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Review

A review of allodiversity in Lake Naivasha, Kenya: Developing conservation actions to protect East African lakes from the negative impacts of alien species

Francesca Gherardi[a,*], J. Robert Britton[b], Kenneth M. Mavuti[c], Nic Pacini[d], Jonathan Grey[e], Elena Tricarico[a], David M. Harper[f,*]

[a] Dipartimento di Biologia Evoluzionistica "Leo Pardi", Università degli Studi di Firenze, Via Romana 17, 50125 Firenze, Italy
[b] School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB, UK
[c] School of Biological Sciences, University of Nairobi, Nairobi, Kenya
[d] Dipartimento di Ecologia, Università degli Studi della Calabria, 87030 Arcavacata di Rende, Italy
[e] School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK
[f] Department of Biology, University of Leicester, University Road, Leicester LE1 7RH, UK

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ABSTRACT

The biodiversity of developing countries is increasingly threatened by introductions of invasive alien species. This study on the allodiversity in Lake Naivasha, Kenya reviews the pathways, establishment rates and outcomes of introduced species, and provides the basis for determining conservation actions that, if implemented, could prevent potentially harmful effects of similar events in other East African lakes. Introductions into Naivasha commenced in the 1920s with the release of a sport fish and have since produced an allodiversity of 23 species. This includes species that are no longer present (e.g., some tilapia species), presumed no longer present (e.g., the Nile perch *Lates niloticus*) or whose distribution is highly localised and ecologically neutral (e.g., the coypu *Myocastor coypus*). It also includes species that established successfully and invoked major changes in lake ecology (e.g., the red swamp crayfish *Procambarus clarkii*) and a species that is producing apparent economic benefits to the local population (i.e., the common carp *Cyprinus carpio*). The most frequent donor continents were the Americas and most species were the result of secondary introductions. The main introduction vector was active release that aimed to enhance fishery production. Alien species now dominate each main level of the lake's food web and produce impacts that are rarely restricted to a single ecosystem service. With a few exceptions, the majority of introductions translate into socioeconomic costs that contribute to rising social conflicts and exacerbating poverty. Development of appropriate conservation management tools within a regulatory framework could help protect Naivasha from further damage and could be used elsewhere in East African lakes to ensure that subsequent introductions enhance ecosystem services without affecting biodiversity.

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* Corresponding authors. Tel.: +39 055 2288216/215; fax: +39 055 222565 (F. Gherardi), tel.: +44 (0) 116 252 3346; fax: +44 (0) 116 252 3330 (D.M. Harper).
E-mail addresses: francesca.gherardi@unifi.it (F. Gherardi), dmh@le.ac.uk (D.M. Harper).

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1. Introduction

The search for effective conservation measures in Africa has reached a critical stage: forests and grasslands are threatened by agro-fuel production, wildlife is losing habitat and is being consumed by increasing numbers of malnourished human populations, surface waters are drained and degraded to support intensive agro-business or just subsistence food production, and governments are lured by continuing prospects of industrial extraction of minerals and oil (Abrams et al., 2009). A further, under-studied threat to the integrity of African wildlife comes from the introduction of alien species and from the consequent "ecological explosion" that a fraction of them, the invasive alien species, may trigger (Elton, 1958; Mack et al., 2000). Invasive alien species may in fact impact many biodiversity hotspots in Africa, potentially leading to substantial changes in the functioning of ecosystems and in the services they provide. Their impacts will ultimately affect all components of human well-being, including the basic material needs for a good life, health, good social relations, security, and freedom of choice and action (MEA, 2005).

The drivers of the introductions of alien species in Africa are primarily economic, with managers introducing new species to enhance ecosystem services through, for example, increased fish production in either aquaculture or captive fisheries (Nuñez and Pauchard, 2010). These introductions often raise conflicts between ecological and biodiversity impacts and socioeconomic benefits, as demonstrated by the introduction of Nile perch (*Lates niloticus*) into Lake Victoria in 1954 for fishery enhancement. This was successful in the context of increased fish production and exports, albeit concentrated in the hands of a small minority of fishermen (Kasulo, 2000), but it has also been a major factor in the mass extinction of native haplochromine cichlids (Ogutu-Ohwayo and Hecky, 1991; Kaufman, 1992; Goldschmidt et al., 1993; Witte et al., 2000; Aloo, 2003; Hecky et al., 2010; but see Verschuren et al., 2002; Gurevitch and Padilla, 2004; Paterson and Chapman, 2009).

These conflicts at Lake Victoria between biodiversity conservation and socioeconomic factors are embedded in a wider debate on the role of economic development in driving alien species introductions, with robust evidence that the number of alien species in a given country – its allodiversity *sensu* Barthlott et al. (1999) – generally increases with the economic development of that country (Jenkins, 1996; Vitousek et al., 1997; Taylor and Irwin, 2004; Thuiller et al., 2005; Pyšek et al., 2010; Essl et al., 2011). Since the extent of biological invasions is positively correlated with the openness of a country to a globalised world – its extroversion (Dalmazzone, 2000) – it can be expected that the increased standards of living in developing countries and their growing economies will raise the demand for imported products and human mobility (Vilà and Pujadas, 2001; Nuñez and Pauchard, 2010), with a consequent intensification of the "bombardment" by alien species (Elton, 1958).

To help reconcile the conflict between economic growth and biodiversity conservation (Czech, 2008), we argue that studies on African allodiversity should be intensified given that, up to now, research on biological invasions has shown a strong geographical bias towards developed countries (Pyšek et al., 2008). Indeed, a deeper knowledge of allodiversity will influence management strategies for the control of the growing problem of biological invasions (Nuñez and Pauchard, 2010) and help understand which actions, including preventative measures (surveillance of pathways of introduction, licensing, inspections, quarantines, etc.), should be undertaken. Indeed, due to the abundance of highly diverse natural habitats, the developing countries in Africa and elsewhere in the world are where science-based attempts to control invasions promise to be more beneficial, from a global perspective (Myers et al., 2000).

Here we review the conflicts between introductions of alien species and economic growth that have occurred in Lake Naivasha (Rift Valley Province, Kenya) since the 1920s. Lake Naivasha is a unique case study for East Africa due to the long-term monitoring across floral and faunal communities, with data available since 1982 from teams coordinated by D.M.H. and K.M.M. We synthesise the succession of species introductions into Lake Naivasha and characterise their ecological and socioeconomic effects. The potential or documented impacts on the lake's ecosystem services are reviewed and the role of alien species in driving the ecology of the lake is analysed. Finally, conservation-based actions are suggested that would minimise subsequent negative impacts on the lake, with these also having the potential to be applied to similar ecosystems elsewhere in East Africa.

2. Materials and methods

2.1. Lake Naivasha catchment

Lake Naivasha (0°45′S, 36°20′E; 1890 m a.s.l., 3–6 m depth) is the second largest lake in Kenya after Lake Victoria and constitutes a vital freshwater resource in Kenya's Rift Valley (the Eastern or Gregory Rift), which is otherwise dominated by soda lakes. This lake lies on the rift floor, 80 km northwest from Nairobi, and receives drainage from two perennial rivers, the Malewa, draining the Nyandarua (Aberdare) Mountains (drainage area: 1730 km^2), and the Gilgil, draining the Rift Valley escarpment ridges from the North (drainage area: 420 km^2). Overviews of the lake's general ecology, hydrology and other physical attributes can be found in Harper et al. (1990), Becht and Harper (2002) and Everard et al. (2002). The ecological value of Lake Naivasha was internationally recognised in 1995 when it was declared as the second Ramsar site in Kenya (Ramsar, 2009a). This declaration emphasised the important bird diversity of this freshwater lake and its contrast to the first Ramsar site, the alkaline-saline Lake Nakuru. Currently, however, the ecological status of the lake has become seriously compromised, and the Government has considered downgrading the lake and placing it in the "Montreux Record" of threatened Ramsar wetland sites (Ramsar, 2009b) "where changes in ecological character have occurred, are occurring or are likely to occur".

