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Non-native species have multiple abundance-impact curves

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28 **Abstract**

29 The abundance-impact curve is helpful for understanding and managing the impacts of
30 non-native species. Abundance-impact curves can have a wide range of shapes (e.g., linear,
31 threshold, sigmoid), each with its own implications for scientific understanding and
32 management. Sometimes the abundance-impact curve has been viewed as a property of the
33 species, with a single curve for a species. I argue that the abundance-impact curve is determined
34 jointly by a non-native species and the ecosystem it invades, so that a species may have multiple
35 abundance-impact curves. Models of the impacts of the invasive mussel *Dreissena* show how a
36 single species can have multiple, non-interchangeable abundance-impact curves. To the extent
37 that ecosystem characteristics determine the abundance-impact curve, abundance-impact curves
38 based on horizontal designs (space-for-time substitution) may be misleading and should be used
39 with great caution, if at all. It is important for scientists and managers to correctly specify the
40 abundance-impact curve when considering the impacts of non-native species. Diverting attention
41 from the invading species to the invaded ecosystem, and especially to the interaction between
42 species and ecosystem could improve our understanding of how non-native species affect
43 ecosystems and reduce uncertainty around the effects of management of populations of non-
44 native species.

45 **Introduction**

46 Non-native species are of concern because of their impacts. Whether the invader affects
47 biodiversity, ecosystem function and services, human economies, or human health (e.g.,
48 Lockwood et al. 2013; Ricciardi et al. 2013; Blackburn et al. 2014; Gallardo et al. 2015), it is the
49 impacts of the invader, rather than the invader itself, that usually is the primary concern. Despite
50 the central importance of impacts, many useful contributions about the impacts of specific
51 invaders (e.g., Higgins & Vander Zanden 2010; Vilà et al. 2011), and some general frameworks
52 and empirical studies that apply broadly across taxa (e.g., Parker et al. 1999; Blackburn et al.
53 2011; Dick et al. 2014; Pearse et al. 2019; Crystal-Ornelas & Lockwood 2020), we are far from
54 having satisfactory understanding or predictive power about the impacts of non-native species
55 (e.g., Ricciardi et al. 2013; Strayer et al. 2019a; Crystal-Ornelas & Lockwood 2020).

56 One useful general approach that links the invader with its impacts is the abundance-
57 impact curve (Fig. 2) (=density-impact function [DIF]; Norbury et al. 2015), in which some
58 measure of the abundance (e.g. population density, biomass) of a non-native species is plotted

59 against some measure of its total impact (e.g., Yokomizo et al. 2009; Sofaer et al. 2018). The
60 abundance-impact curve represents a substantial advance over earlier approaches (e.g., Parker et
61 al. 1999) because it accommodates non-linear relationships between abundance and impact, in
62 which the marginal per capita effect can vary with invader abundance. It therefore identifies a
63 critical distinction between the average and marginal per capita effects of an invader. The shape
64 and parameters of this curve are highly relevant to management, because they allow managers to
65 estimate the expected benefits of reducing the population of the invader by a given amount,
66 which can be weighed against the expected costs of that reduction (e.g., Yokomizo et al. 2009;
67 Sofaer et al. 2018). Especially in the last decade, scientists have published abundance-impact
68 curves of problematic invaders (e.g., Thiele et al. 2010; Benkwitt 2015; Strayer et al. 2019a), as
69 well as broad empirical analyses of the impacts of non-native species that are based on
70 abundance-impact curves (e.g., Norbury et al. 2015; Bradley et al. 2019; Pearse et al. 2019).
71 These studies have provided insights into the basic ecology of species invasions, as well as
72 information that could be useful to managers.

73 A potential problem with impact theories in general, and with abundance-impact curves
74 in particular, is that impacts have been regarded chiefly as a property of the invading species
75 (e.g., Ricciardi et al. 2013; Sofaer et al. 2018). Thus, it is common to see reference to *the*
76 abundance-impact curve of a species, as if each species had a single abundance-impact curve. If
77 the invaded ecosystem has been considered at all, it has been included implicitly (e.g., in the per-
78 capita effect term of Parker et al.'s [1999] equation), or treated as a secondary modulator of
79 impacts. I argue here that the invading species and the invaded ecosystem are partners in
80 determining impact, and that both must be considered explicitly in effective theories of impacts.
81 Furthermore, once we include the invaded ecosystem, we see that there generally will not be a
82 single abundance-impact curve for a species, but multiple, non-interchangeable abundance-
83 impact curves, each of which applies over limited domains (types of ecosystems, types of
84 invaders, types of impacts). I will explore these ideas using simple models of the expected
85 impacts of *Dreissena* (zebra and quagga mussels), ecologically and economically important
86 invaders that have been well studied (e.g., Higgins & Vander Zanden 2010; Gallardo et al. 2016;
87 Crystal-Ornelas & Lockwood 2020).

88 **Abundance-impact curves of *Dreissena*: two examples**

89 *Dreissena* species (Fig. 1) are native to the Ponto-Caspian region of southeastern Europe
90 and southwestern Asia. Since the early 19th century, they have been spread widely through
91 western Europe and North America, chiefly through commercial shipping and recreational
92 boating (van der Velde et al. 2010; Benson et al. 2019). They often form dense populations, and
93 have large ecological and economic impacts (summarized by Ricciardi 2003; Connelly et al.
94 2007; Strayer 2009; Higgins & Vander Zanden 2010) as a result of their suspension-feeding,
95 shell-building, and fouling. *Dreissena* has impacts that are broadly similar to many other species
96 of freshwater, estuarine, and coastal marine bivalves that have been spread widely around the
97 world by humans (e.g., *Corbicula*, *Limnoperna*, *Mytilopsis*, *Rangia*, and various species of
98 oysters and mussels), and so represents an important class of invaders.

