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

26 The ecological impact stemming from a biological invasion is considered the most poorly 27 understood aspect of the invasion process. While forecasting methods are generally lacking, a 28 potential means of predicting future impacts is to examine the effects caused by a non-indigenous 29 species (NIS) at previously invaded locations, i.e. its invasion history. However, given the context-30 dependence of impact and the scarcity of data, it is uncertain whether invasion history can in fact 31 be used to forecast the effects of most introduced species. Using a sample of 19 aquatic NIS listed 32 with the IUCN's 100 World's Worst Alien Invasive Species, we reviewed the literature to 33 determine i) the amount of information currently available concerning their ecological impacts, ii) 34 if the effects reported to be caused by each NIS are consistent across multiple studies, and iii) 35 whether their invasion histories provide sufficient quantitative information to assess and forecast 36 the severity of their impacts on recipient environments. As a case study, we conducted a meta-37 analysis and developed models that relate the severity of the impacts of a well-documented invader, 38 common carp (Cyprinus carpio), to two potential predictor variables: biomass and time since 39 introduction. We then tested whether models developed from one set of observations can predict 40 the severity of impacts reported at other sites. Models incorporating biomass and pre-impact 41 conditions explained 91% of the variation in carp impact severity at new locations (i.e. those not 42 used to build the models). For most other NIS, limited availability of comparable quantitative data 43 currently prevents the development of similar empirical models for predicting the severity of 44 future impact. Nonetheless, invasion history can often be used to develop informative predictions 45 concerning the type and direction of impacts to be expected at novel recipient sites. 46

Keywords: impact, invasive species, meta-analysis, *Cyprinus carpio*, common carp, predictive
model, risk assessment

49 Introduction

50 Non-indigenous species (NIS) are often studied at independent stages of the invasion 51 process comprising their transport, establishment, local spread and impacts (Williamson and Fitter 52 1996, Kolar and Lodge 2001). Empirical analysis of previously documented invasions, combined 53 with theoretical knowledge, has yielded several tools which can be used to predict various aspects 54 of these different stages - particularly the establishment and spread of NIS (e.g. Peterson and 55 Vieglais 2001, Hastings et al. 2005, Lodge et al. 2006). Yet, despite growing recognition of the 56 ecological threats posed by introduced species, relatively few studies have explicitly quantified the 57 effects of NIS on their recipient communities (Parker et al. 1999). Consequently, predictive 58 models of impact are lacking for the majority of even the most widespread and disruptive invaders, 59 and generalisable forecasting methods are almost nonexistent. 60 Attempts to prioritize limited management resources towards the most disruptive invaders 61 and vulnerable sites would benefit greatly from reliable estimates of potential impacts (Byers et al. 62 2002), particularly given the growing number of species introduced to new geographic locations 63 each year (Carlton and Geller 1993, Ricciardi 2007). It is generally expected that only a small 64 fraction of these NIS will cause notable damage to their recipient environments (Williamson and 65 Fitter 1996, Ricciardi and Kipp 2008). Some of the factors which may determine whether an 66 introduced species will be detrimental include the absence of natural enemies (Keane and Crawley 67 2002, deRivera, et al. 2005), whether the NIS assumes a novel ecological role in the community 68 (Kats and Ferrer 2003, Ricciardi and Atkinson 2004), and whether the species possesses certain 69 biological traits that predispose it to becoming a nuisance, such as broad environmental tolerances 70 and high reproductive output (Rejmanek and Richardson 1996, Kolar and Lodge 2001, 2002). Yet, 71 attempts to generalize such hypotheses across a broad range of invasions have produced mixed 72 results (Lodge 1993, Agrawal and Kotanen 2003, Colautti et al. 2004, Colautti et al. 2006).

73 Furthermore, while such criteria can be useful for classifying NIS in terms of the relative risk they 74 pose, they cannot offer insight into the specific types of impacts (e.g. effects on a particular native 75 species or ecosystem process) nor the severity of these effects to be expected at recipient locations 76 - information that is necessary to direct management efforts (Vander Zanden and Olden 2008). 77 Estimating the potential impacts of a novel introduced species is a challenging task (Byers 78 et al. 2002). However, knowledge of the effects caused by NIS at previously invaded sites (i.e. 79 invasion history) may be useful for forecasting their impacts in new locations. Indeed, some 80 introduced aquatic species, including the European green crab (*Carcinus maenas*), zebra mussel 81 (Dreisenna polymorpha) and grass carp (Ctenopharyngodon idella), have been shown to cause 82 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 83 84 that, for at least some widespread invaders, information on previous ecological impacts can serve 85 as a basis for generating robust predictions that can inform management decisions (e.g. Branch and 86 Steffani 2004, Vander Zanden et al. 2004, McCarthy et al. 2006, Ward and Ricciardi 2007, Jokela 87 and Ricciardi 2008).