Such downgrading is the result of the synergistic action of two major drivers of change both affecting the integrity of the lake's ecosystem, that is (1) the introduction of alien species and (2) physico-chemical degradation. This degradation has resulted from the rapid population increase that followed the boom, in the last 30 years, of intensive floriculture and horticulture industries. Employment opportunities were developed and tens of thousands of migrants were attracted into the region from across Kenya. The population of the Lake Naivasha catchment passed from 35,000 inhabitants of the urban area in 1989 to 250,000–350,000 in 2005 (LNRA, pers. comm.) and over 500,000 today (2010 census). Unplanned settlements and grazing by livestock have cleared much of the fringing papyrus (*Cyperus papyrus*) (Morrison and Harper, 2009); the proliferation of small scale agriculture throughout the basin has led to the cultivation of river banks that increased erosion and lake sedimentation (Harper and Mavuti, 2004); and excessive water abstraction for agriculture and industrial purposes has lowered the lake level to about a third of its expected value (Becht and Harper, 2002). This industrial boom and exponential growth rate in the human population has followed the influence of species introductions to the lake's ecosystem, which was particularly evident in the 1970s–1980s when the impact of the red swamp crayfish, *Procambarus clarkii* (introduced in 1970; *cf.* Section 3.1; Harper et al., 1990), became apparent.

2.2. Data gathering and analysis

Data were gathered from scientific and grey literature, and from direct communication with Kenyan and international researchers. The focus was primarily on deliberate or accidental introductions, but instances of natural dispersal by species which reached the lake through influent rivers were also considered. The analysis was restricted to aquatic plants and animals. Alien species were classified according to their native range, the date of their first introduction into the wild, their current status (whether established, extinct or rare, i.e., occasionally observed), the mode of introduction (whether intentional or accidental introduction), and the vector/s and the pathway/s of their first introduction.

Table 1
Types of impact on ecosystem services (after Vilà et al., 2010, modified).

Supporting (S)	
S1	Modification of soil and sediments
S2	Modification of nutrient and water cycling
S3	Changes in community
S4	Changes in food web
S5	Changes in refugia
S6	Modification of photosynthesis and primary production
Provisioning (P)	
P1	Loss or gain in food, fresh water, fuel, fibre, biochemicals, etc.
P2	Changes in genetic resources
P3	Loss or gain in ornamental resources
Regulating (R)	
R1	Changes in air quality regulation
R2	Changes in climate regulation
R3	Changes in water regulation
R4	Changes in erosion regulation
R5	Changes in water purification and waste treatment
R6	Changes in disease regulation
R7	Changes in pest regulation
R8	Changes in pollination
R9	Changes in natural hazard protection
Cultural (C)	
C1	Changes in the economic use of species
C2	Effects on recreation and tourism
C3	Changes in the cultural heritage value and sense of place
C4	Effects on aesthetic enjoyment and inspiration value

Dates of first introduction refer to either the exact or the approximate year reported in scientific publications or, when not available, the year of the first known record. Vectors of introduction were classified into four categories: (1) dispersal, if alien species entered the lake as the result of range expansion by active or passive means from populations of the influent rivers; (2) escape, if they escaped from captivity; (3) release, if they were deliberately released into the wild; and (4) transport, if they were transported accidentally by human means.

Pathways of introduction include biocontrol (released into the wild as control agents of other species); culture (imported in association with aquaculture and farming); ornamental (imported in association with aquarium trade or for ornamental purposes); and stock enhancement or stocking (introduced to increase wild production in association with professional or sport fishing). The latter category also includes species used as fish food or bait. In those cases where no documentation is available for a given category or it is dubious or anecdotal, the pathway was marked as "unknown".

Impacts have been classified following the approach suggested by Binimelis et al. (2007) and applied by Vilà et al. (2010). We analyse four categories of ecosystem services, i.e., the benefits that people obtain from ecosystems, following the terminology of the Millennium Ecosystem Assessment framework (MEA, 2005). These include (1) provisioning services, i.e., the products obtained from ecosystems (food, fresh water, fibre, fuel, genetic resources, biochemicals, natural medicines, pharmaceuticals and ornamental resources); (2) regulating services, i.e., the benefits obtained from the regulation of ecosystem processes such as air quality, climate, water, erosion, diseases, pest, pollination and natural hazards; (3) cultural services, i.e., nonmaterial benefits obtained through spiritual enrichment, cognitive development, reflection, recreation and aesthetic experiences; and (4) supporting services, i.e., the services needed for the production of all other ecosystem services (soil formation, photosynthesis, primary production, and nutrient and water cycling). Whereas the changes of provisioning, regulating and cultural services have relatively direct and short-term impacts on people, the impacts inflicted to supporting services are often indirect or occur over a very long time. For each category of ecosystem services, we distinguished the impact types as listed in Table 1, modified from those previously reported by Vilà et al. (2010). Terms, such as "impacts", "changes", "modification", do not necessarily imply a negative meaning. The impacts of each alien species of this study have been directly assessed by the authors and/or reported in previous publications and/or extrapolated from studies conducted elsewhere but assumed to also occur in Lake Naivasha.

Statistical analyses were done using Wilks' test (statistic: G) (Zar, 1999). The level of significance at which the null hypothesis was rejected is $\alpha = 0.05$.

3. Results

3.1. Extent of allodiversity

Twenty-three aquatic species were introduced into Lake Naivasha since the beginning of the 20th century (Table 2). Fig. 1 synthesises the temporal sequence and the mode of introduction of each alien species plus the current status of populations.

Aggregated data indicate a significant increase in the rate of introductions since the 1950s (after 1950: 81%; Binomial test: $p < 0.001$) (Fig. 2). Four introduction phases are identified: (1) intentional fish introductions to enhance the fisheries to 1960; (2) accidental arrivals of invasive floating plants: *Pistia stratiotes* (1960s), *Salvinia molesta* (1962) and *Eichhornia crassipes* (1988); (3) the introduction of *P. clarkii* (1970) and the release of weevils

Table 2
List of the alien species recorded in Lake Naivasha.