99 *Example 1: shell accumulation*

100 *Dreissena* plays many roles in ecosystems (e.g., Ricciardi 2003; Higgins & Vander
101 Zanden 2010); here I will here explore two roles that are simple and well understood enough to
102 analyze with simple, quantitative models. The first is the accumulation of empty shells and shell
103 fragments (“shell hash”) on the sediments. These empty shells change the surface roughness,
104 texture, porosity, permeability, and chemistry of sediments, thereby affecting habitat for benthic
105 animals, interstitial biogeochemistry, near-bottom hydrodynamics, and exchanges of materials
106 between the water and sediments (Gutierrez et al. 2003; Ricciardi 2003). Shell production by
107 *Dreissena* and other mollusks can be large, approaching rates of wood production (in terms of
108 mass) in temperate forests (Gutierrez et al. 2003).

109 The amount of shell hash that accumulates on sediments depends on the rate at which
110 empty shells are produced by dying animals and the rate at which they are dissolved, buried, or
111 washed downstream by the ecosystem. For simplicity, I assume that burial and export are
112 negligible, so that the dynamics of shell hash are determined by production and dissolution, as
113 follows:

114
$$\frac{dS}{dt} = M - kS$$

115 where S is the standing stock of shell hash, M is the quantity of shell material entering the spent
116 shell pool through mortality of living animals, and k is the instantaneous loss rate of spent shells.

117 At steady state, mortality is equal to the production of spent shells (P) and $\frac{dS}{dt} = 0$, so the

118 quantity of shell hash will be $\frac{P}{k}$, where k depends on water chemistry and currents (Strayer &
119 Malcom 2007).

120 I will model shell accumulation in three ecosystems: a hardwater lake in which shell
121 dissolution is slow ($k = -0.05/\text{yr}$; rates estimated from Strayer & Malcom 2007), a moderately
122 hardwater lake in which shell dissolution is moderately fast ($k = -0.3/\text{yr}$), and moderately
123 hardwater river in which shell dissolution is fast ($k = -2/\text{year}$). I chose these three systems
124 because they cover most of the range of conditions under which dense populations of *Dreissena*
125 occur (Whittier et al. 2008). (*Dreissena* does live in waters supersaturated in calcium carbonate,
126 where even smaller absolute values of k would be expected, but not in very soft waters, where
127 shell dissolution would very fast [$k < -2/\text{year}$].)

128 I begin by considering the amount of shell hash that would accumulate, at equilibrium, by
129 *Dreissena* populations of different sizes in each of these three hypothetical ecosystems. Again,
130 the range of *Dreissena* population sizes used roughly matches the range expected in nature
131 (Strayer & Malcom 2007); note that population size is expressed here as the rate of shell
132 production. In this first scenario, the amount of shell hash that accumulates on the sediments
133 depends strongly on both the size of the *Dreissena* population and the characteristics of the
134 ecosystem, to a roughly equal extent (Fig. 3). In this example, the abundance-impact curve is
135 always simple and of the same form (linear) across different ecosystems, and the difference
136 across ecosystems is easily understood and modeled as a simple difference in slopes. The slopes
137 depend on the shell dissolution rate, which can be estimated roughly from water chemistry and
138 movement, or more precisely from simple litter-bag studies (Strayer & Malcom 2007).
139 Furthermore, because shell dissolution rates are a function of shell size and thickness (Strayer &
140 Malcom 2007; Ilarri et al. 2019), it would be possible to extend this simple framework to cover
141 other species of shell-producers.

142 However, the impacts of shell accumulation are cumulative, not instantaneous, so this
143 example has interesting temporal dynamics, which also depend on the characteristics of the
144 ecosystem. I will now relax the assumption of steady state, and model the temporal dynamics of
145 shell accumulation in different ecosystems. In this second scenario, I assume a constant
146 *Dreissena* population, and calculate the time-course of shell accumulation in the three model
147 ecosystems (Fig. 4). As we already saw, the equilibrium amount of shell hash (the asymptotes in
148 Fig. 4) differs among ecosystems. In addition, the rate at which that asymptote is approached

149 differs among ecosystems; systems with high dissolution rates approach equilibrium rapidly
150 (within ~5 years), whereas systems with low dissolution rates take several decades to reach
151 equilibrium. Thus, the ecosystem affects the dynamics of impacts as well as their long-term
152 equilibria.

153 But of course *Dreissena* populations vary over time; in many cases, year-to-year
154 variation is approximately an order of magnitude (Strayer et al. 2019b). I next model the
155 temporal dynamics of shell hash accumulation in different ecosystems that support temporally
156 variable populations of *Dreissena*. Temporal variability of shell production in these populations
157 mimics the year-to-year variation in *Dreissena* biomass in the Hudson River, a population with
158 moderately high interannual variation (Strayer et al. 2019b). For simplicity, I modeled
159 accumulation of shell hash only for the ecosystems with the highest and lowest rates of shell
160 dissolution (i.e., the hardwater lake and the moderately hardwater river).

161 In the river with high dissolution rates, shell accumulation equilibrates rapidly with shell
162 production, shell accumulation closely tracks shell production (Fig. 5, left), and impact measured
163 in any year is still a clear linear function of current *Dreissena* population size (Fig. 5, right).
164 However, when rates of shell dissolution are lower, the ecosystem equilibrates slowly with
165 inputs, shell accumulation is not closely coupled with instantaneous rates of shell production
166 (Fig. 5, left), and there is no apparent relationship between the current impact and *Dreissena*
167 population size (Fig. 5, right). For a cumulative impact such as shell accumulation, impact at any
168 time t will be a weighted function of invader population size over some temporal window
169 preceding that time. Because the ecosystem determines the dynamics of the impact, the width of
170 that window and the appropriate weighting function are determined by the characteristics of the
171 ecosystem and will differ across ecosystems.

