Fish from elsewhere

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Introduction

If the early European explorers were to return today, they would find Australian rivers now harbour many familiar fishes to supplement their travelling rations. Rather than the antipodean perch, cod, bass, herring and catfish, they would find the common carp *Cyprinus carpio* (hereafter 'carp'), brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, goldfish *Carassius auratus* and redfin perch *Perca fluviatilis* ('redfin'). They might still question, now as then, the relative values of native fishes and those introduced from the Old World. Which were more desirable? What effects followed the introductions? Australian rivers have changed greatly in the past two centuries, and 'fish from elsewhere' are both causes and symptoms. That epithet could describe Australian native species introduced to new river systems across catchment boundaries, or species from other continents. It could also refer to different genetic stocks of a native species introduced to another region of a drainage system, beyond a waterfall or other barrier.

In two centuries, technologies, trade and transportation have breached biogeographic barriers that previously isolated freshwater biotas of continents and catchments over millions of years. The study of biological invasions has become a theme in ecology, responding to trends towards globalisation and biological homogenisation (Vermeij 1996; Davis 2009). Homogenisation of plant and animal assemblages is amongst the greatest threats to Earth's biological diversity and ecosystem function (Strayer et al. 2006). Species extinction and declining genetic diversity are associated threats (Moyle and Light 1996a; Rahel 2002). Introductions of non-indigenous species are among the least controlled and least reversible of human impacts on the world's ecosystems, affecting their biodiversity, biogeochemistry, and economic uses (Strayer 2010).

Unlike terrestrial ecosystems, where land-use change has a major effect on biodiversity, biotic exchanges such as fish stocking and translocation are more important for freshwater ecosystems (Sala et al. 2000) because they overcome biogeographic barriers. Climate change and invasive species are two of the greatest threats to biodiversity; when combined, their impacts will be compounded, with increasingly dire consequences (Burgeil and Muir 2010). Climate change will facilitate the spread of invasive species, pressuring ecosystems and limiting their ability to provide ecosystem services, necessitating greater efforts to prevent new invasions and control those already present.

This chapter considers the nature of freshwater fish brought to Australia from elsewhere, how they became established in the wild, and their effects on ecosystems. It also deals with less-obvious issues arising from the movements of native fish to new areas within Australia.

A global issue

Global biodiversity continues to decline. Biological invasions have increased in Europe by 76% in the last 40 years, and invasive species are affecting the conservation of threatened species globally (Butchart et al. 2010), with biodiversity decline and extinctions in freshwater ecosystems (Closs et al. 2004; Canonico et al. 2005; McDowall 2006). Alien fishes reduce native fish populations, degrade habitats, compromise gene pools, and introduce diseases and parasites (Rowe et al. 2008). Strayer (2010) noted totals of 314 native fish 'transplants' within

North America plus 116 established alien species. Europe had 58 transplants plus 95 alien fishes. With globalisation of fish culture, non-indigenous fishes dominate aquaculture and fisheries enhancements (Davis 2009; Gozlan et al. 2010). For example, the production of African tilapia is seven times higher in Asia than it is in Africa; in Chile, non-indigenous salmon provide 30% of world salmon production (Gozlan et al. 2010).

In Australia, the introduction, stocking and translocation of fishes similarly threaten biodiversity (Low 1999; Georges and Cottingham 2002; Olden et al. 2008). Since the mid-1800s, introductions of species for recreation and food, escapes from captivity of ornamental species, and releases of fish for pest control have all increased the species complement. Understanding the full consequences of technological advances have always lagged behind developments, and technologies for massive-scale fish propagation, selective breeding and transport, now mean that almost all Australian regions support fish that originated elsewhere.

