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Title

Managing ecosystem services at Loch Leven, Scotland, UK: actions, impacts and unintended consequences

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This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to *Hydrobiologia*.

Abstract

Rivers, lakes and wetlands are good examples of ecosystems that provide multiple, concurrent, services to mankind. Human society has often exploited these systems by enhancing one ecosystem service at the expense of another. Loch Leven, Scotland, UK, is a good example of this. Over the past 150 years, the lake has been subjected to hydrological modification, fish stocking and pollution control to improve the delivery of key goods and services. This study uses historical records to explore the results of these interventions on the ecosystem services that were targeted for improvement and the knock-on effects on other services provided by the lake. The results suggest that, when management changes are being considered to enhance particular ecosystem services, the potentially damaging effects on other ecosystem services should be taken into account. This requires a better understanding of the role of ecosystem function in delivering ecosystem services, and of the links between multiple ecosystem services, than is currently available. While further research is clearly needed, the value of long term datasets in providing knowledge and understanding through ‘hindsight’ should not be underestimated. The study concludes that successful management actions are likely to be those that incorporate lessons learned from previous decisions.

Introduction

Lakes, rivers and wetlands are good examples of ecosystems that provide a wide range of ecosystem services at the same time. Ecosystem services are the benefits that people obtain from the natural environment (MEA, 2005). They include provisioning services (e.g. delivery of food, water, pharmaceuticals, energy), regulating services (e.g. carbon sequestration, climate regulation, water purification, disease control), supporting services (e.g. nutrient cycling, seed dispersal, primary production) and cultural services (e.g. providing inspiration, facilitating recreation, enabling scientific discovery). These services are produced by complex processes and interactions that are intimately linked in such a way that the exploitation of one ecosystem service can cause knock-on effects on many others (Heal et al. 2001; Pereira et al. 2005; Reid et al., 2005).

In the past, human society has often exploited these systems by enhancing one ecosystem service at the expense of another. For example, water has been used for consumption, irrigation or transport purposes, with little consideration of the impact that this may have on other services such as food supply, flood control, purification of human and industrial wastes, and provision of habitat to support plant and animal life (Baron et al., 2002). This has led to the degradation or loss of many of the services that mankind depends on, including those that are difficult, if not impossible, to replace (Huisman, 1995). This is an important issue because the degradation or loss of any part of an ecosystem can reduce its resilience, i.e. its capacity to adapt to environmental alterations such as climate change (Folke et al., 2004).

Loch Leven, a shallow eutrophic lake in the lowlands of Scotland, UK, is a good example of a waterbody that supplies a wide range of ecosystem services across local, national and international scales. Over the past 150 years, this system has been subjected to a range of management initiatives that have sought to improve some of the key goods and services provided by the lake. These activities have been carefully documented in terms of their original aims and subsequent outcomes, generating a wealth of historical information that enables us to explore the effects of these management activities with the benefit of hindsight. This study uses these records to investigate, not only the results of management intervention on the ecosystem service that was targeted for improvement, but also the knock-on effects on other services that the lake provides. These results are reviewed in terms of their wider implications for the sustainable management of other complex systems and the ecosystem services that they deliver.

Site description

Loch Leven is a shallow, eutrophic lake lying at about 107 m above sea level in the lowlands of Scotland, UK (56°10'N; 3°30'W). It has a surface area of 13.3 km², and mean and maximum depths of 3.9 m and 25.5 m, respectively (Kirby, 1971). The lake is a world famous trout fishery, internationally recognised conservation area (SSSI, Ramsar, SAC, Natura 2000) and a source of water supply to downstream industry (May & Spears, this volume).

The lake lies within a catchment that covers an area of about 145 km² and ranges in altitude from 107 m.a.o.d to 482 m.a.o.d. Most of the catchment is intensively farmed, with the best quality land being used for high-value potato and vegetable crops, as well as cereal and oilseed rape (Castle et al., 1999). Livestock rearing (cattle and sheep) is mainly restricted to the more upland areas, which tend to be further away from the lake (LLCMP, 1999). However, there is a small area of intensive poultry production near to one of the main inflows, the South Queich. A small amount (*ca.* 11%) of the catchment is wooded and the remainder (*ca.* 2%) is used for habitation.

The catchment is sparsely populated, with only about 11,000 people living in the area (Frost, 1996). Of these, about 60 % live in the towns of Kinross, Milnathort and Kinnesswood (Perth & Kinross Council, 2004), in properties that are served by mains sewerage systems. A further 650 households, in the more remote parts of the catchment, rely upon septic tank systems for the management of their domestic waste (Dudley & May, 2007).

In general, there is little industry within the catchment. However, there have been woollen mills on the banks of one of the main inflows to the lake, the South Queich, since 1840 (Munro, 1994). Until recently, at least one of these mills discharged large quantities of industrial effluent into the lake (D'Arcy, 2006). In addition, sand and gravel extraction is practiced in some areas of the catchment. This is believed to have adversely affected some of the traditional trout spawning beds and nursery areas along the inflows to the lake (Montgomery, 1994).

Management activities to enhance key ecosystem services

Like all lakes, Loch Leven is the 'sink' into which the upstream catchment drains (Baron et al., 2002). As such, both the lake and its catchment are inextricably linked in terms of the wide range of ecosystem services that they provide and the complex nature of their interactions. This study focuses on the key ecosystem services that the lake provides, which are:

Provisioning services

- food (fish)
- water supply to downstream industry

Regulating services

- waste management
- water purification
- flood control

Supporting services

- nutrient cycling
- primary production

Cultural services

- cultural, intellectual and spiritual inspiration

- recreation, tourism and nature conservation
- scientific discovery

Many attempts have been made to enhance some of these services over the last 150 years through targeted management activities. These have focused, primarily, on improving the water supply to downstream industry and enhancing the fishery. However, at the same time, the lake has also been used to process the effluent generated by upstream industry and waste water treatment works (WWTWs). Attempts to enhance the various uses of the lake are reviewed below in relation to their impact on the provision of other ecosystem services, with particular emphasis on conflicts of interest that have arisen amongst stakeholders. Such conflicts have often resulted from the fact that the lake is being used for both provisioning and regulating services at the same time, with the former being dependent upon good water quality and the latter causing a degradation of that water quality. In addition to the above, the economic costs and benefits of these management activities are also noted where sufficient data exist.

Improving water supply to downstream users

Background

Since the early 1700s, Loch Leven has supplied water to downstream industry for use either as a source of power or cooling, or in the manufacturing processes themselves (Munro, 1994). By the 1820s, 40 such industries, including corn mills, sawmills, paper mills, textile mills and bleaching fields, were using water supplied by the lake. As these industries expanded they began to find water in short supply, especially during the summer months. So, it was concluded that there was a need to manage the water from the lake more effectively to support both these industries, and the jobs and income that they provided for the local community.

Various options were considered for improving water supply. Local industrialists preferred the option of raising the level of the lake and, thus, its storage capacity. In contrast, local landowners, whose land would be inundated if the level was increased, strongly supported the alternative option of lowering the level of the lake and building sluice gates to manage the rate of discharge in summer (Munro 1994). It was argued that the latter option would have additional benefits, including the creation of new areas of highly productive farmland around the margins of the lake and the provision of a mechanism for controlling downstream flooding. The second option was approved by an Act of Parliament (1827).

