

1 **A Global Perspective on the Influence of the COVID-19 Pandemic on Freshwater Fish**
2 **Biodiversity**

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5 Biological Conservation – Special Issue on COVID-19
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59

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62 champion of freshwater fish biodiversity and conservation. He will be remembered for
63 his passion for field work, his gift as a mentor, his commitment to capacity building in
64 Africa, and his larger-than-life presence. Tight lines Olaf.

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68

69 **Abstract**

70

71 The COVID-19 global pandemic and resulting effects on the economy and society (e.g.,
72 sheltering-in-place, alterations in transportation, changes in consumer behaviour, loss of
73 employment) have yielded some benefits and risks to biodiversity. Here, we considered the ways
74 the COVID-19 pandemic has influenced (or may influence) freshwater fish biodiversity (e.g.,
75 richness, abundance). In many cases, we could only consider potential impacts using
76 documented examples (often from the media) of likely changes, because anecdotal observations
77 are still emerging and data-driven studies are yet to be completed or even undertaken. We
78 evaluated the potential for the pandemic to either mitigate or amplify widely acknowledged, pre-
79 existing threats to freshwater fish biodiversity (i.e., invasive species, pollution, fragmentation,
80 flow alteration, habitat loss and alteration, climate change, exploitation). Indeed, we identified
81 examples spanning the extremes of positive and negative outcomes for almost all known threats.
82 We also considered the pandemic's impact on freshwater fisheries demand, assessment, research,
83 compliance monitoring, and management interventions (e.g., restoration), with disruptions being
84 experienced in all domains. Importantly, we provide a forward-looking synthesis that considers
85 the potential mechanisms and pathways by which the consequences of the pandemic may
86 positively and negatively impact freshwater fishes over the longer term. We conclude with a
87 candid assessment of the current management and policy responses and the extent to which they
88 ensure freshwater fish populations and biodiversity are conserved for human and aquatic
89 ecosystem benefits in perpetuity.

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91

92 **Introduction**

93

94 Freshwater biodiversity is widely acknowledged to be in crisis (Harrison et al. 2019), with
95 biodiversity loss in freshwater systems exceeding both terrestrial and marine environments
96 (Ricciardi and Rasmussen 1999; Tickner et al. 2020). Freshwater fishes are the most threatened
97 group of vertebrates, after amphibians (Darwall & Freyhof 2016). Moreover, the global
98 extinction rate of fishes (including marine fish) is believed to exceed that of other vertebrates
99 (Dais et al. 2017). More than 60% of freshwater habitat is classified as moderately or highly
100 threatened by human activity (Vörösmarty et al. 2010) and few free-flowing rivers remain (Grill
101 et al. 2019). The threats to freshwater fishes and their aquatic ecosystems are many and varied,
102 spanning long-standing threats (Dudgeon et al. 2006) as well as emerging ones (e.g.
103 nanoparticles; Reid et al. 2019). Recent efforts have recognized the severity of the conservation
104 crisis in freshwater environments and the need to adopt an emergency action plan to recover
105 biodiversity (Tickner et al. 2020).

106

107 The Sars-Cov-2 virus causing COVID-19 and the subsequent global pandemic (hereafter,
108 ‘COVID-19’) have rapidly and dramatically altered patterns of human behaviour, society, and
109 economies. It has been suggested the pandemic is serving as an unprecedented global human
110 confinement experiment as governments around the world institute ‘lockdowns’ (Bates et al.
111 2020). During lockdown periods, large portions of society have been isolated, reducing the
112 regional and global movements of people (Askitas et al. 2020), and altering the trade and
113 distribution of goods (Baldwin and Tomiura 2020). Moreover, the economic status of many
114 individuals and communities has changed rapidly with COVID-19, driving potential changes in
115 human interactions with freshwater fishes and ecosystems (e.g., illegal harvest to ensure food
116 security).

117

118 Early thinking about the effects of COVID-19 has suggested a potential benefit to biodiversity
119 (Pearson et al. 2020) and the environment (Zambrano-Monserrate et al. 2020; Mandal 2020), yet
120 others have suggested both benefits and disbenefits depending on context (Corlett et al. 2020).
121 The first examples arising from the freshwater realm, however, have indicated mixed outcomes
122 (Pinder et al. 2020; Stokes et al. 2020). For example, the rivers of India are cleaner because of
123 dramatic reductions in industrial pollution, but imperiled freshwater fish species are increasingly
124 exploited by food insecure peoples in response to the disruption of their normal livelihoods and
125 economic well being (Pinder et al. 2020). In a global snapshot of expert-perceived impacts to
126 inland fisheries, Stokes et al. (2020) found responses to be spatially variable with more negative
127 impacts associated with less developed areas and high provisioning fisheries. Given the
128 connections between freshwater fishes and individuals, people, and the broader society
129 (Welcomme et al. 2010; Cooke et al. 2016), regional, national, and global events are driving
130 changes in the ways humans interact with freshwater fishes and freshwater ecosystems.

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132 Although formal analyses will yield empirical tests of the impact of COVID-19 on biodiversity
133 (Bates et al. 2020), there is also a need to engage in forward-looking syntheses that consider the
134 potential mechanisms and pathways by which both negative and positive effects may be
135 revealed. To that end, we assembled a team of global experts in freshwater fish biodiversity and
136 conservation (the authors) with the objective of considering ways COVID-19 has influenced (or
137 may influence) wild freshwater fish populations (e.g., health, abundance, diversity). We

138 approached this from the perspective that there are many existing and widely acknowledged
139 threats to freshwater fish populations (e.g., pollution, dams, climate change, overexploitation,
140 invasive species; Reid et al. 2019) and the recognition that COVID-19 has the potential to either
141 mitigate or amplify their effects (Figure 1). Thus, our goal was to elucidate the interaction of the
142 societal disruption caused by the COVID-19 pandemic and the background of pre-existing
143 threats to freshwater ecosystems in order to understand the potential outcomes for global
144 freshwater fish diversity. We also consider how COVID-19 has influenced freshwater fish
145 assessments, research, compliance monitoring, and management interventions. We conclude
146 with a candid assessment of the current management and policy responses and the extent to
147 which they have contributed to ensuring that fish populations and biodiversity are conserved and
148 continue to benefit future generations. Where possible, we use documented examples (often from
149 the media) but recognize that often we are only able to consider potential impacts given that
150 anecdotal observations are still emerging and data-driven studies are yet to be completed or even
151 undertaken.