172 *Example 2: provision of macrophyte habitat*

173 The second example of *Dreissena* impact is the increase in the area of the photic zone
174 available for colonization by submersed macrophytes. *Dreissena* typically increases water clarity
175 by removing phytoplankton and other particles from the water column (Higgins & Vander
176 Zanden 2010; Higgins et al., 2011). This can increase the area of lake or river bottom colonized
177 by rooted plants and benthic algae (Zhu et al. 2006), which in turn can have large and far-
178 reaching effects on the food web, provision of habitat for fish and invertebrates, and

179 biogeochemical processes and exchanges between the sediment and water column (Carpenter &
180 Lodge 1986; Jeppesen et al. 1998).

181 Three pieces of information are needed to connect *Dreissena* abundance with the increase
182 in area available for submersed macrophytes (Fig. 6): (i) the relationship between *Dreissena*
183 abundance (now expressed as aggregate filtration rate of the population) and phytoplankton
184 biomass (as concentration of chlorophyll a); (ii) the relationship between phytoplankton biomass
185 and water clarity; and (iii) the bathymetric map (technically the hypsographic curve) of a body of
186 water. The relationship between *Dreissena* population filtration rate and phytoplankton biomass
187 is known only approximately. For the purposes of this exercise, I assumed that phytoplankton
188 biomass declines exponentially with *Dreissena* filtration rate as (Fig. 6, left):

$$189 \quad chl_{post} = 0.2chl_{pre} + 0.8chl_{pre}e^{(-0.0347DFR)}$$

190 where chl_{pre} and chl_{post} are the chlorophyll concentrations before and after the *Dreissena*
191 invasion, and DFR is the *Dreissena* filtration rate (as % of the water column/day). This equation
192 is consistent with previous analyses and data (Caraco et al. 2006; Higgins & Vander Zanden
193 2010; Strayer et al. 2019a). The relationship between phytoplankton biomass and water clarity
194 was well explored in the classical eutrophication literature; I used the relationship of Rast & Lee
195 (1978) and shown in Fig. 6 (center):

$$196 \quad \log_{10} \text{Secchi depth} = -0.473 \log_{10} \text{chl} + 0.803$$

197 where Secchi depth is in m and chlorophyll (chl) is in $\mu\text{g/L}$. For bathymetry, I will use three
198 contrasting model lakes: (i) a conical basin with a maximum depth of 5m (“shallow”); (ii) a
199 conical basin with a maximum depth of 50m (“deep”); (iii) a lake of intermediate depth
200 (maximum = 15m), but with a pronounced shelf between 2.5m and 3m (“shelf”; such shelves are
201 common in lakes). I ran this model for an unproductive lake (pre-invasion chlorophyll
202 concentration of 3 $\mu\text{g/L}$) and a productive lake (pre-invasion chlorophyll concentration of 30
203 $\mu\text{g/L}$). I further assumed that the light extinction coefficient (η) was equal to the Secchi depth/1.7
204 (Wetzel 2001), and that submersed macrophytes could survive to the depth reached by 5% of
205 surface light (Moss 2010).

206 This model produced several notable results (Fig. 7). In some ecosystems, the
207 relationship between *Dreissena* population size and area available for submersed macrophytes
208 was positive and asymptotic, simply with differences in slope among the different lakes.
209 However, other ecosystem types showed fundamentally different relationships. For the shallow,

210 unproductive lake, the arrival of *Dreissena* had no effect on the area available for submersed
211 macrophytes, regardless of the density of *Dreissena*, because the entire lake bottom was well
212 lighted enough for submersed macrophytes before *Dreissena* arrived. The abundance-impact
213 curve for the productive “shelf” lake was highly nonlinear, with steep increases in macrophyte
214 habitat at *Dreissena* filtration rates of 10-30% of the water column/day contrasting with much
215 lower rates over other parts of the range. Such idiosyncratic responses would occur in the many
216 lakes that have nonlinear hypsographic curves (i.e., non-conical basins).

217 This second example again shows that impacts are a joint property of the *Dreissena*
218 population and the ecosystem, and that a wide range of abundance-impact curves are possible
219 (both in terms of parameters and shapes). Despite this complication, impacts are predictable if
220 we explicitly consider both the invader and the ecosystem. As in the first example, it seems
221 likely that this analysis could be extended to accommodate the activities of other non-native
222 species in the same functional group as *Dreissena* (suspension-feeders in this second example), if
223 we express their population sizes in terms of filtration rates. In contrast to the shell accumulation
224 example, the impacts here are more or less instantaneous (the light environment should closely
225 follow changes in filtration rates, even though there may be some lags in the responses of
226 macrophytes), so that the history of the invasion is less likely to be critical.

227 These two examples show that the characteristics of the ecosystem can be fundamentally
228 important in defining the abundance-impact curve, and must be explicitly considered if we hope
229 to understand that curve. As others (e.g., Ricciardi 2003; Ricciardi et al. 2013; Pearse et al. 2019)
230 have noted, there are different curves for different impacts of a single invader (i.e., shell
231 accumulation vs. water clarification). These differences may be especially marked between
232 instantaneous and slow, cumulative impacts. Furthermore, very different attributes of the
233 ecosystem are important for these different impacts – water chemistry and movement for shell
234 accumulation vs. lake bathymetry and productivity for provision of submersed macrophyte
235 habitat. Likewise, the abundance of the invader may best be expressed in different ways (e.g.,
236 population density, biomass, shell production rate, filtration rate) depending on the impact being
237 considered.