Alien species are both causes and indicators of river health problems (Harris 1995; Kennard et al. 2005). In the Murray-Darling Basin (MDB), the condition of fish communities was a foundation for river health assessments in the Sustainable Rivers Audit (Davies et al. 2010). The proportions of alien species' abundance and biomass constituted the nativeness indicator for the Fish Theme. Sampling yielded 38 species, 10 of which were alien and constituted 43% of individual abundance and 68% of total biomass. Alien species rivalled or outnumbered natives in nine of the 23 MDB valleys, with carp, eastern gambusia *Gambusia holbrooki* ('gambusia') and goldfish, present throughout. Carp were overwhelmingly dominant, being 87% of alien fish biomass and 58% of total fish biomass. In a survey of New South Wales (NSW) rivers, Harris and Gehrke (1997) concluded that fish, as indicators of ecosystem condition, were in severe decline as a result of habitat degradation through sedimentation following catchment damage, river regulation, coldwater pollution below large dams, migration barriers and the effects of alien species. Later assessments (Gilligan 2005a, 2005b) confirmed the decline. Government agencies have shared leading roles in managing non-indigenous fish; the groundbreaking MDB Native Fish Strategy (MDBC 2003) includes controlling alien fish species among six driving actions.

About 73 invasive vertebrate pest animals have established wild populations in Australia (Bomford and Glover 2004). Of these, some 43 species currently are freshwater fish, 34 of which continue to spread (Koehn and McKenzie 2004; Lintermans 2004). The International Union for Conservation of Nature nominated five of these species (carp, Mozambique tilapia *Oreochromis mossambicus* ('tilapia'), gambusia, rainbow trout, brown trout) as among 100 of the world's most invasive species (Lowe et al. 2000). Thirty small aquarium species have been recorded in the wild in Australia (Corfield et al. 2008). Recent proliferations of aquarium fish in Western Australia and Queensland are matched globally only in the southern USA. Corfield et al. (2008) warned that such ornamentals could become pests like carp, degrading environments and demanding costly controls.

Predicting impacts from potential invaders is challenging, requiring risk-assessment procedures (Rowe et al. 2008; Bomford and Glover 2004; Keller et al. 2009). There is no 'generalised invasion theory' of potentially harmful species, and the inadequate understanding of ecological impacts and the need for the *Precautionary Principle* have been stressed (Leprieur et al. (2009). The impacts of alien fish now present in Australia need to be better assessed, based on appraisals of species' ecology, potential for spread, and likely interactions with native fauna and habitats. Furthermore, native fish introduced into watercourses outside their natural geographic distribution may have equivalent effects to those of alien species (Phillips 2003; DSEWPC 2010).

Kinds of non-indigenous fish and an introductions chronicle

Non-indigenous fish may originate in other continents, or in river basins or river reaches elsewhere in Australia (Table 1). These various sources carry differing ecological and management implications, and a consistent set of terms is needed to categorise the classes of fish, but no consensus has emerged and there is little common usage (Davis 2009; Gozlan et al. 2010). Non-indigenous species and genetic stocks can be simply classified as either exotic, alien or translocated (Table 1):

(TABLE 1 NEAR HERE)

Alien fishes began proliferating in the early decades of European colonisation. Many authors have chronicled fish introductions, establishment and spread (e.g. Weatherley and Lake 1967; Tilzey 1980; Fletcher 1986). Figure 1 shows this history of early acclimatisation, beginning in the mid-1800s, then little change in numbers of species over the first half of the 20th Century, followed by steeply increasing numbers from 1960 (Lintermans 2004; Ayres and Clunie 2010). Three salmonids, four cyprinids and a percid were established before 1900; gambusia's introductions before and during World War II brought the total to 10, which remained static for 40 years (Figure 1). A geographic shift featured in this history. For the first century, exotic fishes established alien populations predominantly in southern waters but, since the late 1900s, the balance has moved northwards with the rash of aquarium fish introductions, mostly tropical or subtropical species. The following sections outline the alien species, then the translocated native fishes, plus their distribution patterns and movement vectors.

(FIGURE 1 NEAR HERE)

Alien species

Attention on non-indigenous fishes has mainly focused on alien species; 43 have been recorded in Australia (Table 2). Uncertainty surrounds this exact number; survey data are scarce and unevenly spread across waterways, some recorded species may be self-perpetuating or they may die out. Species totals will inevitably change over time. Of the 43 listed, 18 are cichlids, eight cyprinids, six poeciliids and five salmonids; remaining families have only one or two representatives. All these families have crossed Wallace's Line, the biogeographic boundary in the Indonesian Archipelago separating the Australian biota from that of the Old World (Van Oosterzee 1997). Other than the Gobiidae, there are no naturally occurring Australian members of these alien families.