152

153 **COVID-19's modulating effect on existing threats**

154

155 *Invasive species*

156

157 Invasive species are considered one of the most significant drivers of freshwater biodiversity
158 decline (Reid et al. 2018 and references therein). COVID-19 has both changed the way that
159 invasive species spread between regions and the way humans are able to control this spread.
160 Human-related pathways of species introductions have been altered due to COVID-19. Dramatic
161 reductions in both local and international travel will likely lead to subsequent reductions in
162 invasive species transport associated with pathways such as ballast water exchange, air
163 transportation, the movement of fresh foods, and recreational activities, among others (Hulme
164 2009; Early et al. 2016). For example, significant decreases in trade demand have led to
165 reductions in shipping traffic among all global ports. Research prior to COVID-19 forecasted
166 dramatic increases in species invasions associated with mid- 21st Century shipping traffic (e.g.,
167 ballast water releases; Sardain et al. 2019), but we expect the economic recovery to COVID-19
168 may slow the pace of invasions, at least in the short term. As economies rebuild in the coming
169 years, it seems likely that human-related pathways of species introductions may actually
170 accelerate the pace of invasions. Moreover, there remain uncertainties regarding how COVID-19
171 and other geopolitical issues (e.g., trade wars) may influence trade routes in the coming years
172 and what that may mean for risk of invasive species introductions.

173

174 On the other hand, COVID-19 has led to significant budget reductions for controlling the spread
175 of invasive fishes from intentional introductions, aquaculture releases, and unintentional
176 transport. For example, a US\$8 million project aimed at stopping the spread of invasive Asian
177 carp in Michigan, USA, was vetoed in order to support the state's response to COVID-19 instead
178 (Boomgaard 2020). Furthermore, reduced monitoring and regulatory measures (e.g., boat
179 inspections; see example from Utah, <https://www.sltrib.com/news/environment/2020/04/25/utah-fears-lack-boat/>) for invasive species will likely compromise the success of early detection and
180 rapid response of new introductions, leading to greater spread and costs of control in the future.
181 While the public plays an increasing role in the early detection and control of invasive species
182 (e.g., detected range expansion of lionfish (*Pterois* spp – a marine fish) in the northern Gulf of
183

184 Mexico, Scyphers et al. 2015; and increased abundance of invasive marine fishes in Turkey,
185 Bodilis et al. 2014), community science programs have largely ceased in response to COVID-19
186 because of lockdown restrictions, reducing the ability to notice new or track existing invasive
187 species. Similarly, the public remains central to many invasive species control efforts (Crall et al.
188 2012). For example, sustained public participation is critical to removing invasive lionfish from
189 reef ecosystems (Anderson et al. 2017), but removal events have been cancelled as a result of
190 social distancing. Although those are marine examples, we expect similar reductions in
191 community science in freshwater systems. We also expect that trickle-down effects of reduced
192 community science programs will ultimately decrease science literacy and dampen attitudes
193 towards invasive species in the long-term (Roy et al. 2018). It should be noted however, that
194 COVID-19 may serve as an important example (for outreach and education) of the devastating
195 effects invasive species can have on society. There may also be opportunity for ecologists to
196 learn from the modeling used for COVID-19 to better model invasive species dynamics
197 (Bertelsmeier and Ollier 2020; Nuñez et al. 2020).

198

199 *Pollution*

200

201 The COVID-19 pandemic has altered the way that pollutants (i.e., nutrients, pesticides, toxins
202 and contaminants, microplastics, light and noise, and salinity) are influencing freshwater
203 ecosystems. (Reid et al., 2019; Chen et al., 2020). During the pandemic, global lockdowns and
204 temporary closures of many industries have potentially reduced discharge of nutrients, heavy
205 metals, and other chemicals to water bodies and reduced emissions to the atmosphere (Chow
206 2020). Reduced nitrogen dioxide concentrations observed over Eastern China, Europe, the
207 Northeastern United States, and India have been used as indicators of temporary recovery of
208 urban surface water quality that runs off into waterways (Hallema et al. 2020). In Vembanad
209 Lake, Southern India, an average 15.9% decrease of suspended particulate matter concentration
210 during the lockdown period suggests reduced anthropogenic impacts (Yunus et al., 2020). In
211 China, the percentage of nationwide surface water quality transects at the “good” level increased
212 6.0% between January to May of 2020 (CMEE, 2020). Noise from shipping traffic on aquatic
213 biota may also be reduced during the pandemic (Zajicek and Wolter, 2019). These reductions in
214 water pollution will have positive effects on aquatic organisms and their habitats.

215

216 However, the pandemic has also increased pollution impacts on freshwater fishes. In the UK,
217 disruption to food supply chains has led to dumping wasted food and drink, such as milk, which
218 has entered waterbodies, potentially depleting oxygen levels through eutrophication (Ends report,
219 2020; Salmon and Trout Conservation, 2020). Elsewhere, altered sewage pollution patterns or
220 collapse of the sewage systems could be a major detriment to aquatic biodiversity (Herbig, 2019;
221 Tortajada & Biswas, 2020). Increased use of disinfectants (e.g., hand sanitizers, cleaning
222 products) has likely increased their presence in freshwater systems through runoff and
223 wastewater discharge (Zhang et al., 2020). In addition, heightened concern for hygiene and
224 disease spread has increased pollution associated with packaging and personal protection
225 equipment (Roberts et al. 2020, van Reenan 2020; Aragaw et al. 2020). Moreover, as single-use
226 plastics are a key source of microplastics in fresh waters (Li et al. 2020), such actions will likely
227 contribute to more plastic pollution entering waterways. Disruption to the monitoring, control,
228 and surveillance of freshwater ecosystems could further increase pollution risks from certain
229 unregulated human activities or fail to detect accidental pollution events altogether.

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Fragmentation

Fragmentation of freshwater systems is a major threat to freshwater biodiversity, particularly migratory fishes (Dudgeon et al. 2006; Nilsson et al. 2005). The construction of dams is currently the greatest source of increased fragmentation in freshwater ecosystems as free-flowing rivers are obstructed (Zarfl et al. 2015). The slowdown of industrial development and construction activities during the pandemic has also slowed hydropower projects, particularly in Asia (Bangladesh, China, Nepal, Indonesia, India and Myanmar; Cox 2020), and temporarily suspended further fragmentation of freshwater ecosystems. How long this will persist is unknown, given global changes in energy demand due to COVID-19.

However, as regions prioritise economic recovery post-pandemic, there is evidence that environmental legislation and assessment processes are being side-stepped (Diele-Vegas and Pereira 2020; Canadian Environmental Law Association 2020). It is possible proponents of development projects will attempt to take advantage of a swamped news-cycle, decreased environmental assessment capacity, and a need for economic growth following the lockdown to push forward controversial projects. For example, the Government of India is considering a controversial 3097 MW dam (Dibang Valley Hydropower project) in the Himalayan Biodiversity Hotspot (Chandrashekhar 2020). While many regions of the world are building dams, other regions are removing them (Ding et al. 2019) or constructing fishways to provide passage over such barriers. Funding for such restoration projects may be restricted or diverted during the economic recession to benefit human health and employment security (discussed in Corlett et al. 2020), but to the detriment of river fishes.