Action

Building and land drainage works began in 1831 to lower the level of the lake and install sluice gates on the outflow. By 1850, the water level had been lowered by about 1.5m (Morgan, 1970), causing its surface area and mean depth to be reduced by 25% and 30%, respectively (Kirby, 1974). From this date onwards, the level of the lake was managed to ensure that the lake was full to capacity (i.e. water level *ca.* 107.3 m.a.o.d.) by late spring. Then, its discharge was controlled to ensure that the level of the lake fell only by about 0.18 m per month over the summer period (May &

Carvalho, 2010). The total cost of these ‘improvements’ was about \$US 60,000 at the time, a final figure that was more than double the original estimate (Munro, 1994). This is equivalent to a present day value of about \$US 4.5M.

Consequences

The drainage works successfully met their primary aim of providing a more stable and reliable water supply to downstream users (Sargent & Ledger, 1992). However, the secondary aim of increasing the area of land available for farming around the margins of the lake was only partially met. These works had been expected to provide an additional 440 ha. of good quality land (Committee for the Society for the Sons and Daughters of the Clergy, 1831), whereas, on completion, it was found that only 265 ha. of poor quality land had been reclaimed. In addition, the associated economic benefits were found to be 75% lower than expected (Munro, 1994).

The drainage works also affected a wide range of other ecosystem services that the lake provided. Firstly, amenity value was reduced because the local landowners claimed ownership of the recovered land and began to prosecute ‘trespassers’ found walking along the shore of the lake (Munro, 1994). Secondly, newly erected fencing on the reclaimed land prevented local villagers having access to peatlands that had long been used as a source of fuel, and to reed beds that had previously provided resources for the thatching of house roofs (Munro, 1994). Thirdly, it was estimated that the value of the fishery had been permanently reduced by about 33%, because the new shoreline was less suitable as a feeding ground for fish (Fleming, 1936), especially pike and brown trout (Winfield et al., this volume). Fourthly, and in contrast to expectation, management of the outflow proved to be more difficult than anticipated and actually increased the incidence of downstream flooding, at least initially. This led to several claims for compensation payments from disgruntled farmers whose land was flooded (Munro, 1994). Finally, the general ecology of the lake was disrupted, with macrophytes such as *Isoetes* and *Chara* being lost (Salgado, 2009), Arctic charr becoming locally extinct (Burns-Begg, 1874), and the numbers of wading birds falling (Munro, 1994).

Enhancing the fishery

Background

Loch Leven has been an important fishery since 1314, when the Abbot of Dunfermline was granted permission to set fishing nets (Thorpe, 1974). In 1633, it was deemed necessary to protect the brown trout (*Salmo trutta* L.) stocks in the feeder streams and a private Act of Parliament, banning poaching, was introduced. By the early 18th century, fish stocks appeared to be thriving, with the lake being declared to be ‘full of fish, particularly the finest trouts in the world’ by Defoe (1723). Throughout the 17th and 18th centuries, fish were caught with nets and sold for local consumption (Thorpe, 1974). However, with the development of the railway in the 19th century, economically viable markets opened up further afield in large cities such as Liverpool, Manchester and London (Munro, 1994) and fishing effort was increased. This increased pressure on the resource.

In contrast to the net fishery, which focused on the consumer market, rod fishing (angling) was introduced as a leisure activity in 1844. Enhanced by the arrival of the railway in the 1850s, the sports fishery had become an important generator of income for the owners by 1859. By the late 1800s, Loch Leven had become a world renowned recreational trout fishery (D'Arcy et al, 2006). In parallel to this development, the importance of net fishing declined, ceasing completely in 1873. Because of the local economic importance of the recreational fishery at Loch Leven, several attempts were made to enhance fish stocks and improve angling catches between the late 1800s and 2006.

Action

A range of management activities were implemented to support the recreational fishery. These are documented in detail by Montgomery (1994) and summarised by Winfield et al. (this volume). The main focus of these activities was fish stocking, with hatchery and rearing ponds coming into use in the mid to late 1800s. By 1882, an estimated 60,000 fry and 4,000 two year old brown trout *per* year, from breeding ponds at the nearby Howietoun fishery (Montgomery, 1994), were being placed in the lake's inflow streams. Although these trout were of "unrecorded origin", it seems likely that the original source of fish for this hatchery was Loch Leven (Day, 1887) because many of the ova produced were marketed as such and exported across the world. By the 1920s and early 1930s, up to 300,000 fry were being released each year. It seems likely that these, too, were reared from local stocks (Montgomery, 1994).

The hatchery closed in the late 1930s, but reopened in 1983 following a dramatic decline in fishery performance (Winfield et al., this volume). In that year, 5,000 fish of local origin were stocked directly into the lake (Montgomery, 1994). The number of stocked trout increased each year until 1988, when 166,000 were introduced. Levels of stocking remained in excess of 100,000 brown trout *per* year until 2004, when the number was reduced to 5,000. Stocking with brown trout was discontinued in 2006. In addition to stocking with brown trout, 30,000 non-native rainbow trout (*Oncorhynchus mykiss*) were introduced *per* year between 1993 and 2004 in an attempt to reduce the on-going decline of the fishery and reflect changes in angler preferences (Winfield et al., this volume).

Consequences

It is difficult to assess the benefits of the stocking programme that was undertaken between 1882 and 1936 to the fishery, because there are few records of fish catches over that period. However, the reintroduction of fish stocking in the 1980s does seem to have been partially effective in that it appears to have slowed down the long-term decline in fish catches at the lake, for a few years at least (Winfield et al., this volume). Nevertheless, this apparent response was short-lived and catches began to decline further in the early 1990s.

The introduction of rainbow trout in the early 1990s was, initially, deemed a success from a fisheries point of view, because the catch of rainbow trout almost equalled that of brown trout in the first year of stocking and then greatly exceeded it in subsequent years (Winfield et al., this volume). However, by 2003, this figure had fallen

dramatically and, with only about 10% of the stocked fish being caught by anglers, stocking with rainbow trout was suspended (Montgomery, 2004). By this time, the fishery was losing more than \$US 150,000 *per year* and its operations were scaled down by about 75% (Loch Leven Fisheries, *pers. comm.*).

It was concluded that fish stocking had been ineffective in improving the economic value of the Loch Leven fishery in the longer term. Baer & Brinker (2010) came to a similar conclusion when studying the development of the brown trout fishery in the River Wutach, Germany, after fish stocking ceased in 2001. The results of these studies suggest that augmentation of a natural fishery with stocked individuals does not, necessarily, result in an improvement in the fishery or in angler satisfaction.

The reason for the failure of fish stocking to improve the fishery at Loch Leven is unclear. A range of theories have been suggested, but the one that has received most public attention, and caused most controversy, is the assertion that stocking the lake with small fish may have simply attracted more fish eating birds, primarily cormorants (*Phalacrocorax carbo*), to the site. While Wright (2003) concluded that cormorants had no effect on brown trout abundance or fishery performance in Loch Leven, Stewart et al. (2005) estimated that cormorants probably consumed about 80,800 brown and 5,200 rainbow trout over a seven month period. These results suggested that there was considerable potential for competition between the birds and the fishery for available fish. Stewart et al. (2005) also found a relationship between the level of brown trout stocking in spring and the abundance of cormorants on the lake the following winter. This added weight to the argument that increased stocking may have attracted more cormorants to the lake, causing an increase in predation that negated any of the potential benefits that the stocking programme could have had on fishery yield. As there is considerable uncertainty about the size of the fish populations in Loch Leven, it is not possible to estimate the impact of piscivorous birds on the trout population as a whole (Winfield et al., [this volume](#)). However, the figures obtained by Stewart et al. (2005) indicated that almost 20% of the Rainbow trout stocked into the lake by fisheries managers were being removed by cormorants. This equates to an economic cost of about \$US 7,100 per year (Loch Leven Fisheries, *pers. comm.*).