88 Information on impacts can also be derived through experimental investigation, so we 89 should be able to expand the amount of data available even for NIS that have not yet become 90 widely established. However, despite promising results, studies of invasion history have thus far 91 been relatively rare and quantitative analyses, leading to the development of empirical predictive 92 models, have only been performed for a very small number of species – namely widespread 93 invaders whose impacts have been particularly well documented, such as the zebra mussel (Ward 94 and Ricciardi 2007) and rusty crayfish (Orconectes rusticus) (McCarthy et al. 2006). The 95 feasibility of developing predictions for many other NIS therefore remains to be demonstrated.

96 A number of challenges may impede the use of invasion history as means of forecasting 97 the impacts of most introduced species. First, given the scarcity and heterogeneous quality of 98 information on the impacts resulting from biological invasions (Parker et al. 1999, Byers et al. 99 2002), it is unknown how much data are available concerning the effects of any particular NIS, 100 whether this information is comparable across previous observations, or amenable to quantitative 101 analysis. Furthermore, introduced species cause multiple distinct types of impacts, and the 102 magnitude or even the direction of any particular effect can vary substantially across space and 103 time (e.g. McIntosh 2000, Ross et al. 2003, Branch and Steffani 2004, Strayer et al. 2006, 104 Ricciardi and Kipp 2008). Given this variability and the constraints of data limitation, it remains to 105 be determined whether invasion history can be generally employed to predict the type, direction 106 and severity of future impacts.

107 Variations in the severity of impact caused by an invasive species are arguably the result of 108 a multitude of differences in extrinsic conditions between recipient habitats. However, it is also 109 possible that a substantive proportion of this variability can be explained by a relatively small 110 number of predictable factors. In particular, it has been suggested that the magnitude of the 111 impacts caused by an introduced species should be correlated with its abundance across invaded 112 locations (Parker et al. 1999, D'Antonio and Kark 2002). This intuitive relationship has been 113 demonstrated empirically for several aquatic NIS (e.g. Madsen 1998, Ricciardi 2003, Chumchal et 114 al. 2005, Pintor et al. 2009). Therefore, we may be able to explain much of the variation in the 115 severity of impacts caused by particular invaders by accounting for differences in their local 116 densities or the local environmental factors that control their abundances. However, our ability to 117 test such relationships and determine their predictive value will be limited by the amount and 118 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.

126 Specifically, we evaluated whether for a given NIS similar types of impacts are reported 127 across multiple studies and tested if these studies are consistent in their conclusions regarding the 128 direction of the observed impacts. We then examined whether studies reporting categorically 129 similar effects had provided quantitative information that could be combined to statistically assess 130 variation in impact severity. Finally, using a meta-analytical approach, we conducted a case study 131 for common carp (*Cyprinus carpio*) to demonstrate how quantitative data can be used to explain 132 variability in the severity of impacts observed across invaded locations. Specifically, we developed 133 empirical models that relate the magnitude of several impacts to carp biomass and time since 134 introduction, as reported by multiple studies, and tested whether predictions from such models can 135 be extrapolated to new situations.

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137 Methods

138 *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 illustratethe use of invasion history as a predictive tool.

145 We restricted our analysis to marine and freshwater NIS featured on the list, as biological 146 invasions are particularly prevalent and damaging in aquatic systems (Carlton and Geller 1993, 147 Ruiz et al. 2000; Ricciardi and Atkinson 2004). One aquatic species on the IUCN's list, the zebra 148 mussel Dreissena polymorpha, was excluded from our study because its invasion history has been 149 examined in detail elsewhere (Ricciardi 2003, Ward and Ricciardi 2007). Furthermore, we did not 150 consider species listed as either amphibious or semi-aquatic (e.g. cane toad Bufo marinus; red 151 eared slider turtle *Trachemys scripta*). Finally, due to similar morphology and impacts that 152 sometimes result in misidentification or taxonomic uncertainty (Komak and Crossland 2000, 153 Rawlings et al. 2007), information on *Gambusia holbrooki* and *Pomacea insularum* was combined 154 with that of their congeners G. affinis and P. canaliculata, respectively. 155 We limited our search to peer-reviewed journal articles to ensure the quality of the data 156 used in our analyses and because we assumed the scientific literature to be representative of the 157 quantity of information available concerning the impact of each species. Given the variable nature 158 of the impacts caused by NIS, we set several preliminary criteria for the inclusion of publications 159 in our study. First, for logistical feasibility, we restricted our definition of impact to a reported 160 change in the abundance, distribution, fitness or behaviour of native species, or in the diversity, 161 community composition or abiotic properties of the recipient system or experimental treatment, 162 that had been attributed to the NIS. We thus excluded studies that documented only socioeconomic 163 impacts. We also explicitly excluded studies that had examined the effects of our sample NIS on 164 other introduced species, or those conducted within their native ranges. 165 To reduce bias, the literature search was conducted by two researchers and cross-validated

166 by a third researcher (Gates 2002). Relevant publications were located through several online

167 databases including Science Citation Index Expanded (SCI-EXPANDED, 1900-April 2009), 168 BIOSIS previews (1969-April 2009) and Aquatic Sciences and Fisheries Abstracts (ASFA, 1971-169 April 2009). Initial search terms included (1) invasive, non-indigenous, introduced, exotic or alien 170 species, (2) the scientific and common names of each NIS and (3) impact, effect, affect and 171 *influence*. Additional studies were located by searching citations from relevant publications. 172 Review articles or studies which analysed previous research findings were used for locating 173 primary literature but were not included in our analysis. When articles presented the results of two 174 or more distinct approaches (e.g. a lab experiment coupled with a field survey) we considered each 175 as a separate study.

