Acidification and eutrophication: insights into wildfowl–fish competition

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Wildfowl managers are often advised to discourage the introduction of fish into wetlands because competition between fish and wildfowl for invertebrate prey negatively affects the quality of breeding habitat and duckling growth rates. In the last three decades, research on this competition has been performed under the umbrella of two management issues: the effects of acidification on wildfowl and fish in oligotrophic (low-nutrient) lakes and the effects of biomanipulations (fish removals to reduce nuisance algae) on lake communities in mesotrophic to hypertrophic lakes. In both types of studies, regardless of the fish and bird fauna involved, the focus has been on the effects of fish extirpations or removals on invertebrates and thus on the birds that compete with the fish for invertebrate prey. However, some of the ways in which fish are removed or lost from lakes may not necessarily result in benefits to wildfowl, because (1) in acidic lakes, low pH can also have negative effects on the birds and (2) some methods used to remove fish in biomanipulations can negatively affect the very invertebrates upon which birds feed. Thus, although these fish removal/extinction-based studies have addressed the issues of acid precipitation and eutrophication in lakes, they do not always unequivocally show that fish are responsible for reduced invertebrate abundance and reduction of wildfowl habitat quality. Removal studies may not, therefore, provide an adequate basis for advising managers to discourage fish introductions into wetlands. The merits and pitfalls of these fish removal/extinction-based studies of wildfowl–fish competition are reviewed. Additionally, a more direct approach to studying wildfowl–fish competition and to assessing the effects of fish introductions on invertebrates and wildfowl is suggested – namely, adding fish experimentally to wetlands.

Key Words: acidification, biomanipulation, fish, wildfowl, invertebrates

Introduction

Acid precipitation studies in oligotrophic lakes, where fish have been extirpated or their densities greatly reduced, provide extensive insights into wildfowl–fish competition for food (e.g. Bendell & McNicol 1995; Eadie & Keast 1982; Eriksson 1979, 1984; Pehrsson 1984). In these studies, wildfowl appeared to benefit from fish extirpations if they could exploit the nektonic invertebrates, such as Dytiscidae, Hemiptera and Chaoboridae, that increased after fish disappeared, and did not rely solely on acid-sensitive invertebrates such as molluscs. Wildfowl might also benefit from biomanipulations in hypertrophic lakes, where fish are removed to try to reduce nuisance algae (Bergman *et al*. 1999). However, not all wildfowl in acidified lakes can switch invertebrate prey, and the methods used in biomanipulations, such as poisoning lakes with rotenone, can be detrimental to invertebrates upon which wildfowl might rely (Miskimmin & Schindler 1994). Recent studies of fish colonisations and studies that involve adding fish to mesocosms may add valuable insights into the effects of fish on invertebrates and hence on breeding wildfowl. Insights on wildfowl–fish competition obtained from acid precipitation studies and biomanipulation studies for wildfowl are reviewed below. New evidence based on adding fish to waterbodies instead of on removing them is suggested as a basis for further insights into wildfowl–fish competition. Data from these new methods may be more useful to wildfowl managers who must deal with issues such as stocking of sport or bait-fish in lakes than traditional fish removals, which are costly, invasive and labour-intensive.

Methods

This review is based on a literature search in Cambridge Scientific Abstracts and the Web of Science databases, and on some input from reviewers. The literature on acid precipitation and biomanipulations is extensive, and so the focus was almost exclusively on those studies that dealt directly with wildfowl, or those whose findings could be extrapolated feasibly to wildfowl–fish competition. A search for studies that had been performed in Europe and North America covered as broad a range of biomes as possible. Since biomanipulation was not a widely used or well-developed technique before 1975, and since acid precipitation began to be a serious issue only at that point, searches were restricted to 1975 or after. Because there are many studies that repeat the information presented here, this review cites a subset of about 50 references that most comprehensively cover the findings of the 388 studies found.

Competition in oligotrophic lakes: acidification and fish–wildfowl interactions

Acidification studies demonstrated that competition with fish is one of the principal limiting forces for wildfowl that feed on invertebrates in oligotrophic lakes. Eriksson (1978, 1979) showed that Common Goldeneye *Bucephala clangula* used fishless oligotrophic lakes in southwest Sweden more than oligotrophic lakes with Perch *Perca fluviatilis* or Roach *Rutilus rutilus*. Odonata and Dytiscidae were less abundant in oligotrophic lakes with fish, and Goldeneye increased their use of a lake from which fish were removed (Eriksson 1978, 1979). In eastern Canada, Eadie & Keast (1982) found 80% diet overlap between Goldeneye ducklings and Yellow Perch *P. flavescens* based on prey size, and 71% overlap for prey types (mostly Ephemeroptera nymphs). These studies were conducted in lakes that were becoming acidified; the basic information on wildfowl–fish–invertebrate interactions that they revealed was a valuable source of background information for later studies that were more directly management-focused.

