

1 **Preventing and controlling non-native species invasions to bend the curve of global**
2 **freshwater biodiversity loss**

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43 **Abstract**

44

45 The Emergency Recovery Plan for freshwater biodiversity recognises that addressing non-
46 native species is one of six principal actions needed to bend the curve in freshwater biodiversity
47 loss. This is because introduction rates of non-native species continue to accelerate globally
48 and, where these species develop invasive populations, they can have severe impacts on
49 freshwater biodiversity. The most effective management measure to protect freshwater
50 biodiversity is to prevent introductions of non-native species. Should a non-native species be
51 introduced, however, then its early detection and the implementation of rapid reaction measures
52 can avoid it establishing and dispersing. If these measures are unsuccessful and the species
53 becomes invasive then control and containment measures can minimise its further spread and
54 impact. Minimizing further spread and impact includes control methods to reduce invader
55 abundance and containment methods such as screening of invaded sites and strict biosecurity
56 to avoid the invader dispersing to neighbouring basins. These management actions have
57 benefitted from developments in invasion risk assessment that can prioritise species according
58 to their invasion risk and, for species already invasive, ensure that management actions are
59 commensurate with assessed risk. The successful management of freshwater non-native
60 species still requires the overcoming of some implementation challenges, including non-native
61 species often being a symptom of degraded habitats rather than the main driver of ecological
62 change, and eradication methods often being non-species specific. Given the multiple
63 anthropogenic stressors in freshwaters, non-native species management must work with other
64 restoration strategies if it is to deliver the Emergency Recovery Plan for freshwater
65 biodiversity.

66

67

68 **1. Introduction**

69

70 Freshwater ecosystems are subjected to considerable physical, chemical, and biological
71 alteration through the exploitation of their provisioning ecosystem services, with these factors
72 driving substantial declines in biodiversity (Tickner *et al.* 2020). One of these modifications is
73 the introduction of non-native species (Moorhouse and Macdonald 2015; also see Box 1).
74 Although only a proportion of the introduced species establish populations that then disperse,
75 it is these invasive populations that can severely impact freshwater ecosystems across large
76 spatial areas (Gozlan *et al.* 2010; Gallardo *et al.* 2016). Impacts of freshwater invasive species
77 can manifest at levels from individual to ecosystem, and can include substantial declines in the
78 diversity of native species (Cucherousset and Olden 2011; Flood *et al.* 2020) and altered
79 ecosystem functioning (Vilizzi, Tarkan and Copp 2015), as well as causing major economic
80 consequences (Cuthbert *et al.* 2021). Correspondingly, the ‘Emergency Recovery Plan’ of
81 Tickner *et al.* (2020) recognised the successful management of non-native species as one of six
82 principal actions needed to ‘bend the curve’ in freshwater biodiversity loss.

83 With the impacts of non-native species described by the International Union for
84 Conservation of Nature as ‘immense, insidious, and usually irreversible’, it is not unexpected
85 that management measures to restore invaded systems are challenging, with intensive efforts
86 often needed for reducing the population abundances of non-native species and avoiding their
87 further dispersal (Britton, Gozlan and Copp 2011a). Whilst efforts to manage non-native
88 species in the wild have had some successes for fishes (Rytwinski *et al.* 2019) and macrophytes
89 (Coetzee *et al.* 2021), the results for other invasive freshwater taxa have been more mixed, with
90 the control of widely distributed invaders - such as non-native crayfish - being particularly
91 difficult (e.g., Gherardi *et al.* 2011). Management control and containment efforts can also be
92 resource intensive when applied over large spatial scales, thus pointing to the importance of

93 preventing introductions as a key goal in the management of non-native species (Russell *et al.*
94 2017).

95 In the last decade, decision-making relating to the management of non-native species has
96 been assisted by substantial developments in invasion risk assessments, with growing
97 advancements in establishing minimum standards (e.g., Leung *et al.* 2012; Roy *et al.* 2018).
98 Eradication feasibility assessment schemes have also helped prioritise the management of new
99 and emerging invasive species (e.g., Booy *et al.* 2017; Booy *et al.* 2020). Thus, while invasive
100 species continue to be a major driver of freshwater biodiversity decline, risk-based tools can
101 enhance the prevention of high-risk invasive species being introduced and identify those
102 species already present that require rapid management actions to prevent their invasion.

103 The primary aim of this study is to consider how managing non-native species can help
104 ‘bend the curve’ in freshwater biodiversity loss within the Emergency Recovery Plan for
105 freshwater biodiversity (Tickner *et al.* 2020). Through syntheses of existing knowledge, we
106 identify the contemporary issues associated with non-native species in freshwaters, before
107 outlining the strategies available for preventing, controlling, and coping with freshwater
108 invasions (Fig. 1). We then discuss the integration of these tools into risk-based management
109 programs, and outline the barriers to their successful implementation.

110

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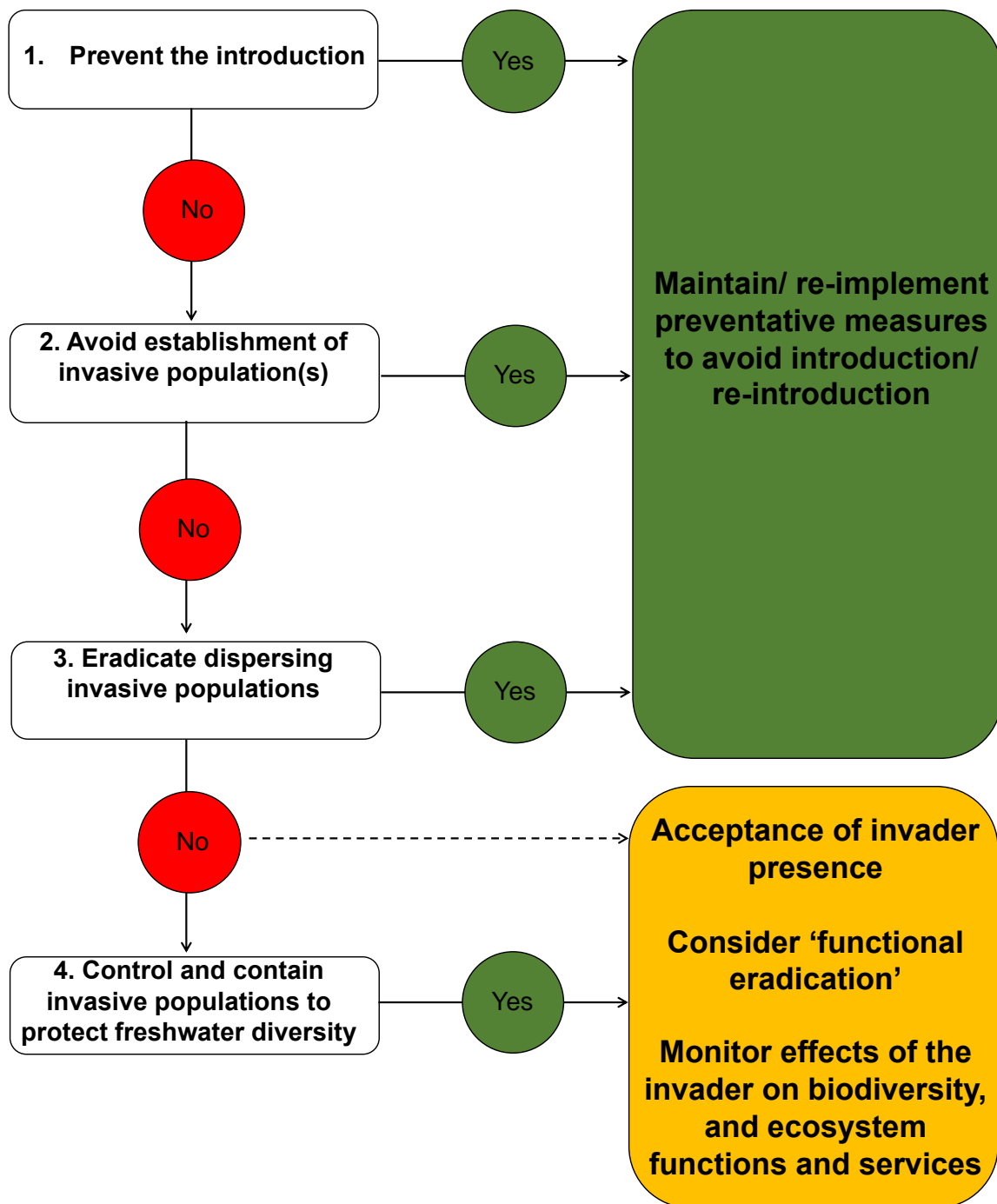