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177 Data summary and analysis

178 Articles meeting our criteria were reviewed by two researchers and summarized according 179 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 180 181 location where the research was carried out; the impacted variables under investigation (a 182 particular indigenous species, a certain functional group, an abiotic parameter, etc.); the direction 183 of the effect – positive, negative, or a non-directional change; the proposed mechanism by which 184 the effect occurred (e.g. predation, habitat modification) and other relevant information, such as 185 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. Non-directional 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 informationpresented in the article.

193 The resulting database was used to quantify the amount of information available 194 concerning the invasion history of each NIS and to determine whether this information could be 195 used to gain a predictive understanding of their impacts. First, to assess whether certain NIS are 196 likely to possess more detailed invasion histories than others, we tested whether the number of 197 studies reporting impacts varied between marine and freshwater taxa or between vertebrate and 198 invertebrate invaders. Owing to unequal variances between groups and skewed distributions, we 199 used Welch's t-test and restricted our comparisons to two-tailed tests (Ruxton 2006). Using least-200 squares regression, we also examined whether the number of studies reporting the impacts of each 201 NIS was dependent upon the extent of its invaded range, estimated by the number of countries in 202 which a species has become established. Both variables were log-transformed prior to analysis to 203 achieve normality. For these and subsequent tests, results were considered significant at $p \le 0.05$.

204 Data for each NIS were then grouped according to affected taxon, abiotic parameter, 205 functional group, or other biologically relevant impact categories. This was done to determine the 206 quantity of information available for any particular type of impact and to test whether the direction 207 of the various effects attributed to each species were consistent across multiple studies, with the 208 greatest degree of resolution possible. To assess consistency within each impact category we used 209 a G-test to determine if the number of observed positive and negative effects differed from that 210 expected by chance. Impacts categorized as non-directional changes, which made up less than 5% 211 of all records, were not considered. We also restricted our tests to impact categories where the 212 number of cases expected under the null hypothesis for each outcome was no less than 3 (Sokal 213 and Rohlf 1995).

214 Finally, to examine whether invasion history could be used to derive quantitative 215 information suitable for assessing the severity of impacts, we first identified the most commonly 216 documented impact category for each NIS. When five or more published studies were located, we 217 revisited relevant articles to determine if sufficient information (i.e. raw data, statistics, graphical 218 information) was available to quantify impact severity and if these estimates were directly 219 comparable across studies. For each impact category examined, we then determined the maximum 220 number of studies that could be combined using meta-analysis or other statistical techniques. We 221 also identified the main impediments to combining quantitative information from multiple 222 publications.

223 The results derived from these analyses were then used to rank each NIS according to the 224 relative degree of utility of invasion history for generating impact predictions. Based on the most 225 commonly cited impact category for each species, the 19 NIS were ordered hierarchically 226 according to the following criteria: (i) the number studies, providing comparable quantitative data 227 regarding the severity of the reported impacts; (ii) the level of agreement among studies 228 concerning the direction of the effect (either significantly different from random, not significantly 229 different or insufficient data); and (iii) the total number of studies reporting the particular 230 ecological impact.

231

232 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.

244 Rather than using the more conventional approach of converting the statistics reported in 245 each publication to standardized effect sizes (Hedges 1992), we opted to employ a meta-analysis 246 procedure based on linear mixed-effect models (LMEM). LMEM provide an appropriate 247 framework in which to analyze data with an inherently grouped and thus non-independent 248 structure, such as those derived from the same study or experiment (Pinheiro and Bates 2004). By 249 incorporating both fixed (i.e. across-study) parameters and random (i.e. within-study) effects, this 250 approach allowed us to use multiple observations from a wide range of published studies to examine the relationship between various impact categories and carp biomass, while accounting 251 252 for intrinsic variations among studies.

253 Raw data were first compiled from the text, tables or figures (i.e. by digitizing graphs) 254 presented in each article. For each observation of impact, we recorded the corresponding biomass 255 density (kg/ha) of carp as reported nearest the time when the impact was measured, most often at 256 the conclusion of the experiment. When density was not reported directly, it was calculated from 257 the reported carp biomass and the enclosure or water body size, where possible. Given that the 258 impacts of carp might also vary with the amount of time since they have become established in the 259 recipient system, we also recorded experimental duration -i.e. the number of days between the 260 introduction of carp and the measurement of impact.

