Wetland fishes avoid a carbon dioxide deterrent deployed in the field

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Biological invasions are poorly controlled and contribute to the loss of ecosystem services and function. Altered watershed connectivity contributes to aquatic invasions, but such hydrologic connections have become important for human transport. Carbon dioxide (CO₂) deterrents have been proposed to control the range expansion of invasive fishes, particularly through altered hydrologic connections, without impeding human transport. However, the effectiveness of CO₂ deterrents needs to be further evaluated in the field, where fishes are situated in their natural environment and logistical challenges are present. We deployed a proof-of-concept CO₂ deterrent within a trap-and-sort fishway in Cootes Paradise, Ontario, Canada, to determine the avoidance responses of fishes attempting to disperse into a wetland. We aimed to describe deterrent efficiency for our target species, common carp, and for native fishes dispersing into the wetland. Our inexpensive inline CO₂ deterrent was deployed quickly and rapidly produced a CO₂ plume of 60 mg/l. Over 2000 fishes, representing 13 species, were captured between 23 May and 8 July 2019. A generalized linear model determined that the catch rates of our target species, common carp (n = 1662), decreased significantly during deterrent activation, with catch rates falling from 2.56 to 0.26 individuals per hour. Aggregated catch rates for low-abundance species (n < 150 individuals per species) also decreased, while catch rates for non-target brown bullhead (n = 294) increased. Species did not express a phylogenetic signal in avoidance responses. These results indicate that CO₂ deterrents produce a robust common carp avoidance response in the field. This pilot study deployed an inexpensive and rapidly operating deterrent, but to be a reliable management tool, permanent deterrents would need to produce a more concentrated CO₂ plume with greater infrastructural support.

Keywords: non-structural deterrent, non-physical barrier, invasive species, fishway, Cyprinus carpio, common carp, Carbon dioxide

Introduction

Human activities have drastically altered the biodiversity of freshwater systems (Su et al., 2021). Threats, such as biological invasions, are poorly controlled (Strayer, 2010), but contribute to the loss of ecosystem diversity and resilience (Ricciardi and MacIsaac, 2011; Downing et al., 2012). Freshwater ecosystems experience high invasion rates due to ballast-
water transport, authorized and unauthorized release and altered system connectivity (Strayer, 2010). While the construction of dams have restricted access to critical habitats (Milt et al., 2018), canals have allowed for the hydrologic connection of historically separated basins (Strayer, 2010; Rasmussen et al., 2011).

Non-structural deterrents have been proposed to control the range expansion of invasive fishes without altering human transport. Non-structural deterrents can alter fish behaviour to produce avoidance responses as documented for acoustic, visual or low-concentration CO2 deterrents (Vetter et al., 2015; Cupp et al., 2016; Dennis et al., 2015; Putland and Mensinger, 2019; Dennis and Sorensen, 2020), or they can alter fish physiology to limit the capacity to move, as documented for electrical (Noatch and Suski, 2012) and visual or low-concentration CO2 deterrents (Vetter et al., 2015; Donaldson et al., 2016; Suski, 2020). Increased CO2 concentrations are often associated with decreased O2 concentrations, but can also affect gas exchange at the gills and induce hyperventilation (Gilmour, 2001; Perry and Gilmour, 2002).

Recent deterrent efforts have been applied towards limiting the continued dispersal of invasive bigheaded carps (Hypophthalmichthys spp.) within the Mississippi river basin (Kates et al., 2012; Donaldson et al., 2016). However, most CO2 deterrent studies have been conducted in the laboratory (see Kates et al., 2012; Dennis et al., 2015; Dennis et al., 2016; Cupp et al., 2017; Tucker et al., 2018) or within artificial environments (see Donaldson et al., 2016; Cupp et al., 2016; Schneider et al., 2018). There remains a paucity of information on CO2 deterrent performance within realistic site conditions (but see Cupp et al., 2018). Field deterrents present challenges that do not exist in the laboratory such as inclement weather and suboptimal infrastructure. Deterrents must also produce an avoidance response in fishes that exist within their natural contexts, but behaviours in the laboratory and field can vary widely (Calisi and Bentley, 2009). Field tests are needed to describe in situ CO2 deterrent efficiency. Furthermore, deterrent efficiencies should be described for both target species and native fishes likely to be affected by deterrent deployment.