238 **Implications of ecosystem sensitivity for horizontal studies (space-for-time substitution) in**
239 **invasion ecology**

240 Up until now, I have not been explicit about what the points in the abundance-impact
241 curve (Fig. 2) represent. In fact, there are at least three distinct versions of the abundance-impact
242 curve, depending on what the points represent. These three versions will generally not be
243 interchangeable in terms of their shapes, parameters, or applications. All three curves have the
244 abundance of the invader on the x-axis and one of its impacts on the y-axis (as in Fig. 2). In the
245 first formulation (“within system”), the points on the graph come from a single ecosystem. This
246 could be either a single ecosystem in nature sampled over different times, each with a different
247 abundance of the invader, or experimentally manipulated to produce different abundances, or
248 from an experiment using different abundances of the non-native species in replicates of the
249 same ecosystem. In the second formulation (“cross-system snapshot”), the points are snapshots,
250 each representing a single sample from different ecosystems. In the third formulation (“cross-
251 system, long-term”), the points are long-term means from different ecosystems.

252 To see the difference among these three abundance-impact curves, consider a very simple
253 example in which within-system impacts are non-cumulative, linear on invader abundance, but
254 with different slopes in different types of ecosystems. Further assume that invader abundance
255 varies over time in each ecosystem, and that different landscapes hold three types of ecosystems
256 (with a high slope, moderate slope, and low slope, respectively, to their abundance-impact
257 curves) in different proportions. Snapshot samples taken from such a landscape will produce data
258 points whose distribution depends on (i) the within-system abundance-impact curves; (ii) the
259 distribution of invader densities over time within each ecosystem; and (iii) the proportion of each
260 kind of ecosystem in the landscape (and possibly (iv) the proportion of each kind of ecosystem in
261 the sample, if the ecosystems are not sampled using a representative sampling design). The three
262 selected examples in Fig. 8 show that highly varied distributions of points, and therefore highly
263 varied abundance-impact curves, can be produced from snapshot samples taken from a single
264 simple system. It doesn’t take much imagination to see that almost any distribution of data points
265 and any shape of abundance-impact curve can be obtained from cross-system snapshot sampling,
266 even if the system has a very simple underlying structure, if different ecosystems have different
267 abundance-impact curves. This problem becomes even more severe if the system has a more
268 complex underlying structure (e.g., abundance-impact curves that are nonlinear or different in
269 shape in different ecosystems, cumulative impacts). Except in the case of coincidence, the
270 abundance-impact curves obtained by snapshot sampling (the black lines in Fig. 8) will generally

271 not match any of the within-system abundance-impact curves in shape, parameters, or even sign.
272 Specifically, the fitted lines will not accurately predict the results of changing invader
273 abundances in any ecosystem in the landscape, and can even (as in Fig. 8b) produce predictions
274 of the wrong sign.

275 If we sample the ecosystems in this simple example repeatedly to get their long-term
276 mean abundances and impacts, we will obtain less noisy versions of plots like those shown in
277 Fig. 8. If the abundance of the invader does not vary much over time, the long-term curve will
278 closely resemble the snapshot curve, whereas if invader abundance within ecosystems varies
279 greatly over time, the long-term curve will look a lot cleaner than the snapshot version. However,
280 neither cross-system curve will generally resemble the within-system curves, in either shape or
281 parameters.

282 If the within-system abundance-impact curve is non-linear (which will often be the case;
283 e.g., Norbury et al. 2015; Benkwitt 2015; Strayer et al. 2019a), the snapshot and long-term cross-
284 system curves will also differ from one another in shape and parameters. They will differ
285 because the mean value of a dependent variable evaluated at a series of points along a non-linear
286 function is not the same as the value of the dependent variable evaluated at the mean value of the
287 independent variable (cf. Karamata's Inequality or Jensen's Inequality – Denny 2017). This
288 problem can range in severity from negligibly small to large depending on the degree of non-
289 linearity in the within-system abundance-impact curves and the amount of temporal variation in
290 invader abundance.

291 Thus, even if the impact of the invader is not a cumulative function of invader
292 abundance, the three different abundance-impact curves are equivalent only under special
293 conditions. The within-system curve and the snapshot curve will be the same only if invader
294 impact is unaffected by the characteristics of the ecosystem (i.e., if a single abundance-impact
295 curve applies to all ecosystems in the sample). The snapshot curve and the long-term cross-
296 system curve will be the same only if all within-system invader-impact curves are linear. And all
297 three curves will be the same only if both of these conditions apply – if the abundance-impact
298 curve is linear and identical in all ecosystems in the sample. These conditions seem unlikely to
299 apply to many impacts of invaders.

300 Cumulative impacts introduce additional complications. We have seen that if we wish to
301 obtain an interpretable within-system abundance-impact curve for cumulative impacts, we must

302 consider (and weight) invader abundance over some window of time, and both the width of the
303 time-window and the weighting function can differ across ecosystems. Consequently, even if
304 abundance-impact curves are similar across all ecosystems, the snapshot approach will not
305 produce interpretable results for cumulative impacts, unless the impact equilibrates rapidly (e.g.,
306 the blue line in Fig. 5, left) or the invader's abundance is stable over time. Nor will the long-term
307 cross-system abundance-impact curves equal the within-system curves, even if abundance-
308 impact curves are similar across all ecosystems (although they may be less erroneous than the
309 snapshot results), because the temporal weighting functions will generally be nonlinear. This
310 further restricts the conditions under which cross-system and within-system abundance-impact
311 curves will resemble one another.