	Kingdom	Phylum/division	Family	Species	Authority	Native range	Date of introduction
1	Plantae	Magnolyophyta	Pomtederiaceae	*Eichhornia crassipes*	(Mart.) Solms	S. America	1988
2	Plantae	Alismatales	Araceae	*Pistia stratiotes*	Linnaeus, 1753	S. America	1960s
3	Plantae	Pteridophyta	Salviniaceae	*Salvinia molesta*	D. Mitchell	S. America	1962
4	Animalia	Annelida/Oligochaeta	Tubificidae	*Branchiura sowerbyi*	Beddard, 1892	Asia (China, Indonesia, Japan), Australia	Unknown
5	Animalia	Mollusca/Gastropoda	Physidae	*Haitia acuta*	(Draparnaud, 1805)	N. America	1950
6	Animalia	Arthropoda/Crustacea/Cladocera	Daphniidae	*Daphnia pulex*	Leydig, 1860	Cosmopolitan	Unknown
7	Animalia	Arthropoda/Crustacea/Decapoda	Cambaridae	*Procambarus clarkii*	(Girard, 1852)	N. America (south-central USA, N.E. Mexico)	1970
8	Animalia	Arthropoda/Hexapoda/Coleoptera	Curculionidae	*Cyrtobagous salviniae*	Calder and Sands, 1985	S. America	1995
9	Animalia	Arthropoda/Hexapoda/Coleoptera	Curculionidae	*Neochetina bruchi*	Hustace, 1926	S. America	1996 and 1999
10	Animalia	Arthropoda/Hexapoda/Coleoptera	Curculionidae	*Neochetina eichhorniae*	Warner, 1970	S. America	1996 and 1999
11	Animalia	Arthropoda/Hexapoda/Coleoptera	Curculionidae	*Neohydronomus affinis*	Hustace, 1926	S. America	1999
12	Animalia	Osteichthyes	Centrarchidae	*Micropterus salmoides*	Lacépède, 1802	N. America	1929, 1940s, 1951
13	Animalia	Osteichthyes	Cichlidae	*Oreochromis leucostictus*	(Trewavas, 1933)	Africa (Lakes Edward, George and Albert and affluent rivers)	1956
14	Animalia	Osteichthyes	Cichlidae	*Oreochromis niloticus*	(Linnaeus, 1758)	Africa	1967
15	Animalia	Osteichthyes	Cichlidae	*Oreochromis spilurus niger*	Günther, 1894	Africa (Athi River and tributaries)	1925
16	Animalia	Osteichthyes	Cichlidae	*Tilapia zillii*	(Gervais, 1848)	Africa, Asia	1956
17	Animalia	Osteichthyes	Cyprinidae	*Barbus paludinosus*	Peters, 1852	Africa	1920s and 1982
18	Animalia	Osteichthyes	Cyprinidae	*Cyprinus carpio*	(Linnaeus, 1758)	Asia (China, India, S.E. Asia, Siberia), Europe	1999
19	Animalia	Osteichthyes	Latidae	*Lates niloticus*	(Linnaeus, 1758)	Africa (Ethiopia)	1970s
20	Animalia	Osteichthyes	Poeciliidae	*Gambusia affinis holbrooki*	Girard, 1859	N. America	1960s
21	Animalia	Osteichthyes	Poeciliidae	*Poecilia reticulata*	Peters, 1859	S. America	1950s-1960s
22	Animalia	Osteichthyes	Salmonidae	*Oncorhynchus mykiss*	(Walbaum, 1792)	E. Asia, N. America	<1925
23	Animalia	Mammalia	Myocastoridae	*Myocastor coypus*	(Molina, 1782)	S. America	1965

	Mode of arrival	Vector	Pathway	Status	References
1	Unintentional	Dispersal	Unknown	Established	Adams et al. (2002)
2	Unintentional	Dispersal	Unknown	Established	Adams et al. (2002)
3	Unintentional	Dispersal	Ornamental	Established	Adams et al. (2002)
4	Unknown	Unknown	Unknown	Established	Adams et al. (2002) and Raburu et al. (2002)
5	Unknown	Unknown	Unknown	Established	Adams et al. (2002)
6	Unintentional	Release	Stocking	Established	Mergeay et al. (2005)
7	Intentional	Release	Stocking	Established	Harper et al. (2002a) and Smart et al. (2002)
8	Intentional	Release	Biocontrol	Unknown	Foster and Harper (2006b)
9	Intentional	Release	Biocontrol	Unknown	Adams et al. (2002) and IUCN (2003)
10	Intentional	Release	Biocontrol	Established	IUCN (2003)
11	Intentional	Release	Biocontrol	Unknown	IUCN (2003)
12	Intentional	Release	Stocking	Established	Harper et al. (1990) and Seegers et al. (2003)
13	Unintentional	Release	Stocking	Established	Hickley et al. (2002, 2004b)
14	Intentional	Release	Stocking	Extinct	Hickley et al. (2008)
15	Intentional	Release	Stocking	Extinct	Harper et al. (1990) and Lévêque (1997)
16	Intentional	Release	Stocking	Established	Hickley et al. (2002, 2004b)
17	Intentional/unintentional	Release and dispersal	Stocking	Established	Harper et al. (1990), Hickley et al. (2002, 2004b, 2008)
18	Unintentional	Escape	Culture	Established	Britton et al. (2007)
19	Intentional	Release	Stocking	Extinct	Hartley (1984) and Harper et al. (1990)
20	Intentional	Release	Biocontrol	Extinct	Seegers et al. (2003)
21	Intentional	Release	Biocontrol	Established	Seegers et al. (2003)
22	Unintentional	Dispersal	Stocking	Rare	Hickley et al. (2002, 2004b)
23	Unintentional	Escape	Culture	Rare	Harper et al. (1990)

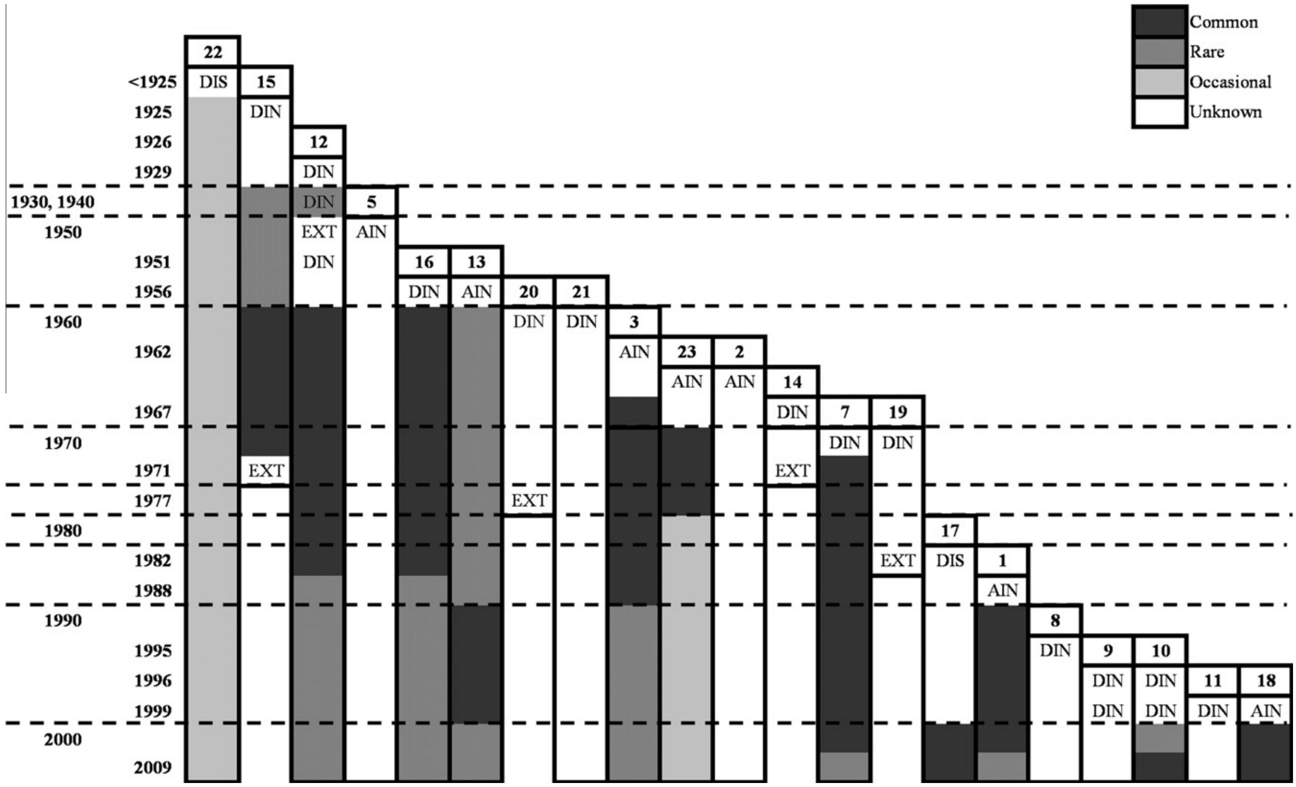

Fig. 1. Sequence of introductions with indication of the abundance of the populations of each alien species (see number coding in Table 2) in Lake Naivasha. Species of unknown date of introduction (*Branchiura sowerbyi* and *Daphnia pulex*) are excluded. AIN = accidental introduction; DIN = deliberate introduction; DIS = natural dispersal; EXT = extinct.