261	We were able to investigate eight impact categories, including the effects of carp on rooted
262	macrophytes, benthic macro-invertebrates, phytoplankton, turbidity, total nitrogen, total
263	phosphorus, total suspended solids and inorganic suspended solids (Table 2). Observations within
264	each category were converted to the most commonly reported unit of measurement, where possible,
265	or were otherwise discarded from the analysis. Although several studies reported the impacts of
266	carp on zooplankton, the reported metrics varied greatly, sometimes involving density
267	(individuals/L), biomass (g/L), species richness or diversity (e.g. Shannon-Weaver index) of the
268	zooplankton community. As a result, these data could not be confidently standardized and this
269	impact category was not examined in the meta-analysis. For each impact category, studies with
270	fewer than three observations were retained for validation of the fitted models.
271	

Model development

For each impact category we then developed a series of models to examine (i) the variability in the severity of carp impacts across different studies, (ii) the relationship between impact severity and carp biomass, and (iii) 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_i) was estimated by a single across-study mean impact term (β_0) (equation 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_{ik}) for observation *i* from study *k* was estimated by equation 2.

$$283 \qquad Y_j = \beta_0 + \mathbf{E}_j \tag{1}$$

 $Y_{jk} = \beta_0 + U_{0k} + E_j$ (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 (equation 3), as well as a fixed slope (β_2) for experimental duration (*D*) (equation 4).

291
$$Y_{jk} = \beta_0 + C\beta_1 + U_{0k} + E_j$$
 (3)

292
$$Y_{jk} = \beta_0 + C\beta_1 + D\beta_2 + U_{0k} + E_j$$
 (4)

293

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}) as described by equations 5 and 6.

- 298 $Y_{jk} = \beta_0 + C\beta_1 + CU_{1k} + U_{0k} + E_j$ (5) 299 $Y_{jk} = \beta_0 + C\beta_1 + D\beta_2 + CU_{1k} + U_{0k} + E_j$ (6)
- 300

301 The optimal model for each impact category was selected by comparing the residual 302 variance, Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) 303 associated with each model described above. Both AIC and BIC measure the compromise between 304 the fit given by a particular model and its complexity, i.e. the number of parameters included 305 (Johnson and Omland 2004). Although BIC penalizes more heavily than AIC for each additional 306 parameter, models with the lowest values for both criteria were considered to be the most 307 informative. All analyses were conducted using R statistical software (R Development Core Team, 308 2008) and packages "lme4" and "nlme" (Bates 2005).

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

316 **Results**

317 *Literature review*

318 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 319 320 identify only 218 published articles that met our criteria. Several of these articles reported the 321 results of multiple approaches (e.g. a lab experiment and a field study) or the impacts of more than 322 one of our sample NIS, yielding what we considered as 237 (103 observational and 134 323 experimental) case studies. The number of studies reporting the effects of each NIS ranged 324 between 1 for walking catfish and 46 for common carp (Figure 1A). We found no significant 325 difference between the number of studies reporting the impacts of freshwater versus marine taxa (t 326 = 1.14, df = 15, p = 0.27), or between vertebrate and invertebrate invaders (t = 1.90, df = 9, p = 1.14, df = 15, p = 0.27), or between vertebrate and invertebrate invaders (t = 1.90, df = 9, p = 0.27). 327 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 = 3.25, p =328 329 0.089).

Many articles had reported the effects of their focal NIS on multiple factors (e.g. different taxa, several abiotic parameters, etc.), thus we were able to extract a total of 353 different records for impact, ranging from 1 to 113 for each invader (Figure 1B). The most commonly cited

333 mechanisms by which NIS affected their recipient communities were direct predation (n = 143), 334 competition with native species (73), and indirect effects resulting from either trophic cascades (35) 335 or habitat modification (138). Several studies had stated that more than one mechanism was likely 336 responsible for the observed impact; however, carp accounted for more than 70% of the 337 documented effects associated with habitat modification (Figure 2). By categorizing the impact 338 records for each NIS into groupings of similar effects, we identified 66 unique impact categories, 339 which varied from 1 (for several species) up to 10 (for carp) (Figure 1C), whereas the number of 340 records within each individual impact category ranged between 1 and 22 (Figure 1D). A full 341 summary of the compiled impact data and source publications is provided in Appendix A.

342

343 *Direction and severity of impacts*

Over a quarter of the impact categories identified had but a single record – i.e. only 1 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 ($p \le 0.05$). 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 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
behaviour. However, only 8 of these 12 comparable studies provided quantitative estimates of the
observed impacts.

360 Lack of compatibility between the specific types of effects (i.e. effect size estimates) 361 reported across studies was also found to be a major limitation. For *Caulerpa taxifolia*, 9 of 10 362 studies that reported impacts on other macroalgae also provided substantial quantitative 363 information in the form statistical results and graphical data. Among these, 5 studies reported 364 quantitative estimates of impacts on the productivity of native species, and the remaining studies 365 focused on other aspects, such as the diversity or composition of the recipient community. 366 Consequently, information from all of these 9 quantitative studies would not be amenable to 367 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.

382

383 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.