Flow alteration (hydropower and water extraction)

Flow regimes in rivers have been modified to accommodate societal needs, leading to changes in hydrogeomorphological processes and ecosystem functioning (Anderson et al. 2019). Agricultural water use accounts for about 70% of water withdrawals from aquatic ecosystems, and associated irrigation and drainage infrastructure also contributes greatly to fragmentation of aquatic habitats (Wisser et al. 2008; Vörösmarty et al. 2010). Changes in irrigation demand and management has major impacts on fish biodiversity and fisheries (Nguyen Khoa et al. 2005; Lorenzen et al. 2007). Along with other sectors, agricultural water demand initially decreased during the COVID-19 crisis, due to impacts on supply and trade systems and the reduced availability of agricultural labor (with irrigated agriculture being more dependent on all of these factors than traditional rainfed farming systems). However, a need to re-invigorate irrigated agriculture quickly to avert food shortages and stabilize the world food system is widely recognized. While the net effect of these shifts in demand and technology are difficult to predict, such changes will affect aquatic ecosystems in multiple ways, including the disconnection of irrigated areas and altered flooding patterns.

Water use and energy demand during the pandemic has varied across spatial scales based on pre-existing usage. In the United States, estimated residential water-demand increased by 21% in April compared to February when the lockdown first began (as per smart-water monitoring company 'Phyn'; Mendoza 2020). In Turkey, consumption of potable water increased by 60%,

276 compounding the impact of regional drought and concerns for water availability (Daily Sabah
277 2020). Conversely, non-residential uses of water have decreased. While it is unclear how net
278 water demand has been affected, it appears water bodies near large metropolitan areas would
279 have experienced reductions in water extraction, while water bodies sourcing primarily
280 residential areas have experienced moderate increases in water extraction (Cooley 2020).
281 Disruption to global food production and trade has raised food security fears, and countries are
282 considering increasing their domestic production, including irrigated agriculture (Cambodia New
283 Vision 2020). Increased water use will likely compound existing changes in flow regimes, with
284 associated impacts on fishes and aquatic biota, such as loss of productivity, increased risk of
285 poor water quality and fish kills, and reduced cues for spawning, recruitment and movements.
286 Likewise, with the onset of lockdown measures during COVID-19, global energy demand
287 dropped precipitously, with less industrial production (International Energy Agency 2020). The
288 International Energy Agency estimated overall energy demand contracted by 6%, with a
289 concurrent reduction in the use of fossil fuels and a shift towards renewable energy sources,
290 inclusive of hydropower. As a consequence, hydropower production appears to have changed
291 little during the crisis and thus regulated flow patterns have been sustained. Consequently, little
292 relief from the impact of hydropower operations on freshwater fish populations and biodiversity
293 is expected.

294

295 *Habitat loss and alteration*

296

297 Hydropower dams, aggregate mining, pollution, and land-use change have all been implicated in
298 the extensive degradation and loss of freshwater habitats (Dudgeon 2019). Depending on
299 geographical region, key anthropogenic stressors of freshwater habitats have both declined as
300 well as increased under COVID-19. In India, the combined effects of reductions in pollution and
301 commercial activity are predicted to improve habitat quality in the Ganges,
302 facilitating/improving spawning migrations of the anadromous hilsa (*Tenualosa ilisha*; Anon,
303 2020). Despite some evidence of improvements in habitat quality, it is uncertain whether these
304 reduced impacts will continue and help rejuvenate these systems, or whether efforts to kick-start
305 economies during pandemic recovery will aggravate threats and intensify habitat loss.

306

307 Indeed, many examples exist where habitats and entire ecosystems have suffered greater damage
308 during COVID-19. In India, sand mining, an emerging threat to freshwater ecosystems
309 (Koehnken et al., 2020), increased due to reduced enforcement mechanisms (Kannan, 2020), but
310 was considerably reduced in other parts of South Asia (e.g., Sri Lanka and Bangladesh) due to
311 lockdown and associated mobility issues (S. Lockett Pers. Comm.). In the Amazon, deforestation
312 rates increased by 55% from January to April 2020, compared with the same period in 2019
313 (Brown, 2020) due to reduced enforcement (Schwartz et al., 2020). This is intensifying pressures
314 on the already vulnerable freshwater ecosystems of the region (Castello et al., 2013).

315

316 *Climate change*

317

318 Climate change is a widely recognized threat to freshwater fish populations (Lynch et al.,
319 2016a). COVID-19 and associated changes in global emissions could reduce climate impacts
320 over the short term, indirectly benefitting freshwater fishes. Global travel restrictions and
321 reduced industrial activity have dramatically decreased fossil fuel consumption worldwide

322 (Gössling et al. 2020). These large-scale changes have resulted in a temporary reduction in CO₂
323 emissions during lockdown (average reduction of 26%, Le Quere et al., 2020). The timescale of
324 these reductions is likely too short to affect long-term climate change trends or freshwater habitat
325 conditions, yet these temporary shifts could translate to longer term change depending on
326 societal responses, i.e., whether economic recovery efforts follow a return to ‘business as usual,’
327 or instead, embrace the implementation of new climate policies that drive further reductions in
328 energy use and shifts to clean energy. A shift towards working from home could be a significant
329 longer-term change that reduces emissions (Hern 2020). Perhaps the most important long-term
330 consequence of COVID-19 on climate change is the unplanned global experiment revealing that
331 dramatic reductions in carbon emissions are possible if societal and political will exist. Whether
332 this realisation, together with a renewed public exposure to scientific evidence as a result of
333 COVID-19 media coverage, will alter societal willingness to address climate change is unknown.
334

335 While there have been some short-term wins for the environment due to the pandemic, they may
336 be counterbalanced by other losses. In Brazil, decreased emissions related to fossil fuels were
337 offset by increased deforestation in the Amazon (SEEG, 2020). Similarly, electricity
338 consumption has generally decreased in response to lockdowns, largely due to reduced demand
339 from commercial and industrial users (e.g., forecasted decline of 4.2% in the US in 2020, US
340 EIA, Short-term energy outlook July 2020). Additionally, some environmental regulations have
341 already been rolled back. In California, USA, for example, a law passed in 2016 banning
342 restaurants and grocery stores from providing single-use plastics to customers was suspended in
343 April-2020 by Executive Order N-54-20 due to health concerns. Plastics have a large carbon
344 footprint (Zheng and Suh, 2019); they are energy-intensive to produce and transport, and
345 contribute substantially to greenhouse gas emissions when incinerated. Importantly, there is a
346 risk that COVID-19 has taken attention away from climate change as a preeminent world ‘crisis.’
347 Given the manifold effects of climate change on freshwater fish, diversion of attention from
348 climate change may harm fish populations and the fisheries and communities that rely on them.
349