We deployed a proof-of-concept CO2 deterrent within a trap-and-sort fishway in Coote’s Paradise, Ontario, Canada. This same fishway was previously outfitted with an acoustic fish deterrent (Bzonek et al., 2021), allowing for a comparison of deterrent technology. Coote’s Paradise is a 250-ha drowned river-mouth marsh and a significant nursery for Lake Ontario fishes (Thomassen and Chow-Fraser, 2012). The fishway, in operation since 1997, was constructed to exclude invasive common carp (Cyprinus carpio) from the marsh.

Common carp is a globally invasive species with high fecundity and broad biotic and abiotic tolerances (Weber and Brown, 2009). Introduced common carp can cause ecosystem-level changes by increasing sediment mixing and reducing aquatic vegetation through benthic foraging (Bajer and Sorensen, 2014; Huser et al., 2016). In Coote’s Paradise, common carp had dominated the community prior to the installation of the fishway. It had comprised 90% of the fish community biomass (Loughheed et al., 2004) and increased turbidity by 45% (Loughheed et al., 1998).

We aimed to determine whether the CO2 deterrent was effective at reducing the catch rates of fishes attempting to disperse into the wetland. The catch rates of the target species, common carp, and all other fishes were recorded across alternating deterrent and control trials. We predicted that the CO2 deterrent would reduce the catch rate of all regularly encountered fish species.

**Methods**

To quantify the effectiveness of a non-structural CO2 deterrent, the catch rates of fishes entering the fishway under ambient conditions were compared to the catch rates of fishes entering fishway during the deterrent treatment. The Royal Botanical Gardens fishway is a physical structure that separates the Coote’s Paradise wetland from Hamilton Harbour at the western end of Lake Ontario (43°16′47.0″N 79°53′35.0″W). Native and non-native fishes regularly challenge the fishway to gain access into the wetland. The fishway blocks the outlet of Coote’s Paradise with metal grating (spacing, 5.4–6.2 cm), such that small fishes can pass through the grating but large fishes wider than the grating spacing are funnelled towards six traps (four active) to be manually processed. For a detailed description of fishway operation, see (Bzonek et al., 2021).

Traps were operated between 23 May and 8 July 2019; however, deterrent trials (n = 7) were not operated between 31 May and 24 June due to logistical constraints (i.e. flooding). Lake Ontario experienced record-high water levels in summer 2019 (Orr, 2019), which flooded the only access road to the Royal Botanical Gardens fishway and prevented CO2 dewar gas delivery.

The CO2 deterrent was installed in one of four active fishway traps and activated on alternating days, typically Monday, Wednesday and Friday. The traps were typically processed twice a day, Monday–Friday, at approximately 0800 and 1400 h with trap exposure time ranging from 6 (0800–1400) to 18 (1400–0800) hours. Traps were closed between Friday at 1400 and Sunday at 0800, then remained open until the traps were emptied on Monday at 0800 for a 24-hour exposure time. Each time that the deterrent-integrated trap contents were processed, the data were recorded as a deterrent or control treatment. During the sorting process, fishes were identified to species and counted by Royal Botanical Gardens technicians. During deterrent trials, CO2 was pumped into the water continuously, with carbonation starting 20 minutes
prior to the trap opening and running until the trap was closed for processing. During the 30 minutes of trap processing, CO2 concentrations would return to ambient levels and we reset the trap for the next ambient trial.