Figure 1. Step-wise process outlining the different actions to be considered for managing the impacts of a non-native species in freshwaters, where ‘yes’ indicates success of the measures underlying the action (see Table 1), ‘no’ indicates failure of the measures, solid arrows indicate primary pathway through the process, the dashed line indicates where no management interventions are taken against the presence of an invader. For information on functional eradication, see Green and Grosholtz (2021).

112 **2. Non-native species in fresh waters**

113 There are two major contemporary issues associated with non-native species in freshwaters: (i)
114 their continued high rates of introductions; and (ii) for those introduced species, their ecological
115 impacts on freshwater biodiversity.

116

117 ***2.1 Introduction rates***

118 Major introduction pathways (i.e., the routes by which a species is transported from its native
119 range to the new range; Saul *et al.* 2017) of freshwater non-native species vary taxonomically,
120 and their strength and geographic routes have changed, and will continue to change over time.
121 Primary motivations for early non-native species introductions were for extensive fish culture
122 and stocking of plants and animals for the ‘national good’ (e.g., acclimatisation societies)
123 (Hickley and Chare 2004). For example, initial introductions of common carp *Cyprinus carpio*
124 to Western Europe occurred about 2000 years ago and were most likely facilitated by the
125 Romans and later by Catholic monks who reared them in monastery ponds for food (Copp *et*
126 *al.* 2005). Over the last 150 years, however, freshwater introduction rates have accelerated in
127 association with the substantial increases in global trade, human population sizes, and tourism
128 (Mormul *et al.* 2022). Since World War II, a more pronounced increase in the number of
129 freshwater introductions has coincided with the shift towards more intense global trade and
130 productivity (Seebens *et al.* 2017; Vitule *et al.* 2019). This increased number of introductions
131 is consistent across continents and is projected to continue until at least 2050 (Seebens *et al.*
132 2021). As non-native freshwater species are widely used in the aquaculture and ornamental
133 trade, high introduction rates are apparent across diverse taxa (e.g., fish, algae, crustaceans and
134 molluscs; Dawson *et al.* 2017).

135 Contemporary introduction pathways for non-native species into freshwaters are diverse,
136 although typically involve aquaculture practices sport angling, the ornamental trade, shipping

137 and boating activities, cultural activities, and stocking for biocontrol (Dawson *et al.* 2017).
138 Although many introductions of non-native species are intentional, especially where they are
139 being used to increase food production and enhance sport angling, unintentional introductions
140 are frequent, such as from ship ballast water releases, biosecurity lapses involving trade in
141 ornamental pets, and the transfer of propagules attached to recreational boats that move
142 between waterbodies (Gozlan *et al.* 2010; Mangiante *et al.* 2018). The ability of an introduced
143 species to establish a population, disperse, and impact native biodiversity is elevated when the
144 receiving freshwater has been extensively modified by anthropogenic activities, such as
145 including the building of impoundments (promoting establishment) and canals (assisting
146 dispersal) (Craig *et al.* 2017).

147

148 **2.2 Ecological impacts**

149 Freshwater invasive species can cause considerable negative ecological impacts through
150 various processes (e.g., predation, competition, genetic introgression, pathogen transmission)
151 that can manifest across different levels of organisation (i.e., genetic to ecosystem) and scales
152 (i.e., local to global). The genetic impacts of aquatic invasive species include changes in genetic
153 introgression leading to hybridization that can decrease genetic integrity in native populations
154 through genetic pollution (e.g., hybrid swarms), as seen between non-native rainbow trout
155 *Oncorhynchus mykiss* and native cutthroat trout *Oncorhynchus clarkii* subspecies and other
156 salmonids in North American streams (Muhlfeld *et al.* 2009).

157 Population level impacts include changes in the abundance and distribution of native species
158 and the transmission of pathogens and parasites. For instance, non-native crayfishes reduce the
159 abundance of basal resources like aquatic macrophytes and aquatic invertebrates (e.g., snails,
160 mayflies) through direct predation, and competition for habitat and prey with native crayfish,
161 amphibians, and fish (Twardochleb, Olden and Larson 2013). Indeed, comparative functional

162 responses (relationships between resource availability and resource uptake rate) have
163 consistently revealed that invaders with high ecological impacts tend to have higher maximum
164 consumption rates than trophically analogous natives (Dick *et al.* 2017), such as in invasive
165 channel catfish *Ictalurus punctatus* versus native *Rhamdia quelen* in Brazil (Faria, Alexander
166 and Vitule 2019). Invaders with lower consumption rates than native species are also often
167 predicted to have substantial ecological impacts due to their relatively high population
168 abundances, such as in topmouth gudgeon *Pseudorasbora parva* (Dick *et al.* 2017)

169 At the community level, freshwater invaders contribute to the local extinction of native
170 species, and modify species composition and diversity. For example, the giant reed *Arundo*
171 *donax* has invaded many Mediterranean-climate and subtropical riparian areas of the world,
172 resulting in the decreased diversity of riparian vegetation that leads to lower abundance and
173 diversity of riparian invertebrates and birds (Maceda-Veiga *et al.* 2016). The modification of
174 species composition and diversity patterns through introductions has dramatically
175 homogenised the present-day biogeography of the world's freshwaters, with distant regions
176 now demonstrating striking similarities in their faunas and floras (Olden, Comte and Giam
177 2018).

178 Freshwater invaders can also alter ecosystems through 'ecosystem engineering' (Gallardo
179 *et al.* 2016) where, for example, invasive bivalves (e.g., freshwater golden clam *Corbicula*
180 *fluminea* and golden mussel *Limnoperna fortunei*) capture and consume suspended particles,
181 produce faeces and pseudofaeces, function as an important resource subsidy, and bio-amplify
182 pollutants throughout the food chain (Sousa *et al.* 2014). The high filtration rates of bivalves
183 also typically reduce phytoplankton, increase water clarity, and thus change primary
184 productivity and food web structure (e.g., shifts to more macrophytes) (Higgins and Vander
185 Zanden 2010).

186

187 **3. Managing freshwater non-native species**

188 Managing freshwater non-native species involves preventing introductions (via mechanisms
189 supported by horizon scanning, risk assessment and appropriate biosecurity at holding
190 facilities), preventing introduced species from establishing and containing their secondary
191 spread (via early detection and rapid response), and then controlling invasive populations to
192 suppress their ecological impacts and reduce their rate of dispersal (Fig. 1). Where this step-
193 wise process is unsuccessful then there is the option of living with the invader and, ideally,
194 monitoring the consequences of this for freshwater biodiversity, and ecosystem functions and
195 services (Fig. 1; Table 1).

196

197 **3.1 Preventing new introductions**

198 Effective strategies for preventing new species introductions involve the application of a series
199 of tools and approaches, such as enforcement of strong legislation and regulation, horizon
200 scanning and risk assessment, and the application of effective biosecurity measures coupled
201 with education schemes.

