = 0.31$) and those of carp on zooplankton ($P = 1.0$), there was substantial agreement among studies regarding the directionality of observed impacts (Table 3).

Among the most commonly documented impacts for each of our sample NIS, 12 impact categories possessed a sufficient number of studies to be evaluated further. The fraction of studies providing comparable quantitative estimates for the severity of impacts caused by each

TABLE 3. Summarized results of the *G* test for the 23 impact categories with sufficient data for the analysis, including the number of negative (Neg.) and positive (Pos.) effects, *G* statistic, and corresponding *P* value for each category.

		Effect			
Species	Impact category	Neg.	Pos.	*G*	*P*
Carcinus maenas	bivalves	11	0	15.25	<0.001
	decapods	6	0	8.32	0.004
Caulerpa taxifolia	marine macroalgae	8	1	6.20	0.013
Cercopagis pengoi	zooplankton	6	0	8.32	0.004
Cyprinus carpio	macrophytes	21	1	22.36	<0.001
	turbidity	0	19	26.34	<0.001
	benthic invertebrates	13	0	18.02	<0.001
	total phosphorus	0	12	16.64	<0.001
	phytoplankton	0	12	16.64	<0.001
	zooplankton	**5**	**5**	**0.00**	**1**
	total nitrogen	0	8	11.09	<0.001
	total suspended solids	0	7	9.70	0.002
Gambusia spp.	fish	12	0	16.64	<0.001
	amphibians	10	0	13.86	<0.001
Lates niloticus	fish	9	2	4.82	0.028
Micropterus salmoides	fish	10	0	13.86	<0.001
Mnemiopsis leidyi	zooplankton	7	0	9.70	0.002
Mytilus galloprovincialis	**gastropods**	**6**	**3**	**1.02**	**0.313**
	bivalves	7	0	9.70	0.002
Oncorhynchus mykiss	fish	15	0	20.79	<0.001
	amphibians	7	0	9.70	0.002
Salmo trutta	fish	16	0	22.18	<0.001
	benthic invertebrates	6	1	3.96	0.047

Notes: The grouping of impact observations for each invasive species into impact categories is described in *Methods: Data summary and analysis*. The numbers of positive and negative effects are shown only for those categories having a sufficient number of observations to be tested statistically. For each invasive species, the impact categories listed are those that were the most commonly cited within the reviewed literature (having six or more observations as a minimum requirement for the *G* test). For example, rainbow trout (*O. mykiss*) has had negative effects on native amphibian species across all seven documented cases. Boldface type indicates impact categories where the number of reported negative and positive effects did not differ from that expected by chance.

TABLE 4. List of the 19 nonindigenous species (NIS) examined in this study, ranked in order of decreasing utility of their invasion histories for predicting future impacts, based on the most commonly cited impact category of each species.

Rank	Species	Most common impact category	Comparable quantitative studies	Directional agreement	Total number of studies
1	*Cyprinus carpio*	macrophytes	†	SDR	22
2	*Gambusia* spp.	fish	9	SDR	13
3	*Salmo trutta*	fish	8	SDR	16
4	*Oncorhynchus mykiss*	fish	8	SDR	15
5	*Carcinus maenas*	bivalves	7	SDR	11
6	*Micropterus salmoides*	fish	5	SDR	10
7	*Caulerpa taxifolia*	marine macroalgae	5	SDR	10
8	*Mnemiopsis leidyi*	zooplankton	5	SDR	7
9	*Lates niloticus*	fish	4	SDR	10
10	*Cercopagis pengoi*	zooplankton	4	SDR	6
11	*Mytilus galloprovincialis*	gastropods	4	NSDR	8
12	*Undaria pinnatifida*	marine macroalgae	3	ID	6
13	*Pomacea* spp.	macrophytes	‡	ID	4
13	*Asterias amurensis*	bivalves	‡	ID	4
14	*Oreochromis mossambicus*	fish	‡	ID	3
15	*Eriocheir sinensis*	bank erosion	‡	ID	2
15	*Eichhornia crassipes*	benthic invertebrates	‡	ID	2
16	*Corbula amurensis*	phytoplankton	‡	ID	1
16	*Clarias batrachus*	amphibians	‡	ID	1

Notes: The level of agreement among studies regarding the direction of the reported impacts is denoted as either significantly different from random (SDR), not significantly different from random (NSDR), or insufficient data (ID). Several species tied in rank.

† Predictive model developed for impact severity.

‡ Species for which impact categories were not examined in further detail.