**Deterrent stimulus**

A simple CO2 deterrent was deployed at the Royal Botanical Gardens fishway and integrated within the centremost trap, which historically had the greatest ambient common carp catch rate (RBG, unpublished data). A submersible pump with a check valve moved wetland water through polyethylene pipe (diameter, 2.54 cm) into an injection manifold (Figure 1). CO2 gas was pumped from a liquid CO2 dewar (CD MLC230-350; Praxair) into the injection manifold at 10 psi, where the gas line ended with two terminal aerators (10 × 10 × 5 cm) secured inside the manifold. The manifold was a 38 × 28 × 15 cm ABS junction box plumbed to receive the incoming water and gas lines and the outgoing carbonated water line. Aerated CO2 bubbles resisted the downward flow of water, increasing bubble/water interface time within the water line. The mixing of CO2 and water was assisted with two 25-mm static mixers placed directly below, and ∼10 m downline, from the manifold. Inline water flow downstream of the second static mixer held a CO2 concentration of ∼400 mg/l and a flow rate of 240 ml/s. The line of carbonated water was then distributed equally among four hoses with a four-way garden hose manifold, where each hose distributed carbonated water to a different region of the modified fishway trap (dimensions, 1.2 × 0.6 m) (Figure 1). The carbonated water maintained a CO2 plume directly adjacent to the fishway trap, with minimal plume disruption caused by wetland water flow (see Cupp et al., 2018) (flowrate at trap, 0.016 ± 0.025 m/s; mean ± standard deviation). CO2 concentrations 1 m downstream of the fishway trap and outflow apparatus were 70 ± 5 mg/l (mean ± standard deviation) (Figure 2). Such CO2 concentrations have been observed to produce consistent avoidance responses in bigheaded carps in outdoor arenas (Cupp et al., 2016).

**Experimental constraints**

CO2 mapping was limited due to equipment vandalism inside the locked, gate-secured field site. Underwater CO2 probes
Figure 2: CO₂ concentrations measured at 1 and 5 m from the CO₂ deterrent-integrated fishway trap.

(eosGP; eosense; Dartmouth, Nova Scotia) were deployed to continuously log CO₂ ppm throughout the field season. In June 2019, the CO₂ probes were vandalized while other equipment such as the data-logging laptop and Jon boat used to access the site were stolen. Backed-up data from the underwater CO₂ probes did not substantially overlap with experimental treatments. Therefore, CO₂ concentrations reported here were manually calculated with titrations (Hach Company, Loveland, CO, USA; Titrator Model 16 900; CO₂ Kit No. 2272700 and Total Alkalinity Kit No. 2271900) conducted on water samples from the remaining trials at distances 1 and 5 m downstream of the deterrent-integrated trap, and at a depth of 0.6 m. CO₂ titrations were collected immediately after samples were collected.

Statistical analysis

To determine if fish avoided the CO₂ deterrent, catch abundance for the deterrent-integrated trap of the fishway was analysed in a general linear model. Catch abundance was offset by log-transformed trap exposure time to calculate catch rate. Catch abundances were right-skewed and zero-inflated, so abundance was fit with a Poisson distribution and a log link function. We included species identity and treatment levels as fixed effects that were allowed to interact. Dispersal into the wetland is seasonal and species specific (Bzonek et al., 2021), so we included date as a covariate that was allowed to interact with species identity. We tested for a phylogenetic signal in the species-specific response to the deterrent (Bzonek et al., 2021). Branch lengths and phylogenetic relationships for the species in this study (excluding the common carp x goldfish hybrid C. carpio x Carassius auratus) were obtained by pruning the species tree from Rabosky et al. (2018). We used the phylosig function in the phytools package (Revell, 2012) to test for a phylogenetic signal in the percent change in catch rates across species. The statistical significance of the phylogenetic signal was evaluated using Pagel’s λ and Blomberg’s K indices of trait evolution. All statistical analyses were performed in R (version 4.0.2; R Foundation for Statistical Computing, Vienna).