Weatherley and Lake (1967: p217) wryly observed, '... amazingly little attention has been paid to the general biology of the unique fish fauna of [Australia's] rivers, estuaries, lakes and ponds. From the first, anglers and acclimatizationists were primarily concerned to establish here numerous fish species already familiar to them in the northern hemisphere.' Even in the late 1970s, one state fisheries department head, while striving to establish even more salmonids, was still expressing the extraordinary opinion that Australian freshwater fish had limited value for recreational fisheries.

Salmonids

Zealous introductions of salmonids and other prized northern fishes were driven by acclimatisation societies (Brinsley 2011), some of which still persist, albeit under government regulation. Colonists wished to import familiar animals and plants from Europe, and enhance the food-producing and recreational opportunities of streams. Supported by strong public interest in Tasmania and Victoria, a Salmon Commission and individuals such as James Youl, repeatedly struggled to introduce salmonids. From 1852, ice and fresh water were used to cool and aerate fertilised eggs of Atlantic salmon and brown trout during the 3–month journey from England in sailing ships across the Equator and steamy tropics. They suffered many failures until Youl applied new research from America (Halverson 2010), delaying ova development by packing them in layers of ice and moss (Roughley 1951). Youl was knighted when he eventually succeeded in hatching and liberating trout and salmon near Hobart in 1864.

Nearly 500,000 Atlantic salmon eggs were imported in these determined attempts at Tasmanian acclimatisation, and 3,000 larvae were released (Weatherley and Lake 1967), but salmon have not established in the wild. Propagule pressure (see later) may have been insufficient for establishment, or local maritime conditions may be unsuitable. Nevertheless, hatchery-bred salmon currently escape from maritime farms in Tasmania and these fish may establish. In 1963, a century after the early acclimatisation work, Atlantic salmon were reared in NSW from Canadian eggs and released in the Murrumbidgee River. These fish have since supplied regional aquaculture stocks (Brinsley 2011).

Rainbow trout continue to support aquaculture and fisheries in Australia and around the world in regions where supplies of cool, high-quality water are available (Halverson 2010). Eggs were first imported from California through New Zealand in 1894 (Roughley 1951; Brinsley 2011). As well as fish for the table, industry and government hatcheries routinely provide young fish to support fisheries in upland streams and impoundments of southern states.

Other alien species

Three carp strains have established in Australia (Shearer and Mulley 1978; Davis et al. 1999; Haynes et al. 2009). The ‘Prospect strain’ was the first alien fish imported to Australia, being established near Sydney in 1850-1860 (McDowall 1996). Carp and tench were imported into Tasmania soon afterwards (Roughley 1951); acclimatisation societies then distributed them in Victoria. The domesticated, ornamental strain, ‘koi carp’, first escaped into the Murrumbidgee in 1876 (McDowall 1996) and koi continue to invade many new areas (Davis et al. 1999; Haynes et al. 2009). An aquaculturist in southeast Victoria in 1961 illegally imported the third (‘Boolara’) strain of carp from Europe for fish farming. They soon escaped into the MDB, with disastrous consequences (see later), despite Government eradication attempts.

Redfin was the second species introduced, with 11 fish liberated in Tasmanian streams in 1862 (Roughley 1951). Redfin tolerate temperatures up to 31°C (Weatherley and Lake 1967), which enabled their transport by sailing ship from England (Roughley 1951). Acclimatizationists soon released redfin into mainland waters.

TABLE 2 NEAR HERE

The aquarium trade

A booming aquarium industry, fuelled by air transport and international trade, spawned the continuing invasion by alien species from the 1960s (McKay 1977; Arthington and McKenzie 1997; Lintermans 2004) (Figure 1). These aquarium fishes were poeciliids, cichlids and the cobitid weatherloach (Table 2). At least 1181 freshwater species have been imported for the trade (McNee 2002); 33 of these exotics escaped into waterways and now dominate (77%) alien species (Arthington 1991; Ansell and Jackson 2007) (Table 2). Fishes escaping ornamental ponds to populate watercourses include goldfish, guppies, weatherloach and koi carp. The Commonwealth now uses risk-assessment modelling to prevent importation of exotic species likely to become pests (Bomford and Glover 2004; Ansell and Jackson 2007), but this does not affect over 1000 species already present.