350 *Exploitation*

351
352 Overexploitation of freshwater fishes is another major driver of freshwater biodiversity loss
353 (Reid et al. 2018 and references therein). The immediate impact of COVID-19 on freshwater
354 fisheries differs regionally and between sectors and is closely tied to market demands and
355 consumer behaviour. Small-scale freshwater fisheries were impacted by reduced demand during
356 the initial phases of the pandemic, resulting in reduced harvest. In Maine (USA), the reduced
357 demand for juvenile eels (*Anguilla rostrate*) resulted in a 75% reduction in market price (Chase,
358 2020a) and in Ontario, Canada, the closure of restaurants and supermarket fish counters delayed
359 the start of the fishing season on Lake Erie (Chase, 2020b). Similar economic conditions
360 combined with movement restrictions has reduced pressure on freshwater fisheries in Brazil,
361 Namibia, India, and China (Stokes et al. 2020). In Kenya, flood conditions coincided with
362 COVID-19 which collectively led to reductions in fish harvest in inland waters (Auru et al.,
363 2020). Challenges in data collection of diffuse, small-scale fishing activities limit analysis of the
364 pandemic on exploitation at this point in time. However, observed changes potentially impacting
365 exploitation include changes in preference for local fishes (OECD 2020), export bans on fish
366 products (Pisei 2020), and altered fisher behaviour (Indian Council of Agricultural Research
367 2020a, 2020b). There were also extensive restrictions on recreational fisheries in some regions

368 (e.g., across much of North America; reviewed in Paradis et al., In Press; and in South Africa).
369 Some recreational fisheries closures or other restrictions that limit access and reduce effort may
370 reduce fishing mortality (i.e., harvest or catch-and-release mortality) but we are unaware of any
371 data to support that idea.

372
373 Over the longer term, however, the impacts of COVID-19 can be expected to amplify
374 exploitation and unsustainable fishing practices. Freshwater fisheries make important
375 contributions to the food, nutritional, and income security of rural people in the developing
376 world. Even under normal conditions, many rural people fish as part of diversified livelihood
377 strategies, and in times of crisis when other options are reduced, fishing has a well-documented
378 safety net function (Smith et al. 2005; Martin et al. 2013). Job losses in urban areas and the
379 return of migrant workers to their rural homes (Mukhra et al., 2020) will increase fishing effort
380 and may lead to fishing practices that will impact negatively on imperilled fishes, such as the
381 Critically Endangered hump-backed mahseer (*Tor remadevii*; Pinder et al., 2020). This is
382 coupled with evidence of increased illegal fishing activities because of reduced surveillance and
383 enforcement activities.

384
385 Increased effort and exploitation have also been documented in many recreational fisheries
386 around the world as many people have sought outdoor spaces while under lockdown and many
387 countries have incentivized recreational fishing as a socially-distanced activity (e.g., free fishing
388 days). Many areas are seeing an increase in the sales of fishing licenses relative to the same
389 periods in 2019, including Texas, USA (39 % increase; CBS Local 2020), Vermont, USA
390 (resident license have increased 50%, Gribkoff and Trombly, 2020), England (increase of 120%
391 in rod licenses; Cuff, 2020), among many other fisheries worldwide. In some areas, restrictions
392 have affected international travel for recreational fishing and related tourism (Gössling et al.
393 2020), which is likely to reduce local income and compromise co-management agreements
394 aimed at maintaining high abundances of large-bodied freshwater fishes for recreational anglers.
395 Examples include conservancies for tigerfish (*Hydrocynus vittatus*) in Namibia (Cooke et al.,
396 2016), *Arapaima* spp. in Guyana (Lynch et al., 2016b), and mahseer (*Tor* spp.) in India (Pinder
397 and Raghavan, 2013). In northern Thailand, despite no restrictions on in-country travel, several
398 communities temporarily blocked access to self-governed fish reserves by even compatriot
399 anglers out of fear of introducing COVID-19 locally, forgoing important revenues during the
400 tourism season. For many, the lost income from decreased fishing tourism might be replaced by
401 an increase in fishing effort to supplement food sources and income.

402 403 **COVID-19's modulating effect on conservation/management**

404 405 *Enforcement and policy compliance*

406
407 Strong regulation and policies are important for arresting the global decline in freshwater
408 biodiversity (Dudgeon et al., 2006; Reid et al., 2019). Enforcement measures are often supported
409 by high levels of regulatory surveillance that encourage user compliance (Eggert and Lokina,
410 2010) but during COVID-19 lockdown periods these efforts were often restricted (See Figure 2).
411 For instance, some Canadian fisheries and conservation enforcement officers were reassigned to
412 enforce border travel restrictions (Verenca 2020). In China, enforcement has struggled to address
413 increased illegal fishing activities, which usually occur in the winter-spring transition period

414 (e.g., January through March) during the lockdown period. There is evidence that decreased
415 policy compliance of freshwater biodiversity regulations has compromised the protection of
416 some threatened species. For example, Pinder et al. (2020) suggested poaching pressure on large-
417 bodied, threatened fishes, such as mahseers, increased in many developing countries during
418 lockdown, especially in areas where food supply chains and employment levels had collapsed.
419 Indeed, many of the increased exploitation pressures on freshwater fishes during lockdown likely
420 relate to reduced compliance with harvest policies. Food insecurity and reduced enforcement
421 have been suggested as dual causes of increased subsistence fishing (some of which may be
422 illegal) in many regions, including the Mekong, Zambezi system (D. Tweddle pers. comm.), and
423 across South Asia and South America.

424
425 In some regions of the world, surveillance for some species and regions, such as in many
426 national parks and protected areas, was maintained (Corlett et al., 2020). Aspects of this were
427 evident in England, where enforcement controls were maintained for conservation priority
428 species (e.g., Atlantic salmon, *Salmo salar*; European eel, *Anguilla anguilla*), despite population
429 monitoring programmes being halted (e.g., Anglers Mail, 2020). Elsewhere, reduced travel has
430 increased policy compliance. For example, the closure of South African nature reserves and
431 national parks increased regulatory compliance as fewer people had access to these areas of
432 conservation importance.

433 434 *Restoration activities*

435
436 Every year, considerable effort is devoted to the restoration of aquatic biodiversity focusing on
437 habitat (e.g., wetland creation, stream enhancement) and populations (e.g., conservation
438 hatcheries), with such activities expected to intensify (prior to COVID-19) as we enter the UN
439 Decade for Ecosystem Restoration (Young and Schwartz, 2019). Although restoration remains
440 an imperfect science (Cooke et al., 2019), it is one of the primary ways to mitigate threats to
441 freshwater fishes. For some recently implemented conservation and restoration activities, the
442 reduction in human mobility has allowed for greater success of existing restoration actions (e.g.,
443 year-classes of fish protected from angling activity, new habitat not impacted by foot traffic).
444 Many planned or ongoing restoration activities, however, have been reduced or postponed
445 because of COVID-19, particularly those projects involving multiple countries or jurisdictions
446 where international travel/work is necessary (e.g., international research, monitoring projects).
447 Also, many activities involving volunteer groups have been suspended due to concerns about
448 assembling large groups and because many such initiatives rely on volunteers in vulnerable age
449 groups. Where restoration has been undertaken, it has purposefully reduced involvement of local
450 communities who normally provide volunteer labour (e.g., community organizations, students,
451 outdoor clubs). In the Yangtze River Basin, many shoreline restoration projects ceased during
452 the lockdown and in northern China, the largest freshwater restoration initiative in Baiyangdian
453 Lake was stopped because of the lockdown (Y. Chen, Personal Observation). In South Africa,
454 the Working for Water programme, a public works initiative which has a strong focus on
455 removal of alien plants (see van Wilgen et al., 2020), was halted over the lockdown. In the
456 longer term, the need to provide employment in rural areas following the economic impact of
457 COVID-19 may provide for new opportunities to link public-works programmes to well
458 designed and effectively implemented aquatic ecosystem restoration programs.