Results

Over 2000 fishes, representing 13 species, were captured within the deterrent-integrated trap between 23 May and 8 July 2019 (Table 1). Common carp was the most abundant species, representing ~70% of the individuals captured, with a total catch of 1662 individuals. Brown bullhead (Ameiurus nebulosus) was also abundant, with 294 individuals captured throughout the field season. The remaining 11 species represented a catch abundance of 338 individuals, with goldfish (C. auratus) and common carp x goldfish hybrids captured in abundances greater than 100 individuals (Figure 3). Common carp catch rates in the deterrent-integrated traps were significantly lower during deterrent activation (Table 2). Catch rates decreased from 2.56 individuals per hour during control trials to 0.26 individuals per hour during deterrent trials (Figure 4). There was an increase in catch rates for brown bullhead, from a control catch rate of 0.31 individuals per hour to a stimulus catch rate of 1.01 individuals per hour. There were no significant statistical differences in catch rates between the control and stimulus treatments for the remaining, less abundant, species. However, when the catch rates of less abundant species were aggregated there was a significant decrease in catch rates, from the control catch rate of 0.77 fish per hour to stimulus catch rate of 0.31 fish per hour. No phylogenetic signal was observed in the species-specific avoidance responses of all regularly captured fishes (Pagel’s λ < 0.01, Blomberg’s K = 0.41, P < 0.05).

Discussion

The CO₂ deterrent produced a strong avoidance response in the target species, common carp, by decreasing catch rates to 10% of their ambient rate. When aggregated, low-abundance species also significantly avoided the deterrent, but abundant brown bullhead did not. Unlike a comparable acoustic deterrent (Bzonek et al., 2021), fishes did not express a phylogenetic signal in avoidance responses. This study exposed several practical challenges relevant to deterrent deployment such as stochastic flooding and equipment vandalism. The
Table 1: Catch data for fishes caught in the CO2 deterrent-integrated trap at the Royal Botanical Gardens fishway, 23 May to 8 July 2019

| Species scientific name | Common name | Ambient catch rate (fish/hour) | Deterrent catch rate (fish/hour) | Total abundance | Percent change |
|-------------------------|-------------|--------------------------------|----------------------------------|-----------------|---------------|
| C. carpio              | common carp | 2.565                          | 0.267                            | 1662            | −90%          |
| A. nebulosus           | brown bullhead | 0.308                        | 1.009                            | 294             | 228%          |
| C. auratus             | goldfish    | 0.288                          | 0.110                            | 105             | −62%          |
| C. carpio x C. auratus | common carp x goldfish hybrid | 0.289                        | 0.184                            | 133             | −36%          |
| Ictalurus punctatus    | channel catfish | 0.144                        | 0.000                            | 87              | −100%         |
| Dorosoma cepedianum    | gizzard shad | 0.017                          | 0.000                            | 7               | −100%         |
| Aplodinotus grunniens  | freshwater drum | 0.011                        | 0.000                            | 4               | −100%         |
| Micropterus salmoides  | largemouth bass | 0.006                        | 0.000                            | 2               | NA            |
| Amia calva             | bowfin      | 0.005                          | 0.000                            | 2               | NA            |
| Lepomis gibbosus       | pumpkinseed | 0.000                          | 0.022                            | 1               | NA            |
| Oncorhyncus mykiss     | rainbow trout | 0.003                        | 0.000                            | 1               | NA            |
| Catostomus commersonii | white sucker | 0.003                        | 0.000                            | 1               | NA            |

The inline CO2 deterrent used here performed well and may be suitable for continued small-scale, temporary deterrent uses in low flow areas. The results of this proof-of-concept field deterrent are promising for the continued development and deployment of non-physical CO2 fish deterrents.

Avoidance response of target species and greater wetland fish community

Common carp was effectively deterred by the CO2 plume and catch rate decreased by 90%, far greater than the 16% decrease caused by the acoustic deterrent in Bzonek et al. (2021). A 10-fold decrease in common carp wetland immigration rates could reduce population growth rates if the reduced adult immigration was coupled with wetland harvest (Caskenette et al., 2018). Such harvest is regularly conducted at Cootes Paradise (Loughed et al., 2004), indicating that, in the context of common carp exclusion at this specific site, a permanent CO2 deterrent could have been a viable alternative to a physical barrier. Common carp exclusion can be an effective tool in wetland restoration (Loughed et al., 1998), and the development of non-structural deterrents may provide greater flexibility for management efforts when physical barriers are not feasible (Noatch and Suski, 2012).