Regulatory inadequacies among jurisdictions allowed many incoming species to bypass border controls (McNee (2002); any exotic fish species sought has been available through one avenue or another. Of the 1181 exotic species recorded in the preceding 40 years, only 481 (41%) were on the permitted species lists. In 2002 around 40% of the 22 million pet fish in Australia were imported rather than locally bred, and hundreds of species were smuggled in to avoid restrictions and quarantine (McNee 2002). Invasions increase, despite improving regulation of aquarium species imports (Figure 1).

Ballast-water introductions

Australia fortunately lacks shipping ports in freshwater environments. Elsewhere, as in the American Great Lakes and large European rivers, ballast water discharges from ships carry many ecologically damaging organisms between continents (Lodge 1993; Moyle and Light 1996b). Catastrophic invasions of North American ecosystems by zebra mussels and quagga mussels (*Dreissena* spp.) (Davis 2009) provide compelling examples. Although ballast water has introduced coastal invaders to Australia, only two euryhaline gobies have penetrated fresh water.

Relocated native fish: the translocated angling species

River-basin boundaries are almost always naturally impassable for freshwater fish; Table 3 lists sources of natural and human-mediated species relocations. Examples of translocated species include Macquarie perch *Macquaria australasica* in Victoria (Cadwallader 1981) and near Canberra (Lintermans 2007), cod species in Victoria (Cadwallader and Gooley 1984), climbing galaxias *Galaxias brevipinnis* in the upper Murray River, and stocked Murray cod *Maccullochella peelii* in headwaters of the Gwydir River (Davies et al. 2010). The genetically isolated stocks of golden perch *Macquaria ambigua*, silver perch *Bidyanus bidyanus* and freshwater catfish *Tandanus tandanus* (Keenan et al. 1997), Australian bass *Macquaria novaemaculeata* (Chenoweth and Hughes 1997) and barramundi *Lates calcarifer* (Chenoweth et al. 1998) flag the risks of translocations and more research is needed to describe stock structure among native fishes. Many fish-stocking programs have been undertaken with little knowledge of the genetic character of stocked fish or their relationship to wild populations (Rowland and Tully 2004). Encouragingly though, Rourke et al. (2010) found genetic diversity and effective population size of Murray cod were unchanged after lengthy stocking with this moderately migratory species in high-connectivity rivers, where broodstock were sourced locally.

The robustness of species like catfish, eels, cods and perches, the human appreciation for them, plus the proximity of headwaters of different drainages, have combined to facilitate relocation, often with little documentation. Translocated native species are mostly angling targets, forage species or bait. Murray cod, trout cod *Maccullochella macquariensis*, golden perch, Macquarie perch, Australian bass and freshwater catfish were released into new drainages in Victoria, Queensland and New South Wales (Cadwallader and Backhouse 1983; Cadwallader and Gooley 1984; McDowall 1996). Murray cod are particularly valued and there have been other attempts to establish them outside their native distribution, especially in Western Australia.

Research in southeastern mainland states since the 1960s focused on techniques for propagating native fish (e.g. Lake 1967, Rowland 1983a, 1996; Cadwallader and Gooley 1985) and is still continuing (Russell and Rimmer 2004; Battaglene and Selosse 2008; Ingram 2009). These efforts aim to enhance recreational fisheries, develop aquaculture for table fish, or conserve threatened species.

Unintended species have sometimes contaminated stocking shipments. Under limited regulation until recently, hatcheries mostly drew their water supplies directly from watercourses, with little or no effective filtration. Larvae and eggs of aquatic biota populated hatcheries' ponds, and were then difficult to remove from stocking shipments. At least four fish species (gudgeons, redfin, carp, barred grunter *Amniataba percoides*) and amphibians have been introduced to new waterways by this route (Rowland 2001).

Conservation programs, water transfers and bait buckets

Three other groups of fish have been translocated (Table 3). First are the threatened species relocated into new drainages for conservation purposes (e.g. Australian grayling *Prototroctes maraena*, Queensland lungfish *Neoceratodus forsteri*, Tasmanian galaxiids, purple-spotted gudgeon *Mogurnda adspersa)*, usually as relatively few wild-caught fish (Phillips 2003). A few Pedder galaxias (*Galaxias pedderensis*) were transferred to other Tasmanian lakes to preserve the species following its decline in Lake Pedder after hydropower development, eventually becoming Australia's first fish to be classed as 'Extinct in the wild' (Threatened Species Section 2006). Similarly, Lintermans (2006) translocated Macquarie perch to re-establish the Queanbeyan River population. Hatcheries support more-extensive conservation programs for trout cod, Mary River cod and eastern cod (Douglas et al. 1994; Ingram 2009).