The introduction of the rainbow trout coincided with an apparent change in the ecosystem functioning of the lake, as reflected by a significant increase in the chlorophyll *a*:total phosphorus (TP) ratio from the early 1990s onwards (Figure 1). This may reflect changes in grazing pressure on algae from the zooplankter, *Daphnia*, which forms part of the diet of rainbow trout at this site (Duncan, 1994). Therefore, stocking with rainbow trout may have increased the likelihood of algal blooms developing in the lake at the same time as significant sums of money, i.e. about \$US 7.1M, were being invested in reducing the likelihood of algal blooms by lowering the nutrient input to the lake from sources within the catchment (May et al., [this volume](#)).

Finally, stocking the lake with brown trout from the Howietoun rearing ponds in the late 1800s, or with imported rainbow trout between 1993 and 2004, may have affected the biodiversity of the resident fish population. However, the rainbow trout populations were unable to establish a viable population, and any introduced trout

were of the same species as those already in the lake. So, the fish stocking programme probably had less of an impact on the biodiversity of the system than some of the other management activities implemented, such as lowering the level of the lake and controlling the outflow (see above).

Better management of waste from industry and WWTWs

Background

In the early 1800s, the catchment of Loch Leven underwent a significant increase in population size. The local town of Kinross, for example, grew from about 2,100 inhabitants in 1801 to more than 3,200 inhabitants in 1851. This, together with an associated increase in local industries and more intensive farming activity within the catchment, led to more polluted effluent and runoff entering the lake *via* its inflows. At that time, there was an underlying assumption that the natural drainage system would simply carry the waste away, and little consideration was given to the likely impacts of these discharges on the lake and the ecosystem services that it provides.

The development of textile mills on one of the main inflows, the South Queich, has been a particular problem in terms of impacts on water quality and ecosystem services. One of these mills, which was established in 1867 and continues to the present day (Munro, 1994), discharged high levels of phosphorus (P) and pesticides into the lake for many years. The P-laden effluent resulted from manufacturing processes that used sodium hexametaphosphate, tetrasodium pyrophosphate and phosphoric acid (Holden & Caines, 1974), while the pesticide residues resulted from the use of the mothproofing agents Dielmoth (Dieldrin) from the 1950s to 1964, Eulan WANEW (Chlorphenylid) from 1964 to 1980 and Mitin LP (Chlorphenylid & Flucofenwon) from 1980-1988 (D'Arcy et al., 2006). Discharges of P from this source amounted to 2.6 – 7.8 t P y⁻¹ in the late 1960s/early 1970s (Holden & Caines, 1974) and about 6.3 t P y⁻¹ by the mid 1980s (Bailey-Watts et al., 1987), i.e. about 50-60% of the annual P input to the lake in the earlier years and about 30% of the input in the later years. The exact level of discharge of pesticide residues is unknown.

Treated effluent from WWTWs within the catchment was also a significant source of P input to the lake. In the late 1960s/early 1970s, this contribution was estimated to be about 1.7 t P y⁻¹, or 20% of the total P input to the lake (Holden & Caines, 1974). By 1985, this figure had risen to 5.3 t P y⁻¹, or 27% of the total input (Bailey-Watts et al., 1987). Other sewage related sources, such as septic tanks, have also been estimated to contribute 10-14% of the overall P input to this system (Frost, 1996; Dudley & May, 2007).

Using the lake and its inflows for the disposal of both nutrient laden waste and pesticide discharges had a marked detrimental effect on the lake's ecological structure. The increased supply of P resulted in excessive algal growth (Bailey-Watts et al. 1987), while pesticide residues (especially from dieldrin) appear to have reduced the ability of *Daphnia* to control algal biomass through grazing (Holden, 1966; D'Arcy, 2006). Although the evidence for the latter is mainly circumstantial, it is clear that *Daphnia*, which had been common in the lake before the 1950s (Scott, 1891, 1899; Morgan, 1970), disappeared from the system at about the same time as the mill began

discharging dieldrin. It reappeared in the early 1970s (Leven IBP Project Report, 1970 - 1971), when these discharges had stopped and levels in the lake, as indicated by fish tissue analyses, had dropped by about 99% (Wells & Cowan, 1984).

Together, the two pollutants described above appear to have encouraged troublesome algal blooms to develop in the lake by increasing algal productivity and reducing grazing losses at the same time. These blooms decreased water clarity, lowering the aesthetic, economic and amenity values of the lake, and reducing the depth to which rooted, submerged vegetation was able to grow (May & Carvalho, 2010; Dudley et al., this volume). The blooms also limited the ability of the lake to support other ecosystem services, such as supplying clean water and providing good quality habitat for aquatic birds, especially those that are dependent on underwater plants (Allison & Newton, 1974). By the early 1980s, it had become clear that management intervention was required to improve the water quality of the lake and the wide range of ecosystem services that had been damaged by both nutrient pollution and pesticide residues. Although the economic cost of the earlier water quality problems have not been documented, it has been estimated that a single algal bloom in 1992 cost the local community more than \$US 1.5M in lost revenue over a single summer period.

Action

Although several different mothproofing agents had been used by the woollen mill and discharged into the lake over many years, the main ecological impacts seem to have been related to the use/discharge of Dielmoth (dieldrin) from the early 1950s until 1964. This product was initially replaced by other mothproofing agents (see above) but, in 1988, the mill voluntarily stopped using mothproofers altogether (D'Arcy et al., 2006).

Phosphorus inputs to the lake were reduced significantly between 1985 (*ca.* 20 t y⁻¹) and 1995 (*ca.* 8 t y⁻¹) (Bailey-Watts & Kirika, 1999), mainly by reducing outputs from the mill and the WWTWs. The former was achieved initially by effluent diversion and then by changing the chemical processes used; the latter was achieved by upgrading the works and introducing tertiary treatment (i.e. P-stripping). The total cost of these improvements was estimated to be more than \$US 6.5M (LLCMP, 1999). In addition to controlling these larger point source discharges of P, households in rural areas of the catchment were also encouraged to manage their septic tanks more effectively, and more stringent planning regulations were put into place to reduce the likelihood of P discharges from new housing developments in unsewered areas polluting the lake (LLCMP, 1999; Dudley & May, 2007).

Consequences

Reducing the discharge of dieldrin based pesticides to the lake had a significant effect on ecosystem functioning. *Daphnia*, the main grazer of algae in the lake and an important source of food for fish, re-appeared in the summer of 1970 and, by July 1971, had achieved a maximum population density of 74.4 ind. l⁻¹ (Johnson & Walker, 1974). Although there is no direct evidence of this link, *Daphnia* are known to be particularly sensitive to some pesticides because they accumulate larger amounts of these substances in their body tissue than other aquatic invertebrates (Walsh, 1978).

Daphnia magna, for example, concentrated photodieldrin by a factor of x 63,000 when exposed to contaminated media by Khan & Khan (1974) and their reproductive ability was inhibited when they were exposed to other pesticides, such as DDT, by Maki & Johnson (1975). Sprules (1975) has shown that zooplankton species vary in their sensitivity to pollutants and that this can affect community structure. It seems likely that dieldrin pollution had a similarly differential effect on zooplankton species composition in Loch Leven, reducing the number of *Daphnia* significantly while apparently having little impact on other species such as *Cyclops* (Johnson & Walker, 1974). Even though the discharge of dieldrin stopped in 1964, low, but discernable, concentrations of up to 26 $\mu\text{g kg}^{-1}$ were still being detected within the crustacean zooplankton community up to 15 years later (Wells & Cowan, 1984).