The mid-1980s saw the start of a more direct focus on the effects of acidification and restoration on lake fauna (**Table 1**). The Swedish oligotrophic lakes from Eriksson's (1978, 1979) studies were good candidates for liming (adding calcium carbonate to neutralise acid) to restore fish stocks (Eriksson 1987). At this time, many studies suggested that some wildfowl might actually benefit from loss of fish due to acidification – and the evidence presented was compelling. Pehrsson (1984) found that Mallard *Anas platyrhynchos* pair densities were higher in Swedish oligotrophic lakes that were losing fish due to acidification. Imprinted ducklings obtained more food when released into fishless lakes than into lakes with fish. Fishless lakes had significantly more and larger invertebrates than fish lakes had (Pehrsson 1984). Common Goldeneye were thought to benefit from acidification because they could exploit aquatic insects that expanded into the open water following fish extirpation (Eriksson 1984) and were less dense after liming than before (Eriksson 1987).

Studies in North America also implied a positive effect of acidification on wildfowl, mediated by loss of fish, and this was supported by fish–invertebrate studies. For example, Bendell and McNicol (1987) showed that fishless lakes supported nekton-dominant assemblages of invertebrates, including Dytiscidae, Hemiptera and Chaoboridae, irrespective of pH. Black Duck *A. rubripes* ducklings on fishless lakes changed their diets to invertebrates that were unavailable to them in the presence of fish (Hunter *et al*. 1986). Ducklings on fish lakes showed greater dietary overlap with their fish competitors (50–70%) than they did with other ducklings on fishless lakes (38–50%), where other ducklings were the main competitors. DesGranges & Rodrigue (1986) found that Common Goldeneye and Black Duck ducklings spent less time feeding and gained weight faster on acidic lakes from which Brook Trout *Salvelinus fontinalis* were extirpated than they did on acidic lakes to which these fish were added. Thus, loss of fish, and subsequent increases in nektonic invertebrates, appears to have been the main mechanism for changes in wildfowl diets and abundances that came with acidification. Results of long-term studies of restored lakes in Scandinavia still confirm this: recovery of Perch results in reduction of both macroinvertebrate and Goldeneye

Table 1: The main findings of 10 of the acid rain studies that deal with wildfowl–fish competition. 1= Eriksson 1978, 2 = Eriksson 1979, 3 = Eadie & Keast 1982, 4 = Eriksson 1983, 5 = Pehrsson 1984, 6 = Eriksson 1987, 7 = DesGranges & Rodrigue 1986, 8 = Blancher *et al*. 1992, 9 = McNicol & Wayland 1992, 10 = Bendell & McNicol 1995.

Wildfowl	Fish	Invertebrate prey	Location	Methods	Conclusion	Source
Common Goldeneye Bucephala clangula	Perch Perca fluviatilis Roach Rutilus rutilus	Odonata, Coleoptera	Sweden	Fish removal and compared lakes with and without fish.	Exploitation. Competition.	1,2
Common Goldeneye	Yellow Perch P. flavescens	Ephemeroptera	Canada	Compared lakes with and without fish, duckling and fish. Gut contents.	Competition over large geographic areas.	3
Mallard Anas platyrhynchos, Teal A. crecca Common Goldeneye	Perch, Roach, Pike Esox lucius	Not sampled	Sweden	Duckling abundance correlated with fish densities and some habitat characteristics.	Competition only with diving ducks & fish.	4
Mallard, Teal, Common Goldeneye	Perch, Roach, Pike	Coleoptera, Odonata, Trichoptera, Diptera	Sweden	Food availability, feeding success, breeding pair and duckling counts on lakes with and without fish.	More food gained in fishless lakes.	5,6
Common Goldeneye, Black Duck A. rubripes	Brook Trout Salvelinus fontinalis, Yellow Perch	Coleoptera, Hemiptera, Diptera	Canada	Sampling invertebrates, monitoring duckling behaviour and duckling gut contents.	Ducklings forage more on lakes with fish.	7,8,9,10

duckling abundance (e.g. Rask *et al*. 2001).