NIS ranged from 40% to 70%. For most species the main impediment to combining results from multiple publications was a lack of quantitative information. For example, of the 15 studies reporting the impacts of rainbow trout on native fish populations, 12 had specifically documented changes in the abundance of one or more native species, and the remainder focused on changes in their diet or behavior. However, only 8 of these 12 comparable studies provided quantitative estimates of the observed impacts.

Lack of compatibility between the specific types of effects (i.e., effect size estimates) reported across studies was also found to be a major limitation. For *Caulerpa taxifolia*, 9 of 10 studies that reported impacts on other macroalgae also provided substantial quantitative information in the form statistical results and graphical data. Among these, five studies reported quantitative estimates of impacts on the productivity of native species, and the remaining studies focused on other aspects, such as the diversity or composition of the recipient community. Consequently, information from all of these nine quantitative studies would not be amenable to combined statistical assessment.

Finally, we also noted that studies reporting quantitative information for several widespread NIS were often conducted in only a small portion of the species' invaded range. This might hinder generalization to other invaded regions, given substantive spatial variation in observed impacts (Ricciardi and Kipp 2008). For example, 75% of studies that provide comparable quantitative estimates of the impacts caused by brown trout on native fish populations have been conducted in either New Zealand or Australia, which represents only a small fraction of the NIS global invaded range (Lever 1996).

Given the findings presented above, each NIS was ranked to reflect the relative degree of utility of its invasion history for generating predictions regarding its most prevalent impact category (Table 4). Common carp was ranked as having the most informative invasion history, followed by several other freshwater fish species, including mosquitofish as well as brown trout and rainbow trout. Two NIS, the Asiatic clam *Corbula amurensis* and the walking catfish *Clarias batrachus*, had the least informative invasion histories; in either case only a single study had documented the particular ecological impact.

Common carp meta-analysis

Of the publications reporting the impacts of carp, 30 studies presented data that could be used in our meta-analysis. Most articles provided information on two or more impact categories, and many had reported impacts across a range of different carp densities, resulting in a total of 331 observations. Six studies had insufficient information to be used in the model fitting process and thus were used exclusively for validating fitted models, whereas four studies had enough information to fit models for certain impact categories and to validate others.

For most impacts examined, models that incorporated a flexible intercept term (Eq. 2) resulted in a substantially lower AIC, BIC, and residual standard deviation compared to those that incorporated only a fixed-effect estimate (i.e., Eq. 1). Carp biomass was found to be a significant predictor of impact severity for all categories

TABLE 5. Parameter estimates and Akaike's and Bayesian information criterion (AIC and BIC) derived from the six models examined for each impact category in the carp meta-analysis.