202

203 ***Legislation and regulatory frameworks***

204 The legislation and regulation of freshwater non-native species is largely reactive and
205 implemented at national scales, despite the major pathways of introduction usually involving
206 international transportation (Padilla and Williams 2004). An exception is the Ballast Water
207 Management Convention (<https://www.imo.org/>), which aims to reduce the transfer and impact
208 of aquatic organisms transported in the ballast water and sediment of ships (Gollasch *et al.*
209 2007). Several studies have investigated the capacity of ballast water exchange and treatment
210 to remove the number of organisms (*cf.* Lakshmi, Priya and Achari 2021), and some success
211 has been reported for the North American Great Lakes (Ricciardi and MacIsaac 2022). Yet its

212 overall effectiveness at reducing the rate of introduction of new invasive species remains
213 difficult to measure, especially with all aspects of the Convention yet to be fully implemented.
214 Nevertheless, the Ballast Water Management Convention sets the example for the regulation
215 of other major introduction pathways in fresh waters, notably the pet and aquaculture trade, for
216 which ‘safe’ lists are a way to reduce intentional and accidental introductions, where such lists
217 can be based on risk assessment processes (Padilla and Williams 2004).

218 At the pan-continental scale, the European Regulation 1143/2015 of Invasive Alien Species
219 lists 30 freshwater species out of 88 ‘invasive alien species’ as priorities for introduction
220 prevention and invasion management. International trade is restricted for the species in the
221 Union List that are not yet present in Europe; Member States must also design management
222 plans adapted to their current levels of invasion. This legislation uses formal risk assessment
223 processes for potentially invasive taxa (economic-, environmental-, and disease-focused)
224 (CIRCABC 2022). The use of such approaches can result in the development of statutory lists
225 (Roy *et al.* 2018), where ‘black’ and ‘white’ lists identify prohibited and permitted taxa
226 respectively (Simberloff 2006; Roy *et al.* 2018). While list-based approaches can be relatively
227 straightforward to apply but fail for many cryptic species where immature individuals can be
228 difficult to distinguish and so are frequently misidentified (e.g., aquarium fish species, juvenile
229 crayfish) (Morais and Reichard 2018). Post-border controls often commence with compliance
230 or quarantine inspections, which, while valuable, do not detect subclinical diseases and cannot
231 deal with risks from newly emerging pathogens (Peeler *et al.* 2011).

232

233 ***Horizon scanning***

234 Horizon scanning is the systematic process of conducting a contextualised search for potential
235 threats and opportunities that need identification to inform future decision-making and policy
236 development (Roy *et al.* 2014; Roy *et al.* 2019; Vilizzi *et al.* 2021). This is an essential tool for

237 anticipating which non-native species are most likely to arrive in the scanned area and which
238 will cause the greatest impacts, such that preventative actions can be taken (e.g., Roy *et al.*
239 2014; Roy *et al.* 2019). Several approaches with different strengths and weaknesses can be
240 adopted for horizon scanning (from interview to modelling approaches; Roy *et al.*, 2019), but
241 generally a large set of species is reduced to a prioritized list according to the probability of
242 their introduction, establishment, spread, and impact (although with assessments that are not
243 as thorough as for full risk assessment). The approach on consensus-building proposed by Roy
244 *et al.* (2014) for the UK has been increasingly used at national and continental levels (e.g.,
245 Peyton *et al.* 2019; Lucy *et al.* 2020). For example, Roy *et al.* (2019) identified 66 high-risk
246 species at European level, with many of these then considered for full risk assessment and
247 included in the Union list of invasive species of the EU Regulation 1143/2014 (e.g., among
248 aquatic species (*Channa argus*, *Faxonius rusticus*, *Limnoperna fortunei*, *Morone americana*).

249

250 ***Risk assessment***

251 Risk assessment is a systematic approach to prioritise both current and future threats, which
252 assesses the scale and likelihood of arrival (through pathway analysis), establishment, spread,
253 and impact of potentially invasive species that can be either absent or present in the assessed
254 area. A complete risk assessment considers all of the main factors responsible for biological
255 invasions, where Roy *et al.* (2018) identified 14 criteria for assessment, including introduction
256 pathways, impacts on biodiversity, ecosystems, ecosystem services socio-economics, and
257 uncertainty levels in responses. Risk assessments thus generate outputs (e.g. risk-based scores)
258 that are suitable for policy development on invasive species, and managing invasions impacts
259 (Roy *et al.* 2018; Robertson *et al.* 2021). They can also be used developing draft lists of species
260 (e.g., black (prohibited) or white (permitted)), and are important components of trade rules
261 relating to importations (e.g., a risk assessment must have been conducted that identifies

262 significant risk of establishment and harm before a species can be banned from importation)
263 (Robertson *et al.* 2021). Risk assessment is widely used around the world and has produced
264 many lists of prioritized species at national, regional, and continental levels (e.g., Kolar and
265 Lodge 2002; Peyton *et al.* 2019). Examples of risk assessments for a wide range of freshwater
266 species (and other taxa) are available for a number of regions, including England (GB NNSS
267 2022a), Australia (e.g., Queensland; Queensland Government 2021) and the European Union
268 (CIRCABC 2022).

269 Different forms and tools of risk assessment exist (Roy *et al.* 2018), with qualitative or
270 quantitative outcomes. The set of minimum risk assessment standards proposed by Roy *et al.*
271 (2018) included uncertainty and impacts on ecosystem services, as well as assessing
272 invasiveness both under current and future climate conditions. Risk assessment (coupled with
273 initial horizon scanning to prioritise species for full assessment) is thus advantageous for
274 competent agencies to implement as resources can be focussed on the most likely high impact
275 invaders, with appropriate targeted management actions. It is important to couple any risk
276 assessment with the appropriate risk management when considering the feasibility and costs of
277 the species that are then prioritized for management (Robertson *et al.* 2021).

278

279 ***Biosecurity and education***

280 ‘Biosecurity’ involves measures taken to reduce the risk of accidental introduction and spread
281 of invasive species. National biosecurity campaigns, such as ‘Check Clean Dry’ in the UK and
282 ‘Clean Boats Clean Waters’ in the USA, aim to raise awareness of non-native species and
283 biosecurity, and provide clear guidance to stakeholders to reduce the risk of the spread of these
284 species (GB NNSS 2022b). These campaigns focus on three simple steps - visual inspection,
285 cleaning, and drying - to remove and/or kill non-native species that are attached to vessels.
286 Specific practices, including the use of hot water and duration of drying, have been informed

287 by studies assessing mortality of freshwater non-native species (e.g., Shannon *et al.* 2018;
288 Bradbeer *et al.* 2020). In recent years, further specific biosecurity guidance has been developed
289 for high risk pathways, such as angling and boating, although the efficacy of such schemes can
290 depend on the availability of appropriate cleaning facilities (Sutcliffe *et al.* 2018). Engagement
291 by sporting national governing bodies, such as the Angling Trust and British Canoeing in the
292 UK, has enhanced both the appropriateness of guidance and the distribution of education
293 material to members.

294 Assessing water users' compliance with biosecurity guidance presents challenges (Golebie
295 *et al.* 2021). Since the campaign launch in 2011, awareness of 'Check Clean Dry' in the UK
296 has increased amongst water-users, as has the number of anglers and boaters reporting
297 compliance with biosecurity behaviours, although the risk of non-native species spread via
298 these pathways remains apparent (Smith *et al.* 2020). The identification and engagement with
299 all pathways are vital and there is growing recognition of the risk presented by, and biosecurity
300 requirements of, field-based operations in governmental, private, and educational sectors
301 (Sutcliffe *et al.* 2018). Whilst education is an important pillar of biosecurity interventions,
302 campaigns must enhance stakeholders' motivation, capacity, and opportunity to comply with
303 biosecurity guidance (McLeod *et al.* 2015).