312 Some of the problems with horizontal designs can be solved by careful matching of study
313 sites, so that differences in a relevant ecosystem characteristic are minimized (i.e., so that the
314 study ecosystems all fall along a single abundance-impact curve, as do points of the same color
315 in Fig. 8), or by explicitly including the relevant ecosystem characteristics in the abundance-
316 impact model. Indeed, both of these strategies have been recommended or used in horizontal
317 studies of impacts (e.g., Thiele et al. 2010; Pyšek et al. 2012; Staska et al. 2014; Jackson et al.
318 2015). Nevertheless, such strategies may fail to produce reliable abundance-impact curves if the
319 sites are poorly matched, the within-system abundance-impact curve is nonlinear, or impacts are
320 cumulative. All of these problems are likely to be common. Furthermore, because the different
321 impacts of a single species may be sensitive to different ecosystem characteristics (as in the two
322 *Dreissena* examples), a set of study sites that is well-matched for studying one impact may be ill-
323 suited to study another impact of the same species.

324 **Why does this matter?**

325 It has been well appreciated that ecosystem characteristics help to determine the
326 establishment, spread, and local abundance of non-native species (e.g., Leung & Mandrak 2007;
327 Lockwood et al. 2013; Lewis et al. 2017). The examples presented here emphasize that
328 ecosystem characteristics can also strongly affect the abundance-impact curve. That is,
329 ecosystems help to set not only the occurrence and abundance of a non-native species at a site,
330 but also its per capita effects.

331 Abundance-impact curves can be important to several important scientific and
332 management problems (e.g., Yokomizo et al. 2009; Thiele et al. 2010; Sofael et al. 2019). Most

333 obviously, an accurate abundance-impact curve can help managers evaluate the benefits and
334 costs of proposed management actions to reduce the abundance of a non-native species
335 (Yokomizo et al. 2009). Abundance-impact curves are essential to schemes to assess the regional
336 impacts of non-native species (e.g., Thiele et al. 2010; Vander Zanden et al. 2017). They can also
337 provide a standardized way by which to compare impacts of one non-native to another, or natives
338 to non-natives (Pearse et al. 2019). Using the wrong parameters and shape for an abundance-
339 impact curve can therefore have serious consequences for scientific understanding, and incur
340 unnecessary monetary and environmental costs from inappropriate management actions (e.g.,
341 Yokomizo et al. 2009).

342 I have shown here that within- and across-system abundance-impact curves can be
343 radically different in shape and parameters (Fig. 8). Nevertheless, previous studies have
344 generally failed to recognize the existence of different kinds of abundance-impact curves,
345 regarded them as interchangeable (e.g., Sofaer et al. 2018), used across-system curves to judge
346 how the impacts of a non-native species would change if its abundance were to change (e.g.,
347 Bradley et al. 2019), or mixed different kinds of abundance-impact curves (e.g., Norbury et al.
348 2015). Such uncritical use of abundance-impact curves is likely to cause confusion and slow
349 scientific progress, lead to misleading understanding of the impacts of non-native species, cost
350 money (Yokomizo et al. 2009), and damage ecosystems that are subject to inappropriate
351 management actions.

352 **The way forward**

353 Ecosystems can strongly influence abundance-impact curves of non-native species,
354 complicating their use and interpretation. The examples presented here for *Dreissena*, which are
355 relatively realistic, show that the ecosystem is of first-order importance, roughly as important as
356 *Dreissena* abundance, in determining two selected impacts (shell accumulation and provision of
357 macrophyte habitat). There has been little systematic examination of how other per capita
358 impacts of *Dreissena* vary across ecosystems, but the information that is available suggests that
359 these impacts do vary substantially across different kinds of ecosystems. Thus, apart from any
360 effect of *Dreissena* abundance, Caraco et al. (1997), Higgins et al. (2011), and Sarnelle et al.
361 (2012) found that impacts on phytoplankton depend on epilimnetic volume, stratification,
362 turbidity, and nutrient content; Strayer et al. (2004, Fig. 8 and associated text) suggested that
363 impacts on fish communities depend greatly on system morphometry, hydrology, and turbidity,

364 as well as the species composition of the fish community; impacts on native bivalves may
365 depend on hydrodynamics and sediment type (Zanatta et al. 2015; Strayer & Malcom 2018); and
366 Strayer et al. (1999, Fig. 9) found large differences in many attributes of ecosystems that were
367 invaded by *Dreissena* populations of similar density. It therefore seems likely that many impacts
368 of *Dreissena* depend substantially on ecosystem characteristics and cannot be reduced to a single
369 abundance-impact curve.

370 These conclusions about *Dreissena* probably apply to other non-native species. Many of
371 the impacts of non-native species may depend on the characteristics of the invaded ecosystem, in
372 addition to the abundance of the invader, and the list of relevant ecosystem characteristics must
373 be diverse, depending on the impact being considered. For instance, the impacts of a nitrogen-
374 fixing plant or a nitrogen-recycling animal must depend on whether the ecosystem is strongly
375 nitrogen limited or nitrogen replete (e.g., Scherer-Lorenzen et al., 2007; Luo et al. 2014;
376 Atkinson et al. 2017). More generally, we can expect impacts of non-native species to depend on
377 factors such as the structure of the food web (e.g., Vander Zanden et al. 2004), whether the
378 ecosystem is rich or poor in nutrients (as for nitrogen), productive or unproductive (as in the
379 second *Dreissena* example), highly retentive or rapidly flushed (e.g., Lucas & Thompson 2012),
380 stable or highly disturbed, highly heterogeneous or relatively uniform (e.g., MacRae & Jackson
381 2001; Lucas et al. 2016), to name a few obvious possibilities. Therefore, for many invaders it
382 will be more useful to think of multiple abundance-impact curves, each applying to a defined
383 range of impacts, functional groups of species, and types of ecosystems, and each with its own
384 scientific and management applications, rather than a single curve.