Impact category and equation	β_0	τ_{0k}	β_1	τ_{1k}	β_2	σ	AIC	BIC	P biomass
Macrophyte density									
1	1.67					0.79	118.48	122.27	
2	1.65	0.72				0.37	68.53	74.21	
3	**2.08**	**0.74**	**−0.20**			**0.30**	**52.67**	**60.24**	**<0.001**
4	3.23	1.18	−0.20		−0.67	0.28	53.53	62.99	
5	2.09	0.3	−0.21	0.00		0.29	53.44	64.79	
6	3.44	0.46	−0.21	0.00	−0.78	0.28	55.25	68.5	
Benthic invertebrate density									
1	0.10					0.42	14.18	14.78	
2	0.10	0.00				0.40	16.18	17.09	
3	**0.51**	**0.00**	**−0.23**			**0.30**	**12.06**	**13.27**	**0.041**
4	−0.74	0.00	−0.24		0.57	0.27	13.59	15.84	
5	0.51	0.00	−0.23	0.00		0.29	16.06	17.88	
6	−0.74	0.00	−0.24	0.00	0.57	0.27	14.59	16.71	
Phytoplankton biomass									
1	1.31					0.62	74.40	77.68	
2	1.40	0.57				0.32	48.07	52.99	
3	1.21	0.58	0.12			0.27	41.20	47.75	
4	**−0.26**	**0.59**	**0.11**		**0.16**	**0.25**	**37.06**	**45.24**	**0.002**
5	1.21	0.61	0.11	0.02		0.27	44.77	54.59	
6	−0.25	0.59	0.11	0.00	0.16	0.25	41.06	52.52	
Total phosphorus									
1	2.12					0.41	51.35	55.01	
2	2.20	0.43				0.10	−36.68	−31.20	
3	**2.11**	**0.43**	**0.05**			**0.09**	**−44.96**	**−37.64**	**0.002**
4	1.66	0.40	0.04		0.02	0.09	−43.51	−35.36	
5	2.11	0.46	0.05	0.02		0.09	−42.57	−31.60	
6	1.60	0.43	0.04	0.02	0.03	0.09	−43.56	−30.76	
Total nitrogen									
1	3.04					0.39	36.08	39.13	
2	3.07	0.41				0.15	−5.49	−0.91	
3	**2.99**	**0.41**	**0.05**			**0.13**	**−11.86**	**−5.76**	**0.005**
4	2.84	0.39	0.05		0.09	0.13	−9.97	−2.34	
5	2.99	0.42	0.05	0.01		0.13	−8.01	1.15	
6	2.85	0.40	0.05	0.01	0.09	0.13	−6.11	4.58	
Turbidity									
1	1.24					0.59	144.70	149.46	
2	1.23	0.47				0.36	101.41	108.56	
3	**0.87**	**0.42**	**0.20**			**0.26**	**54.45**	**63.98**	**<0.001**
4	0.36	0.38	0.20		0.27	0.26	54.83	66.24	
5	0.86	0.38	0.21	0.02		0.26	57.63	71.92	
6	0.41	0.35	0.21	0.01	0.24	0.26	57.86	74.53	
Total suspended solids									
1	1.91					0.68	64.53	67.34	
2	**1.98**	**0.52**				**0.51**	**60.85**	**65.05**	
3	1.67	0.55	0.14			0.48	61.14	66.74	
4	1.59	0.54	0.14		0.04	0.48	63.13	70.14	
5	1.67	0.54	0.14	0.00		0.48	65.14	73.54	
6	1.47	0.58	0.14	0.02	0.09	0.48	67.10	76.90	
Inorganic suspended solids									
1	1.52					0.35	18.78	20.97	
2	1.49	0.11				0.32	20.34	23.61	
3	1.09	0.00	0.20			0.25	9.69	14.05	
4	1.15	0.00	0.20		−0.03	0.25	11.56	17.02	
5	**1.00**	**0.42**	**0.24**	**0.20**		**0.13**	**2.13**	**8.67**	**0.044**
6	1.09	0.41	0.25	0.20	−0.05	0.14	3.96	11.59	

Notes: Parameter estimates include the fixed-effect intercept (β_0); the standard deviation of the flexible intercept term (τ_{0k}); slope estimates for carp biomass effect (β_1); the standard deviation of the flexible carp biomass slope term (τ_{1k}); experimental duration slope estimate (β_2), and the standard deviation of the residual error (σ). Results in bold indicate the optimal model for each impact category along with corresponding P values for the across-study carp biomass slope.

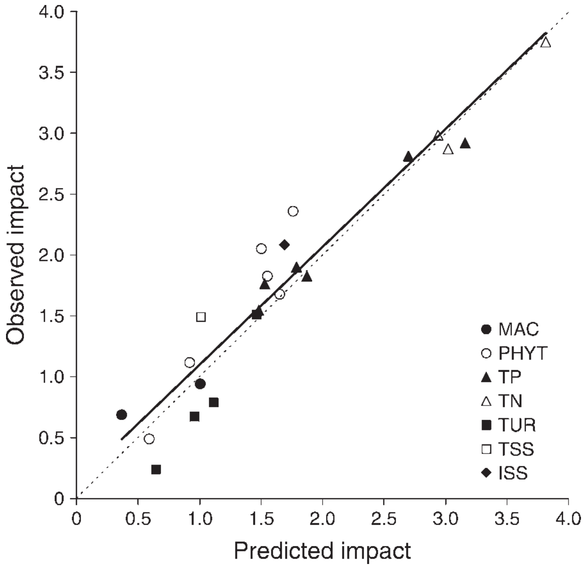

FIG. 3. Relationship between the predicted and observed severity of the impacts caused by carp, derived from the 10 studies used for model validation. Log-transformed data for seven of the eight impact categories examined in the carp meta-analysis are shown. Impact category abbreviations are given in Table 2.

($P \leq 0.04$), with the exception of total suspended solids (Table 5). Based on comparisons of AIC and BIC, the model in the form of Eq. 3 provided an optimal description for most forms of impact. This would suggest that, for most of the categories examined, there is a comparable change in impact severity for each unit increase in carp biomass, but that there is considerable variation among studies in the response variable in the absence of carp (i.e., initial or pre-impact conditions) and a limited effect of experimental duration. However, the best model for describing impacts on phytoplankton biomass also included a fixed-effect slope term for experimental duration, whereas that for inorganic suspended solids included a random carp biomass slope, suggesting that the relationship between this parameter and carp biomass varies considerably among studies.