However, McNicol & Wayland (1992) suggested that not all wildfowl benefit from fish extirpations in acidified lakes, because not all wildfowl can exploit the nektonic invertebrates that increase as fish are lost (Bendell & McNicol 1995; Blancher *et al.* 1992). Acid-sensitive invertebrates such as clams, snails and crayfish are lost with decreasing pH (Scheuhammer *et al.* 1997). These invertebrates provide breeding wildfowl and wetland-associated birds with calcium for egg formation. Although calcium deficiency has not been directly documented in wildfowl from these lakes (D. McNicol, personal communication), important wildfowl prey such as Odonata, Notonectidae and Gyrinidae all had significantly lower calcium content in acid-stressed lakes than in non-stressed lakes (Scheuhammer *et al*. 1997). Goldeneye ducklings also gained weight faster and spent less time searching for food on circumneutral lakes with fish and fishless acidic lakes than on acidic lakes with fish (DesGranges & Rodrigue 1986). Thus, although nektonic invertebrates consumed by breeding wildfowl are more abundant in the absence of fish, this does not imply that a loss of fish due to acidification is good for wildfowl. Mitigation techniques such as liming may help restore fish that compete with wildfowl, but this is surely a more favourable outcome than loss of fish and a calcium-deficient prey base for breeding wildfowl.

Because acidification studies demonstrated that competition with fish is one of the principal limiting forces for wildfowl that feed on invertebrates in oligotrophic lakes, they allow the suggestion that wildfowl might be managed by manipulating fish. The same general pattern appeared in oligotrophic lakes in Europe and North America (**Table 1**) although they supported different fish and wildfowl species: fish reduced the abundance of invertebrates such as Ephemeroptera and Odonata, and this was associated with reduced growth rates of ducklings and reduced numbers of wildfowl.

The studies described above focussed on oligotrophic lakes prone to acidification, and so the evidence that wildfowl benefited from fish extirpation can only be reasonably applied to oligotrophic, acidification-prone lakes. However, the fish extirpation effect also applies to eutrophic systems where fish are often removed in biomanipulations to improve water quality. Many biomanipulation operations quite rightly focus on changes to zooplankton, phytoplankton and macrophyte communities following fish removals (Bergman *et al*. 1999). They can, however, provide valuable insights into wildfowl–fish competition in eutrophic lakes.

Biomanipulation: implications for competition in eutrophic lakes

Multiple anthropogenic nutrient inputs to lakes have led to widespread eutrophication (see Bergman *et al*. 1999 and Meijer *et al*. 1999 for reviews in relation to European lakes). One of the arguably more successful (Phillips *et al*. 1999) restoration techniques for these lakes, biomanipulation, involves removing fish. First developed by Shapiro *et al.* (1975), biomanipulation takes its rationale from the precursors of trophic cascade theory. Removing planktivorous fish reduces predation on grazing zooplankton, allowing increased numbers of zooplankton to consume and significantly reduce nuisance algae. Removals of benthivorous fish, which stir up lake sediments when foraging, result in decreased lake turbidity. These changes result in increased macrophyte development whilst maintaining the same level of primary productivity (Scheffer *et al*. 1993). The shift from a turbid, algal-dominated stable state to a clear, macrophyte-dominated stable state (*sensu* Scheffer *et al*. 1993) provides good habitat for macroinvertebrates.

It may readily be extrapolated and suggested that these fish removals, which lead to increases in water clarity, macrophyte development and macroinvertebrate habitat, would benefit wildfowl that rely on macroinvertebrates. However, there have been few biomanipulation studies that focus on wildfowl in that particular context. Some studies suggest that herbivorous wildfowl such as Coot *Fulica atra* and Mute Swan *Cygnus olor* can retard recovery of macrophytes following a biomanipulation if birds are at high enough densities (Lauridsen *et al.* 1993; Marklund *et al*. 2002; Mitchell & Perrow 1998; Søndergaard *et al*. 1997; Van Donk & Otte 1996). However, these latter studies do not give direct insights into competition between fish and wildfowl for invertebrates (**Table 2**) and so will not be discussed below.