385 Furthermore, although this essay has focused on non-native species, it should be obvious
386 that these considerations apply equally to native species, and so have broad application in
387 ecology. Ecologists and managers often consider trying to increase the abundance of a native
388 species to increase the ecosystem services it provides (e.g., Coen et al. 2007; Kreeger et al.
389 2018), or reduce the abundance of a native species to reduce its harmful impacts (e.g., Beguin et
390 al. 2016). Abundance-impact curves can help to predict the likely changes in impacts resulting
391 from a projected change in abundance and thus assess the costs and benefits of management
392 actions. As for non-native species, it will be essential in such applications to correctly choose
393 and parameterize the abundance-impact curve.

394 But although it seems clear that ecosystems *can* strongly influence the abundance-impact
395 curve, surely there must also be many cases in which the influence of the ecosystem is small
396 enough to ignore, especially if the domain of study systems is carefully defined. But how often
397 *do* ecosystems matter? Can we identify the conditions under which ecosystems are most likely to
398 matter? Clearly, we need better theoretical and empirical explorations of how (and how much)
399 ecosystems affect abundance-impact curves. In many cases, we know enough about the
400 mechanisms of impact that we should be able to predict what characteristics of an ecosystem
401 ought to affect a specified impact (as in the *Dreissena* examples), and use models, experiments,
402 or field observations to assess the importance of ecosystem characteristics to invader impacts. It
403 may eventually be possible to develop a theoretical or empirical basis for separating the
404 situations in which impacts are sensitive to ecosystem characteristics from those in which
405 impacts are robust to variation in ecosystems.

406 How should we proceed in the interim until we satisfactorily understand the importance
407 of ecosystem characteristics to abundance-impact curves? If scientific studies show that the
408 ecosystem has little or no influence on the abundance-impact curve, then a single abundance-
409 impact curve can be applied for a given impact of a non-native species across sites, and any of
410 several methods can be used to estimate the abundance-impact curve (keeping in mind the
411 caveats about cumulative impacts discussed above). However, to the extent that the impacts of
412 non-native species do depend on the characteristics of the invaded ecosystem as well as those of
413 the invader, any satisfactory understanding of invader impacts will have to explicitly consider
414 ecosystems as well as species. This means that we will need to gather and analyze data
415 separately for each kind of ecosystem (cf. Thiele et al. 2010; Norbury et al. 2015) or include
416 ecosystem characteristics in general models of impacts (e.g., Pyšek et al. 2012), limit
417 extrapolations to well defined domains (of impact type, species functional group, and ecosystem
418 type) (Norbury et al. 2015), and take care to apply the correct kind of abundance-impact curve to
419 each application. In particular, unless until ecosystems are shown to have little influence on a
420 given impact, abundance-impact curves derived from cross-system designs should be viewed
421 skeptically and used very cautiously. Likewise, if abundance-impact curves are to be used for
422 management, it will be important to consider whether such curves are reliable and have been
423 based on sound science. But to make an obvious point, management of non-native species is
424 based on considerations other than abundance-impact curves, as valuable as they may be, so

425 there is no reason to postpone management of a non-native species until reliable abundance-
426 impact curves become available.

427 The problems raised in this essay will complicate analyses of abundance-impact curves
428 and non-native species impacts. However, addressing these problems should improve our
429 understanding of how non-native species affect ecosystems and reduce uncertainty around the
430 effects of management of populations of non-native species. Furthermore, as the *Dreissena*
431 examples suggest, these are likely to be tractable problems, and can be solved if invasion
432 ecologists divert some of their attention from the invading species to the invaded ecosystem, and
433 especially to the interaction between species and ecosystem.