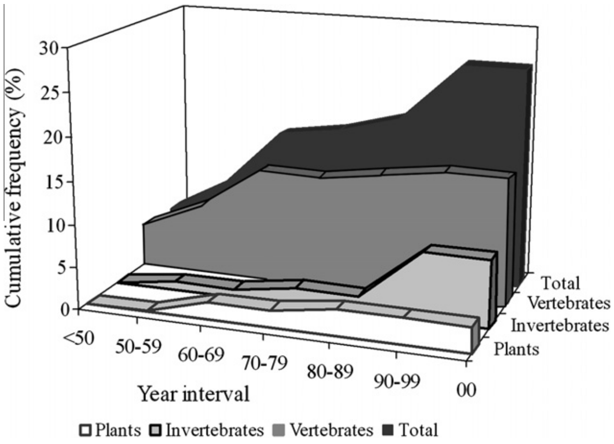

Fig. 2. Increase with time in the frequency of alien species in Lake Naivasha. Dates refer to the exact or approximate year of introduction into the wild or, when this datum is absent, to the year of the first record in the published literature. Species of unknown date of introduction (*Branchiura sowerbyi* and *Daphnia pulex*) are excluded.

for *E. crassipes* biocontrol (1996–2000) and (4) the accidental arrival of carp *Cyprinus carpio* (in 1999). North and South America were the most frequent continents of origin ($G = 21.95$, d.f. = 4, $p < 0.001$), but most species were the result of secondary introductions (Foster and Harper, 2007).

No significant difference was found between modes of arrival (excluding unknown cases, Binomial test: $p = 0.26$). The main vector for introduced species was active release (excluding unknown cases, $G = 12.07$, d.f. = 2, $p < 0.01$), particularly in relation to stocking and culture ($G = 12.63$, d.f. = 3, $p < 0.01$). Two fishes (*Micropterus salmoides* and *Tilapia zillii*) were introduced to enhance the fishery (Harper et al., 1990; Hickley et al., 2002), whereas *P. clarkii* was released to provide an additional fishery export and food to *M. salmoides* (Foster and Harper, 2007). *Oreochromis leucostictus*, which dominated catches prior to *C. carpio* introduction, was released as a contaminant of a batch of *Oreochromis niloticus* (see below). Similarly, *C. carpio* entered the lake as escapees almost certainly from a dam in the upper River Gilgil (see below).

3.2. Extinct and occasional aliens

Not all introduced species have thrived in the lake. Populations of four introduced fishes are no longer present (*Oreochromis spilurus niger*, *Gambusia affinis holbrooki*, *L. niloticus* and *O. niloticus*; Table 2). Reasons for their failure have not been tested but were likely to include competition with established species, predation by *M. salmoides* and habitat changes (Siddiqui, 1977; Seegers et al., 2003). The South American coypu, *Myocastor coypus*, imported to Kenya in 1950 for fur farming, escaped into the lake about 1965 and gave rise to a large population in the 1970s. They have since largely disappeared through hunting although occasional sightings still occur (Brock, 2005). Rainbow trout, *Oncorhynchus mykiss*, are sometimes recorded in the lake, although these fish come from the River Malewa where they were introduced between 1905 and 1910.

3.3. Extant aliens

Of the 17 alien species occurring today in Lake Naivasha, 14 are known to have established (Fig. 1). The status of the remaining three species is unknown. Alien aquatic plants are three floating South American ornamental macrophytes, including *E. crassipes* which is a globally invasive and problematic plant (Howard and Chege, 2007). All these plants form dense mats on the surface and reproduce asexually, dispersing by wind and water currents. *S. molesta* mats were observed in 1989, when 81% of surveyed sites had cover of >75%, decreasing to 5% by 1993, when *E. crassipes* reached >75% cover in 63% of the sites (Adams et al., 2002). Control of these plants was attempted through introductions of the coleopteran *Cyrtobagous salviniae* in the early 1990s and *Eichhornia* weevils (*Neochetina bruchi*, *N. eichhorniae*, and *Neohydronomus affinis*) in 1996–2000 (IUCN, 2003). Although *E. crassipes* has been widely damaged by the most recent weevil introduction since 2000 and reduced in vigour and mat thickness (Harper et al., submitted for publication), other factors, such as relatively low water temperatures (mean annual value of 21 °C against the preferred 28 °C for water hyacinth), may have also been involved (Adams et al., 2002).

Alien invertebrates, other than the aforementioned Coleoptera, include the annelid *Branchiura sowerbyi*, the gastropod *Haitia acuta* (formerly *Physa acuta*) and two North American crustaceans (a strain of *Daphnia pulex* and *P. clarkii*). No information is available on *B. sowerbyi* and *H. acuta* and their status (Clark et al., 1989). The annelid, native to the Sino-Indian region, is a global invader that is highly diffused in Europe and North America (Brinkhurst and Jamieson, 1971). In Naivasha, it contributes to the benthic primary production by approximately 60%, with its biomass reaching 2.4 g m^{-2} y^{-1} (dry weight; Raburu et al., 2002). The cryptic invasion of *D. pulex* was discovered through genetic analyses of material in sediment cores (Mergeay et al., 2005). All known Kenyan populations belong to the North American clade of the species complex, suggesting it might have been accidentally introduced with *M. salmoides* (Mergeay et al., 2005).

In the 1980s–1990s, prior to the invasion of *C. carpio*, *P. clarkii* played the role of keystone species *sensu* Paine (1995) (Smart et al., 2002); its introduction to Kenya and Lake Naivasha catchment is summarised in Box 1. A repeated cycle of *P. clarkii* decline and consequent plant recovery, and *vice versa*, was apparent between 1975 and 1999 (Fig. 3). A significant inverse correlation was detected between macrophyte cover and crayfish abundance in this period (Harper, 1992; Hickley and Harper, 2002) but it appears less strong today (Fig. 3). This is most likely due to a breakdown of *E. crassipes* mats starting from late November 2000 as a consequence of weevil activity that reduced refugia, but other factors could have contributed, including (i) a 1-m drop in lake level from late 1999 to late 2000 that left littoral zones dry (Foster and Harper, 2006a), (ii) spread of the crayfish muscle-wasting disease (Foster and Harper, 2007); and (iii) overexploitation by the fishery. Crayfish abundance was almost certainly maintained low by predation and competition with *C. carpio* (Britton et al., 2007).

Box 1 The story of *P. clarkii* in Kenya and Lake Naivasha catchment.