In addition to the potential impact of pesticides on *Daphnia*, fish from the lake were found to have relatively high dieldrin concentrations in both their muscle and liver tissues during the 1960s (Holden, 1972). In 1964, those levels amounted to 0.34 mg kg^{-1} and 0.3 mg kg^{-1} , respectively, for trout, 0.78 mg kg^{-1} and 1.2 mg kg^{-1} , respectively, for perch, and 0.38 mg kg^{-1} and 6.1 mg kg^{-1} , respectively, for pike (Wells & Cowan, 1984). Following the change from dieldrin to Eulan WANew in 1964, fish tissue samples analysed between 1963 and 1970 showed a steady decline in dieldrin concentrations, with levels of residue having fallen by 99% after 4-7 years (Wells & Cowan, 1984). Although the biological effect of dieldrin on the ecology of the fish populations is unclear, the fact that they were known to be contaminated probably reduced the value of the fishery amidst concerns about the health risks to anglers of eating contaminated catches (D'Arcy, 2006).

As a result of this sudden increase in *Daphnia* abundance in the early 1970s, grazing losses increased and chlorophyll *a* concentrations fell (Bailey-Watts, 1974). This led to a significant lowering of the chlorophyll *a*:TP ratio in the lake (Figure 1) and an associated reduction in the frequency of algal blooms. This caused a temporary improvement in water clarity and an increase in the abundance of submerged macrophytes (Johnson & Walker, 1974; [Dudley et al., this volume](#)). However, as P inputs to the lake continued to increase ([May et al., this volume](#)), algal growth outstripped loss processes, even with the increase in zooplankton grazing, and algal blooms became more common, again.

Amidst concerns about the continuing decline in water quality at the lake, and its impacts on the fishery, tourism and downstream industry, targets were set for the restoration of this waterbody in 1993. These were based on P and chlorophyll *a* concentrations, water clarity and macrophyte growing depths (D'Arcy et al., 2006; [Carvalho et al., this volume](#)). However, when P discharges from WWTWs and the mill were reduced by 60% between 1993 and 1999, the expected recovery in water quality did not occur immediately. Instead, a prolonged recovery trajectory was observed as a result of internal release of phosphorus from the lake sediments (Spears et al., this volume). During the recovery phase, open water P concentrations have fallen ([Carvalho et al., this volume](#)), water clarity has increased (especially in spring), and submerged macrophytes have been observed to recolonise deeper areas of the lake (May & Carvalho, 2010). These improvements were associated with increases in species composition and abundance of macrophytes and invertebrates ([Dudley et al.,](#)

this volume; Gunn et al., this volume) and an improvement in the habitat available to fish communities (Winfield et al., this volume).

Conflicts and trade offs

Throughout the documented history of management intervention at Loch Leven, it is clear that changes focused on improving one particular ecosystem service have been made with little or no prior consideration of the knock-on effects on others. In some cases, these effects have been significant. The most important of these are summarised below.

The impact of the drainage works on ecosystem services at Loch Leven is summarised in Figure 2. While these works improved the water supply to downstream industry, resulting in economic benefits to mill owners as intended, they did not deliver the expected increase in good quality farmland, better control of downstream flooding or economic benefits to local landowners. Instead, changes in the water level of the lake led to increased downstream flooding, the loss of marginal macrophyte beds, damage to fish habitat and food supply, and lower amenity value. In addition, fencing of reclaimed areas of land restricted the access of local people to traditional sources of fuel and building materials.

Fish stocking aimed to boost the fishery in terms of increasing angling catches and improving its economic value. However, there is little evidence that either of these aims was achieved successfully and it is possible that this activity may have led to detrimental effects on other ecosystem services provided by the lake. These include reducing the ability of *Daphnia* to control algal blooms through their grazing activity, lowering the aesthetic and economic value of the lake by attracting large numbers of cormorants, and undermining the conservation value of the lake through the introduction of non-native species. These effects are summarised in Figure 3.

Using Loch Leven and its tributaries to dispose of nutrient and pesticide wastes from industry and WWTWs also affected the ecosystem services that the lake provides. When these inputs were reduced, P concentrations decreased, water clarity improved (at least in spring) due to the re-appearance of key zooplankton grazers, and macrophytes began to grow in deeper water. In addition, the level of pesticide residues within the zooplankton and fish communities fell, more extensive macrophyte beds developed providing a better habit for fish and their invertebrate food, and the biodiversity of many plant and animal communities increased. These responses are summarised in Figure 4.

The results outlined above, and summarised in Table 1, clearly demonstrate that management for the benefit of one ecosystem service can often be at the expense of a whole range of others, as suggested by Holling & Meffe (1996). So, it is important to understand the relationships that exist across all of the services that an ecosystem provides before deciding on an appropriate management strategy. Balancing these effects, or considering ecosystem service ‘trade-offs’, must take into account the type, magnitude, and relative mix of services that ecosystems can provide under different management scenarios. However, realistically, such informed decision making can only be applied effectively to systems that are well understood; if not, other ‘trade-

offs' may arise without premeditation or even awareness that they are taking place, leading to unwelcome, unexpected or unintended consequences (Rodríguez et al., 2006). In managing these trade-offs, human preferences tend to focus first on provisioning services, then on regulating, cultural, and supporting services, in that order (Foley et al., 2005; Pereira et al., 2005; Rodríguez et al., 2006; van Jaarsveld et al., 2005), the latter generally being "taken for granted" (Rodríguez, et al 2006). This approach is unlikely to provide sustainable solutions to the management of ecosystem services, as this study on Loch Leven demonstrates.

Discussion

The results from the long term monitoring studies at Loch Leven clearly show that the management of ecosystem services often results in unexpected or unintended consequences, especially if the complexity of the system being managed is not sufficiently well understood. Such outcomes show that the so-called 'law' of unintended or unanticipated consequences (Merton, 1936; Norton, 2010), which is widely used in the social sciences (e.g. economics, history, philosophy, political science, and sociology) but less commonly applied to the environmental sciences, is equally applicable to the management of lakes. The wide range of examples given by Tenner (1997) in his book entitled "Why things bite back: Technology and the revenge of unintended consequences", provide further evidence of the wide applicability of this concept.

Although unintended consequences can be either positive or negative, the 'law' of unintended consequences warns that intervention in a complex system without taking into consideration the relationships between one component and another always creates unanticipated, and often undesirable, results. Merton (1936) suggests that there are five possible causes of unexpected consequences when management actions are planned and implemented. These are as follows:

- Lack of knowledge, leading to incomplete analysis of the problem
- Error, leading to incorrect analysis of the problem
- Immediate interest, which may override long-term interests
- Basic values, which may prohibit certain actions even if the long-term result might be unfavorable
- Self-defeating prophecy, whereby fear of the consequences drive people to find solutions before the problem occurs

The examples from Loch Leven illustrate how the management of ecosystem services in the natural environment can lead to a wide range of unintended consequences. In particular, they show how Causes 1-3, i.e. lack of knowledge, incorrect analysis of the problem and addressing immediate (especially economic) interests, can cause a wide range of problems that threaten the long-term sustainability of the system and the services that it provides. In contrast, Causes 4 and 5 have been less applicable to problems that have arisen from management intervention at this site over the years.