304

305 **3.2 Preventing invasions of newly introduced species**

306 Early detection of newly introduced species is key for preventing their establishment (Vander
307 Zanden and Olden 2008); this requires methods to reliably detect species when they are at low
308 abundance levels (Britton *et al.* 2011c). Although this is often difficult with capture-based
309 methods, environmental DNA (eDNA) increasingly provides a rapid and low-cost alternative
310 (Larson *et al.* 2020), where 'first detection' capability can be targeted around high-risk
311 introduction areas (e.g., urban centres, ports). Previously time-consuming sample filtering and

312 contamination issues are being addressed with automated sampling equipment, with real-time
313 methodologies also available (Doi *et al.* 2020). Metabarcoding approaches with eDNA can
314 screen for multiple species simultaneously and could be used as a standard screening technique
315 for non-native species in freshwaters (King *et al.* 2022).

316 Other early detection methods include harnessing or interrogating citizen science platforms
317 across biomes or interrogating social media and internet sources, such as iEcology approaches
318 (Jarić *et al.* 2020a; Unger *et al.* 2021) and aquatic culturomics (Jarić *et al.* 2020b). Citizen
319 science is already contributing to formal records of alien species in marine ecosystems
320 (Kousteni *et al.* 2022). Harnessing the large numbers of naturalists/general public, a high risk
321 group that recreate on or around aquatic habitats, will greatly enhance detection capacity and
322 speed, with many platforms now collecting high resolution georeferenced images from
323 smartphones, with a series of experts quickly verifying images to species (Larson *et al.* 2020).

324 Preparation of rapid response plans for priority taxa can enhance the likelihood of
325 eradicating or controlling newly detected species or populations. Consideration of which taxa
326 to plan for could include the development of national ‘watch’ lists (Reaser, Frey and Meyers
327 2020a). Contingency plans for rapid response can include the most effective means for
328 delineating the extent of dispersal, focussed effective control methods, responsibilities,
329 resources, partners to be involved, and monitoring requirements, with identification of the
330 lines of authority and funding also being critical components (Beric and MacIsaac 2015;
331 Reaser *et al.* 2020b; Section 4.1). However, early detection can be hampered by incomplete
332 taxonomy and misidentifications (Ng *et al.* 2018; Palandačić, Witman and Spikmans 2022).

333 Eradication of many freshwater invaders is possible, but generally at small scales and is
334 costly, usually requiring lengthy management effort (Rytwinski *et al.* 2019). However,
335 successful eradications have occurred for crayfish (Peay *et al.* 2006; Kouba, Petrussek and
336 Kozák 2014; Duggan and Collier 2018), fish (Bardal 2019; Rytwinski *et al.* 2019), plants

337 (Simberloff 2021), molluscs, and other freshwater groups (Roda *et al.* 2016; Hammond and
338 Ferris 2019). Methods include mechanical removal (for fish and crayfish: nets, traps, harvest,
339 electrofishing; for plants: hand-pulling, cutting, dredging/drying), biocides or herbicides
340 (rotenone, antimycin (fish), synthetic or natural pyrethroid (crayfish)), selected herbicides
341 (plants), and biocontrol (diseases, predators/consumers (plants and fish)), and habitat
342 manipulation (lake/wetland drawdown, draining; flow management, physical habitat
343 alteration) (Hussner *et al.* 2017; Rytwinski *et al.* 2019; Sandodden 2019; Simberloff 2021).
344 Chemical treatments are probably the most effective for eradications of fish and crayfish
345 (Rytwinski *et al.* 2019; Sandodden 2019) but have non-target effects and, consequently,
346 significant policy and legislative hurdles.

347

348 **3.3 Eradicating and controlling dispersing populations of invaders**

349 The reason why early detection and rapid response measures are important to implement is that
350 once a non-native species invades a relatively large area, its eradication becomes highly
351 challenging and expensive. Where risk assessment has indicated a specific invader is of high
352 risk of impacting freshwater biodiversity, but surveys have indicated it has already achieved a
353 wide spatial distribution, then decisions on the most appropriate management actions must also
354 incorporate feasibility assessments and resourcing (Britton *et al.* 2011b). In situations where
355 resources are limited, they are likely to be applied more effectively against a newly introduced
356 or recently established species, rather than one that has already dispersed widely (Britton *et al.*
357 2011b). Indeed, the success of an eradication effort is dependent on a myriad of factors ranging
358 from the species' invasion biology and distribution, the recipient ecosystem (habitat,
359 connectivity etc) and the available control measures.

360 Where population eradications are assessed as the commensurate management action
361 against an invader then the eradication method must be selected. This method selection should

362 aim to consider all possible foreseen risks associated with the method, especially where the
363 method is not species selective, such as the applications of chemical treatments against invasive
364 crayfish and fishes (Simberloff 2009). Eradication has been an effective management tool in
365 removing terrestrial invaders from islands, including rodents, plants, and insects (Howald *et*
366 *al.* 2007; Simberloff 2009) - and river basins effectively represent 'biogeographic islands' that
367 can provide a closed management area (Leprieur *et al.* 2009; Saunders *et al.* 2010). Thus, using
368 river basins as management units for freshwater non-native species can provide discrete spatial
369 areas in which eradication and control programs can be implemented that considers both the
370 native biodiversity present (e.g., the extent of endemism) and extent of extant invasions.

371 The spatial extent of the invasion can mean that an eradication attempt is not feasible.
372 Alternatively, an eradication attempt might have been attempted but was unsuccessful, such as
373 attempts to prevent the establishment and invasion of zebra mussel in Lake Winnipeg through
374 potash application (Depew *et al.* 2021). In both cases, population control and containment
375 methods can then be considered, where the ultimate aim is to reduce invader impact (control)
376 and stop their further spread (containment) (Fig. 1; Table 1; Britton *et al.*, 2011a,b; Rytwinski
377 *et al.*, 2019). Indeed, the concept of functional eradication has recently been proposed by Green
378 and Grosholtz (2021), where they suggest that in situations where absolute eradication is not
379 feasible, suppressing invasive populations to a level where their ecological impacts are
380 minimised within high priority habitats is more appropriate. To reduce invader abundance to
381 levels where their impacts are reduced or eliminated, the influence of control methods on the
382 magnitude and direction of invader impacts must be understood. This can be complex, as
383 impact severity can also be influenced by the life-stages present and time since introduction
384 (Vilizzi, Tarkan and Copp 2015; Haubrock *et al.* 2022), plus a range of mechanistic context
385 dependencies (i.e. impacts contrast under different ecological and spatiotemporal conditions)
386 (Catford *et al.* 2022). Moreover, the relationship between invader abundance and impact is

387 often non-linear, where impact accelerates considerably once abundance thresholds are
388 exceeded (Jackson, Ruiz-Navarro and Britton 2015; Vilizzi, Tarkan and Copp 2015). In these
389 situations, control methods would need to reduce abundances below these thresholds to
390 minimise impact. Containment measures that restrict the invader to its current range include
391 screening and barrier construction that prevent dispersal; these are increasingly applied at local
392 or small scales to protect threatened taxa or other high-value assets (e.g., wetlands) (Dunham
393 *et al.* 2020; Jones *et al.* 2021). Eradication and control methods that have been used against a
394 range of invasive taxa in freshwaters are now discussed using a case study approach, where
395 emphasis is both on the effectiveness of the control measure(s) and the response of native
396 communities to resultant reductions in invader abundance.