1966: *P. clarkii* (already in Uganda) was introduced to Kenya (Solai and Subukia dams) by the Kenyan Fisheries Department from Uganda to increase fish production and to prey on the gastropods *Biomphalaria pfeifferi* and *B. glabrata*, intermediate hosts of schistosomiasis (Hofkin et al., 1992).
1970: Approximately 300 individuals of *P. clarkii* from Subukia Dam (Kenya) were released in the vicinity of Marina Bay, in the southeast margin of Lake Naivasha (Oluoch, 1990) to provide food to the largemouth bass (Foster and Harper, 2007); *P. clarkii* was subsequently introduced to various sites around the lake (Oluoch, 1990) and farmers also contributed to its spread.
1974: *P. clarkii* was recorded from several Kenyan river basins (e.g., Athi/Galana).
1975: Commercial exploitation of *P. clarkii* began; catches of several hundred metric tonnes per annum were exported alive, mainly to Europe (Sweden and Germany).
1981: Catches of *P. clarkii* reached a maximum of 500 metric tonnes (*ca.* 19 million adults).
1983: EU banned the import of live crayfish from Kenya due to concerns about cholera.
1999: *P. clarkii* was first recorded from the Gilgil and Malewa rivers, as the result of natural upstream movements or deliberate introduction to control leeches (Foster and Harper, 2006a).
2002: Catches of *P. clarkii* in the lake amounted to about 40 metric tonnes per annum for local consumption (mainly tourism).
2005: *P. clarkii* was recorded at Njunu Springs (altitude: 2300 m).
2009: *P. clarkii* was recorded in some sites of the Gilgil and Malewa rivers (e.g., Langa Langa) living in syntopy with the indigenous river crab *Potamonautes loveni*.

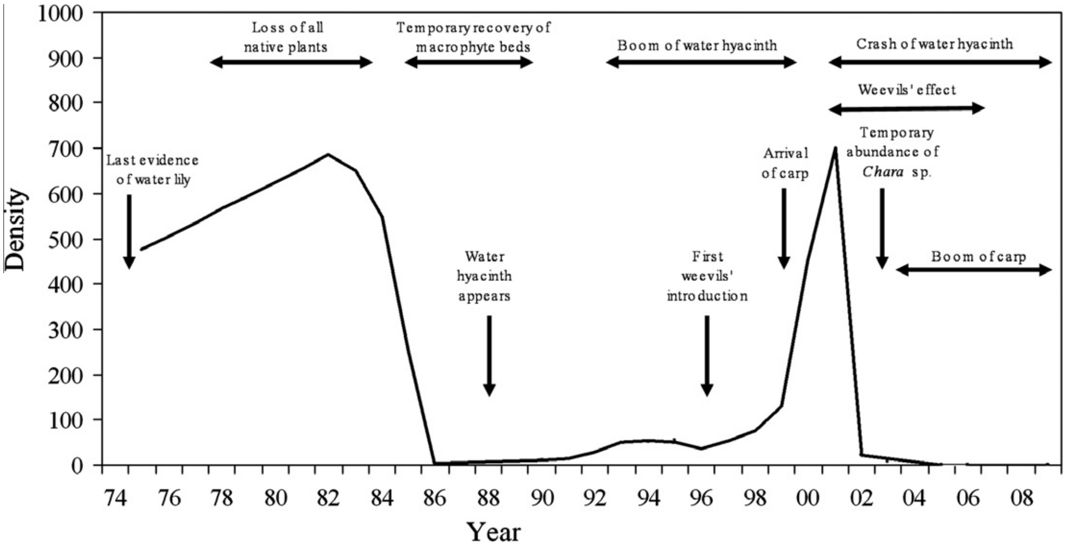

Fig. 3. Temporal changes in the population density of the red swamp crayfish *Procambarus clarkii* in Lake Naivasha compared with some events occurring in the ecosystem. The species was introduced in 1970. Data come from Harper et al. (2002a) and Britton et al. (2007). Density is inferred by qualitative observations between 1974 and 1989 and obtained through sampling (in crayfish m^{-2}) between 1990 and 2010. Crayfish were sampled in quadrants between 1990 and 1999 and with baited traps after 1999.

Extant alien vertebrates comprise six finfish species, *Barbus paludinosus*, *C. carpio*, *M. salmoides*, *O. leucostictus*, *Poecilia reticulata* and *T. zillii*. Prior to 1929, the lake was inhabited by a single fish species, the small, endemic, but commercially unimportant Naivasha lampeye, *Aplocheilichthys* spec. "Naivasha", but this has not been reported since 1962 (Elder et al., 1971), almost certainly driven to extinction by predation from *M. salmoides*. This paucity of fish species, unusual for a tropical lake, was seemingly due to the complete drying-out of the lake during the Makalian and Nakurian post-pluvial events (Leakey, 1931) and probably several times in the past 1000 years (Verschuren et al., 2000).

M. salmoides, a North American sport fish, was first released in 1929 to support angling, with subsequent releases in the 1940s and 1951 (Siddiqui, 1977; Lévêque, 1997). In 1956, the herbivorous redbelly tilapia, *T. zillii*, was introduced from Lake Victoria, together with the blue spotted tilapia, *O. leucostictus*, native to Congo and Uganda, as a contaminant of a batch of *O. niloticus* (Lévêque, 1997; Hickley et al., 2008). After 1959, these three species formed an important fishery (Muchiri and Hickley, 1991). *P. reticulata* was introduced for mosquito control in the late 1950s and early 1960s (Muchiri and Hickley, 1991). The current population of the small riverine fish *B. paludinosus* appears to be the result of migration from the inflowing rivers (Harper, 1984), although its status as native or introduced to the catchment is not clear (Muchiri and Hickley, 1991; Hickley et al., 2008; Britton et al., 2010). The species is now abundant in the lake fish community, possibly due to the rich planktonic food resources offered by the present-day eutrophic lake (Britton et al., 2010).

Table 3

Impact types on ecosystem services of the extant alien species in Lake Naivasha. Occasional or debated species (*Myocastor coypus*, *Oncorhynchus mykiss* and *Barbus paludinosus*) are excluded. The type of impact is indicated by S: supporting, P: provisioning, R: regulating, and C: cultural. See Table 1 for the codes of each impact type. The impact types that have been documented in Lake Naivasha are denoted in bold. See the text for bibliographical references.

Species	Taxonomic group	Impact types			
Eichhornia crassipes	Plantae, Magnolyophyta	S2, **S3**, **S4**, **S5**, **S6**		**R5**, R6	**C1**, **C2**, C3
Pistia stratiotes	Plantae, Alismatales	S2, **S3**, **S4**, S5, **S6**		**R5**, R6	**C1**, **C2**, C3
Salvinia molesta	Plantae, Pteridophyta	S2, **S3**, **S4**, S5, **S6**		**R5**, R6	**C1**, **C2**, C3
Branchiura sowerbyi	Animalia, Annelida	S1, S3	P1		
Haitia acuta	Animalia, Mollusca	S3, S4			
Cyrtobagous salviniae	Animalia, Arthropoda			R6	
Daphnia pulex	Animalia, Arthropoda	S3	P1		
Neochetina bruchi	Animalia, Arthropoda			R6	
Neochetina eichhorniae	Animalia, Arthropoda			R6	
Neohydronomus affinis	Animalia, Arthropoda			R6	
Procambarus clarkii	Animalia, Arthropoda	S1, **S2**, **S3**, **S4**, **S5**, **S6**	**P1**	R4, **R5**, **R6**	**C1**, **C2**
Cyprinus carpio	Animalia, Osteichthyes	S1, S2, **S3**, **S4**, S5, S6	**P1**	R5	**C1**
Micropterus salmoides	Animalia, Osteichthyes	**S3**, **S4**			**C1**, C2
Oreochromis leucostictus	Animalia, Osteichthyes	**S3**, **S4**	P2		**C1**
Poecilia reticulata	Animalia, Osteichthyes	S3, S4		R6	
Tilapia zillii	Animalia, Osteichthyes	**S3**, **S4**, S5, S6	**P1**		**C1**