Other species were also affected by the deterrent. Brown bullhead was captured in greater abundance when the deterrent was activated. However, deterrent treatment catch rates for this species were driven by rare, high-abundance trials, including one event where 35 individuals were captured over a 6-hour exposure time. When this large-group outlier is removed, brown bullhead catch rates also decreased with deterrent activation. It is currently unknown whether brown bullhead avoidance responses are affected by group size. Tucker and Suski (2019) found that, for Bluegill (Lepomis macrochirus), groups of fish avoided CO2 to a greater extent than individuals in isolation, as groups were likely less vulnerable to habituation, learning or inter-individual variation. Bzonek et al. (2021) found that group size had no impact on common carp avoidance to an acoustic deterrent. An alternate explanation may be that ictalurids have altered sensitivity, tolerance or behavioural responses to CO2 (see Caprio et al., 2014). The 11 remaining fish species represented 14% of the total catch. The catch rates of these species had generally decreased during the deterrent treatment (Table 1), but not significantly. When the catches of all low-abundance species were aggregated, there was a significant decrease in catch rate during the deterrent treatment. Furthermore, closely related species were no more likely to respond similarly to each other than more distantly related species. This result occurred because all species, except brown bullhead, exhibited general avoidance.

Species specificity in deterrent responses may aid in mitigating the ecological impacts of deterrents on non-target species. In contrast to the general avoidance to the CO2 deterrent used in this study, an acoustic deterrent deployed at the same site produced a greater avoidance response in ostariophysian fishes than in non-ostariophysian fishes (Bzonek et al., 2021). However, our results indicate that CO2 deterrents are likely to alter the dispersal of both target and non-target fish species. Watershed connectivity is a critical factor for many ecological processes (Crook et al., 2015), and the benefits of preventing range expansions of invasive fishes should be balanced against the consequences of limiting the movement of native species. Fausch et al. (2009) proposed a conceptual framework for balancing the benefits of invasive species barrier against the costs of population isolation.
Deterrent stimulus

We used CO2 as a non-physical deterrent stimulus to prevent common carp entry into a wetland. Such CO2 deterrents have shown consistent success in producing avoidance responses in target species (Donaldson et al., 2016; Cupp et al., 2016, 2018; Schneider et al., 2018). This study did not isolate the component of the CO2 stimulus to which fishes were responding. Fishes may have avoided the deterrent due to the elevated CO2 concentrations. Alternatively, fish may have been avoiding a resultant decrease in O2 and pH caused by the elevated CO2 (Gilmour, 2001; Perry and Gilmour, 2002). However, we are not certain if either O2 or pH decreased in our study to a level that would cause deterrence and recommend future studies monitor both environmental variables. Determining the specific impetus for deterrent avoidance may become important when optimizing the deterrent stimuli but was not critical when establishing proof-of-concept for the deterrent in the field. If the avoidance found in this study was...
caused by the indirect effects of CO\textsubscript{2}, the stimulus would still be suitable for deterrent use as it is relatively inexpensive, safe to store/transport and effective at altering the water chemistry of the immediate environment.

Additional factors contributed to the suitability of CO\textsubscript{2} as a deterrent. Water flow across the deployment site was generally static, and ambient CO\textsubscript{2} concentrations were relatively high. Flow velocity and water discharge have a direct impact on plume development, as moving water carries CO\textsubscript{2} to store/transport and effective at altering the water chemistry of the immediate environment. Flow velocity and water discharge have a direct impact on plume development, as moving water carries CO\textsubscript{2} to store/transport and effective at altering the water chemistry of the immediate environment.

The strong common carp avoidance response produced by a low-magnitude, temporary CO\textsubscript{2} deterrent is promising for the development of dedicated, large-scale deterrents. Our deterrent maintained a CO\textsubscript{2} plume with a 5-m radius and a concentration of ∼60 mg/l. This concentration is sufficient to produce an avoidance response in most individuals; however, a higher concentration may be necessary to elicit sufficient avoidance in an unresponsive subset of the population. Large-scale, dedicated deterrents can achieve CO\textsubscript{2} plumes with higher concentrations than seen here to surpass interindividual variation in CO\textsubscript{2} tolerances (Zolper, Cupp, and Smith, 2018). Stronger CO\textsubscript{2} deterrents may also transition from a behavioural deterrent to a physiological deterrent.