When unintended consequences occur, it is often difficult to turn back the clock. At Loch Leven, for example, the drainage works and consequent change in water level caused a wide range of ecological and hydrological problems, but it is unlikely that

this significant amount of engineering work will ever be reversed. Even if it were, it is doubtful that this would result in the complete restoration of the lake's ecology to pre-drainage conditions without considerable management intervention. This issue of reversibility, which is very important when considering restoration options for impacted ecosystems, has also been raised in relation to the management of many other systems such as the River Rhine. Husiman (1995) showed that the concept of reversibility, i.e. the "clean up the water and life will return" approach, did not work when waste water treatment was improved and levels of pollution in the river were reduced. He concluded that damaged ecosystems and the services that they provide could only be restored through a significant change of approach, i.e. from a one-sided promotion of individual interests to a more integrated and sustainable method of management.

It is now generally accepted that the ecological structure and function of lakes will be altered as a result of anthropogenic climate change (Carpenter et al., 1992). In Loch Leven, climate induced changes in ecological structure are expected to be driven mainly by wind speed and direction (Spears & Jones, 2010), temperature (Carvalho et al., this volume) and rainfall (Carvalho et al., this volume). Additionally, the performance of pivotal ecosystem functions such as internal nutrient cycling (Spears et al., 2008; Spears et al., this volume), zooplankton seasonality and abundance, and, therefore, grazing pressure (Ferguson et al., 2008), are expected to vary in Loch Leven as a result of climate change. However, the importance of other key drivers of biodiversity, including land use change, atmospheric deposition and biotic exchange (which is expected to be the most important driver of global freshwater biodiversity loss in this century according to Sala et al., 2000), are not well understood in Loch Leven. It is clear that in order to mitigate against decline, and ideally to maximise the future provision of ecosystem services in Loch Leven, a better understanding of the drivers of feedbacks between biodiversity and ecosystem functioning is required (Covich et al., 2004).

Conclusion

More than 40 years ago, Ehrlich and Ehrlich (1970) correctly warned mankind that "the most subtle and dangerous threat to man's existence ... is the potential destruction, by man's own activities, of those ecological systems upon which ... the human species depends". For this reason, when management changes aimed at enhancing one particular ecosystem service are being considered, it is important that potentially damaging effects on others are also taken into account. In practice, taking this approach requires a better understanding of the role and complexity of ecosystem function, and of species interactions in delivering ecosystem services, than is currently available. While further research is clearly needed, the value of long term datasets in providing knowledge and understanding through 'hindsight' should not be underestimated. Valuable insight can be gained from studies such as that on Loch Leven to help ensure that future decision making takes into consideration the full range of benefits expected and the likelihood of unintended, especially harmful, effects on the delivery of other ecosystem services. Our results support the view of Rodriguez et al. (2006) that, in the longer term, successful management policies are likely to be those that incorporate lessons learned from previous decisions into future management actions.

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References

Act of Parliament, 1827. The River Leven Improvement Act.

Allison, A. & I. Newton, 1974. Waterfowl at Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh*, B, 74: 365-381.

Bailey-Watts, A. E., 1974. The algal plankton of Loch Leven, Kinross. *Proceedings of the Royal Society Edinburgh*, B, 74: 136 - 156.

Bailey-Watts, A. E. & A. Kirika, 1987. A re-assessment of the phosphorus inputs to Loch Leven (Kinross, Scotland): rationale and an overview of results on instantaneous loadings with special reference to runoff. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 78: 351-367.

Bailey-Watts, A. E. & A. Kirika, 1999. Poor water quality in Loch Leven (Scotland) in 1995, in spite of reduced phosphorus loadings since 1985: the influences of catchment management and inter-annual weather variation. *Hydrobiologia* 403: 135-151.

Baer, J. & A. Brinker, 2010. The response of a brown trout stocks and perception of anglers to cessation of brown trout stocking. *Fisheries Management and Ecology* 17: 157-164.

Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, N. G. Hairston, R. B. Jackson, C. A. Johnston, B. D. Richter & A. D. Steinman, 2002. Meeting ecological and societal needs for freshwater. *Ecological Applications* 12: 1247-1260.

Burns-Begg, R., 1874. *The Loch Leven angler*. Barnett, Kinross, U.K.

Carvalho, L., C. Ferguson, I. Gunn, H. Bennion, B. Spears, A. Kirika & L May, this volume. Water quality of Loch Leven: responses to enrichment, restoration and climate change. *Hydrobiologia* 0: 000-000.

Carpenter, S. R., S. G. Fisher, N. B. Grimm & J. F. Kitchell, 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23: 119-139.

Castle, K., C. A. Frost & D. F. Flint, 1999. The Loch Leven Project – Buffer strips in practice on a catchment scale. *Aspects of Applied Biology* 54: 71-78.

Committee for the Society for the Sons and Daughters of the Clergy, 1839. The New Statistical Account of Scotland: Fife, Kinross.

Covich, A., M. C. Austen, F. Barlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner & B. Moss, 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54: 767-775.

D'Arcy, B. J., L. May, J. Long, I. R. Fozzard, S. Greig & A. Brachet, 2006. The restoration of Loch Leven, Scotland, UK. *Water Science Technology* 53: 183-91.

Day, F., 1887. On the Loch-Leven trout (*Salmo levenensis*). *Journal of the Linnaean Society of London, Zoology* 20: 71-90.

Defoe, D., 1723. *A Journey through Scotland*. London.

Dudley, B., I. D. M. Gunn, L. Carvalho, I. Proctor, M. T. O'Hare, K. J. Murphy & A. Milligan, this volume. Changes in aquatic macrophyte communities in Loch Leven – evidence of recovery from eutrophication? *Hydrobiologia* 0: 000-000.

Dudley, B. & L. May, 2007. Estimating the phosphorus load to waterbodies from septic tanks. Report to the Scottish Environment Protection Agency and Scottish Natural Heritage, 45 pp.

Duncan, W., 1994. The fish community in Loch Leven. In Hutchinson, P. & A. Walker (eds), *The Loch Leven Trout Fishery - its Future*. Institute of Fisheries Management, Pitlochry: 29-38.

Ehrlich, P. R. & A. Ehrlich, 1970. *Population, resources, Environment: Issues on Human Ecology*. W.H. Freeman, San Francisco.

Ferguson, C. A., L. Carvalho, E.M. Scott, A. W. Bowman & A. Kirika, 2008. Assessing ecological responses to environmental change using statistical models. *Journal of Applied Ecology* 45: 193-203.

Fleming, J., 1936. Interim report by the Reverend Dr Fleming as valuator of the damage done to the fishings by the drainage of Loch Leven, Kinross. Manuscript, Sheriff Court, Kinross.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F.S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty & P. K. Snyder, 2005. Global consequences of land use. *Science* 309: 570–574.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, C. S. Holling, 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics* 35: 557-581.