The majority of the studies retained for validation had reported one observation of the variable being investigated in the absence of carp (i.e., before introduction or as a control treatment) and one estimate for impact at a particular carp density. All optimal models included a flexible intercept term, indicating that some of the variability in the magnitude of the impacts reported by different studies was the result of site-specific differences in initial conditions. To validate our models we therefore generated our predictions using the control observation reported in each publication as an estimate of the intercept (i.e., the pre-impact state of the response variable) and the fixed effect slope estimates derived from the best fit model for each category. The relationship between the observed and predicted magnitude of impact across all categories (Fig. 3) was highly significant ($R^2 = 0.91$, df $= 21$, $F_{1,21} = 210.3$, $P < 0.0001$).

DISCUSSION

Our review and analysis of impact data for our sample NIS suggest that a broad spectrum of conclusions, varying in resolution, can be drawn based from invasion history. For most NIS multiple studies had reported categorically similar impacts across a wide range of systems. Although limited data currently presents a major barrier to the development of generalizations even for some widely introduced species (e.g., grass carp *Ctenopharyngodon idella*; Dibble and Kovalenko 2009), and context dependence can generate spatial heterogeneity in impacts (e.g., McIntosh 2000, Ricciardi 2003, Ross et al. 2006, Ricciardi and Kipp 2008) some NIS cause similar impacts in most parts of their invaded ranges. For example, Grosholz and Ruiz (1996) had qualitatively demonstrated that the European green crab (*Carcinus maenas*) has had comparable impacts on bivalve molluscs and other crab species in most of its invaded range, and Ricciardi (2003) showed that the zebra mussel (*Dreissena polymorpha*) has broadly similar effects on a variety of biotic and abiotic parameters in both European and North American lakes. Our results are consistent with these findings. Thus, at a minimum, invasion history can generally be used to reveal the types of impacts expected to occur at new recipient locations.

For all but two of the impact categories for which sufficient data were available to test for consistency, there was substantial agreement among studies regarding the direction of effects. Such consistency has provided a predictive basis for particular impacts caused by several aquatic NIS. For example, in a meta-analysis of multiple experimental studies, McCarthy and colleagues (2006) found that several species of invasive crayfish consistently caused reductions in zoobenthic densities and that these findings could be extrapolated to natural systems. However, such directional consistency is absent in several of the impact categories examined in our study.

Five of the eight articles that document the effects of *M. galloprovincialis* on the abundance of grazing gastropod species had reported reductions, two reported increases and one article reported contrasting effects on the same native species. Similarly, carp were reported to have both positive and negative effects on zooplankton communities and, although not tested formally, inconsistencies were also noted for several other impact categories, including the effects of largemouth bass on benthic invertebrates and those of green crab on marine macroalgae. Yet even for these cases, variation in the observed direction of effects can often be explained by the influence of simple moderator variables, such as the size of the affected native species or variation in extrinsic habitat characteristics (e.g., Branch and Steffani 2004). Thus, information on previous impacts can also be used to infer the direction of particular effects in many cases.

Invasion history can thus often form the foundation for generating informative predictions of impact, given future invasions. For example, from the data presented in Tables 3 and 4, we predict that at novel recipient sites *Mnemiopsis leidyi* will cause reductions in zooplankton abundance, rainbow trout will reduce or extirpate fish populations occupying similar or lower trophic levels, *Caulerpa taxifolia* will compete with other macroalgae and thus reduce the productivity of native species and that *M. galloprovincialis* will alter the densities of grazing gastropods. However, the magnitude and in some cases even the direction of these impacts may vary substantially across space and time (Ricciardi 2003, Ross et al. 2003, Strayer et al. 2006). Further analysis is therefore necessary to determine the confidence we can assign to such predictions and to generate quantitative estimates of the severity of the impacts to be expected at potential recipient locations.