459

460 Public aquaria play an important role in freshwater biodiversity conservation through activities
461 including, but not limited to species reintroduction programs, habitat restoration and ex-situ
462 research programs (see Murchie et al. 2018). The global pandemic has had serious financial
463 implications for numerous nonprofit institutions such as public aquariums, that rely heavily on
464 ticket and membership sales, along with donations to operate (AZA 2020, WAZA 2020, WCS
465 2020). Indeed, numerous NGOs that play a critical role in public communication of freshwater
466 biodiversity issues and inspire the public to action are currently at risk of losing capacity to
467 maintain the level of engagement that is urgently needed to reverse species loss and restore
468 degraded habitats. However, there have been instances where online engagement has been highly
469 successful. For instance, the biennial World Fish Migration Day reached a greater number of
470 people in 2020 than in its previous three years (Twardek et al. 2020). COVID-19 has also
471 impacted government finances but in some regions there may be federally based stimulus
472 funding, at least over the short-term, to help kick-start economies. NGOs are working to ensure
473 these actions are “green,” including large-scale restoration initiatives (e.g., Carlson and Roe,
474 2020). Given the urgent need to reverse the decline of biodiversity loss and restore degraded
475 habitats (Tickner et al., 2020), postponing restoration activities (e.g. lack of dam removals, water
476 quality restoration) could have devastating effects on aquatic ecosystems over the longer-term.

477 478 *Regulations*

479
480 Fishing, habitat restoration, assessment and enforcement activities were strongly impacted by
481 COVID-19-related restrictions on travel and social distancing guidelines. During full lockdowns,
482 recreational fishing was often initially classified as a non-essential activity while commercial and
483 subsistence fishing was generally permitted as essential. Lobbying efforts by recreational fishing
484 organizations resulted in recreational fishing being given essential status in some jurisdictions in
485 the USA within weeks of initial lockdowns (see Paradis et al., In Press). Outside of strict
486 lockdowns, restrictions persisted with respect to travel distances, congregation at boat ramps and
487 on the water, and the number of people allowed on recreational vessels (Game and Fish, 2020).
488 These restrictions are likely to have resulted in a net reduction and spatial redistribution of
489 recreational fishing effort in the early stages of the pandemic. However, there is also evidence
490 that widespread reductions in working hours and working from home arrangements may have
491 increased the overall level of fishing activity (see above). Due to the suspension of many routine
492 creel surveys and other assessment methods, precise estimates may be difficult to attain, but
493 fishing license sales appear to have increased in many jurisdictions world-wide.

494
495 Concurrently, enforcement of fishing and environmental regulations has generally declined
496 during the pandemic due to restrictions on travel and face-to-face interactions by enforcement
497 personnel. Many agencies such as the USA Environmental Protection Agency have explicitly
498 and temporarily relaxed certain reporting requirements and enforcement actions, but not the
499 regulations being enforced (Beitsch 2020). Such actions have fueled widespread speculation in
500 many countries, including the USA and South Africa, that there will be a push to relax
501 environmental regulations to aid economic recovery from COVID-19. There may also be efforts
502 to push through deregulation efforts at times when press coverage is focused on COVID-19
503 issues. On the other hand, government programs to promote recovery may fast-track
504 modernization of certain industries, for example adoption of ‘smart irrigation’ technologies in
505 agriculture, which may result in an overall reduction of agricultural water withdrawals and in

506 South Africa, the Inland Fisheries Policy may be fast-tracked to help deal with COVID-19
507 impacts.

508
509 *Monitoring and stock assessment*

510
511 The COVID-19 crisis has resulted in disruptions to routine environmental monitoring (Cheval et
512 al., 2020) and impacted fisheries management and stock assessment practice (FAO, 2020) across
513 the globe. Government-mandated suspension of environmental assessments and protections for
514 freshwater ecosystems have been reported for Canada (Paterson et al., 2020), the USA (Beitsch,
515 2020), India (Chandrashekhar, 2020), and Brazil (Spring, 2020), and mobility restrictions for
516 environmental managers have meant reductions in the monitoring of populations, watersheds,
517 and fishery landing sites (FAO, 2020). In the UK, monitoring and stock assessment were
518 suspended during lockdown. For anadromous fishes that are only present in UK rivers in spring
519 (e.g., European shads, *Alosa* spp.; sea lamprey, *Petromyzon marinus*), the opportunity to collect
520 data on their 2020 migrations has been lost, and as lockdowns persist and are reinstated,
521 information on other migratory species like Atlantic salmon and sea trout (*Salmo trutta*) will be
522 missed. In China, complete lockdown of Hubei Province and the city of Wuhan – China’s
523 epicentre of freshwater fisheries research – has resulted in major reductions in fish monitoring
524 activities. In Brazil, many fish monitoring projects have been paralyzed during the pandemic
525 resulting in large data gaps.

526 Although closures of formal fisheries in many regions during lockdown have caused temporary
527 reductions in usual harvest pressures (FAO 2020b), interruptions to other food production sectors
528 have led many local communities to rely on freshwater fisheries as an emergency food source
529 (Pinder et al., 2020). An influx of inexperienced fishers and introduction of more damaging gear
530 types might lead to increased risk of overexploitation to nearshore stocks as fishers target these
531 more accessible habitats. Although reductions in monitoring capacity were initially predicted to
532 be short-term (Cheval et al., 2020), in several cases suspensions have extended throughout 2020
533 and will presumably extend into 2021. As lockdowns are lifted, there will be a critical need to
534 undertake rigorous assessments to understand the longer-term responses of fish biodiversity
535 impacts and their recovery. However, such increased monitoring might not be adequately
536 funded. A potential positive outcome of COVID-19 is that, in some regions, the restriction of
537 human activity represents a major change from the norm and thus is an opportunity to study the
538 effects of humans on freshwater ecosystems (e.g., Bates et al. 2020). Of course, this will only be
539 possible in instances where stock assessment and monitoring occurred during the pandemic
540 lockdown.