- Frost, A., 1996. Loch Leven and diffuse pollution. In Petchey, A., B. D'Arcy & C. Frost (eds.), Diffuse pollution and agriculture. Scottish Agricultural College, Aberdeen: 174-182.
- Gunn, I. D. M., M. T. O'Hare, P. S. Maitland & L. May, this volume. Trends in Loch Leven invertebrate communities. *Hydrobiologia* 0: 000-000.
- Heal, G., G. C. Daily, P. R. Ehrlich, J. Salzman, C. Boggs, J. Hellman, J. Hughes, C. Kremen & T. Ricketts, 2001. Protecting natural capital through ecosystem service districts. *Stanford Environmental Law Journal* 20:333–364.
- Holden, A. V., 1966. Organochlorine insecticide residues in salmonid fish. *Journal of Applied Ecology* 3 (Supplement): 45 - 53.
- Holden, A. V., 1972. The effects of pesticides on life in freshwater. *Proceedings of the Royal Society London, Series B* 180: 383 – 394.
- Holden, A. V. & L. A. Caines, 1974. Nutrient chemistry of Loch Leven. *Proceedings of the Royal Society Edinburgh (B)*: 101 - 122.
- Holling, C. S. & G. K. Meffe, 1996. Command and control and the pathology of natural resource management. *Conservation Biology* 10:328–337.
- Huisman, P., 1995. From one-sided promotion of individual interests to integrated water management in the Rhine basin. *Water Science and Technology* 31: 59-66.
- Johnson, D. & A. F. Walker, 1974. The zooplankton of Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh (B)* 74: 285-294.
- Khan, H. M. & M. A. Q. Khan, 1974. Biological magnification of photodieldrin by food chain organisms. *Archives of Environmental Contamination and Toxicology* 2: 289 – 301.
- Kirby, R. P., 1971. The bathymetrical resurvey of Loch Leven, Kinross. *Geography Journal* 137: 372–378.
- Kirby, R. P., 1974. The morphological history of Loch Leven, Kinross. *Proceedings of the Royal Society Edinburgh, B*, 74: 57 - 68.
- LLCMP, 1999. Loch Leven Catchment Management Plan: The Report of the Loch Leven Area Management Advisory Group, 93 pp.
- Loch Leven IBP Project Report, 1970-1971, 22 pp.
- McMichael, M. T., P. Pingali, C. Samper, R. Scholes, R. T. Watson, A. H. Zakri, Z. Shidong, N. J. Ash, E. Bennett, P. Kumar, M. J. Lee, C. Raudsepp-Hearne, H. Simons, J. Thonell & M. B. Zurek, 2005. Millennium Ecosystem Assessment. Island Press, Washington.

Maki, A. W. & H. E. Johnson, 1975. Effects of PCB ('Aroclor' 1254) and p,p'-DDT on production and survival of *Daphnia magna* Strauss. Bulletin of Environmental Contamination and Toxicology 13: 412 – 416.

May, L. & L. Carvalho, 2010. Maximum growing depth of macrophytes in Loch Leven, Scotland, United Kingdom, in relation to historical changes in estimated phosphorus loading. Hydrobiologia 646: 123 – 131.

May, L., L. Carvalho, I.D.M. Gunn & A. Kirika, 2007. The impact of trophic interactions on the recovery of Loch Leven after reduction in phosphorus loads. In Heckrath, G., G. H. Rubæk & B. Kronvang (eds.), Diffuse Phosphorus Loss. Risk assessment, mitigation options and ecological effects in river basins. Aarhus, Denmark, National Environment Research Institute, University of Aarhus, 71-73, 4pp. (DJF Plant Science, 130).

May, L., L. H. Defew, H. Bennion & A. Kirika (this volume) Historical changes in external phosphorus loads to Loch Leven, 1905 to 2005. Hydrobiologia 0: 000-000.

May, L. & B. M. Spears (this volume) A history of scientific research at Loch Leven. Hydrobiologia 0: 000-000.

Merton, R. K., 1936. The unanticipated consequences of purposive social action. American Sociological Review 1: 894 – 904.

Millennium Ecosystem Assessment (MEA), 2005. Ecosystems and Human Well-Being: Wetlands and Water Synthesis. World Resources Institute, Washington, DC.

Montgomery, D., 1994. Management of the Loch Leven trout fishery. In Hutchinson, P. & A. Walker (eds), The Loch Leven Trout Fishery - its Future. Institute of Fisheries Management, Pitlochry: 26-28.

Montgomery, J., 2004. Loch Leven Fisheries – Executive Summary, 7 pp.

Morgan, N. C., 1970. Changes in the fauna and flora of a nutrient enriched lake. Hydrobiologia 35: 545 -553.

Munro, D., 1994. Loch Leven and the River Leven – A landscape transformed. The River Leven Trust, Markinch, 196 pp.

Norton, R., 2010. Unintended Consequences. The Concise Encyclopedia of Economics, Library of Economics and Liberty.

Perth & Kinross Council, 2004. Kinross Area Local Plan 2004. 106 pp.

Pereira, H. M., B. Reyers, M. Watanabe, E. Bohensky, S. Foale, C. Palm, M. V. Espaldon, D. Armenteras, M. Tapia, A. Rincón, M. J. Lee, A. Patwardhan & I. Gomes, 2005. Condition and trends of ecosystem services and biodiversity. In Capistrano, D., C. Samper, M.J. Lee & C. Raudsepp-Hearne (eds), Ecosystems and human well-being: multi scale assessments, Volume 4. Findings of the Sub-global

Assessments Working Group of the Millennium Ecosystem Assessment. Island Press, Washington.

Reid W. V., H. A. Mooney, A. Cropper, D. Capistrano, S. R. Carpenter, K. Chopra, P. Dasgupta, T. Dietz, A. K. Duraiappah, R. Hassan, R. Kaspersen, R. Leemans, R. M. Rodríguez, J. P., T. D. Beard Jr., J. Agard, E. Bennett, S. Cork, G. Cumming, D. Deane, A. P. Dobson, D. M. Lodge, M. Mutale, G. C. Nelson, G. D. Peterson & T. Rodríguez, J. P., T. D. Beard Jr., E. M. Bennett, G. S. Cumming, S. Cork, J. Agard, A. P. Dobson & G. D. Peterson, 2006. Trade-offs across space, time, and ecosystem services. *Ecology and Society* 11: 28. [online] URL: <http://www.ecologyandsociety.org/vol11/iss1/art28/>

Sargent, R. J. & D. C. Ledger, 1992. Derivation of a 130 year runoff record for the Loch Leven catchment, south-east Scotland. *Proceedings of the Institute of Civil Engineers Water, Maritime and Energy* 96: 71–80.

Salgado, J., S. Sayer, L. Carvalho, T. Davidson & I. Gunn, 2009. Assessing aquatic macrophyte community change through the integration of palaeolimnological and historical data at Loch Leven, Scotland. *Journal of Paleolimnology* 43: 191 - 204.

Sala, O.E., F.S. Chapin, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker & D.H. Wall, 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Scott, T., 1891. The invertebrate fauna of the inland waters of Scotland. Part II. In 9th Annual Report of the Fisheries Board of Scotland, Part III: 269 – 296.

Scott, T., 1899. The invertebrate fauna of the inland waters of Scotland – report on special investigation. In 17th Annual Report of the Fisheries Board of Scotland, Part III: 161 - 165.

Spears, B. M., L. Carvalho, R. Perkins, & D. M. Paterson, 2008. The effects of light on sediment nutrient flux and water column nutrient stoichiometry in a shallow lake. *Water Research* 42: 977-986.

Spears, B. M., L. Carvalho, R. Perkins, A. Kirika & D. M. Paterson (this volume) Long-term variation and regulation of internal loading in Loch Leven. *Hydrobiologia* 0: 000-000.

Spears, B. M. & I. Jones, 2010. The long-term (1979-2005) effects of the north atlantic oscillation on wind induced wave mixing in Loch Leven (Scotland). *Hydrobiologia* 646: 49-59.

Sprules, W.G., 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. *Journal of the Fisheries Research Board of Canada* 32: 389 – 395.