390 For most impacts examined, models that incorporated a flexible intercept term (equation 2) 391 resulted in a substantially lower AIC, BIC, and residual standard deviation compared to those that 392 incorporated only a fixed-effect estimate (i.e. equation 1). Carp biomass was found to be a 393 significant predictor of impact severity for all categories ($p \le 0.04$), with the exception of total 394 suspended solids (Table 5). Based on comparisons of AIC and BIC, the model in the form of 395 equation 3 provided an optimal description for most forms of impact. This would suggest that, for 396 most of the categories examined, there is a comparable change in impact severity for each unit 397 increase in carp biomass, but that there is considerable variation among studies in the response 398 variable in the absence of carp (i.e. initial or pre-impact conditions) and a limited effect of 399 experimental duration. However, the best model for describing impacts on phytoplankton biomass 400 also included a fixed-effect slope term for experimental duration, whereas that for inorganic 401 suspended solids included a random carp biomass slope, suggesting that the relationship between 402 this parameter and carp biomass varies considerably among studies.

403 The majority of the studies retained for validation had reported one observation of the 404 variable being investigated in the absence of carp (i.e. before introduction or as a control treatment) 405 and one estimate for impact at a particular carp density. All optimal models included a flexible 406 intercept term, indicating that some of the variability in the magnitude of the impacts reported by 407 different studies was the result of site-specific differences in initial conditions. To validate our 408 models we therefore generated our predictions using the control observation reported in each 409 publication as an estimate of the intercept (i.e. the pre-impact state of the response variable) and 410 the fixed effect slope estimates derived from the best fit model for each category. The relationship 411 between the observed and predicted magnitude of impact across all categories (Figure 3) was highly significant ($R^2 = 0.91$, df = 21, F = 210.3, p < 0.0001). 412

413

414 **Discussion**

415 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 416 417 multiple studies had reported categorically similar impacts across a wide range of systems. 418 Although limited data currently presents a major barrier to the development of generalizations 419 even for some widely introduced species (e.g. grass carp *Ctenopharyngodon idella*; Dibble and 420 Kovalenko 2009), and context dependence can generate spatial heterogeneity in impacts (e.g. 421 McIntosh 2000, Ricciardi 2003, Ross et al. 2006, Ricciardi and Kipp 2008) some NIS cause 422 similar impacts in most parts of their invaded ranges. For example, Grosholz and Ruiz (1996) had 423 qualitatively demonstrated that the European green crab (Carcinus maenas) has had comparable 424 impacts on bivalve molluscs and other crab species in most of its invaded range, and Ricciardi 425 (2003) showed that the zebra mussel (Dreissena polymorpha) has broadly similar effects on a 426 variety of biotic and abiotic parameters in both European and North American lakes. Our results

427 are consistent with these findings. Thus, at a minimum, invasion history can generally be used to428 reveal the types of impacts expected to occur at new recipient locations.

429 For all but two of the impact categories for which sufficient data were available to test for 430 consistency, there was substantial agreement among studies regarding the direction of effects. 431 Such consistency has provided a predictive basis for particular impacts caused by several aquatic 432 NIS. For example, in a meta-analysis of multiple experimental studies, McCarthy and colleagues 433 (2006) found that several species of invasive crayfish consistently caused reductions in zoobenthic 434 densities and that these findings could be extrapolated to natural systems. However, such 435 directional consistency is absent in several of the impact categories examined in our study. 436 Five of the eight articles that document the effects of *M. galloprovincialis* on the 437 abundance of grazing gastropod species had reported reductions, two reported increases and one 438 article reported contrasting effects on the same native species. Similarly, carp were reported to 439 have both positive and negative effects on zooplankton communities and, although not tested 440 formally, inconsistencies were also noted for several other impact categories, including the effects 441 of largemouth bass on benthic invertebrates and those of green crab on marine macroalgae. Yet 442 even for these cases, variation in the observed direction of effects can often be explained by the 443 influence of simple moderator variables, such as the size of the affected native species or variation 444 in extrinsic habitat characteristics (e.g. Branch and Steffani 2004). Thus, information on previous

445 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.

- 457
- 458 *Predicting the impacts of common carp*

459 The magnitude of impacts caused by a NIS at any given site is hypothesized to be a 460 function of its local abundance (Parker et al. 1999, D'Antonio and Kark 2002, Ricciardi 2003). 461 While this relationship has been demonstrated empirically for a few aquatic invasive species, it is 462 not clear whether differenced in abundance can generally explain a significant portion of the 463 variation in impacts observed across multiple invaded locations. In particular, a number of studies 464 have shown that the severity of multiple impacts caused by introduced carp vary as a function of 465 biomass (e.g. Robel 1961, Breukelaar et al. 1994, Tatrai et al. 1997, Lougheed et al. 1998). 466 Furthermore, several authors have previously combined findings from other studies with their own 467 experimental data, in order to examine the generality of such relationships (Crivelli 1983, 468 Chumchal et al. 2005). Yet such analyses have thus far been restricted to relatively few impact 469 categories and a narrow range of observations, and the ability to predict carp impacts at new sites 470 had not been previously tested.

471 Carp consistently cause several types of impacts, most of which stem from their ability to
472 substantially modify the physical characteristics of invaded habitats (Matzusaki et al. 2009).