### Table 2: Summary table for the generalized linear model and marginal means describing the catch abundances of species within the deterrent-integrated trap

| Species scientific name | Species common name | Treatment     | Estimate | Lower confidence level | Upper confidence level | Standard error | Z score | P value |
|-------------------------|---------------------|---------------|----------|------------------------|------------------------|----------------|---------|---------|
| *C. carpio*             | common carp         | Ambient       | 32.7322  | 31 3                   | 35 7                   | 0.8241052      | 9.367   | <.0001 |
| *A. nebulosus*          | brown bullhead      | Ambient       | 1.3636   | 1 2                    | 2 5                    | 0.1942901      | −5.272  | <.0001 |
| Aggregate of species below | Ambief Deterrent | 6.2412  | 6 2                  | 1 1                    | 0.3675215          | 3.232     | 0.0012 |
| *C. auratus*            | goldfish            | Ambient       | 1.6775   | 1 2                    | 2 2                    | 0.1997788      | 1.871   | 0.0614 |
| *C. carpio x C. auratus*| common carp x goldfish hybrid | Ambient Deterrent | 2.2118  | 2 3                    | 3 3                    | 0.223782       | 1.285   | 0.1989 |
| *Ictalurus punctatus*   | channel catfish     | Ambient       | 1.7676   | 1 2 Inf                | 2 Inf                 | 0.1898237      | 0.002   | 0.9982 |
| *Dorosoma cepedianum*   | gizzard shad        | Ambient       | 0.1297   | 0 0                    | 0 Inf                 | 0.0536849      | 0.002   | 0.9981 |
| *Aplodinotus grunniens* | freshwater drum     | Ambient       | 0.0781   | 0 0                    | 0 Inf                 | 0.0406611      | 0.002   | 0.9985 |
| *Amia calva*            | bowfin              | Ambient       | 0.0398   | 0 0                    | 0 Inf                 | 0.0287776      | 0.002   | 0.9984 |
| *Micropterus salmoides* | largemouth bass     | Ambient       | 0.0252   | 0 0                    | 0 Inf                 | 0.0268144      | 0.002   | 0.998  |
| *Lepomis gibbosus*      | pumpkinseed         | Ambient       | 0 0.0711 | 0 0                    | 0 Inf                 | 0.0000006      | −0.006  | 0.995  |
| *Oncorhyncus mykiss*    | rainbow trout       | Ambient       | 0.0201   | 0 0                    | 0 Inf                 | 0.0203504      | 0.002   | 0.9985 |

The marginal means were estimated from the general linear model reported in the results using the R package ‘emmeans’. The predicted catch abundances of each species were allowed to independently vary across time within the general linear model, so the marginal means presented here were predicted for the median date of the study, 13 June 2019. The catch abundance of each species in each trial was also standardized across trap exposure time; therefore, the catch abundances were predicted for the median trap exposure time of 12.6 hours. Catch rates between each treatment were compared for each species in a pairwise post hoc Tukey-Kramer test. An estimated marginal mean was also predicted for the aggregation of all low abundance species (per species).
by surpassing an individual’s tolerance to hypercarbia and induces equilibrium loss (Suski, 2020).

Our inline CO2 delivery system operated more efficiently than the terminal-diffuser systems used in comparable outdoor CO2 deterrents (Cupp et al., 2016, 2018). When CO2 is extruded through porous media at the target site, the resultant bubbles quickly travel through the water column and off-gas into the atmosphere at the surface, dramatically limiting the CO2 mass transfer within the water column (see Li et al., 2019). With our design, CO2 was diffused into a water line to increase the exposure time of the gas-water interface before the mixture was released at the terminal site. We achieved CO2\textsubscript{aq} concentrations of ~400 mg/l within our lines, which allowed for the rapid development of CO2 plumes at the target site. Our plume concentrations reached 60 mg/l in less than 1 hour, while terminal diffuser systems have required 4–6 hours (Cupp et al., 2016) or >8 hours (Cupp et al., 2018) to produce similar concentrations. Current outdoor deterrent studies have utilized simple deployment designs constructed with relatively common equipment (Cupp et al., 2018). Permanent, large-scale CO2 deterrents will require more complex and efficient delivery systems with specialized equipment and access to large volumes of CO2. Such deterrents are currently being assessed (Zolper et al., 2018). The deterrent system described here is more suitable for temporary, low flow, small-scale studies where funding, development and operation are limiting factors in deterrent design.