541 *Research on freshwater fish biodiversity*

542
543 Shelter-in-place policies enforced by governments and research institutions have resulted in
544 suspensions and cancellations to both laboratory and field-based research (Corlett et al., 2020,
545 Wilson, 2020). In many countries (e.g., Canada, USA, UK, Germany), freshwater biodiversity
546 research has been suspended for much of 2020 (Bath, 2020; Wilson, 2020; Bunk, 2020).
547 Research activities that have been maintained are primarily maintenance-related (i.e., caring for
548 populations of live fish, upkeep of sensitive battery-powered monitoring equipment) and
549 ensuring long-term monitoring activities in only limited situations. In southern Africa, research

550 on the upper Zambezi floodplains has been suspended despite one of the largest flood years on
551 record. In Asia, major international research initiatives on the Mekong River have been delayed,
552 and in India all freshwater studies, including laboratory and field-based work, were suspended
553 for at least two months. For some research programs, the height of the lockdown coincided with
554 key monitoring months. In India, for example, research on subterranean (e.g., cave, aquifer)
555 aquatic biodiversity during summer months (i.e., May through August) is facilitated by low
556 water levels, and even short lockdowns during that timeframe have resulted in an entire year of
557 research on these species being lost. The consequence of suspended or cancelled research on
558 aquatic biota is that the status of populations, stocks, and migrations are not being appraised.
559 This is of particular concern for endangered fishes and sensitive, threatened freshwater
560 ecosystems. Furthermore, halting research – especially in the long term – could result in
561 overlooking conservation priorities or opportunities to protect freshwater resources (Corlett et
562 al., 2020). In most cases, research is expected to resume as pandemic restrictions are lifted, but
563 there is concern that the economic consequences of lockdowns will limit research funds,
564 typically available from governments and conservation foundations. Reductions in funding could
565 permanently halt or diminish conservation programs around the globe (Corlett et al., 2020).

566 A silver lining for some researchers unable to conduct field research is the increased time for the
567 analysis and publication of pre-existing data. Yet, not all researchers have benefitted equally and
568 long-lasting productivity disparities are emerging (see Viglione, 2020). For example, journal
569 submission rates during the pandemic have increased for male researchers but decreased for
570 female researchers, a result with high potential to exacerbate existing gender-based inequalities
571 in publishing and pay rates through reductions in women being granted tenure (Collins, 2020). It
572 is unclear how this will influence those working in the realm of freshwater fish biodiversity.

573 *Training and capacity building*

574 Freshwater fisheries science and management is inherently hands on – whether setting nets,
575 identifying fish species in local markets, or conducting door-to-door harvest studies in rural
576 communities. These activities (as well as the examples related to restoration, research, etc
577 outlined above) all depend largely on trained fisheries professionals. COVID-19 has changed
578 college and university education in many ways with cancellation of field-based internships and
579 rapid transition to online instruction (Bao, 2020). Some aspects of fisheries science training can
580 be adapted to online formats with relative ease (e.g., quantitative stock assessment) yet we
581 require fisheries practitioners to interact directly with fish, habitats, and people (Hard, 1995).
582 Consequently, there is concern that there is a cohort of trainees that are currently moving through
583 the system that may not have hands on training experiences needed to engage in various
584 activities that span and integrate the natural sciences, health, humanities and social sciences.
585 Graduate students that are conducting their research in 2020 may be delayed and mental health
586 issues among this cohort are on the rise (Langin 2020). Due to the financial constraints facing
587 doctoral students, the proportion expecting they will drop out has increased greatly (Johnson et
588 al. 2020). In the Anthropocene, we are in desperate need for the next generation of
589 environmental professionals to be well equipped for solving complex problems (Jeanson et al.,
590 2020) and that will be impeded if training is incomplete and limited to text books and videos.
591 Similarly, freshwater fisheries practitioners around the world routinely participate in professional
592 development (continuing education) training courses to improve their skills and proficiency

593 (Rassam and Eisler, 2001). In some regions where freshwater fisheries science and management
594 capacity is lacking, efforts focused on capacity building are crucial to enable effective local
595 governance and science-based fisheries management (Espinoza-Tenorio et al., 2011). Both
596 professional development and capacity building have been severely hampered by COVID-19. As
597 educators and trainers adapt their curricula, pedagogy, and delivery to COVID-19 realities (see
598 Singh et al. 2020 for example of how medical school has adapted), there is certainly need for
599 creativity to ensure that learners are provided with opportunities to learn through experiential
600 means. There is also uncertainty regarding how COVID-19 may alter enrollment in fisheries-
601 relevant programs. If students perceive such programs to be less desirable given lack of
602 opportunity for experiential education, they could be declines in enrollment which could have
603 consequences for the profession and freshwater ecosystems.

604 The rapid transition to online formats for many facets of work also creates opportunities to
605 normalize virtual conferences and even participating remotely once in-person opportunities
606 resume. Online formats have low barriers to participate and can increase engagement for those
607 typically unable to travel due to financial burdens, other obligations, or both. Subsidies for
608 international participation (particularly from Low and Middle Income Countries) and on-demand
609 formats can accommodate asynchronous participation across time zones.

610 **Beneficial outcomes and opportunities for freshwater fish biodiversity stemming from** 611 **COVID-19**

612
613 Turning short-term benefits to aquatic ecosystems into long-term opportunities for freshwater
614 fish conservation will involve harnessing newly found environmental stewardship. Increased
615 participation in freshwater fisheries activities during the COVID-19 crisis is evident globally, be
616 it in response to food or income security or for recreation. The crisis has highlighted important
617 benefits of inland fisheries, their contributions to social and economic resilience, and the need to
618 conserve and restore the ecosystems upon which they depend. Importantly, these benefits and
619 needs transcend socio-economic strata and geographical boundaries. Increased angling licence
620 sales can contribute to funding increases for fisheries management and potentially greater
621 freshwater fish biodiversity conservation through increased stakeholders and advocates. New and
622 more energized stakeholders can push for broader policies for improved water quality and
623 restoration of freshwater ecosystems. However, we are unaware of any evidence showing that
624 increases in angling interest yield improvements in stewardship. An important step forward is the
625 recent EU strategy on biodiversity for 2030 (released in May 2020) that provides substantial
626 funding to restore connectivity in European rivers. In pandemic recovery mode, as public work
627 programmes are used to rebuild national economies (e.g., Subbarao et al., 2012), conservation
628 initiatives may serve as a foundation for efforts, especially in rural areas. South Africa's
629 Working for Water programme, which pursues conservation, employment, and development
630 (Turpie et al., 2008), could be a model for other public works initiatives.