397

398 **Case study 1: Eradicating non-native fishes in South Africa**

399 Within South Africa's Cape Floristic Region, non-native fishes such as smallmouth bass
400 *Micropterus dolomieu*, bluegill *Lepomis macrochirus*, sharptooth catfish *Clarias gariepinus*,
401 rainbow trout *Oncorhynchus mykiss* and banded tilapia *Tilapia sparrmanii* have impacted more
402 than half of the 42 fish species native to this area (Weyl *et al.* 2014; Ellender *et al.* 2017). The
403 Rondegat River reach, a system invaded by *M. dolomieu*, underwent South Africa's first non-
404 native fish eradication and river restoration in 2012 and 2013. Using rotenone, a fish killing
405 pesticide, the eradication project was conducted along a 4 km stretch of the river with the
406 ultimate goal of protecting and preserving local fish species. Within the invaded lower reaches,
407 native *Labeobarbus capensis* was detected at very low densities, while three other native fish
408 species (i.e., *Austroglanis gilli*, *Barbus calidus*, *Pseudobarbus phlegethon*) were not detected
409 but they were observed within the non-invaded zone (Weyl *et al.* 2014). Furthermore, non-
410 native fishes were not detected above a barrier waterfall that was 5 km upstream of the river's
411 confluence with a reservoir. Invertebrate assemblages were found to be sensitive to invasion

412 from *M. dolomieu*, with the non-native fish eliminating native insectivorous fish predators,
413 thereby reducing predation on invertebrate prey, with consequent food web effects (Lowe *et al.*
414 *al.* 2008). In the presence of *M. dolomieu*, Baetidae and Chironomidae abundances increased,
415 whereas Elmidae and Heptageniidae abundances were moderately reduced (Bellingan *et al.*
416 2015).

417 A total of 470 *M. dolomieu* and 139 *L. capensis* were removed from the treatment zone
418 during the rotenone operation, with no fish being detected within this zone after rotenone
419 treatment (Weyl *et al.* 2013). Native fishes rapidly re-colonised this reach where the non-native
420 *M. dolomieu* had been eradicated, with native fish densities reaching control site densities after
421 three years of non-native fish absence. The successful removal of non-native *M. dolomieu*
422 resulted in increased invertebrate and fish biodiversity, and this has encouraged more native
423 fish restoration projects in South Africa, such as the Cape Floristic Region's non-native fish
424 eradication programs within farm reservoirs (e.g., targeting *L. macrochirus*, *C. carpio* and *O.*
425 *mykiss*; see Dalu *et al.* 2020). These studies provide important background knowledge for
426 conservation authorities considering the removal of invasive non-native fishes from lotic water
427 systems using rotenone.

428

429 **Case study 2: Eradicating *Gyrodactylus salaris* from Norwegian salmon rivers**

430 The salmon fluke *Gyrodactylus salaris* is a freshwater Atlantic salmon *Salmo salar*
431 ectoparasite native to the Baltic region, and an invasive species in Norway that was first
432 detected in the 1970s. This parasite is one of the most severe threats against Norwegian Atlantic
433 salmon. It was unintentionally introduced with live fish transports and distributed in Norwegian
434 rivers through stocking. Norwegian Atlantic salmon populations are highly susceptible to the
435 parasite, with an average reduction of parr densities of 86 % (48-99 %) in infected rivers
436 (Johnsen and Jensen 1991).

437 The Norwegian government declared a goal to eradicate the parasite from Norwegian rivers.
438 As *G. salaris* is a viviparous, obligate parasite, restricted to freshwater, and survives for only
439 a few days without its host, then eradication of all hosts with the chemical rotenone has been
440 the main strategy for its eradication (Sandodden *et al.* 2018; Adolfsen, Bardal and Aune 2021).
441 The eradication campaign has been ongoing for more than 40 years, with the parasite now
442 eradicated from 39 of 51 Norwegian rivers where it has been detected, with four rivers still
443 under post-treatment surveillance awaiting eradication confirmation. In areas targeted for *G.*
444 *salaris* eradication, local strains of sea trout *Salmo trutta* and Atlantic salmon in the treated
445 anadromous zone undergo an extensive program for preservation and restocking to minimise
446 the long-term impacts of eradication (O'Reilly and Doyle 2007). Studies on benthic
447 invertebrates in rotenone treated rivers suggest short term impacts, with increasing effects at
448 higher water temperatures and rotenone concentrations, and longer exposure times. Although
449 most invertebrate taxa recolonize within a year (Kjærstad *et al.* 2021), recolonization can take
450 several years if the rotenone treatment comprised most of the basin (Mangum and Madrigal
451 1999).

452

453 **Case study 3: Controlling invasive macrophytes**

454 Invasive macrophyte infestations threaten freshwater ecosystems throughout the world. While
455 a number of key traits are exhibited by the majority of invasive macrophytes which increase
456 their invasiveness, their presence in a system is usually a symptom of anthropogenic spread
457 combined with increasing urbanisation, industry, and agriculture, which ultimately results in
458 eutrophication (Coetzee and Hill 2012). Both floating aquatic macrophytes, such as water
459 hyacinth *Pontederia crassipes*, giant salvinia *Salvinia molesta*, and water lettuce *Pistia*
460 *stratiotes*; and submerged invasive macrophytes such as *Elodea* spp., *Hydrilla verticillata*,

461 *Egeria densa*, and *Lagarosiphon major*, are among the most prolific invasive aquatic weeds
462 worldwide, with significant socioeconomic and ecosystem impacts (Cuthbert *et al.* 2021).

463 A number of management options are available for the control of invasive macrophytes,
464 with varied success. Floating macrophytes may be manually removed, chemically controlled,
465 and/or utilised, particularly by poor rural communities which are perceived to benefit from
466 using them (e.g., as fuel in South Africa) (Hill *et al.* 2020). Unfortunately, these methods are
467 rarely effective in the long term due to the effort and cost required to remove/control significant
468 amounts of high water content biomass, and may even promote their spread. Biological control,
469 using host specific natural consumers ('enemies'), has been particularly effective in controlling
470 floating macrophyte invasions (Coetzee *et al.* 2021), especially in tropical and subtropical parts
471 of the world. In southern Africa, the invasive red water fern *Azolla filiculoides* from South
472 America was successfully controlled through the release of the frond-feeding weevil
473 *Stenopelmus rufinasus*, imported from Florida (McConnachie, Hill and Byrne 2004). Their
474 release resulted in the local extinction of red water fern at 81 % of release sites over an average
475 of 7 months. In temperate areas, an integrated strategy using a variety of methods is often
476 required to obtain acceptable control (Shearer and Nelson 2002).

477 In contrast to floating macrophyte species (whose presence is known at the early stages of
478 invasion), submerged plant invasions often remain undetected for long periods of time,
479 (Hussner *et al.* 2017) although that is being overcome through eDNA methods (Doi *et al.*
480 2021). Similar management strategies (e.g., manual removal, chemical control, shading;
481 Schooler 2008) are also used for their control, again with varied success due to fragmentation
482 and regeneration following control operations. While biological control of floating aquatic
483 plants has many successful examples, the biological control of submerged aquatic macrophytes
484 has been variable with, for example, the successful use of grass carp *Ctenopharyngodon idella*
485 in control programs, such as in North America, being tempered with the invasion of these fish

486 following biosecurity lapses, other than where sterile fish have been used (Chilton and
487 Muoneke 1992).

488

489 **Case study 4: Managing populations of invasive bivalves**

490 Through the formation of dense and expansive populations, invasive freshwater bivalves such
491 as *Corbicula* clams and *Dreissena* mussels can substantially alter ecosystem functioning and
492 biodiversity. Notably, their presence has transformed nutrient cycling in the Laurentian Great
493 Lakes (Li *et al.* 2021) and underpinned the escalated growth of problematic macrophytes, such
494 as in Lough Erne, Ireland (Crane *et al.* 2020). Mass die-offs can lead to deoxygenation and
495 acute nutrient-based toxicity, while the persistence of empty shells may detrimentally alter
496 habitats and community composition (McDowell and Sousa 2019; Coughlan *et al.* 2022).
497 Further, living and dead biomass can foul anthropogenic infrastructure, such as the internal
498 surfaces of pipework and irrigation systems. Consequently, bivalve infestations along with
499 costly management interventions often result in negative socio-economic effects (Haubrock *et*
500 *al.* 2022).