The common carp, *C. carpio*, was assumed to have reached the lake in 1999 during heavy rains following an El Niño event (Britton et al., 2007). It was initially supposed that juveniles escaped from a flooded fish farm in the Malewa River (Hickley et al., 2004a). It now seems more likely that they came from a 90-ha dam which impounds the upper Gilgil: both carp and trout were stocked into the dam by a community self-help group in 1998 (D.M. Harper, pers. comm.). Carp have since established and dominated the fish community and fishery catches, as a consequence of the thermal and habitat conditions favouring their rapid growth and reproduction (Britton et al., 2007). In 2008, the total landing of *C. carpio* was 207,922 kg compared with a combined total catch of 16,872 kg for other species.

3.4. Impacts of alien species on ecosystem services

Table 3 synthesises the types of impact on ecosystem services (see Table 1) that each alien species exerts (as indicated in bold) or is likely to exert (*cf.* Section 2.2). The aggregated data revealed that supporting and regulating services tend to be more affected than provisioning and cultural services, although this was not significant ($G = 2.21$, d.f. = 3, $p > 0.1$). Considering only impact types with at least one record, impacts on supporting ($G = 6.63$, d.f. = 5, $p > 0.1$), regulating (with data aggregated in two classes, Binomial test: $p > 0.1$) and cultural services ($G = 2.29$, d.f. = 2, $p > 0.1$) are equally distributed among types, although S3 (i.e., changes in community), R6 (i.e., changes in disease regulation) and C1 (i.e., changes in economic use of species) appear more intense (Fig. 4). On the contrary, for the provisioning services, alien species significantly exert more the impact type P1 (i.e., loss or gain in food, fresh water, fuel, fibre, biochemicals, etc.; with data aggregated in two classes, Binomial test: $p = 0.02$) (Fig. 4).

Crayfish, the floating macrophytes and common carp have a broad effect on the four ecosystem services and exhibit a larger number of impact types than others, with 12 types reported for *P. clarkii*, 10 for the three plant species and 9 for carp.

3.4.1. Impacts of P. clarkii

Procambarus clarkii tends to be the largest invertebrate where it is introduced, causing cascading effects and impacting the trophic structure of the invaded food webs (Gherardi, 2006, 2007, 2010). In Lake Naivasha, crayfish are important components of the diet of fish (*M. salmoides* and *C. carpio*), birds (e.g., herons, African fish eagles *Haliaeetus vocifer* and cormorants) and mammals (e.g., the African clawless otter *Aonyx capensis*) (Smart et al., 2002). The species has drastically changed the composition of the community (impact type S3) and food web (impact type S4). Crayfish have replaced river crabs *Potamonautes loveni* as the primary food item of the African clawless otter in adjacent rivers (Ogada et al., 2009), so any fluctuation of their population size might lead to otter decline in the rives Malewa and Gilgil, into which they have penetrated (impact type S3). In the areas of syntopy, *P. clarkii* may prey on the indigenous river crab *P. loveni* and transmit pathogens (Foster and Harper, 2006a), including *Aphanomyces astaci*, the etiological agent of the "crayfish plague" (impact types S3 and R6): there is in fact evidence that the plague may affect other decapods (Benisch, 1940). Crayfish are also suspected to be intermediate hosts of numerous helminth vertebrate parasites and a vector of the bacterium *Francisella tularensis*, the causative agent of human tularemia (impact type R6) (Anda et al., 2001).

P. clarkii has had marked impacts on Naivasha's floating and submergent macrophytes by consumptive and non-consumptive destruction, except water hyacinth (Harper et al., 1990; Gouder de Beauregard et al., 1998; Adams et al., 2002), with a preference, at least in the laboratory, for the pioneer species *Potamogeton*

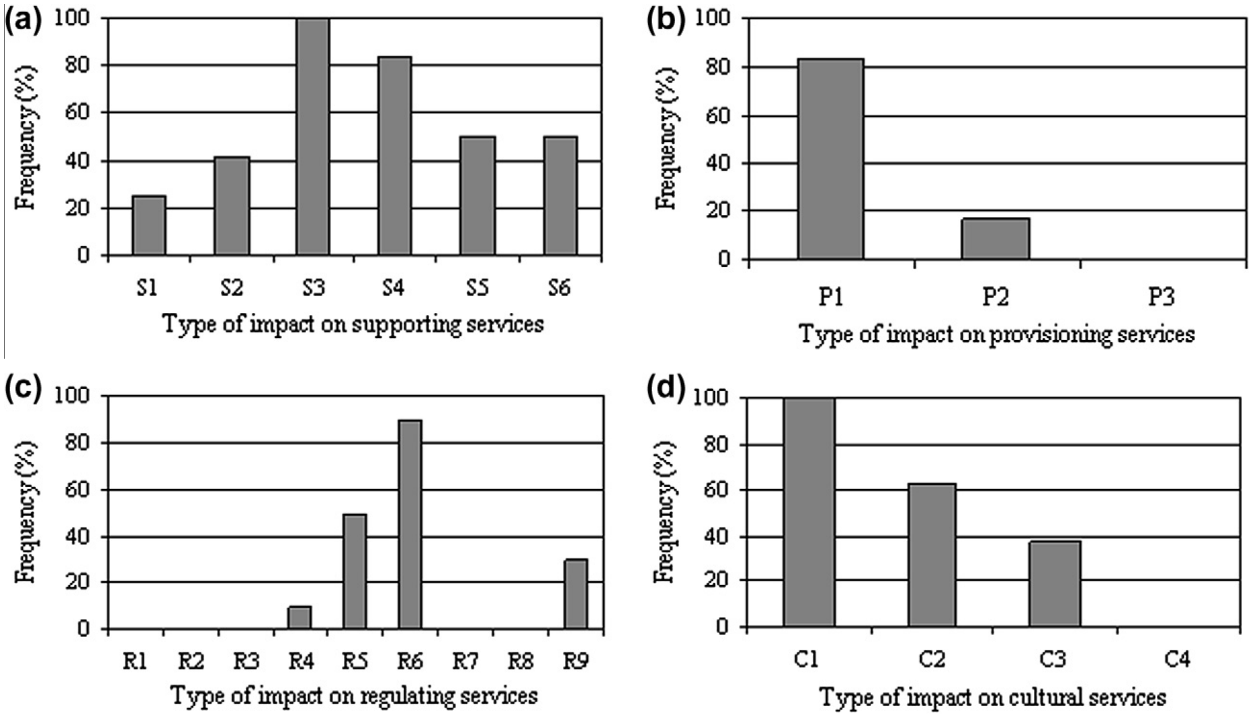

Fig. 4. Frequencies (in%) of species (on a total of 12 for a, 6 for b, 10 for c and 8 for d) exerting a type of impact on each of the four ecosystem services analysed (a: supporting, b: provisioning, c: regulating and d: cultural). See Table 1 for the meaning of abbreviations.

octandrus (Smart et al., 2002). Indeed, the blue water lily *Nymphaea nouchalii* var. *caerulea* and other floating-leaved and submerged macrophytes declined in coincidence with crayfish population expansion in 1974–1980 (Root and Root, 1978; Hickley and Harper, 2002), with evidence of direct consumption (Smart et al., 2002; Harper and Mavuti, 2004) (impact types S3 and S4). *P. clarkii* has changed patterns of primary production (impact type S6) (Harper, 1990) and impacted the availability of food and shelter for Mollusca, Hirudinea, Trichoptera and Ephemeroptera (Clark et al., 1989) (impact types S4 and S5). It can also modify nutrient cycling (impact type S2), as a result of removing the stabilising effect of macrophytes upon littoral sediments. The loss of macrophyte beds has also reduced food resources for red-knobbed coot (*Fulica cristata*), yellow-billed duck and African jacana (impact type S4) (Taylor and Harper, 1988), so affecting feeding opportunities for the African fish eagle (impact types S3 and S4) (Harper et al., 2002b). An indirect effect on tourism, particularly ornithological tourism (impact type C2), is thus likely.