Stewart, D. C., S. J. Middlemas, W. R. Gardiner, S. Mackay & J. D. Armstrong, 2005. Diet and prey selection of cormorants (*Phalacrocorax carbo*) at Loch Leven, a major stocked trout fishery. *Journal of the Zoological Society of London* 267: 191-201.

Tenner, E., 1997. *Why things bite back: Technology and the revenge of unintended consequences*. Vantage Books.

Thorpe, J. E., 1974. Trout and perch populations at Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh, B*, 74: 296-313.

van Jaarsveld, A. S., R. Biggs, R. J. Scholes, E. Bohensky, B. Reyers, T. Lynam, C. Musvoto & C. Fabricius, 2005. Measuring conditions and trends in ecosystem services at multiple scales: the Southern African Millennium Ecosystem Assessment (SAfMA) experience. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360: 425–441.

Walsh, G. E., 1978. Chapter 12: Toxic Effects of Pollutants on Plankton. In *Principles of Ecotoxicology*, pp. 257 – 274.

Wells, D. E. & A. A. Cowan, 1984. Fate and Distribution of the Mothproofing Agents Dieldrin and Eulan WA New in Loch Leven, Kinross, 1964-1979. *Environmental Pollution (Series B)* 7: 11-33.

West G., 1910. A further contribution to a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habitat in Scottish lakes. *Proceedings of the Royal Society of Edinburgh* 30: 65-181.

Winfield, I. J., Adams, C. E., Armstrong, J. D., Gardiner, R., Kirika, A., Montgomery, J., Spears, B. M., Stewart, D.C., Thorpe, J.E. & Wilson, W. (this volume). Changes in the fish community of Loch Leven: untangling anthropogenic pressures. *Hydrobiologia* 0: 000-000.

Wright, G. A., 2003. Impact of cormorants on the Loch Leven trout fishery and the effectiveness of shooting as mitigation. In Cowx, I. G. (ed), *Interactions between fish and birds: implications for management*. Fishing News Books, Blackwell Scientific Publications, Oxford: 288-297.

Table

Table 1. Summary of the positive (+), negative (-) and neutral (+/-) effects of management for the benefit of one key ecosystem service (Column 1) at Loch Leven on the provision of other such services (Row 1).

	Water supply	Waste management	Flood control	Recreation
Water supply	+	-	-	-
Waste management	-	+	+/-	-
Flood control	-	-	+	-
Recreation	+/-	-	-	+

Figure captions

Fig. 1 Chlorophyll *a*:total phosphorus (TP) ratio in Loch Leven showing changes that occurred when *Daphnia* re-appeared in the early 1970s and when rainbow trout were introduced in 1993. Differences in three treatment populations (i.e. 1964-1972: mean = 0.95, standard deviation (s.d.) = 0.15); 1973-1992: mean = 0.52, s.d. = 0.12; 1993-2008: mean = 0.66, s.d. = 0.13) were tested using analysis of variance (total degrees of freedom = 41; $F = 30.35$; $p < 0.001$). Each population was assumed to be normally distributed (i.e. $p > 0.05$) following an Anderson-Darling test. Tukey *post-hoc* analysis indicated significant differences between all populations (after May et al., 2007).

Fig. 2 Summary of the impacts of water level change and outflow management on ecosystem services at Loch Leven.

Fig. 3 Summary of the impacts of fish stocking on ecosystem services at Loch Leven.

Fig. 4 Summary of the impacts of reductions in pesticide and phosphorus inputs on ecosystem services at Loch Leven.