- 473 Cumulatively, these impacts can result in shifts between pristine, clear-water conditions
- 474 characterized by high macrophyte densities to heavily degraded turbid water states (Scheffer et al.

475 2001, Zambrano et al. 2001). In particular, the presence of carp has been shown to affect 1) rooted 476 macrophyte densities, mainly through physical disturbance and increased turbidity (e.g. Robel 477 1961, Crivelli 1983, Miller and Crowl 2006); 2) benthic invertebrate densities, through predation 478 and habitat modification (Richardson et al. 1990, Wilcox and Hornbach 1991, Zambrano and 479 Hinojosa 1999); 3) phytoplankton biomass, by altering the availability of various nutrients through 480 excretion and bioturbation (Angeler et al. 2002, Chumchal and Drenner 2004, Driver et al. 2005, 481 Roozen et al. 2007); 4) zooplankton abundance, either indirectly through their effects on 482 phytoplankton (Drenner et al. 1998, Parkos et al. 2003, Matsuzaki et al. 2007) or directly through 483 planktivory by juvenile carp (Cardona et al. 2008); and 5) the abundance of native fish species, 484 through multiple indirect effects including those described above (Forester and Lawrence 1978, 485 Drenner et al. 1997, Cardona et al. 2008). However, the limited amount of comparable 486 quantitative information for these latter two impact categories prevented us from addressing them 487 in our meta-analysis.

488 Our results demonstrate the generalisability of previous findings that the severity of the 489 impacts caused by carp is largely dependent on its local density. Although some studies have 490 found no evidence to suggest a significant relationship between carp density and the magnitude of 491 certain impacts (e.g. turbidity; Fletch et al. 1985, Crivelli 1983) and others have found that several 492 effects vary as a nonlinear function of carp biomass (e.g. Matzuzaki et al 2009, Lougheed et al. 493 1998), with the exception of changes in total suspended solids (TSS), substantial variation in the 494 impact categories noted above could be explained by linear models relating impact severity to carp 495 biomass. Thus, despite some heterogeneity in previous findings, our meta-analysis demonstrates 496 that, at a broad inter-regional scale, the invasion history of this NIS can in fact be used to develop 497 informative predictions regarding the severity of multiple impacts expected to occur at different 498 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.

501 Our results, as well as previous findings, also illustrate the degree to which the impacts of 502 carp are context-dependent. Each of our models included a flexible intercept term, suggesting that 503 the severity of the impacts expected to occur at a particular carp density depend largely on 504 experimental or site-specific conditions. Furthermore, for one of the categories examined, 505 inorganic suspended solids, the relationship with carp density varied substantially between studies. 506 The ability of carp to influence suspended solids and other water clarity measures depends largely 507 on the type of sediment that they disturb (Roberts 1995, Parkos et al. 2003), thus variation in 508 sediment size and composition may preclude a significant relationship between carp biomass and 509 measures of suspended solids across sites.

510 Similarly, the degree of susceptibility of aquatic vegetation to the effects of carp has been 511 shown to vary with different macrophyte species (Zambrano and Hinojosa 1999, Evelsizer and 512 Turner 2006), while the impacts of carp on several water quality parameters may also depend on 513 the depth of the invaded water body (Zambrano et al. 2001). Further, while experimental duration 514 was found to be a relevant predictor for only the phytoplankton biomass category, several studies 515 have illustrated that carp impacts can vary substantially over time (Tatrai et al. 1997, Zambrano 516 and Hinojosa 1999, Matsuzaki et al. 2007). The studies examined in our meta-analysis consisted 517 mainly of experiments conducted in controlled environment over relatively short time-spans, and 518 thus may not fully reflect the potential variation in impact severity that may occur under natural 519 conditions. Unfortunately, given the lack of historical baseline data for carp introductions 520 throughout much of its invaded range, we were unable to assess the predictive power of our 521 models in natural systems.

522

523 The utility of invasion history for predicting impacts

524 Our results illustrate that invasion history can be used to develop informative predictions 525 pertaining to the type and direction of ecological impacts caused by many introduced species. 526 Furthermore, for at least some NIS, the severity of impacts to be expected at novel recipient sites 527 can be estimated from a few key variables. As demonstrated for carp, substantial variance in 528 impact severity can be explained by empirical models linking the invader's biomass to the 529 magnitude of various forms of impact, when sufficient quantitative data are available. By 530 incorporating information on initial (i.e. pre-impact) conditions at potential recipient locations, 531 such models can generate useful quantitative predictions for the severity of the impacts to be 532 expected. Although similar approaches have been used to model the ecological effects of a few 533 other high-profile aquatic invaders, especially the zebra mussel Dreissena polymorpha (Ward and 534 Ricciardi 2007, Jokela and Ricciardi 2008) and rusty crayfish Orconectes rusticus (McCarthy et al. 535 2006), several challenges – namely the lack of comparable quantitative data – currently inhibit similar analyses for the majority of introduced species. 536