The extensive burrowing of *P. clarkii* means that this species is also a bioturbator (impact types S1 and R4), thus reducing water transparency (impacts type S6 and R5) and affecting the foraging of long-tailed cormorants, fish eagles and *M. salmoides* (Harper et al., 2002b; Britton et al., 2010) (impact types S3 and S4). This has led to declines in *M. salmoides* abundance and catches (impact types S3, C1 and C2) (Britton et al., 2010). The fishery is also affected by crayfish damaging fish and nets (impact type C1) (Lowery and Mendes, 1977). Bioturbation also contributes to increased eutrophication: in the late 1990s, the total primary productivity exceeded 160 mg C m^{-3} h^{-1}, indicative of highly eutrophic conditions (Harper, 1990; Hubble and Harper, 2002) (impact types S6 and R5). Algal blooms are now characterised by a community shift from diatoms to cyanobacterial dominance (Hubble and Harper, 2002), with recorded blooms since 2005 of *Microcystis* sp. (Harper et al., 2006). Some strains produce toxins, which may bioaccumulate in *P. clarkii* (Tricarico et al., 2008), thus potentially affecting the health of consumers, including humans (impact type R6).

At the beginning of its invasion, crayfish supported commercial catches and their export to Europe, whereas today their annual harvest is less than 40 tonnes (0 tonnes in 2009). Although offered to international tourists (Harper et al., 1990), they are rarely consumed by local people who view them as "insects" (Foster and Harper, 2007) or "red scorpions" (F. Gherardi, pers. obs.). The ban posed on live fish exports to Europe in 1983 led to a significant drop in their exploitation (Foster and Harper, 2006a) (impact types P1 and C2).

3.4.2. Impacts of E. crassipes, P. stratiotes and S. molesta

The dense mats formed by these invasive floating plants lower oxygen concentration by blocking the air–water interface (impact type R5) and by preventing light from reaching the water column, thus affecting survival and production of submerged macrophytes (such as *P. octandrus*) (impact types S3 and S6), at least in the years when they have flourished during the population decline of *P. clarkii* (Ngari et al., 2009). Floating rafts in the shallows also impede fish eagle foraging (impact type S4) (Harper et al., 2002b). However, *E. crassipes* does offer refuge to many invertebrates, specifically Oligochaeta (mainly *Alma emini*), Insecta and Arachnida, while juveniles of *P. clarkii* and *Micronecta scutellaris* find refugia amongst roots (Adams et al., 2002) (impact type S5). Roots could also provide breeding grounds to mosquitoes, potential disease vectors (impact type R6): although Naivasha's altitude is above the malarial belt now, this could change, as the air temperature is showing an increase (N. Stranadko, pers. comm.). Decomposition of the abundant dead sinking plant material causes a significant modification of nutrient cycling (impact type S2). Floating macrophyte mats in the littoral zone block boat movements, hampering navigation and fishing (impact types C1 and C2). Domination of the littoral zone by alien floating plants in the shallows in place of the native water lilies has changed the sense of place of long-term riparian residents (impact type C3).

3.4.3. Impacts of *C. carpio*

The benthic foraging of *C. carpio* tends to increase water turbidity (impact type S6), can make water less suitable for swimming or drinking (impact type R5), reduces the abundance of aquatic plants (impact types S2, S3, S4 and S5; see the explanations above for *P. clarkii*) and resuspends sediments (impact type S1) (Titus et al., 2004; Hickley et al., 2008). However, their frequent feeding at the surface does provide an abundant food resource for the African fish eagle (Hickley et al., 2008) (impact types S3 and S4), almost certainly contributing to its increased population to 150 birds between 2002 and the end of 2008 (M.M. Harper, pers. obs.).

Both direct (consumption) and indirect effects (mechanical damage, uprooting) on submerged macrophytes have been observed in other locations invaded by carp (Parkos et al., 2003; Hinojosa-Garro and Zambrano, 2004; Lougheed et al., 2004). In experimental enclosures, the abundance of *Potamogeton pectinatus*, a species native to Lake Naivasha, significantly increased when carp were excluded (Miller and Crowl, 2006). In Naivasha, macrophyte regeneration positively correlated with increased carp abundance was observed in 2001–2003 contrary to predictions, although it may be too early to quantify their full ecological impact (Britton et al., 2007). Stable isotope evidence collated in 2001–2008 indicates that carp have had a strong impact upon crayfish, by preying on juveniles (Britton et al., 2007) (impact type S4) and reducing their trophic niche (impact type S5). Thus, *C. carpio* has now replaced *P. clarkii* as a keystone species in Lake Naivasha with expected further changes in the food web (impact type S4). Despite being less appreciated by consumers in comparison to the tilapias, the carp currently represents the only option for viable commercial fishery exploitation (Britton et al., 2007); carp also have a high socioeconomic value, because their large size means a single fish being used for family meals (impact types P1 and C1).

4. Discussion

4.1. Allodiversity of Lake Naivasha

The influence of multiple species introductions on the ecology of Lake Naivasha has been profound. Today alien species dominate the food web (Harper et al., 2002a) with up to three alien species being (or having been) represented with abundant populations at each main trophic level. The only exceptions are top consumers, which remain exclusively composed of indigenous birds (Harper et al., 2002b). This alien-dominated food web is beneficial in supporting a commercial fishery that represents the third most important socioeconomic activity gained from the lake (after the flori- and horticulture industry and tourism). Since the opening of fishery in 1963, it has provided income to more than 1000 Kenyans (Kundu et al., 2010), particularly belonging to the Luo community. The dependency of the fishery upon alien species is direct, since the target species are all introduced, but it is also indirect, since the target fish populations depend on food resources almost entirely represented by alien species (e.g., *P. clarkii*). Catch declines were due to crashes in the abundance of these alien species that ultimately led to periods of closure of the fishery (e.g., in 2001).

The communities of the lake have been subjected to rapid and drastic temporal changes in terms of both species composition and their population abundances. Dramatic population collapses have been recorded in species such as *P. clarkii* and associated with population cycles of "prey" species out of phase. The causes of analogous collapses in alien species' populations in other ecosystems have been rarely studied experimentally and/or quantitatively (Simberloff and Gibbons, 2004). In Lake Naivasha, population abundance shifts may also be largely associated with trends in water level changes, with periodic dry spells and low lake levels (Verschuren et al., 2000). However, over-abstraction now causes low lake levels to drop even lower and to be more prolonged (Becht and Harper, 2002), exacerbating other negative ecological impacts: a decline in fishery returns (especially *O. leucostictus*), an increase in eutrophication and higher demands from residents per unit area of shore/volume of lake water. All these occur at times when the whole country appears to be experiencing longer and deeper droughts (Becht and Harper, 2002). These fluctuations in prey populations have then impacted species in higher trophic levels, such as the 'umbrella' species, the African fish eagle, whose main prey items (fish and coot) both declines over the period 1986–1997, resulting in an eagle population decline of 50% of its maximum (70 birds; Harper et al., 2002b).