501 The control of established populations of invasive bivalves can be exceedingly difficult,
502 particularly in open waterbodies (Sousa *et al.* 2014), which has been evidenced by numerous
503 attempts to control bivalves at locations across Europe and North America, such as the River
504 Barrow, Ireland (Sheehan *et al.* 2014) and Lake Tahoe in California, USA (Wittmann *et al.*
505 2012). Although no evidence for complete eradication of *Corbicula* from natural waterways
506 exists, techniques such as dredging, hand or suction harvesting, deoxygenation, thermal shock,
507 and the application of various molluscicides can reduce *Corbicula* abundances (Sheehan *et al.*
508 2014; Sousa *et al.* 2014; Coughlan *et al.* 2021). Contrastingly, many of these techniques have
509 been used to successfully eradicate *Dreissena* mussels (e.g., molluscicides, deoxygenation),
510 such as from Millbrook Quarry, Virginia, USA (Sousa *et al.* 2014), although approaches in

511 Lake Winnipeg were unsuccessful (Depew *et al.* 2021). In industrial settings, physical removal,
512 electrocution, desiccation, thermal, and chemical treatments have been successfully used to
513 control and eradicate bivalve infestations (Sousa *et al.* 2014). Nevertheless, the efficacy of
514 these approaches can vary and all management interventions, even those performed in
515 industrial settings, can have substantial negative consequences for native freshwater
516 biodiversity.

517

518 **3.4 Living with invasive species**

519 In freshwater systems with high levels of socio-economic and recreational activity, there tends
520 to be high introduction rates of non-native species; as some of these species develop highly
521 invasive populations, efforts to eradicate, contain and control these invasions are highly
522 challenging (Fig. 1; Table 1). In regions where non-native species are continuing to be
523 introduced and management efforts to control their invasions are increasingly expensive and/
524 or ineffective, then there is an option to also ‘live with invasive species’, where some
525 populations continue to be exploited without any further control, whereas other populations
526 might continue to be controlled and contained to prevent further damage to biodiversity and/
527 or ecosystem services (Fig. 1). The following case studies on the Laurentian Great Lakes,
528 USA/Canada and Lake Naivasha, Kenya, highlight two regions where aspects of living with
529 invasive species have been adopted.

530

531 **Case study 5: Laurentian Great Lakes, USA and Canada**

532 The Laurentian Great Lakes of North America are an interconnected system of five freshwater
533 lakes that all rank among the seventeen largest lakes in the world (Herdendorf 1982). A
534 multijurisdictional system, managed by two federal governments (USA, Canada), as well as
535 multiple state, provincial, and tribal agencies, the Laurentian Great Lakes have a long history

536 of living with invasive species (Campbell and Mandrak 2019). Records of unintentional
537 introductions date to as early as 1819 and deliberate introduction and stocking of non-
538 indigenous species can be found as early as 1870 (Emery 1985). Currently, the main pathways
539 for introduction include commercial shipping, live trade, recreational boating and angling, and
540 stocking (Mandrak and Cudmore 2010). Over 180 species that are non-native to the basin have
541 been successfully introduced and established within the past two centuries (Pagnucco *et al.*
542 2015), with a small number of species having radically altered the ecosystem community
543 structure. For example, invasion of sea lamprey *Petromyzon marinus*, along with overfishing
544 and habitat alteration, caused devastating impacts for the Great Lakes commercial fisheries -
545 particularly lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*, and
546 deepwater ciscos *Coregonus* spp. (Siefkes *et al.* 2013). Zebra and quagga mussels have also
547 drastically altered the lakes' aquatic food webs and water clarity (Mayfield *et al.* 2021).

548 The aggregate cost of aquatic invasive species to the basin is estimated to be well over
549 US\$100 million annually (Fantle-Lepczyk *et al.* 2022). Interventions used against these species
550 range from active support for maintaining populations of desirable species to multi-pronged
551 control and eradication attempts, and the most common response, no intervention at all. The
552 efforts to control sea lamprey are the most extensive in the basin, with a control program
553 involving lampricide applications in combination with physical and electromechanical barriers
554 (Siefkes *et al.* 2013).

555 The spatial scale of the Great Lakes, coupled with their highly modified state, means that
556 eradication of many invaders is not a viable option. At this stage, most management efforts are
557 vested towards prevention of new invasions, such as the extensive efforts to exclude bighead
558 carp *Hypthalmichthys nobilis* and silver carp *Hypthalmichthys molitrix* (Kokotovich and
559 Andow 2017) or reducing, but not eliminating, impacts from established species, such as the
560 goals of the sea lamprey control program (Siefkes *et al.* 2013). Acceptance of the persistence

561 of invasive species has induced the Great Lakes management agencies to optimize best suited
562 strategies for living with these species.

563

564 **Case-study 6: Lake Naivasha, Kenya**

565 Lake Naivasha is one of only two freshwater lakes wholly in Kenya and thus provides a wide
566 range of ecosystem provisioning services at national (e.g., agricultural/ horticultural jobs,
567 export income), regional (e.g., potable water, fisheries, power) and international (e.g.,
568 provision of non-seasonal flowers and vegetables) scales (Hickley *et al.* 2004; Hickley *et al.*
569 2015). Allied to these provisioning services is the introduction of numerous non-native species
570 in the last 100 years, including mammals, crayfish, plants and fish (Gherardi *et al.* 2011b).

571 The red swamp crayfish *Procambarus clarkii*, introduced intentionally in 1970 for fishery
572 enhancement, was key in the lake's transformation from a macrophyte dominated and clear
573 water state to an algal dominated and turbid state (Gherardi *et al.* 2011b). Despite this shift in
574 the lake's stable state, the artisanal fishery remained dominated by two tilapia species
575 (introduced in the 1950s) up to the early 2000s, when a combination of further lake degradation
576 (e.g., continued nutrient enrichment) and high exploitation resulted in their catches declining
577 until the stocks were not viable for fishing in 2009/10 (Oyugi *et al.* 2011). However, the
578 accidental introduction of non-native *C. carpio* into the lake in the late 1990s, and their
579 subsequent establishment, has since provided an alternative target species that is also capable
580 of tolerating the increasingly eutrophic and degraded lake conditions (Hickley *et al.* 2015).

581 Although *C. carpio* catches supported the fishery catches throughout the last 20 years, local
582 fishers and consumers continued to prefer tilapia and so the fishery management of the lake
583 decided to release the non-indigenous Nile tilapia *Oreochromis niloticus* in 2011, a globally
584 invasive species that can also tolerate relatively degraded conditions, with *Clarias gariepinus*
585 also escaping into the lake from on-shore aquaculture systems (Hickley *et al.* 2015). Both

586 species established and now feature in fish catches (Waithaka *et al.* 2020; Keyombe, Waithaka
587 and Obegi 2015). Thus, to maintain and enhance food security in the region, fishery managers
588 have manipulated the fish community of the lake using non-native fishes, with these species
589 providing abundant stocks for exploitation, despite the shift in lake stable state and on-going
590 nutrient enrichment. Active management of these fishes primarily relates to the enforcement
591 of fishery regulations that determine the extent of fishing pressure and monitors catch rates by
592 species. Legislation is in place that means new introductions can be completed after risk
593 assessment, although issues of food security and the potential for deriving socio-economic
594 benefits from new species mean that these introductions of ecologically damaging species
595 might still occur (Hickley *et al.* 2015).

596

Table 1. Summary of the three sequential stages, and their actions and details, that can be brought together within strategies to bend the curve of freshwater biodiversity loss from the harmful effects of freshwater non-native species.