Predicting the impacts of common carp

The magnitude of impacts caused by a NIS at any given site is hypothesized to be a function of its local abundance (Parker et al. 1999, D'Antonio and Kark 2002, Ricciardi 2003). While this relationship has been demonstrated empirically for a few aquatic invasive species, it is not clear whether differences in abundance can generally explain a significant portion of the variation in impacts observed across multiple invaded locations. In particular, a number of studies have shown that the severity of multiple impacts caused by introduced carp vary as a function of biomass (e.g., Robel 1961, Breukelaar et al. 1994, Tatrai et al. 1997, Lougheed et al. 1998). Furthermore, several authors have previously combined findings from other studies with their own experimental data, in order to examine the generality of such relationships (Crivelli 1983, Chumchal et al. 2005). Yet such analyses have thus far been restricted to relatively few impact categories and a narrow range of observations, and the ability to predict carp impacts at new sites had not been previously tested.

Carp consistently cause several types of impacts, most of which stem from their ability to substantially modify the physical characteristics of invaded habitats (Matsusaki et al. 2009). Cumulatively, these impacts can result in shifts between pristine, clear-water conditions characterized by high macrophyte densities to heavily degraded turbid-water states (Scheffer et al. 2001, Zambrano et al. 2001). In particular, the presence of carp has been shown to affect (1) rooted macrophyte densities, mainly through physical disturbance and increased turbidity (e.g., Robel 1961, Crivelli 1983, Miller and Crowl 2006); (2) benthic invertebrate densities, through predation and habitat modification (Richardson et al. 1990, Wilcox and Hornbach 1991, Zambrano and Hinojosa 1999); (3) phytoplankton biomass, by altering the availability of various nutrients through excretion and bioturbation (Angeler et al. 2002, Chumchal and Drenner 2004, Driver et al. 2005, Roozen et al. 2007); (4) zooplankton abundance, either indirectly through their effects on phytoplankton (Drenner et al. 1998, Parkos et al. 2003, Matsuzaki et al. 2007) or directly through planktivory by juvenile carp (Cardona et al. 2008); and (5) the abundance of native fish species, through multiple indirect effects including those described above (Forester and Lawrence 1978, Drenner et al. 1997, Cardona et al. 2008). However, the limited amount of comparable quantitative information for these latter two impact categories prevented us from addressing them in our meta-analysis.

Our results demonstrate the generalizability of previous findings that the severity of the impacts caused by carp is largely dependent on its local density. Although some studies have found no evidence to suggest a significant relationship between carp density and the magnitude of certain impacts (e.g., turbidity; Crivelli 1983, Fletcher et al. 1985) and others have found that several effects vary as a nonlinear function of carp biomass (e.g., Lougheed et al. 1998, Matsuzaki et al. 2009), with the exception of changes in total suspended solids (TSS), substantial variation in the impact categories noted above could be explained by linear models relating impact severity to carp biomass. Thus, despite some heterogeneity in previous findings, our meta-analysis demonstrates that, at a broad interregional scale, the invasion history of this NIS can in fact be used to develop informative predictions regarding the severity of multiple impacts expected to occur at different recipient sites. Indeed, when models developed from one set of published studies were used to estimate the magnitude of impacts, based on initial conditions and carp biomass reported by others, we were able to predict impact severity with a high degree of accuracy.

Our results, as well as previous findings, also illustrate the degree to which the impacts of carp are context dependent. Each of our models included a flexible intercept term, suggesting that the severity of the impacts expected to occur at a particular carp density depend largely on experimental or site-specific conditions. Furthermore, for one of the categories examined, inorganic suspended solids, the relationship with carp density varied substantially between studies. The ability of carp to influence suspended solids and other water clarity measures depends largely on the type of sediment that they disturb (Roberts et al. 1995, Parkos et al. 2003), thus variation in sediment size and composition may preclude a significant relationship between carp biomass and measures of suspended solids across sites.

Similarly, the degree of susceptibility of aquatic vegetation to the effects of carp has been shown to vary with different macrophyte species (Zambrano and Hinojosa 1999, Evelsizer and Turner 2006), while the impacts of carp on several water quality parameters may also depend on the depth of the invaded water body (Zambrano et al. 2001). Further, while experimental duration was found to be a relevant predictor for only the phytoplankton biomass category, several studies have illustrated that carp impacts can vary substantially over time (Tatrai et al. 1997, Zambrano and Hinojosa 1999, Matsuzaki et al. 2007). The studies examined in our meta-analysis consisted mainly of experiments conducted in controlled environment over relatively short time-spans, and thus may not fully reflect the potential variation in impact severity that may occur under natural conditions. Unfortunately, given the lack of historical baseline data for carp introductions throughout much of its invaded range, we were unable to assess the predictive power of our models in natural systems.