Studies performed on flooded gravel pits in England are among the few that deal directly with wildfowl–fish competition in the biomanipulation context (**Table 2**). Bream *Abramis brama,* perch, Tench *Tinca tinca* and other sport fish are often stocked in these lakes (Hill *et al*. 1987). Gut content analyses show that these fish exhibit dietary overlap with dabbling and diving wildfowl such as Mallard and Tufted Duck *Aythya fuligula* for benthic invertebrates such as Chironomidae, Gastropoda and Amphipoda (Giles 1994; Giles *et al*. 1990; Phillips 1992). In experimental mesocosms, fish density was negatively correlated with Mallard duckling growth and Chironomidae density (Hill *et al*. 1987). Giles (1990) removed fish from gravel pit lakes and found increased macrophyte abundance, Chironomidae density and water clarity, with concurrent increases in survival of young Tufted Ducks.

Gravel pit lake studies provided strong evidence that Bream, Tench and Perch competed directly with diving and dabbling wildfowl for invertebrate prey in hypertrophic lakes (Giles *et al*. 1990; Hill *et al*. 1987), much as Perch, Yellow Perch or Brook Trout competed with diving and dabbling wildfowl in oligotrophic, acidified lakes (Eadie & Keast 1982; Eriksson 1978, 1979). They also showed that fish removals, i.e. biomanipulation, benefited wildfowl. However, gravel pit lake studies generally used a combination of imprinted ducklings and mesocosms, rather than natural populations in whole lakes as some of the acid precipitation studies had done (but see Giles 1990). These factors, whilst not diminishing the scientific rigour of these studies, limit the insights into wildfowl–fish competition in eutrophic systems that such studies can potentially provide. Before generalising about wildfowl–

Table 2: The main findings of 10 of the biomanipulation studies that focus on wildfowl. 1 = Giles 1990, 2 = Giles 1994, 3 = Giles *et al*. 1990, 4 = Hill *et al*. 1987, 5 = Marklund *et al*. 2002, 6 = Lauridsen *et al*. 1993, 7 = Mitchell & Perrow 1998, 8 = Hanson & Butler 1994, 9 = Andersson & Nilsson 1999, 10 = Cox *et al*. 1998.

Wildfowl	Fish	Invertebrate prey	Location	Methods	Conclusion	Source
Tufted Duck *Aythya fuligula*	Not sampled	Diptera	England	Imprinted duckling dive times.	Bird foraging effort correlated with food density.	1
Tufted Duck	Bream *Abramis brama*, Roach *Rutilus rutilus*, Perch *Perca fluviatilis*, Pike *Esox lucius*	Diptera	England	Fish removal, fish gut samples, invertebrate sampling, duckling counts.	Removing fish increases duckling survival.	2
Not sampled	Bream, Perch, Roach, Tench *Tinca tinca*	Diptera, Bivalvia	England	Fish gut samples.	Fish and wildfowl have overlapping diets.	3
Mallard *Anas platyrhynchos*	Roach, Bream	Diptera, Ephemeroptera	England	Mesocosms at different fish densities, duckling growth rates.	Higher survival/ weight gain for ducklings at low fish densities.	4
Eurasian Coot *Fulica atra*, Mute Swan *Cygnus olor*	Tench, Perch, Roach	Not sampled	Denmark	Fish removed, macrophyte and bird counts, exclosures.	Grazing wildfowl retard macrophyte recovery.	5,6,7

Table 2 continued

Wildfowl	Fish fauna	Invertebrate	Location	Methods	Conclusion	Source
American Coot *F. americana*, Lesser Scaup *Aythya affinis*, Ring-necked Duck *A. collaris*	Yellow Perch *P. flavescens*, Bluegill Sunfish *Lepomis macrochirus*, Bullhead Catfish *Ictalurus* spp.	Diptera, Cladocera, Amphipoda	Minnesota, USA	Fish removed, birds and invertebrates counted before and after.	Birds and their prey increase after fish removal.	8
Eurasian Coot, Mute Swan, Mallard, Tufted Duck, Pochard *A. ferina*	Roach, Bream	Not sampled	Sweden	Fish removed, bird counts before and after.	Birds increase after fish removal.	9
Mallard	Fathead Minnow *Pimephales promelas*	Diptera	North Dakota, USA	Fish and ducklings placed in artificial wetlands, invertebrate densities and duckling growth rates measured.	Duckling body mass & growth rate correlated with invertebrate density.	10

fish competition in eutrophic systems, researchers and managers must look beyond the evidence from gravel pit lakes.