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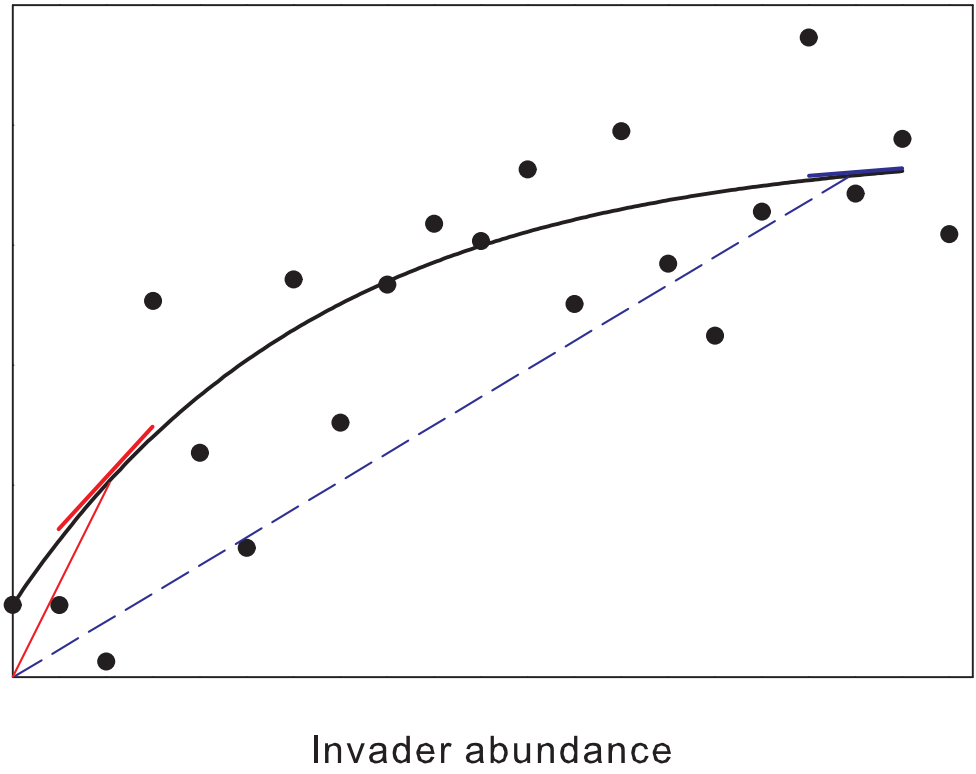
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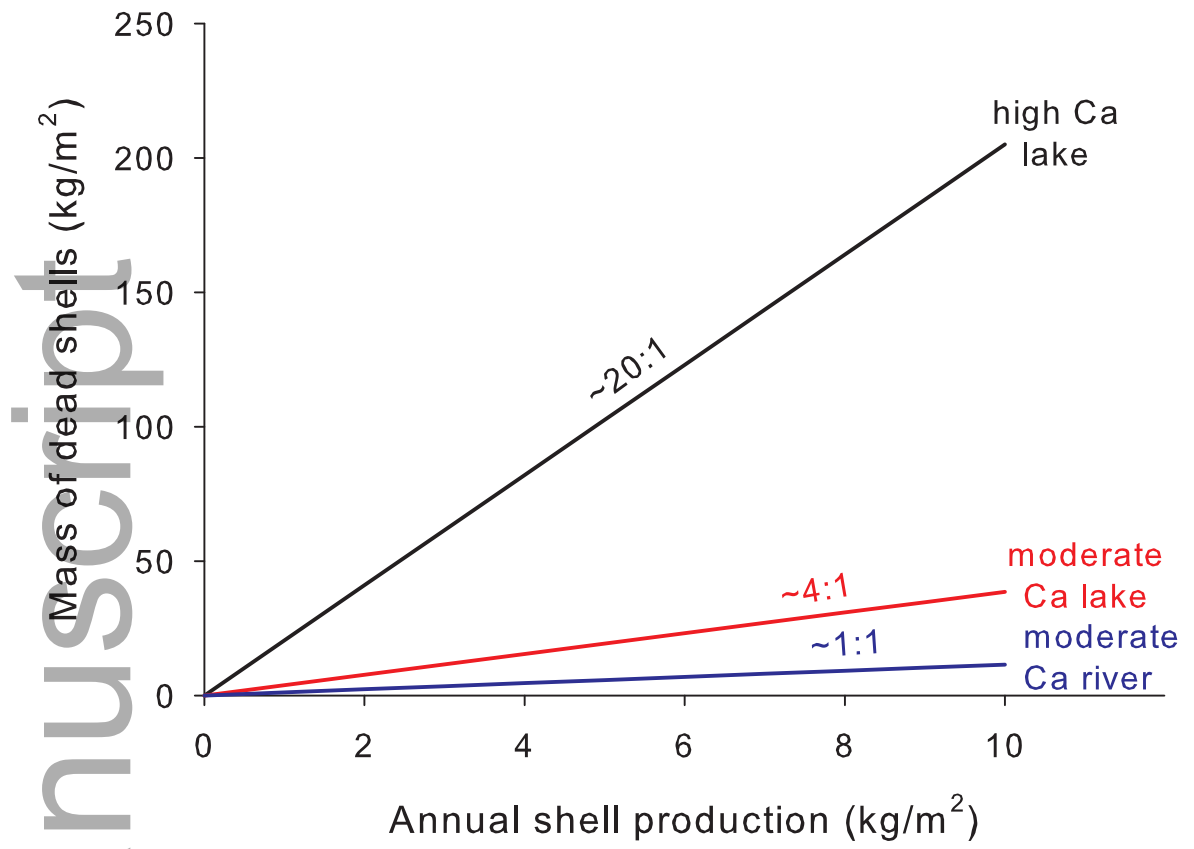