Stage	Action	Detail
1. Introduction prevention	Legislation and regulation	Only permitted/ approved non-native species can be imported/ introduced/ used in closed aquaculture, and following full risk assessment
	Horizon scanning	Identify high-risk species most probable to be introduced in near future
	Pathway surveillance	Implement surveillance of introduction pathways (e.g., for species from horizon scanning)
	Import inspections/ quarantine	Qualified personnel inspect imports for non-native species presence/ use quarantine to provide time for detection
	Enforcement of legislation/ species' lists	Enforce legislation via regulatory frameworks, including lists of permitted/prohibited species (i.e., risk-based)
	Biosecurity approaches	Provide infrastructure and mechanisms for freshwater users to decontaminate equipment of possible non-native species
2. Preventing an invasion following an introduction	Early detection of new introduction	Methods needed to detect newly introduced species prior to establishment, especially in high-risk areas (e.g., near ports, urban centres etc.), including predictive tools.
	Rapid response decision	Following detection, risk-based decisions needed on the appropriate response to protect biodiversity
	Implementation of the rapid response	Where eradication is the decision, rapid implementation is needed to remove introduced individuals before establishment

3. Managing extant invaders	Risk-based management decisions	Where the invasion is underway, risk-based decisions are needed on how to protect/ restore biodiversity from harm
	Control invader abundance	Where local biodiversity impacts are a function of invader abundance, removals can reduce population sizes, including to zero by eradication and suppression to levels where ecological impacts are minimised (‘functional eradication’). Alternative control methods seek to reduce invader abundance through impacting recruitment success (e.g. sterile male release techniques).
	Contain invader to current range	Management actions are implemented that prevent the further dispersal of the invader through connected waters and through anthropogenic means
	Accept invader presence (including monitoring their populations and increasing resilience to impact of native communities)	Where the invader has wide spatial distribution, low risk to biodiversity and/ or control methods are ineffective, an active decision to accept invader presence/ do-nothing is acceptable. Can be coupled with management of physical environment to enhance populations of native species, including measures to increase recruitment and competitive abilities, as well as continued monitoring of the effects of invasive populations on biodiversity, ecosystem functioning and services, with instigation of management and conservation actions should unacceptable impacts start to be detected.
Applicable to all stages	Risk assessment	Process to assess risk posed by non-native species in the environment (assessing probabilities of entry/ establishment/ dispersal/ impact)
	Biosecurity of sites	Sites containing non-native species (aquaculture, fisheries, ornamental) should be bio-secure to minimise colonisation pressure

Education programs

Programs to educate policy makers, practitioners, stakeholders and the general public are needed for all stages and actions. Could be completed with social assessments to inform reasons for non-compliance with regulations and/or management programs.

598 **4. Implementation**

599 **4.1 Implementation strategies and contingency plans**

600 The approaches and measures for managing freshwater non-native species in Table 1 can be
601 incorporated into species-specific strategies through the step-wise process outlined in Figure
602 1. However, when management is dealing with multiple non-native species, where concomitant
603 actions range from introduction prevention to minimising invasives' impacts, these processes
604 can be integrated into wider strategies. Generic contingency plans can outline the actions
605 needed on the first detection of a non-native species (Raymond *et al.* 2011), such as that
606 developed in England for actioning when a disease not native to the European Union was
607 detected, which comprised of a framework response plan to assist and direct the Government
608 response and an operation manual to manage the 'on the ground' response (Oidtmann *et al.*
609 2011).

610 For very high-risk species that have yet to be introduced, species-specific contingency plans
611 can be formulated that are implemented on its first detection in that region (Raymond *et al.*
612 2011). For example, for the countries of the UK, a specific contingency plan has been
613 developed for *G. salaris* (Oidtmann *et al.* 2011), given the high risk it poses to wild and captive
614 populations of salmonid fishes (Case Study 2, Section 3). The contingency plan for Scotland
615 outlines the legislation that permits the control of the parasite, along with the management
616 details, including the roles and responsibilities of government departments and agencies, a risk
617 assessment, details on decision making for containment or eradication, the eradication methods
618 and their application, gene banking processes, and resources (Scottish Government 2011). This
619 ensures that decisions on how to manage the species are made in advance, which can be
620 important given they involve the resolution of ecological, socio-economic, and ethical
621 arguments among conflicting groups (Stokes *et al.* 2006; Finnoff *et al.* 2007). Similar
622 contingency planning exists for other harmful invasive species, such as the Invasive Mussel

623 Collaborative, which comprises 36 different federal, state, provincial, and tribal agencies, plus
624 non-government groups, research institutions, private industries etc., who work together to
625 address the risk of, and response to, zebra and quagga mussel invasions in the US
626 (<https://invasivemusselcollaborative.net>).

627

628 **4.2 Implementation challenges and impediments to managing non-native freshwater** 629 **species**

630 Although some of the challenges in managing non-native species have been overcome (e.g.,
631 substantial developments in invasion risk assessments; Section 3), many still remain. For
632 example, in some jurisdictions, there is no legislation for managing non-native species in
633 freshwaters and/ or there is legislation that promotes their use in aquaculture. In many
634 freshwater biodiversity-rich nations such as Brazil and India, legislation permits the use of non-
635 native fishes within freshwater aquaculture (e.g., Brito *et al.* 2018; Singh 2021), with these
636 species then escaping into the wild during biosecurity lapses (Casimiro *et al.* 2018) and/ or
637 extreme climatic events (Raj *et al.* 2021). Even where national legislation does exist to prevent
638 introductions, the introduction pathway of many freshwater non-native species involves global
639 trade routes and importing species through busy traffic areas (e.g., ports, airports). The
640 opportunities for detecting contaminants of legal animal movements or the illegal import of
641 species is limited (Chapman *et al.* 2017). Nevertheless, the success of ballast-water screening
642 at reducing the numbers of introduced species into the North American Great Lakes (Ricciardi
643 and MacIsaac 2022) emphasises that where pathways are targeted with effective and enforced
644 legislation, strong outcomes for the protection of freshwater biodiversity are possible.

645 The growth of trade through routes that are largely unregulated (e.g., the internet) has also
646 enabled non-native species to be traded in a manner that is difficult for authorities to track
647 (Olden, Whattam and Wood 2021). The potential for unregulated internet trade to provide an

648 introduction pathway for fishes was revealed in Brazil, where a six-month monitoring period
649 of social media groups recorded over 1100 posts advertising the sale of over 5000 specimens
650 of over 600 species, of which 66 % were non-native and 25 % were forbidden by national
651 legislation to be traded (Hirsch *et al.* 2021). There was also a trend for more expensive prices
652 to be associated with species that were non-native, prohibited, and of larger body size (Hirsch
653 *et al.* 2021). Similarly, well-intended religious practices (e.g., Tsethar in Buddhism) have
654 resulted in the release of significant numbers of invasive species, including African catfishes
655 and non-native turtles (Everard *et al.* 2019). The complexities involved in the regulation and
656 enforcement of religious and cultural practices associated with live release means that
657 community-supported and voluntary legislation need to be developed to ensure rituals do not
658 result in environmentally harmful outcomes (Everard *et al.* 2019).

659 These issues of unregulated trade are compounded by a general lack of investment in
660 introduction prevention schemes in many world regions, despite the ability of these schemes
661 to provide substantial long-term savings (Ahmed *et al.* 2022). Counter-intuitively, preventative
662 management is sometimes viewed as riskier than control, as its effectiveness (or lack thereof)
663 at preventing invasions cannot be easily predicted (Finnoff *et al.* 2007). Where budgets are
664 limited but there are multiple conservation demands, expenditure on non-native species is often
665 delayed until impacts have been demonstrated (Ahmed *et al.* 2022). Indeed, Finnoff *et al.*
666 (2007) suggested that such paradoxical decisions stem from the association between
667 preferences for risk-bearing and the technology of risk reduction, with risk-averse managers
668 more likely to use invasion control than introduction prevention, as control can appear less
669 risky (i.e., invaders are seen being removed). Effective management of non-native species also
670 requires considerable political acumen and commitment to liaise with multiple agencies and
671 stakeholder groups to agree on actions. Risk-aversion, coupled with lacking commitment to

672 coordinating and implementing preventative actions, might thus result in river basins with high
673 invasion rates.