Workers in the Norfolk Broads region of England have used a combination of sediment removal and biomanipulation to restore eutrophic shallow lakes to macrophyte-dominated states over the past three decades (Moss *et al*. 1996; Phillips *et al*. 1999). Although these workers were not focusing directly on wildfowl, their studies provide strong evidence at the whole-lake level that zooplanktivorous fish play a pivotal role in the switches between alternative stable states (Blindow *et al.* 1993; Scheffer *et al.* 1993) commonly seen in eutrophic lakes that wildfowl use.

Hanson & Butler (1994) used rotenone to remove planktivorous (Bluegill Sunfish *Lepomis macrochirus* and Yellow Perch) and benthivorous (Bullhead Catfish *Ictalurus* spp.) fishes from a large shallow North American prairie lake. Biomass of grazing zooplankton increased as expected, and turbidity decreased. Subsequently, a spring clear-water phase developed and allowed development of macrophytes and the invertebrates associated with them. The autumn after fish removal, numbers of diving wildfowl increased from < 5000 to 57,000. Similar effects were seen in biomanipulated lakes in Sweden (e.g. Andersson & Nilsson 1999). Thus, removing assemblages of large and small-bodied fish prompted increases in water clarity and invertebrate densities in eutrophic lakes – characteristics that some acidification-based studies had also shown to be important for wildfowl in oligotrophic lakes (Eadie & Keast 1982; Eriksson 1979, 1983).

This latter evidence for negative effects of planktivorous or benthivorous fish on wildfowl in productive, biomanipulated lakes is a compelling addition to the insights from gravel pit lakes. However, these added insights for wildfowl–fish competition are not as clear as they at first appear. Wildfowl in the Hanson & Butler (1994) study and the Swedish studies were monitored in autumn. The need for invertebrate protein in wildfowl is most critical earlier in spring and summer, when females are laying and ducklings are less than 17 days old (Swanson & Meyer 1977; Swanson *et al*. 1974; Swanson *et al*. 1985; Taylor 1978). Birds in these studies may have been responding directly to the increased quantity of macrophytes available to them following fish removals rather than to invertebrate changes, since they tend to eat more plant materials in autumn than they do earlier in summer (Owen & Black 1990). Thus, these studies, whilst tying wildfowl directly to fish removal at large spatial extents, did not focus on the most appropriate period in wildfowl life cycles as regards competition with fish.

Secondly, some fish removal methods have direct negative impacts on invertebrates, making it difficult to discern the mechanisms of invertebrate change. Drawdown of water to remove fish (Giles 1990) eliminates invertebrates such as Amphipoda, which lack a terrestrial phase in their life cycles and are important wildfowl prey (Swanson *et al*. 1974, 1985). Rotenone causes short-term reductions in some invertebrates (Aldhous 1996). Toxaphene, a polychlorinated camphene once used for fish removals, reduces invertebrate zooplankton predators such as *Chaoborus* spp. for up to a decade after application (Miskimmin & Schindler 1994). Thus, removal of *Chaoborus* and similar predators, not fish, may cause an increase in grazing zooplankton. These complications suggest that fish removal may not necessarily benefit wildfowl in eutrophic lakes, because invertebrates are also lost. This is a direct contrast to the evidence from gravel pit lakes.

In some cases, large predatory invertebrates can replace removed fish, or there is a gradual build-up of large inedible algae because the smaller edible forms are eaten by the more abundant grazing zooplankton. Benndorf *et al.* (2000) term the functional replacement of small fish by large predatory invertebrates 'overbiomanipulation'. In many biomanipulations (e.g. Hanson & Butler 1994), piscivorous fish are also added to keep any surviving planktivorous fish from successfully recolonising the lake. Thus, large predatory invertebrates, such as midge *Chaoborus obscuripes*, are no longer suppressed by competition with planktivorous fish (Benndorf *et al.* 2000). For these reasons, it is widely acknowledged that maintenance of biomanipulated lakes is required to ensure that fish removals are effective for more than a few years (McQueen 1998; Meijer *et al*. 1999; Phillips *et al*. 1999; Sagehashi *et al.* 2000). To the author's knowledge, there are no studies relating the long-term maintenance of biomanipulations to wildfowl.