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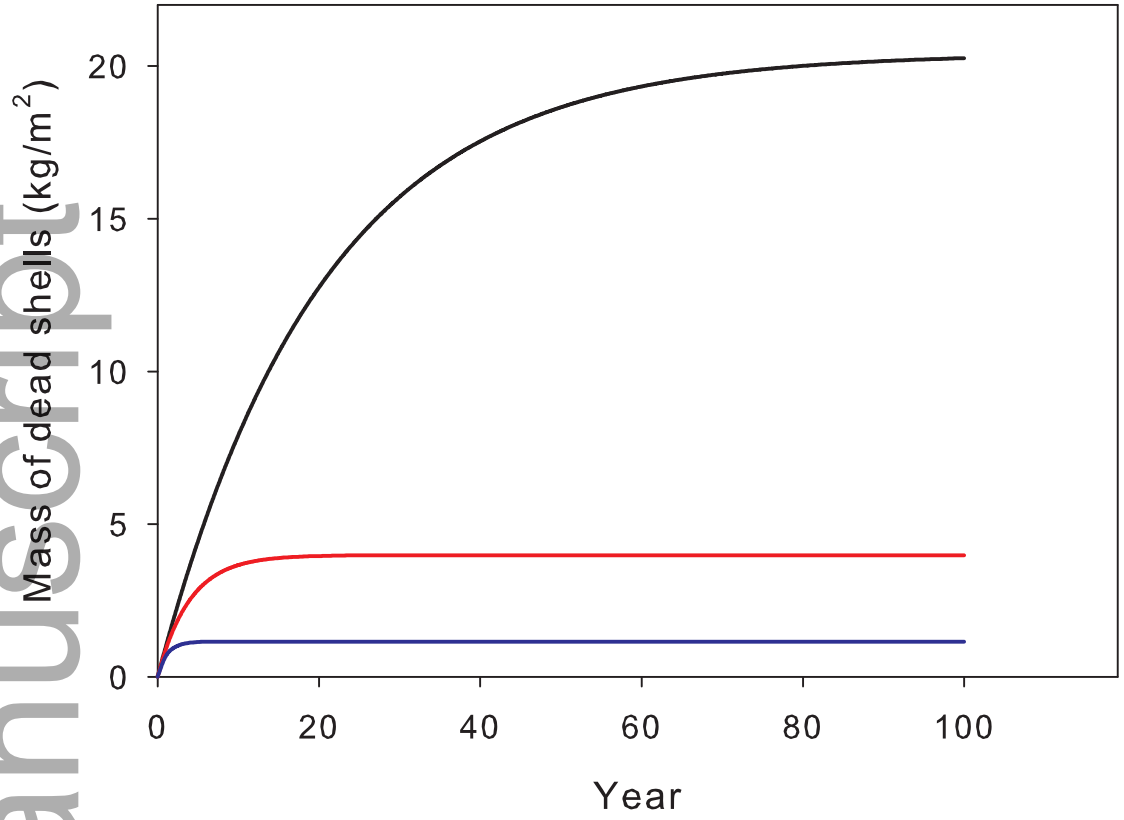
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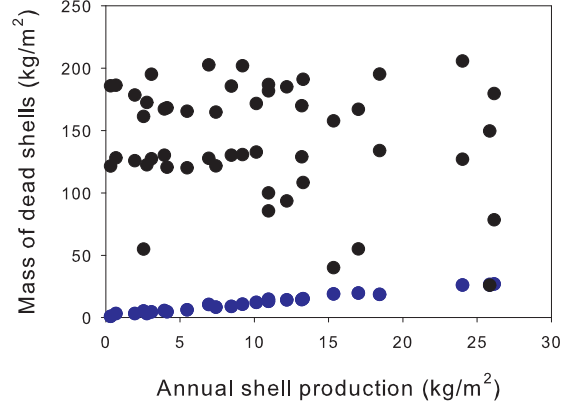
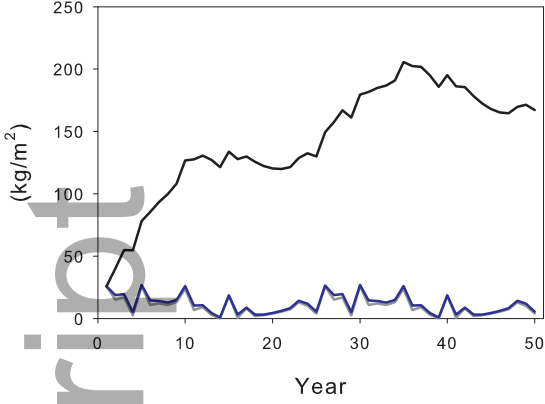
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(for annual shell production = 1 kg/m²)



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Mass or annual production of dead shells
(kg/m²)

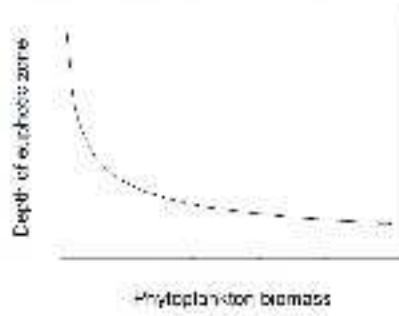


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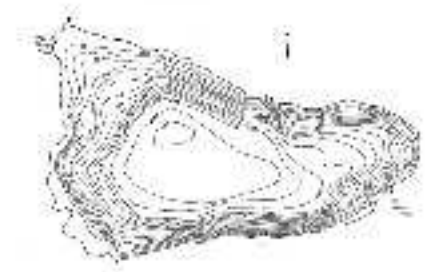
1. Phytoplankton biomass vs. *Dreissena* population size



2. Phytoplankton biomass vs. water clarity

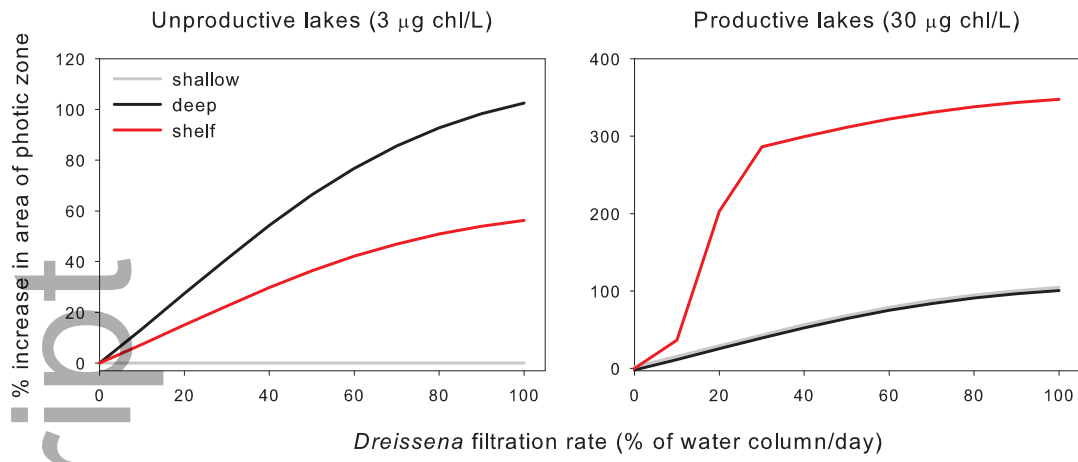


3. Lake bathymetry



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