674 A major implementation challenge to protect and restore fresh waters from non-native
675 species is that these species might represent only one of numerous, potentially interacting,
676 stressors in the environment (Craig *et al.* 2017). Species rich communities are generally
677 considered as providing substantial resistance to the establishment and invasion of introduced
678 species (Alofs and Jackson 2014). However, biotic resistance tends to be relatively weak in
679 fresh waters that have been disturbed through other anthropogenic activities, such as through
680 increased resource availability (e.g., through nutrient enrichment) and modified physical
681 structure of the ecosystem (e.g., river impoundment) (Catford, Jansson and Nilsson 2009).
682 Riverine impoundment generally leads to species-shifts from lotic to lentic and specialist to
683 generalist (Noble *et al.* 2007), which often favour non-native over native species, and
684 potentially elevates propagule pressure through increased recreational use (Johnson, Olden and
685 Vander Zanden 2008). For example, the creation of multiple reservoirs by hydroelectric dams
686 in Southern Brazil has provided opportunities to create sport fisheries based on non-native
687 species such as peacock basses (*Cichla* spp.) (Espínola, Minte-Vera and Júlio 2010), where
688 high predation rates from their invasive populations further decrease native fish species
689 richness and abundance (Britton and Orsi 2012; Pelicice and Agostinho 2009). Indeed,
690 evidence from the USA revealed the likelihood of finding non-native species in impounded
691 rivers was up to 300 times higher than in natural lakes, with reservoirs frequently supporting
692 multiple invaders (Johnson, Olden and Vander Zanden 2008). Correspondingly, non-native
693 species management strategies should be implemented in tandem with other strategies within
694 the wider freshwater biodiversity restoration toolbox to ensure holistic approaches are
695 implemented.

696 Although methods to remove non-native species from fresh waters exist, their application
697 might not always be considered feasible (e.g., the method is ineffective over large spatial areas)
698 or ethical (e.g., due to high mortality rates of non-target species) (Britton *et al.* 2011b). For
699 example, although toxin application is effective at killing target species, it is also usually non-
700 species specific, often resulting in high mortality rates in other species (Britton *et al.*, 2011a),
701 and therefore impractical in river systems harbouring high numbers of both endemic and non-
702 native species. High losses to non-target species have been seen in invertebrate communities
703 in ponds and lakes treated with the piscicide rotenone, although these populations generally
704 recover rapidly (e.g., within six months; Britton and Brazier 2006; Dalu *et al.* 2020). Moreover,
705 even where eradication attempts are made, failures do occur, such as the failed attempt to
706 eradicate Northern pike *Esox lucius* from Lake Davis, USA (Lee 2001). However, these
707 unsuccessful management operations can be used to inform future attempts (Rytwinski *et al.*
708 2019).

709 Novel control measures based on exploiting innate behaviours or weaknesses ('achilles
710 heel') of invaders are increasingly gaining attention. For example, the exploitation of jumping
711 and pushing traits are being utilised in trap, screen, and weir designs (Holthe *et al.* 2005; Stuart
712 and Conallin 2018; Tempero *et al.* 2019) and the overwintering or spawning
713 aggregations/locations of invaders are now used to focus removal actions, such as *C. carpio* in
714 Australia (Taylor *et al.* 2012; Sorensen and Bajer 2020). Moreover, genetic techniques for
715 invasive fish and crayfish control continue to be explored (e.g., daughterless *C. carpio* in
716 Australia; Thresher *et al.* 2014); sterile male release (e.g., non-native crayfish in England;
717 Green *et al.* 2022), as are gene drives (Bajer *et al.* 2019) but have not yet been implemented on
718 a large scale (Kopf *et al.* 2017; Simberloff 2021). Moreover, the use of 'ark' sites, where
719 imperilled native species are protected from extinction through their translocation from donor
720 sites (e.g., threatened with invasion by high impacting species) to refuge sites (e.g., of low

721 invasion risk), can provide extra time for more effective control methods to be developed and
722 then deployed on the high-impacting invader, as seen with imperilled populations of White-
723 clawed crayfish *Austropotamobius pallipes* in the British Isles that are threatened by invasive
724 North American crayfishes (Nightingale *et al.* 2017).

725 Even where risk assessment processes have identified a species as being of high risk to
726 freshwater biodiversity, it does not necessarily follow that management actions commensurate
727 with that risk level will follow. For example, analysis on the global application of the risk
728 assessment tool ‘Freshwater Fish Invasiveness Screening Kit’ (FISK) revealed *C. carpio* was
729 the most widely screened species, with it assessed as having a high risk of invasiveness in all
730 regions (Vilizzi *et al.* 2019), with the species already being recognised as high impacting on
731 most aspects of freshwater biodiversity and functioning (Vilizzi, Tarkan and Copp 2015).
732 However, in countries such as England, the socio-economic value of the species in angling and
733 aquaculture, coupled with its long introduction history and wide spatial distribution, means that
734 it is managed as a naturalised species and so falls outside of legislation controlling non-native
735 species (Hickley and Chare 2004). Similarly, the species has also been translocated widely
736 across Turkey and now supports productive fisheries, despite all risk screenings indicating the
737 species will become highly invasive in the wild (Vilizzi *et al.* 2012).

738

739 **5. Conclusions**

740 Bending the curve for freshwater biodiversity by protecting and restoring species from the
741 harmful effects of non-native species remains highly challenging. Introduction rates of species
742 continue to accelerate globally and although not all of these species will become invasive, those
743 that establish and disperse have the potential to cause deleterious impacts on freshwater
744 biodiversity. Notwithstanding, there have been considerable developments in the last decade
745 on horizon scanning and risk assessment processes that provide the basis for strong

746 introduction and invasion preventative actions, especially when coupled with effective
747 legislation and regulation that enables surveillance of introduction pathways, and
748 implementation of rapid detection methods and reaction protocols. Also, a range of removal
749 methods are available to control non-native species in both lentic and lotic systems and, in
750 some cases, eradicate high-impacting populations. Although these methods tend to be of low
751 technology (e.g., toxins), new methods are being developed that potentially provide more
752 species-specific approaches, with ark sites providing potential protection for highly imperilled
753 native species. However, implementation challenges and impediments to management success
754 remain, including the application of precautionary principles to prevent introductions often
755 being viewed as a risky option and non-native species often acting as an additional stressor in
756 already highly stressed and modified ecosystems. Overcoming these challenges and
757 impediments is, however, crucial if freshwater biodiversity is to be protected and restored from
758 the damaging impacts of non-native species invasions within the Emergency Recovery Plan
759 and so contribute to bending the curve of freshwater biodiversity loss.

760

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766

767 **6. References**

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1282

49:1163–1173.

1283 **Box 1. Definition of terms used in the paper (note these are defined in freshwater terms)**

1284

Term	Definition
Non-native / non-indigenous / alien	A species with a natal origin outside of, or foreign to, the waterbody/ river basin under discussion.
Introduction	The deliberate or accidental release of a species into a waterbody / river basin where it is not found naturally.
Introduced species	A species that has been released into a waterbody / river basin for the first time.
Pathway	A route / mechanism providing the entry of a non-native species into a waterbody / river basin (and its subsequent introduction).
Establishment	The production of a sustainable population from the introduced individuals.
Dispersal	The spread of individuals from the invasion front into areas where the species has not been found previously.
Invasive species / Invasive alien species / Invasive non-native species / Invasive non-indigenous species / Invader	A species with a natal origin outside of, or foreign to, the waterbody/ river basin under discussion that has been introduced, established, and dispersed, and is impacting native biodiversity.
Eradication	The complete removal of all life-stages of the invader from a waterbody / river basin through management actions.
Control	The intentional reduction in invader population abundance (as number and / or biomass) to levels which reduce its impact on native biodiversity.

Containment

The intentional restriction of the invader to its current distribution to prevent its spread.

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