631
632 COVID-19 may also expand certain horizons for freshwater fish biodiversity research.
633 Agricultural frontiers in Brazil, for example, have been linked to infectious diseases leading to
634 calls for more research and conservation (Zimmer, 2019). As there will be greater interest in and
635 funding availability for zoonotic diseases such as COVID-19, 'One Health' approaches that
636 integrate human, animal, and ecosystem health through transdisciplinary research (Osofsky et al.,

637 2005; Zinsstag et al., 2011; Nunez et al., 2020) will be essential components of research
638 portfolios to optimize outcomes for both people and aquatic environments. There is also an
639 opportunity to push for holistic public health systems that recognize the importance of ecosystem
640 health (including fish and aquatic resources) in human health.

641
642 **Management and policy needs to mitigate negative impacts of COVID-19 on freshwater**
643 **fish and fisheries and make them resilient to future pandemics**

644
645 Although we identified a number of benefits for freshwater fish biodiversity arising from
646 COVID-19, there were also a number of negative outcomes or issues identified that will require
647 management or policy actions (Figure 3). Relaxation of regulations in several countries during
648 the pandemic (where environmental issues were already considered as a low priority) is a major
649 concern for freshwater biodiversity (Kavousi et al., 2020). The same scenario will likely
650 continue, and may even be exacerbated, as countries rebuild their economies and bureaucratic
651 hurdles (environmental safeguards) are removed. To ensure biodiversity is not overlooked, it will
652 be essential to link fish biodiversity and environmental integrity to the many other benefits for
653 humanity (e.g., livelihoods, health, well-being), as well as to ensure sustainable fisheries are
654 available into the future (Brooks et al., 2016).

655
656 Adequate environmental policies depend on the active participation of the scientific community
657 (Azevedo-Santos et al., 2017), and on the collection of robust data to support management
658 actions (Brooks et al., 2016, Radinger et al., 2019). Both aspects were directly affected by
659 COVID-19, and the related consequences deserve to be evaluated and monitored. The lack of
660 detection and measurement of the direction of possible changes in freshwater fish populations
661 during the pandemic period is a major concern. There is a need for increasing monitoring,
662 control, and surveillance in the short term, and large-scale restoration projects should be resumed
663 as soon as the pandemic returns to a relatively stable situation. While the mobilization of
664 organized civil society, including academia, is necessary to avoid environmental setbacks and
665 their effects on aquatic biodiversity, different measures can be taken to alleviate potential
666 negative consequences on freshwater fish and fisheries during future pandemics or lockdowns.
667 These measures include investing in more contingency planning for research and management,
668 and maintaining necessary management and monitoring programs instead of complete lockdown.
669 The need to stimulate depressed economies provides an opportunity for employment in
670 conservation and restoration programs (similar to the Civilian Conservation Corps in the U.S.
671 during the Great Depression).

672
673 *1-2 Years from 2020*

674
675 The potential state of freshwater fish biodiversity in the short-term (i.e., one to two years from
676 now) will depend on the state of the pandemic and how society responds in the post-pandemic
677 recovery phase. If the pandemic is ongoing, a possibility given the current increasing global
678 trend in case numbers, then many of the impacts described above are likely to remain relevant.
679 The state of fish populations under the pandemic recovery scenario will be varied across regions
680 and jurisdictions, primarily determined by localised activities, circumstances, and responses.

681

682 One to two years from now, we anticipate freshwater fish biodiversity at the global scale will be
683 in a similar or improved condition relative to if the pandemic had not occurred. Improvements to
684 freshwater habitat quality resulting from the global ‘pause’ in economic development and
685 declines in human disturbance, adapted fishing activities, and reduced pollution all have the
686 potential to benefit fish populations (Rutz et al. 2020). However, the relatively short-time scale
687 of the lock-down period means freshwater fishes are unlikely to exhibit substantial long-term
688 changes.

689
690 However, in some regions of the world, freshwater biodiversity may be in a worse state
691 immediately after the pandemic relative to how things would have been otherwise. Aquatic
692 ecosystems, specifically in and around urban areas, may be degraded by COVID-19-related
693 products (e.g., masks, disinfectants, hand-sanitizers, and other pharmaceutical chemicals;
694 Aragaw 2020). Trade disruptions and loss of income will likely increase exploitation of more
695 accessible and lower value freshwater fisheries, some of which may be already threatened (e.g.,
696 Pinder et al. 2020). Increased water use for irrigated agriculture may compound pre-existing
697 threats to freshwater fishes, especially in semi-arid regions.

698
699 The pandemic has revealed serious flaws in the global food and public health system, which is
700 far from sustainable or equitable (FAO 2018). The pandemic has also heightened political
701 tensions both within and among countries; global trade has been impacted and this may extend to
702 fish and fish products. Indeed, there are already disputed news articles about COVID-19 being
703 spread by salmon and shrimp (Bloomberg 2020). Freshwater fishes in many areas play an
704 important, but largely undocumented, role in local and regional food and nutrition security, trade,
705 and commerce. It is unclear what the impacts of COVID-19 will be for local communities,
706 freshwater fisheries, and biodiversity, but more intense fishing, increased illegal, unreported, and
707 unregulated (IUU) fishing (albeit this is relatively uncommon in freshwater given that fishing is
708 usually smaller-scale subsistence fishing), and decreased fish availability are likely outcomes.
709 Given the food security implications of COVID-19, these impacts could be immediate in many
710 parts of the world.

711 712 *5 Years from 2020*

713
714 On a longer-time scale (i.e., five years), the future state of freshwater fisheries is very likely to be
715 worse than if the pandemic had not occurred. Society’s prioritisation of economic and societal
716 recovery in the post-pandemic phase may pause or demote environmental concerns and
717 expenditure on restoration programs. Indeed, India has already given the green light to
718 controversial development projects during the COVID-19 lockdown period (following relaxed
719 environmental assessment processes; Kaggere and Bengaluru 2020) and the impacts on wildlife
720 will be felt in this later period. Eagerness to return to economic growth may lead to a rebounding
721 period that ultimately accelerates and compounds threats to freshwater fishes existing prior to the
722 pandemic. This dynamic may play out to a greater extent in developing regions because of
723 increased prevalence of food insecurity caused by the pandemic.

724
725 Some of the longer-term negative impacts on freshwater fisheries will be caused by actions taken
726 during the pandemic period. Disruptions in monitoring and interrupted education and training
727 create data and knowledge gaps that will compromise the ability to make robust sustainable

728 fisheries and conservation decisions. Economic impacts, including the evolving recession and the
729 necessary redirection of funding to human health and other priorities, could greatly compromise
730 important resource management and conservation activities, such as the IUCN Red-List
731 assessment. Indeed, the systems most at risk, and thus heavily reliant on management
732 interventions, will be those impacted greatest by the weakening of fish conservation activities.
733

734 The importance of strong environmental policy to protect biodiversity will be emphasised by this
735 pandemic. For example, adoption of the EU Water Framework Directive and Biodiversity
736 Strategy will likely mitigate many of the threats caused by the pandemic to freshwater fishes in
737 Europe. Moreover, an opportunity exists in the creation of new societal behaviors from the
738 global ‘pause,’ and this could manifest as new policy more adept in protecting biological
739 diversity, including freshwater fishes, across the world (Bates et al. 2020). This pandemic
740 provides a global wake-up call to recognise the need to invest in science and policy agendas that
741 allow for preparedness to confront such a crisis. The impacts on freshwater fish populations and
742 biodiversity that result from COVID-19 will largely compound existing stressors that are well
743 known. While supporting science and understanding of these issues are well-established (FAO
744 SOIFR 2019, Beard et al. 2011, Reid et al. 2019), it is a commitment to continued funding and
745 implementation of remedial interventions that is needed to ensure the sustainability of freshwater
746 fish biodiversity, fisheries, and their ecosystems into the post-pandemic future.