Adding fish: an alternative insight into wildfowl–fish competition

As outlined above, acidification and biomanipulation give us insights into wildfowl–fish competition for invertebrates because they involve removal or loss of fish from lakes. These insights are clouded because acidification of lakes and biomanipulation of eutrophic lakes can negatively impact invertebrates. Given these caveats, more insight into understanding wildfowl–fish interactions might be gained by following the examples of Giles (1990) and DesGranges & Rodrigue (1986) and monitoring birds' responses to fish addition instead (described above). This would be more relevant to managers dealing with stocking of fish in lakes for sport or bait (Hanson & Riggs 1995), or with recolonisation by planktivorous fish after biomanipulations. Although fish can be reduced to a density at which they are functionally absent from a system (Meijer *et al*. 1999; Sagehashi *et al*. 2000), any interpretation of results from a fish removal must address one or more of the above caveats.

Fish additions are not a new concept in understanding wildfowl foraging ecology (e.g. Cox *et al*. 1998), but they have not been widely used to study wildfowl–fish competition *per se*. Studies that focus purely on fish and invertebrates have used fish additions to show that fish have negative effects on invertebrates (Batzer 1998; Gilinsky 1984). Since many of these studies show negative effects of fish additions on Chironomidae, which are important wildfowl prey (Taylor 1978; Swanson *et al.* 1985), one can extrapolate and say that fish reduce the food available to breeding wildfowl. However, this extrapolation assumes that wildfowl will not switch to alternative prey when fish are added. Acid precipitation studies clearly show that some wildfowl do switch prey in the presence of fish (e.g. Bendell & McNicol 1995).

Cox *et al*. (1998) added Fathead Minnow *Pimephales promelas* to experimentally flooded prairie pothole wetlands to manipulate invertebrate densities, and showed that Mallard duckling body mass and growth rates were positively related to invertebrate densities. However, in spite of using fish as a tool to create invertebrate-poor wetlands, Cox *et al*. (1998) focused only on the fact that their study sites differed in invertebrate biomasses, and only briefly mentioned that wildfowl managers should discourage fish introductions to fishless wetlands. Zimmer *et al*. (2001) also found that Fathead Minnows caused decreases in aquatic insect abundance when they colonised a prairie pothole in North Dakota, USA. However, the authors followed this with conventional rotenone removal and invertebrate monitoring. Zimmer *et al*. (2001) did not focus on wildfowl despite the importance of prairie potholes as wildfowl breeding habitat (Krapu & Reinecke 1992), but from their work it may be inferred that colonising fishes might reduce food for wildfowl.

Recently, McParland (2004) studied wildfowl habitat use before and after fish addition in aspen parkland potholes, which lie immediately north of the prairies. Adding Fathead Minnow and Brook Stickleback *Culaea inconstans* to a pond reduced numbers of gastropods and breeding Blue-winged Teal *Anas discors*. Like prairie potholes, parkland potholes are shallow and naturally eutrophic, and their water levels fluctuate widely with annual fluctuations in precipitation (Nicholson & Vitt 1994). Fish colonise vacant wetlands in wet years and disappear from them in dry years. These variations are one reason for the great diversity of wildfowl in potholes (Krapu & Reinecke 1992). Wildfowl–fish competition has not been well studied in potholes despite their importance as wildfowl breeding habitat. The tendency for fish to colonise fishless waters periodically makes using fish additions to study competition logical in these systems.

Future directions for wildfowl–fish competition research and application

Studies of acidification impacts and biomanipulations have provided a wealth of direct and indirect insights into wildfowl–fish competition in oligotrophic and eutrophic lakes. Given the complexity of invertebrate responses to fish removals or losses described above, it may be more logical at this point in our understanding of wildfowl–fish competition to study fish additions (Cox *et al.* 1998; McParland 2004) or, in systems where they are relevant, natural colonisations (Zimmer *et al.* 2001) instead. This is a more direct test of the hypothesis that reduction of invertebrates by fish significantly affects breeding wildfowl.

Knowledge of the impacts of fish on invertebrates must be more explicitly integrated with patterns of wildfowl habitat use if these studies are to be applied to wildfowl management. Management can conflict with stocking of lakes with sport fish (Hill *et al.* 1987) or bait-fish (Hanson & Riggs 1995), or with acid mitigation (Hunter *et al.* 1986; Rask *et al.* 2001). It is quite reasonable to advise wildfowl managers to avoid stocking fish inappropriately (e.g. Hanson & Riggs 1995). Such advice could be strengthened by fish addition studies. Adding fish to fishless lakes to determine (1) whether invertebrates of importance to wildfowl change in abundance and (2) whether wildfowl use of lakes subsequently changes is one possible next step in understanding wildfowl–fish competition.

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