To date, it has been impossible to quantify the monetary costs experienced by the lake's residents resulting from the alien species-mediated changes in ecosystem services. It is recommended that cost-benefit analyses are subsequently undertaken, despite their difficulty. These would require an appraisal of the positive and negative effects of alien species on the fisheries, including indirect benefits such as employment and nutrition, and indirect costs such as concentrated income in the hands of a minority of the lake's residents (Kasulo, 2000), control costs (e.g., the cost of water hyacinth in Lake Victoria amounts to about US$ 9.7 millions; Kasulo, 2000) and the loss of profit due to reduced recreational uses (sport fishery and tourism). Finally, human health problems associated with alien species in Lake Naivasha are poorly understood. These problems include the spread of diseases that, together with the associated economic costs and their social implications, contribute to rising social conflicts and ultimately exacerbate poverty.

4.2. Conservation management of Naivasha's allodiversity and implications

Lake Naivasha's Ramsar status recognises its provision of wetland of international relevance for biodiversity conservation, but its current management is more allied to its role as a regional and national hub of agricultural and fisheries activity. It is apparent, however, that these activities are not sustainable, with water quality deteriorating through over-abstraction, siltation, eutrophication as well as alien species impacts (e.g., Becht and Harper, 2002; Harper and Mavuti, 2004; Hickley et al., 2004b). Correspondingly, successful conservation management of the catchment's biodiversity requires an integrated approach that manages the allodiversity in conjunction with all other contributors to its ecological degradation.

A regulatory framework for this sustainable management of the basin's resources already exists. It started with the drafting of the Lake Naivasha Management Plan in 1999 that followed Ramsar status, with this gazetted into law (Musyoka, 2004). Focusing on five broad management issues (water use, catchment and rivers, species management, tourism and recreation, and public access), it is committed to the 'sustainable management and development of the lake ecosystem' (Musyoka, 2004). In 2002, under the Water Act (gazetted 2005), a national Water Resource Management Agency (WRMA) was created with the role of managing catchments in Kenya at sub-basin level through partnerships with local Water Resource User Associations (WRUAs). Lake Naivasha is under one WRUA (LaNaWRUA) and its catchment under a further 11. This has resulted in the production of Sub-Catchment Management Plans (S-CMPs) by each WRUA and a basin-wide Water Allocation Plan (WAP). More recently, there has been a flurry of government-driven conservation activities following the 2009–2010 drought when lake level fell to a 100-year low. These include the launch of the ''Imarisha Naivasha Program'' to coordinate the sustainable management of the ecosystem services of the basin and the declaration of Naivasha as a ''Groundwater Conservation Area''. The lake is also under consideration for declaration as a National Reserve by the Kenya Wildlife Service. Where this regulatory framework is problematic, however, is blurring of the organisations responsible for their policy development and delivery, their resourcing and their transparent implementation. This was recently demonstrated by the reintroduction of *O. niloticus* into the lake in February 2011 for fishery enhancement. Whilst the S-CMP and WAP do not outline the process for management decisions on introductions, the 1999 Lake Naivasha Management Plan does: it states that it will 'stop (the) introduction of alien invasive species without environmental impact assessments (EIA) on the ecology of the lake' (Musyoka, 2004). This release of *O. niloticus* proceeded without an EIA being completed (or at least available for scrutiny), apparently merely on the instructions of the Permanent Secretary of the Ministry of Fisheries. Consequently, for any regulatory framework to be effective in managing Naivasha's allodiversity, the roles of the responsible authorities need to be clarified and properly resourced, and more transparent decision-making processes developed and scrutinised. Moreover, there is the need for the development of a catchment-wide strategy on alien species that clarifies current priorities and management actions in relation to how these contribute to the balance between conserving existing biodiversity and enhancing ecosystem services such as fishing. This is particularly important, since fisheries management responsibilities are currently divided by local authority boundaries, thus the introduction of carp in the late 1990s into a dam built in colonial times – Gwa Kiongo – impounding the upper Gilgil river was made on advice from the Fisheries Office outside the basin but within the local authority district – from the town of Nyandarua.

For an alien species strategy to be effective in the Naivasha catchment (and throughout East Africa more generally) requires the formulation of a range of policy initiatives lying under the regulatory framework which incorporates a range of objectives enabling more informed and transparent management decisions to be made. These require the development of:

- *Education*: the example of the *O. niloticus* reintroduction suggests that there is arguably insufficient technical knowledge available within the catchment to enable objective management decisions based on environmental risk assessments. The building of partnerships between government, non-government and academic organisations should increase knowledge transfer on issues of alien species and how they should better regulated and managed in the environment, and in relation to international conventions such as the Convention on Biological Diversity. There is also a requirement for dissemination of information on alien species to relevant communities and stakeholders (e.g., fishing communities and fishermen) that aim to prevent further accidental and unregulated introductions from occurring.
- *Risk assessment*: To assist the use of EIAs in management decisions as per the Management Plan, then it is recommended that a risk assessment framework is developed that enables full consideration of species' invasiveness in the context of their potential ecological and/or socioeconomic impacts. A range of risk assessment schemes have already been developed that could be calibrated for use at Naivasha, including fish (Copp et al., 2005a,b, 2009), aquatic plants (Pheloung et al., 1999) and invertebrates (Tricarico et al., 2010). As per Gozlan (2008), species approved for subsequent introduction should then only be those assessed as low risk but whose potential economic return is significant.
- *Research*: In order to better understand the environmental, socioeconomic and regulatory relationships of alien species in the Naivasha catchment, research should focus on developing knowledge on the cost-benefits of alien species (*cf*. Section 4.1), the important introduction pathways of alien species, and the traits of successful and unsuccessful alien species in relation to current and future environmental conditions. Moreover, further work is needed on the environmental factors that have assisted the establishment of alien species, for example the role of eutrophication and lake level change in facilitating the invasion of *C. carpio* in a lake previously dominated by tiliapiine fishes.
- *Enforcement*: This should focus on the development of policies that aim to prevent further unregulated introductions whilst promoting the biosecurity of existing species being used in activities across the catchment such as aquaculture. For example, increased surveillance of the major pathways of introduction and the use of licensing, inspections and quarantine within the aquaculture and fishery sectors should decrease rates of accidental or casual, high-risk introductions. Any risky activities in the catchment, such as aquaculture of alien species in closed systems, could be subjected to regular auditing of their biosecurity systems.

5. Conclusions

The Lake Naivasha case study clearly demonstrates that unregulated introductions of alien species can combine with other anthropogenic pressures in making ecosystem functioning and services highly dependent on allodiversity. Although East African lakes reveal ecological and socioeconomic features unique to each of them, we suggest that conservation management frameworks with a robust regulatory and strategical basis should be implemented to prevent the introduction of high risk species and ensure that only benefits accrue from subsequent introductions. Should introductions occur that involve high risk species, then the Naivasha case study indicates substantial ecological and socioeconomic damage may result. Given the low level of conservation management resources available in much of Africa, then such damage is likely to be irreversible.

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