747
748
749

750 **Figure Captions**

751

752 **Figure 1.** COVID-19 impacts to existing threats on freshwater fish, where positive (+) impacts
753 mitigate and negative (-) amplify threats.

754

755 **Figure 2.** COVID-19 impacts to conservation and management of freshwater fish, where
756 positive (+) impacts mitigate and negative (-) amplify threats.

757

758 **Figure 3.** COVID-19 effects and management needs to alleviate potential negative consequences
759 on freshwater fish and fisheries during future pandemics.

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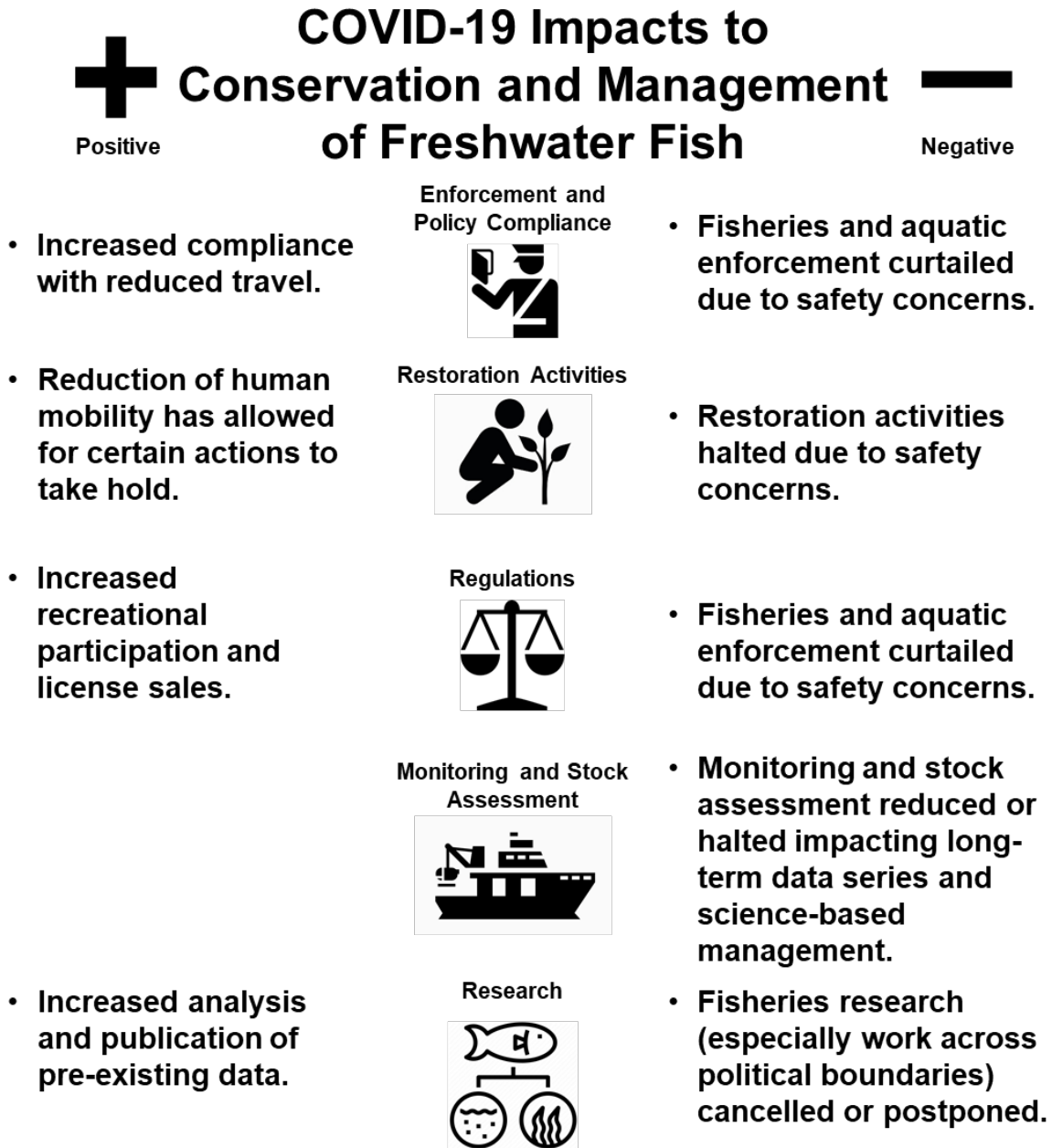
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Figure 2.



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COVID-19 Effects and Management Needs to alleviate potential negative consequences on freshwater fish and fisheries during future pandemics

Invasive Species



- **Variable** (*reduced travel, lower monitoring and control*)
- Ensure control, monitoring, and surveillance resume and are resilient in the case of future lockdowns.

Pollution



- Variable but **overall positive** (*reduction in some pollutants, increase in others*)
- Maintain or strengthen environmental regulations as economies are rebuilt.

Fragmentation



- **Variable** (*temporary delay of some barrier projects, but likely less funding to remove barriers*)
- Ensure environmental regulations are not weakened as economies are rebuilt and reconsider the tradeoffs associated with environmentally-damaging energy and water resource projects.

Flow Regulation



- **Variable** (*increased water extraction in residential areas, decrease in industrial areas, potential increase in irrigated agriculture need*)
- Monitor individual watersheds for modifications in natural and regulated flow regimes.

Habitat Loss



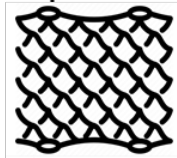
- **Variable** (*greater occurrence of environmentally damaging practices, though a delay in development projects*)
- Ensure environmental regulations are not weakened as economies are rebuilt. Incorporate restoration programs into economic stimulus packages.

Climate Change



- **Reduced** (*global emissions were reduced during lockdowns but effects will likely be short-term*)
- Avoid returning to pre-pandemic global emission levels. Ensure that this issue regains priority post-pandemic.

Exploitation



- **Variable** (*some fisheries experienced reduced demand, though reliance on local food and income sources and interest in outdoor recreation has increased, e.g., recreational fisheries*)
- Manage exploitation in the light of exceptional demand and subsistence or livelihood needs, focus on avoiding destructive practices and conserving vulnerable species.

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793

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795

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