The utility of invasion history for predicting impacts

Our results illustrate that invasion history can be used to develop informative predictions pertaining to the type and direction of ecological impacts caused by many introduced species. Furthermore, for at least some NIS, the severity of impacts to be expected at novel recipient sites can be estimated from a few key variables. As demonstrated for carp, substantial variance in impact severity can be explained by empirical models linking the invader's biomass to the magnitude of various forms of impact, when sufficient quantitative data are available. By incorporating information on initial (i.e., pre-impact) conditions at potential recipient locations, such models can generate useful quantitative predictions for the severity of the impacts to be expected. Although similar approaches have been used to model the ecological effects of a few other high-profile aquatic invaders, especially the zebra mussel *Dreissena polymorpha* (Ward and Ricciardi 2007, Jokela and Ricciardi 2008) and rusty crayfish *Orconectes rusticus* (McCarthy et al. 2006), several challenges—namely the lack of comparable quantitative data—currently inhibit similar analyses for the majority of introduced species.

Indeed, apart from common carp, only seven of the 19 NIS examined in our study (i.e., green crab, largemouth bass, *Caulerpa taxifolia*, mosquitofish, rainbow trout, *Mnemiopsis leidyi*, and brown trout) were the subject of five or more studies that provided comparable quantitative estimates of impact severity. Thus, information necessary for analysis and prediction of future impacts is presently quite limited, even for many of the world worst invaders. Furthermore, only three additional species: *Mytilus galloprovincialis*, Nile perch, and *Cercopagis pengoi*, had sufficient information to statistically test consistency in the direction of reported impacts. As such, quantitative assessments of invasion history can presently be conducted for no more than 60% of the aquatic NIS considered here, and even then only a fraction of the types of impacts caused by most of these species could be examined. For the remaining NIS, invasion history will likely be limited to providing qualitative descriptions of impacts that may arise from future invasions.

Given that our sample of NIS were selected from among the list of the 100 World's Worst Invasive Alien Species, one might conclude that information on impacts may be too limited to develop useful predictions concerning the ecological effects of most other NIS. However, the IUCN's list is largely an educational tool designed to raise awareness of biological invasions. Species are therefore featured not only because they have demonstrated their ability to cause deleterious effects but also because they serve as representative examples of harmful NIS (Lowe et al. 2004). The list omits several introduced aquatic species that have previously been shown to have deleterious effects across a wide range of systems, e.g., Eurasian watermilfoil (Madsen 1998), spiny waterflea *Bythotrephes longimanus* (Boudreau and Yan 2003), and rusty crayfish (McCarthy et al. 2006), presumably because their impacts are similar to those of other listed NIS. Consequently, there are certainly additional species that possess invasion histories sufficiently detailed for the development of quantitative predictions beyond those examined here.

Nonetheless, data on ecological impacts are presently very limited even for some of the world's most disruptive and well-publicized invaders, and the inconsistent manner by which impact data are collected and presented poses a major challenge to risk assessment (Parker et al. 1999, Andersen et al. 2004). Where sufficient quantitative information exists, consideration of predictive attributes such as the relationship between an invader's impact and its abundance may allow for greater resolution regarding which sites are most at risk of damage. Therefore, a priority for the research and management of biological invasions should be to compile, organize and make accessible information on impacts, as well as the factors that mediate them, so that informed predictions can be generated before particularly harmful NIS become widely established and their prioritization and prevention are no longer possible.

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Literature Cited

Agrawal, A. A., and P. M. Kotanen. 2003. Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecology Letters 6:712–715.

Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004. Risk analysis for invasive species: general framework and research needs. Risk Analysis 24:893–900.

Angeler, D. G., M. Alvarez-Cobelas, S. Sanchez-Carrillo, and M. A. Rodrigo. 2002. Assessment of exotic fish impacts on water quality and zooplankton in a degraded semi-arid floodplain wetland. Aquatic Sciences 64:76–86.

Bates, D. M. 2005. Fitting linear mixed models in R. R News 5: 27–30.

Boudreau, S. A., and N. D. Yan. 2003. The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences 60:1307–1313.

Branch, G. M., and C. N. Steffani. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). Journal of Experimental Marine Biology and Ecology 300:189–215.

Breukelaar, A. W., E. Lammens, J. K. Breteler, and I. Tatrai. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. Freshwater Biology 32:113–121.

Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16:630–640.

Cardona, L., B. Hereu, and X. Torras. 2008. Juvenile bottlenecks and salinity shape grey mullet assemblages in Mediterranean estuaries. Estuarine Coastal and Shelf Science 77:623–632.

Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science 261:78–82.

Chumchal, M. M., and R. W. Drenner. 2004. Interrelationships between phosphorus loading and common carp in the regulation of phytoplankton biomass. Archiv für Hydrobiologie 161:147–158.

Chumchal, M. M., W. H. Nowlin, and R. W. Drenner. 2005. Biomass-dependent effects of common carp on water quality in shallow ponds. Hydrobiologia 545:271–277.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8:1023–1037.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Crivelli, A. J. 1983. The destruction of aquatic vegetation by carp *Cyprinus carpio* a comparison between southern France and the USA. Hydrobiologia 106:37–42.

D'Antonio, C. M., and S. Kark. 2002. Impacts and extent of biotic invasions in terrestrial ecosystems. Trends in Ecology and Evolution 17:202–204.

deRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. Ecology 86: 3364–3376.

Dibble, E. D., and K. Kovalenko. 2009. Ecological impact of grass carp: a review of the available data. Journal of Aquatic Plant Management 47:1–15.

Drenner, R. W., K. L. Gallo, R. M. Baca, and J. D. Smith. 1998. Synergistic effects of nutrient loading and omnivorous fish on phytoplankton biomass. Canadian Journal of Fisheries and Aquatic Sciences 55:2087–2096.

Drenner, R. W., K. L. Gallo, C. M. Edwards, and K. E. Rieger. 1997. Common carp affect turbidity and angler catch rates of largemouth bass in ponds. North American Journal of Fisheries Management 17:1010–1013.

Driver, P. D., G. P. Closs, and T. Koen. 2005. The effects of size and density of carp (*Cyprinus carpio* L.) on water quality in an experimental pond. Archiv für Hydrobiologie 163:117–131.

Evelsizer, V. D., and A. M. Turner. 2006. Species-specific responses of aquatic macrophytes to fish exclusion in a prairie marsh: a manipulative experiment. Wetlands 26:430–437.

Fletcher, A. R., A. K. Morisson, and D. J. Hume. 1985. Effects of carp, *Cyprinus carpio* L., on communities of aquatic vegetation of waterbodies in the lower Goulburn River basin. Australian Journal of Marine and Freshwater Research 36: 311–327.

Forester, T. S., and J. M. Lawrence. 1978. Effects of grass carp and carp on populations of bluegill and largemouth bass in ponds. Transactions of the American Fisheries Society 107: 172–175.

Gates, S. 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. Journal of Animal Ecology 71:547–557.

Grosholz, E. D., and G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78:59–66.

Hastings, A. K., et al. 2005. The spatial spread of invasions: new developments in theory and evidence. Ecology Letters 8: 91–101.

Hedges, L. V. 1992. Meta-analysis. Journal of Educational Statistics 17:279–296.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101–108.

Jokela, A., and A. Ricciardi. 2008. Predicting zebra mussel fouling on native mussels from physicochemical variables. Freshwater Biology 53:1845–1856.

Kats, L. B., and R. P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Diversity and Distributions 9:99–110.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199–204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236.

Komak, S., and M. R. Crossland. 2000. An assessment of the introduced mosquitofish (*Gambusia affinis holbrooki*) as a predator of eggs, hatchlings and tadpoles of native and non-native anurans. Wildlife Research 27:185–189.

Lever, C. 1996. Naturalized fishes of the world. Academic Press, San Diego, California, USA.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133–137.

Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, J. T. Carlton, and A. McMichael. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications 16:2035–2054.

Lougheed, V. L., B. Crosbie, and P. Chow-Fraser. 1998. Prediction on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Canadian Journal of Fisheries and Aquatic Sciences 55:1189–1197.

Lowe, B., M. Browne, S. Boudjelas, and M. De Poorter. 2004. 100 of the world's worst invasive alien species. The Invasive Species Specialist Group (ISSG) of the World Conservation Union (IUCN), Auckland, New Zealand.

Madsen, J. D. 1998. Predicting invasion success of Eurasian watermilfoil. Journal of Aquatic Plant Management 36:28–32.

Matsuzaki, S. S., N. Usio, N. Takamura, and I. Washitani. 2007. Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation. Fundamental and Applied Limnology 168:27–38.

Matsuzaki, S. S., N. Usio, N. Takamura, and I. Washitani. 2009. Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. Oecologia 158:673–686.

McCarthy, J. M., C. L. Hein, J. D. Olden, and M. J. Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshwater Biology 51:224–235.