537 Indeed, apart from common carp, only seven of the 19 NIS examined in our study (i.e. 538 green crab, largemouth bass, Caulerpa taxifolia, mosquitofish, rainbow trout, Mnemiopsis leidvi 539 and brown trout) were the subject of five or more studies that provided comparable quantitative 540 estimates of impact severity. Thus, information necessary for analysis and prediction of future 541 impacts is presently quite limited, even for many of the world worst invaders. Furthermore, only 542 three additional species: Mytilus galloprovincialis, Nile perch and Cercopagis pengoi, had 543 sufficient information to statistically test consistency in the direction of reported impacts. As such, 544 quantitative assessments of invasion history can presently be conducted for no more than 60% of 545 the aquatic NIS considered here, and even then only a fraction of the types of impacts caused by

546 most of these species could be examined. For the remaining NIS, invasion history will likely be 547 limited to providing qualitative descriptions of impacts that may arise from future invasions. 548 Given that our sample of NIS were selected from among the list of the 100 World's Worst 549 Invasive Alien Species, one might conclude that information on impacts may be too limited to 550 develop useful predictions concerning the ecological effects of most other NIS. However, the 551 IUCN's list is largely an educational tool designed to raise awareness of biological invasions. 552 Species are therefore featured not only because they have demonstrated their ability to cause 553 deleterious effects but also because they serve as representative examples of harmful NIS (Lowe et 554 al. 2004). The list omits several introduced aquatic species that have previously been shown to 555 have deleterious effects across a wide range of systems, e.g. Eurasian watermilfoil (Madsen 1998), 556 spiny waterflea Bythotrephes longimanus (Boudreau and Yan 2003), rusty crayfish (McCarthy et 557 al. 2006), presumably because their impacts are similar to those of other listed NIS. Consequently, 558 there are certainly additional species that possess invasion histories sufficiently detailed for the 559 development of quantitative predictions beyond those examined here. 560 Nonetheless, data on ecological impacts are presently very limited even for some of the 561 world's most disruptive and well-publicized invaders, and the inconsistent manner by which 562 impact data are collected and presented poses a major challenge to risk assessment (Parker et al. 563 1999, Andersen et al. 2004). Where sufficient quantitative information exists, consideration of 564 predictive attributes such as the relationship between an invader's impact and its abundance may 565 allow for greater resolution regarding which sites are most at risk of damage. Therefore, a priority 566 for the research and management of biological invasions should be to compile, organize and make 567 accessible information on impacts, as well as the factors that mediate them, so that informed 568 predictions can be generated before particularly harmful NIS become widely established and their 569 prioritization and prevention are no longer possible.

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577	
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Species	Common name	Habitat	Native range	Studies
Asterias amurensis	North Pacific seastar	MAR	North-western Pacific	4
Carcinus maenas	Green Crab	MAR	North-western Europe	18
Caulerpa taxifolia	Caulerpa	MAR	Circum tropical	18
Cercopagis pengoi	Fish hook water flea	FW	Ponto-Capian	6
Clarias batrachus	Walking catfish	FW	South-eastern 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 USA	24
Lates niloticus	Nile Perch	FW	Nile River	11
Micropterus salmoides	Largemouth bass	FW	Eastern Canada and USA	10
Mnemiopsis leidyi	Comb jelly	MAR	North and South American Atlantic coast	7

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.

780 (Table 1 continued)

Species	Common name	Habitat	Native range	Studies
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

790 Table 2 Descriptions and abbreviations for the 8 biotic and abiotic impact categories examined in

the carp meta-analysis. The number of studies and total number of observations (indicated in

792	brackets) used to	fit the	models	and v	alidate	model	predictions	are given.
		/						1	0

	A L L	TI:4	# of Studies		
Impact category	Abbreviation	Unit	Fitting	Validation	
Biotic					
Macrophyte density	MAC	g/m ²	6 (49)	2 (2)	
Benthic invertebrate	DI	· 2	2 (10)	0	
density	BI	g/m²	3 (10)	0	
Phytoplankton biomass	РНҮТ	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)	
T 1:14		Nephelometric turbidity units	12 (01)	2	
Turbidity	IUR	(NTU)	13 (81)	3 (4)	
Total suspended solids	TSS	mg/L	5 (30)	1 (1)	
Inorganic suspended	100			4 (4)	
solids	155	mg/L	4 (21)	1(1)	

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. Bold type indicates impact categories where the number
of reported negative and positive effects did not differ from that expected by chance.

Snecies	Impact category	Effect		G	<i>P</i> -value	
species	Impact category	Neg.	Pos.			
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	12	0	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		0	13.86	< 0.001	

804 (Table 3 continued)

Species Impact category		Eff	fect	G	<i>P</i> -value	
		Neg.	Pos.			
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	

Table 4 List of the 19 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. 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).