Figure 1

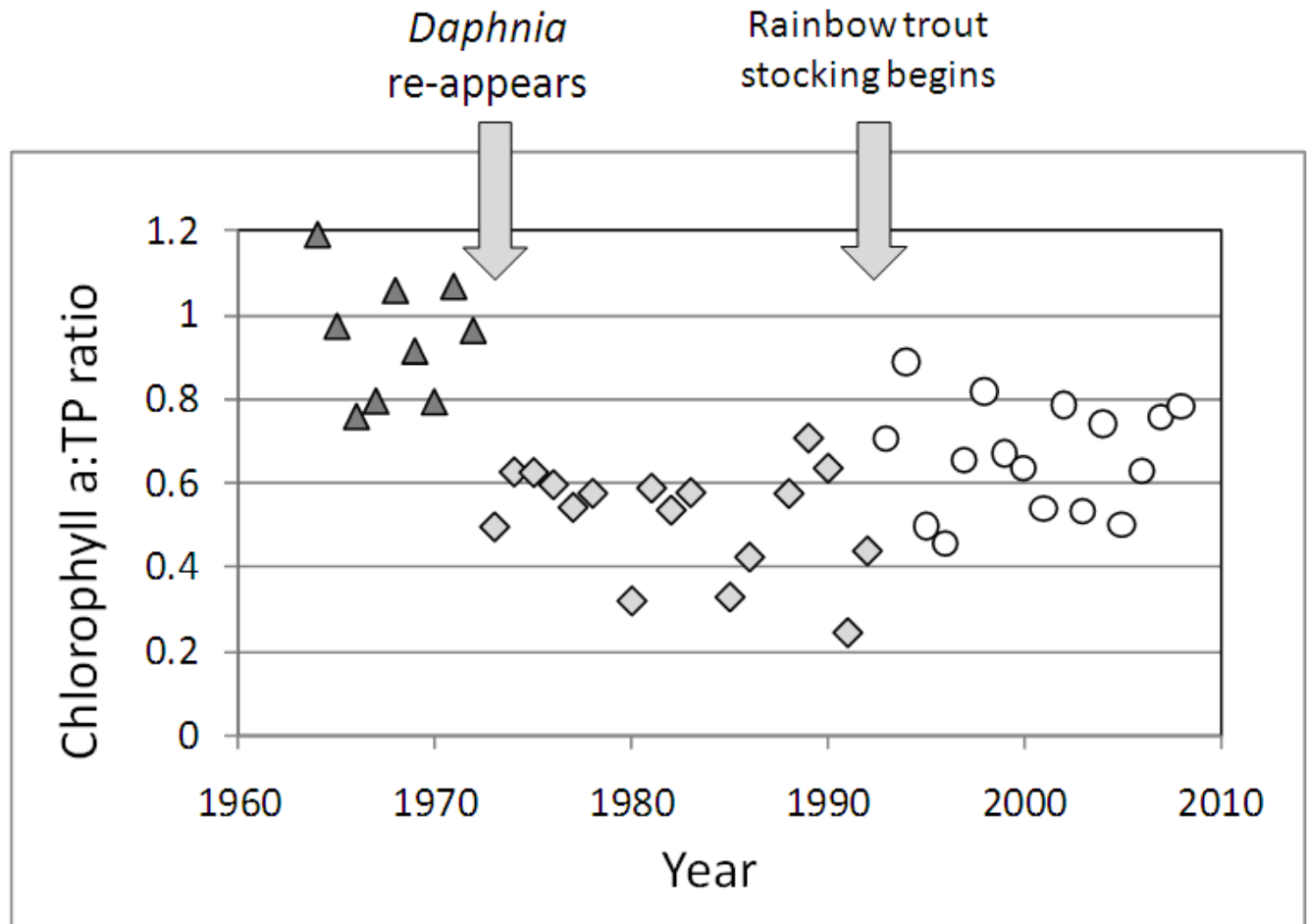


Figure 2

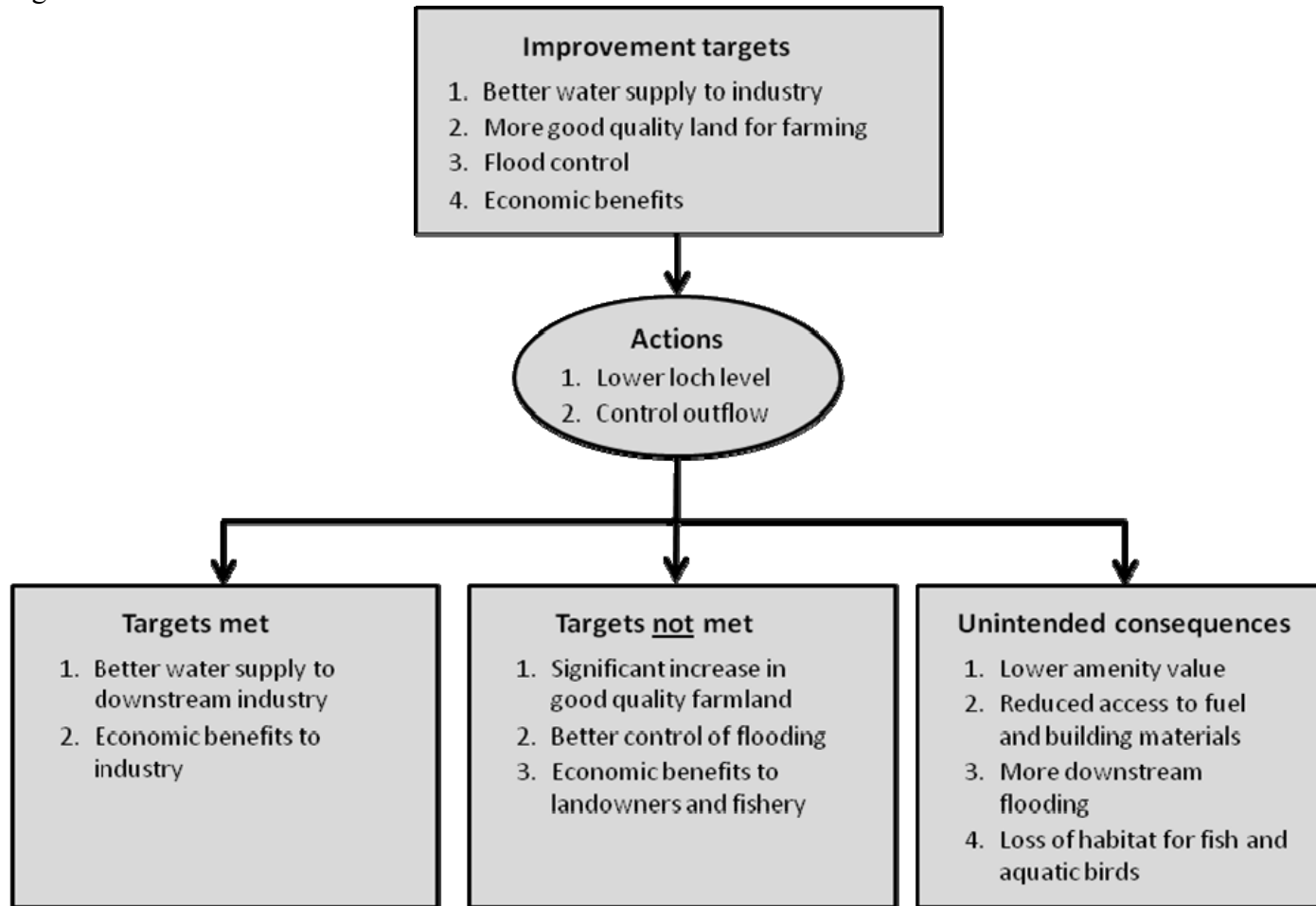


Figure 3

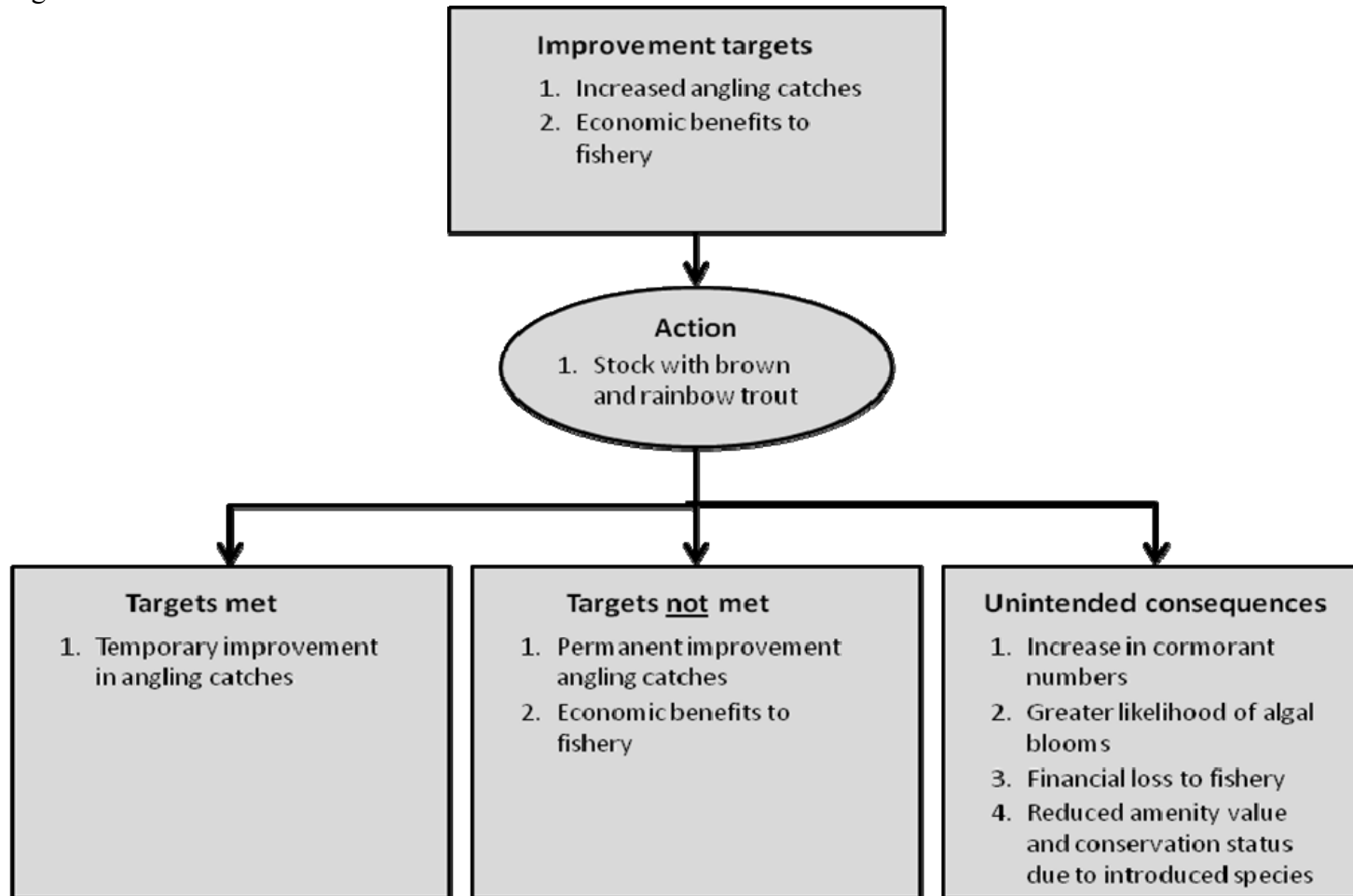


Figure 4