McIntosh, A. R. 2000. Habitat- and size-related variation in exotic trout impact on native galaxiid fishes in New Zealand streams. Canadian Journal of Fisheries and Aquatic Sciences 57:2140–2151.

Miller, S. A., and T. A. Crowl. 2006. Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshwater Biology 51:85–94.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Parkos, J. J., V. J. Santucci, and D. H. Wahl. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. Canadian Journal of Fisheries and Aquatic Sciences 60:182–192.

Peterson, A. T., and D. A. Vieglais. 2001. Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. BioScience 51:363–371.

Pinheiro, J. C., and D. M. Bates. 2004. Mixed-effects models in S and S PLUS. Springer, New York, New York, USA.

Pintor, L. M., A. Sih, and J. L. Kerby. 2009. Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. Ecology 90: 581–587.

R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna, Austria. ⟨www.r-project.org⟩

Rawlings, T. A., K. A. Hayes, R. H. Cowie, and T. M. Collins. 2007. The identity, distribution, and impacts of non-native apple snails in the continental United States. BMC Evolutionary Biology 7:14.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology 48: 972–981.

Ricciardi, A. 2007. Are modern biological invasions an unprecedented form of global change? Conservation Biology 21:329–336.

Ricciardi, A., and S. K. Atkinson. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7:781–784.

Ricciardi, A., and R. Kipp. 2008. Predicting the number of ecologically harmful exotic species in an aquatic system. Diversity and Distributions 14:374–380.

Richardson, W. B., S. A. Wickham, and S. T. Threlkeld. 1990. Foodweb response to the experimental manipulation of a benthivore (*Cyprinus carpio*), zooplanktivore (*Menidia beryllina*) and benthic insects. Archiv für Hydrobiologie 119:143–165.

Robel, R. J. 1961. The effect of carp populations on the production of waterfowl food plants on a western waterfowl marsh. Transactions of the North American Wildlife and Natural Resources Conference 26:147–159.

Roberts, J., A. Chick, L. Oswald, and P. Thompson. 1995. Effect of carp, *Cyprinus carpio* L., an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. Marine and Freshwater Research 46:1171–1180.

Roozen, F., M. Lurling, H. Vlek, E. Kraan, B. W. Ibelings, and M. Scheffer. 2007. Resuspension of algal cells by benthivorous fish boosts phytoplankton biomass and alters community structure in shallow lakes. Freshwater Biology 52:977–987.

Ross, D. J., C. R. Johnson, and C. L. Hewitt. 2003. Variability in the impact of an introduced predator (*Asterias amurensis*: Asteroidea) on soft-sediment assemblages. Journal of Experimental Marine Biology and Ecology 288:257–278.

Ross, D. J., C. R. Johnson, and C. L. Hewitt. 2006. Abundance of the introduced seastar, *Asterias amurensis*, and spatial variability in soft sediment assemblages in SE Tasmania: clear correlations but complex interpretation. Estuarine, Coastal and Shelf Science 67:695–707.

Ruiz, G. M., P. W. Fofonoff, J. T. Carlton, M. J. Wonham, and A. H. Hines. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31:481–531.

Ruxton, G. D. 2006. The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U test. Behavioral Ecology 17:688–690.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walkerk. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology and Evolution 21:645–651.

Tatrai, I., J. Olah, G. Paulovits, K. Matyas, B. J. Kawiecka, V. Jozsa, and F. Pekar. 1997. Biomass dependent interactions in pond ecosystems: responses of lower trophic levels to fish manipulations. Hydrobiologia 345:117–129.

Vander Zanden, M. J., and J. D. Olden. 2008. A management framework for preventing the secondary spread of aquatic invasive species. Canadian Journal of Fisheries and Aquatic Sciences 65:1512–1522.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14:132–148.

Ward, J. M., and A. Ricciardi. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13:155–165.

Wilcox, T. P., and D. J. Hornbach. 1991. Macrobenthic community response to carp (*Cyprinus carpio* L.) foraging. Journal of Freshwater Ecology 6:171–183.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661–1666.

Zambrano, L., and D. Hinojosa. 1999. Direct and indirect effects of carp (*Cyprinus carpio* L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. Hydrobiologia 408:131–138.

Zambrano, L., M. Scheffer, and M. Martinez-Ramos. 2001. Catastrophic response of lakes to benthivorous fish introduction. Oikos 94:344–350.

APPENDIX

Summarized impact data and source publications for each of the 19 aquatic nonindigenous species examined in this study (*Ecological Archives* A021-011-A1).