	S •	Most common impact	Comparable	Directional	Total number
Kank	category		quantitative studies	agreement	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

819 (Table 4 continued)

		Most common impact	Comparable	Directional	Total number
Rank	Species	category	quantitative studies	agreement	of studies
12	Undaria pinnatifida	Marine macroalgae	3	ID	6
13	Pomacea spp.	Macrophytes	-	ID	4
15	Asterias amurensis	Bivalves	-	ID	4
14	Oreochromis mossambicus	Fish	-	ID	3
	Eriocheir sinensis	Bank erosion	-	ID	2
15	Eichhornia crassipes	Benthic invertebrates	-	ID	2
	Corbula amurensis	Phytoplankton	-	ID	1
16	Clarias batrachus	Amphibians	-	ID	1

820

821 ** Predictive model developed for impact severity

822 - Species for which impact categories were not examined in further detail

823

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. Parameters estimates include the fixed effect intercept (B_0); the standard deviation of the flexible intercept term (τ_{0k}); slope estimates for carp biomass effect (B_1); the standard deviation of the flexible carp biomass slope term (τ_{1k}); experimental duration slope estimate (B_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.

Equation	B_{θ}	$ au_{0k}$	B_1	$ au_{1k}$	B_2	σ	AIC	BIC	P biomass
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	
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	
	Equation 1 2 3 4 5 6 1 2 3 4 4 5 6 1 2 3 4 4 5 6 1 2 4 5 6 1 2 4 5 6 1 2 4 5 6 1 2 4 5 6 1 2 4 5 6 1 2 4 5 6 1 2 5 6 1 2 1 2	Equation B_0 11.6721.6532.0843.2352.0963.4410.1020.1030.514-0.74	Equation B_{θ} $\tau_{\theta k}$ 11.6721.650.7232.080.7443.231.1852.090.363.440.4610.1020.100.0030.510.004-0.740.00	Equation B_0 τ_{0k} B_1 11.6721.650.7232.080.74-0.2043.231.18-0.2052.090.3-0.2163.440.46-0.2110.1020.100.0030.510.00-0.234-0.740.00-0.24	Equation B_0 τ_{0k} B_1 τ_{1k} 11.6721.650.7232.080.74-0.2043.231.18-0.2052.090.3-0.210.0063.440.46-0.210.0010.1020.100.004-0.740.00-0.23	Equation B_0 τ_{0k} B_1 τ_{1k} B_2 11.6721.650.7232.080.74-0.2043.231.18-0.2052.090.3-0.210.0063.440.46-0.210.00-0.7810.1020.100.004-0.740.00-0.23	Equation B_{θ} τ_{0k} B_I τ_{Ik} B_2 σ 11.670.7921.650.720.3732.080.74-0.200.3043.231.18-0.20-0.670.2852.090.3-0.210.000.2963.440.46-0.210.00-0.780.2810.100.4220.100.000.4030.510.00-0.230.570.27	Equation B_{θ} $\tau_{\theta k}$ B_1 τ_{Ik} B_2 σ AIC11.670.79118.4821.650.720.3768.5332.080.74-0.200.3052.6743.231.18-0.20-0.670.2853.5352.090.3-0.210.000.2953.4463.440.46-0.210.00-0.780.2855.2510.100.4214.1820.100.00-0.230.570.2713.594-0.740.00-0.240.570.2713.59	Equation B_{θ} $\tau_{\theta k}$ B_I τ_{Ik} B_2 σ AICBIC11.670.79118.48122.2721.650.720.3768.5374.2132.080.74-0.200.3052.6760.2443.231.18-0.20-0.670.2853.5362.9952.090.3-0.210.00-0.780.2953.4464.7963.440.46-0.210.00-0.780.2855.2568.510.1014.1814.7820.100.000.4016.1817.0930.510.00-0.230.570.2713.5915.84

831 (Table 5 continued)

Impact category	Equation	B ₀	$ au_{0k}$	B ₁	$ au_{1k}$	B ₂	σ	AIC	BIC	P biomass
Benthic invertebrate	5	0.51	0.00	-0.23	0.00		0.29	16.06	17.88	
density	6	-0.74	0.00	-0.24	0.00	0.57	0.27	14.59	16.71	
Phytoplankton	1	1.31					0.62	74.40	77.68	
biomass	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	

833 (Table 5 continued)

Impact category	Equation	B_{θ}	$ au_{0k}$	<i>B</i> ₁	$ au_{1k}$	B_2	σ	AIC	BIC	P biomass
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	

837 (Table 5 continued)

Impact category	Equation	B_{θ}	$ au_{ heta k}$	B_1	$ au_{1k}$	B_2	σ	AIC	BIC	P biomass
Total suspended	1	1.91					0.68	64.53	67.34	
solids	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	1	1.52					0.35	18.78	20.97	
solids	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	

840	Figure	legends
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Figure 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 NIS examined, and D) the number of records
per impact category.
Figure 2 Contributions of common carp (CC), other freshwater fish species (OFWF), marine

847 invertebrates (MAR INV), freshwater invertebrates (FW INV) and primary producers (PP) to the

848 four most commonly cited impact mechanisms.

849

850 Figure 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 7 of the 8 impact

852 categories examined in the carp meta-analysis are shown. Impact category abbreviations are given

in Table 1.





Figure 2



Figure 3