Small-scale CO2 deterrents face a number of practical challenges such as the duration of equipment activation and the lack of robust infrastructure. The field site had trail access, but stochastic flooding closed the trail, eliminating vehicle access and conventional gas-canister exchange. Additionally, although the site perimeter was secured, the location was remote and vulnerable to vandalism. Large CO2 deterrents will require secure sites with greater infrastructural access to ensure uninterrupted access and permanent CO2 storage.

Conclusion

Non-structural deterrents have been proposed as a means to control the range expansion of invasive fishes without impeding human transport. Before non-structural deterrents can be successfully implemented to halt the range expansions of invasive species, research must address the uncertainties of scaling laboratory-level successes towards field applications (Cupp et al., 2018). This pilot field study demonstrates that an inexpensive CO2 deterrent constructed with readily available equipment can produce a robust avoidance response in common carp, a species of significant management concern. These findings support the continued development of more permanent CO2 deterrents. Deterrent design should move away from terminal-diffuser systems, which are slower to develop CO2 plumes, and deterrent managers should expect a broad avoidance response to CO2 plumes from most wetland fishes.

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Data Availability

The data underlying this article are available in the online supplementary material.

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Supplementary material

Supplementary material is available at Conservation Physiology online.

References

Bajer PG, Sorensen PW (2014) Effects of common carp on phosphorus concentrations, water clarity, and vegetation density: a whole system experiment in a thermally stratified lake. Hydrobiologia 746: 303–311.

Bzonek PA, Van Nynatten A, Mandrak NE (2021) Phylogenetic signal found in fish–community response to an acoustic common carp deterrent. Freshw Biol 1–11. https://doi.org/10.1111/fwb.13785.

Calisi RM, Bentley GE (2009) Lab and field experiments: are they the same animal? Harm Behav 56: 1–10.

Caprio J, Shimohara M, Marui T, Harada S, Kiyohara S (2014) Marine teleost locates live prey through pH sensing. Science 344: 1154–1156.

Caskenette A, Enders EC, Watkinson D, Wrubleski D (2018) Partial exclusion of spawning Cyprinus carpio to improve coastal marsh habitat may come at the cost of increased carp population growth. Ecol Model 385: 58–64.

Cooke SJ, Cramp RL, Madliger CL, Bergman JN, Reeve C, Rummer JL, Hultine KR, Fuller A, French SS, Franklin CE (2021) Conservation physiology and the COVID-19 pandemic. Conserv Physiol 9: 1–10.

Crook DA, Lowe WH, Allendorf FW, Er T, Finn DS, Gillanders BM, Hadwen WL, Harrod C, Hermoso V, Jennings S et al. (2015) Human effects on ecological connectivity in aquatic ecosystems: integrating scientific approaches to support management and mitigation. Sci Total Environ 534: 52–64.

Cupp A, Erickson R, Fredricks K, Swyers N, Hatton T, Amberg J (2016) Responses of invasive silver and bighead carp to a carbon dioxide barrier in outdoor ponds. Can J Fish Aquat Sci 9: 1–9.

Cupp A, Smerud J, Tix J, Schleis S, Fredricks K, Erickson R, Amberg J, Morrow W, Koebel C, Murphy E et al. (2018) Field evaluation of carbon dioxide as a fish deterrent at a water management structure along the Illinois River. Manag Biol Invasion 9: 299–308.

Cupp A, Tix J, Smerud J, Erickson R, Fredricks K, Amberg J, Suski C, Wakeman R (2017) Using dissolved carbon dioxide to alter the behavior of invasive round goby. Manag Biol Invasion 8: 567–574.

Dennis CE, Adhikari S, Suski CD (2015) Molecular and behavioral responses of early-life stage fishes to elevated carbon dioxide. Biol Invasions 17: 3133–3151.

Dennis CE, Adhikari S, Wright AW, Suski CD (2016) Molecular, behavioral, and performance responses of juvenile largemouth bass acclimated to an elevated carbon dioxide environment. J Comp Physiol 186: 297–311.

Dennis CE, Sorensen PW (2020) High-intensity light blocks bighead carp in a laboratory flume. Manag Biol Invasion 11: 441–460.

Dennis CE, Zielinski D, Sorensen PW (2019) A complex sound coupled with an air curtain blocks invasive carp passage without habituation in a laboratory flume. Biol Invasions 21: 2837–2855.

Donaldson MR, Amberg J, Adhikari S, Cupp A, Jensen N, Romine J, Wright A, Gaikowski M, Suski CD (2016) Carbon dioxide as a tool to deter the movement of invasive Bighead carp. Trans Am Fish Soc 145: 657–670. https://doi.org/10.1080/00028487.2016.1143397.

Downing AS, van Nes EH, Mooij WM, Scheffer M (2012) The resilience and resistance of an ecosystem to a collapse of diversity. PloS One 7: 1–7.

Fausch KD, Rieman BE, Dunham JB, Young MK, Peterson DP (2009) Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conserv Biol 23: 859–870.

Gilmour KM (2001) The CO2–pH ventilatory drive in fish. Comp Biochem Physiol 130: 219–240.

Huser BJ, Bajer PG, Chizinski CJ, Sorensen PW (2016) Effects of common carp (Cyprinus carpio) on sediment mixing depth and mobile phosphorus mass in the active sediment layer of a shallow lake. Hydrobiologia 763: 23–33.

Kates D, Dennis C, Noatch MR, Suski CD (2012) Responses of native and invasive fishes to carbon dioxide: potential for a nonphysical barrier to fish dispersal. Can J Fish Aquat Sci 69: 1748–1759.

Li X, Wang W, Zhang P, Li J, Chen G (2019) Interactions between gas-liquid mass transfer and bubble behaviours. R Soc Open Sci 6: 190136. http://dx.doi.org/10.1098/rsos.190136.

Lougheed VL, Crosbie B, Chow-Fraser P (1998) Predictions on the effect of common carp (Cyprinus carpio) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Can J Fish Aquat Sci 55: 1189–1197.

Lougheed VL, Theyseymeyer T, Smith T, Chow-Fraser P (2004) Carp exclusion, food-web interactions, and the restoration of Cootes Paradise Marsh. J Great Lakes Res 30: 44–57.
Milt AW, Diebel MW, Doran PJ, Ferris MC, Herbert M, Khoury ML, Moody AT, Neeson TM, Ross J, Tresa T, O’Hanley JR, Walter L, Wangen SR, Yacobson E, McIntyre PB (2018) Minimizing opportunity costs to aquatic connectivity restoration while controlling an invasive species. Conserv Biol 32: 894–904. https://doi.org/10.1111/cobi.13105.

Noatch MR, Suski CD (2012) Non-physical barriers to deter fish movements. Environ Rev 20: 71–82.

Orr S (2019) Lake Ontario hits highest water level ever recorded. Democrat & Chronicle.

Perry SF, Gilmour KM (2002) Sensing and transfer of respiratory gases at the fish gill. J Exp Zool 293: 249–263.

Putland RL, Mensinger AF (2019) Acoustic deterrents to manage fish populations. Rev Fish Biol Fish 29: 789–807.

Rabosky DL, Chang J, Title PO et al. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559: 392–395. https://doi.org/10.1038/s41586-018-0273-1.

Rasmussen JL, Regier HA, Sparks RE, Taylor WW (2011) Dividing the waters: the case for hydrologic separation of the North American Great Lakes and Mississippi River Basins. J Great Lakes Res 37: 588–592.

Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3: 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x.

Ricciardi A, Mac Isaac HJ (2010) Fifty Years of Invasion Ecology: The Legacy of Charles Elton. Wiley-Blackwell, Oxford, UK.

Schneider EVC, Hasler CT, Suski CD (2018) Fish behavior in elevated CO2: implications for a movement barrier in flowing water. Biol Invasions 20: 1899–1911.