Secondly, translocations of fish, doubtless with other aquatic biota, result from inter-basin water transfers. For example, climbing galaxias occur naturally in the Murray River's lower reaches, but water transfers from the Snowy Mountains Scheme also established this species in the Murray headwaters (Waters et al. 2002). Water transfers from the Glenelg River into the Wimmera River were probably responsible for introducing common galaxias (*G*. *maculatus*) there, alongside the golden perch that were deliberately stocked for angling (Davies et al. 2008).

Thirdly, small native and alien fish are used as live bait, and escapees produce 'bait-bucket introductions'. The scale of this process is undocumented but anecdotal support and unexplained occurrences of goldfish, weatherloach, gambusia, redfin and carp suggest it has been widespread. So translocated native fish have diverse origins. Table 3 summarises the human-mediated and natural sources that have led to establishment and spread of non-indigenous fishes. The ecological implications of these movements of species and stocks are considered later. Management issues are discussed in Chapter 12.

(TABLE 3 NEAR HERE)

Fisheries stocking

Fish aquaculture is an ancient art, practised in China since 2100 BC, but artificial propagation of fish began in France in 1850, when Joseph Remy first stripped eggs and milt from brown trout and hatched and reared their progeny (Halverson 2010), prompting the government to build a hatchery. The techniques were swiftly adopted in the USA, with brook char being propagated in 1853 followed by rainbow trout in 1872.

Global fish-stock enhancements yield about 2 million tonnes/year, mostly from freshwater fisheries, accounting for 20% of captures (Lorenzen et al. 2001). Cowx (1994) favoured stocking among techniques for rehabilitating freshwater fisheries, especially in repairing damage from fishing or habitat change, manipulating aquatic communities, or creating fisheries in new waterways. Although stocking is widespread, it is generally applied uncritically (Welcomme and Bartley 1998). Despite longstanding questions about stocking's effectiveness, managers and politicians often pin hopes for the future of fisheries on fish-stocking programs (White et al. 1995) in place of more-challenging interventions, such as habitat rehabilitation or fisheries restrictions.

Fish stocking: this almost-agricultural term reflects how stocking is seen. Breed lots of young fish, liberate them in a waterway and later exploit the new-grown fisheries resource. It began early in the Australian colonies, with acclimatizationists' crusading zeal and northern hemisphere fish. State agencies, moving thousands of young fish for hundreds of kilometres, carry most of the present-day burden, but acclimatisation societies still exist (Brinsley 2011), contributing labour and promoting anglers' interests. Landowners also stock fish.

At the turn of the millennium, the Murray-Darling Basin Commission (MDBC 2003) estimated that native fish populations in the MDB generally had fallen to about 10% of pre-European levels, and that a multi-faceted, 50–year rehabilitation program, defined by the Native Fish Strategy (MDBC 2003), would be needed to rehabilitate them to 60%. Declining freshwater fisheries was one of many factors generating enthusiasm for fish stocking in Australia. Dams inundated great reaches of rivers and native fish, many constrained by requirements for riverine spawning (Schiller and Harris 2001; King et al. 2003; Chapter 7), often failed to colonise these expansive artificial habitats. Many were near regional population centres, which drove demands for recreational fishing. Anglers seized on the new fish-propagation technologies. Private and government hatcheries multiplied, so that mass releases of trout in cooler reservoirs, and native species in others became routine. Warm-water fisheries rely on golden perch, silver perch, Australian bass and Murray cod in the south, with barramundi, sooty grunter *Hephaestus fuliginosus* and saratoga *Scleropages leichardti* northwards. Hatcheries routinely produce these native fish in eastern mainland states, together with eastern cod *Maccullochella ikei*, Mary River cod *M. mariensis* and trout cod. But large-scale propagation has remained elusive for others, (freshwater catfish, Macquarie perch, eels *Anguilla* spp.) because of lower fecundity and/or specialized reproductive needs.

Stocking occurs on a massive scale: from 1995/96–2000/01 nearly 37 million young native fish of nine species were stocked in New South Wales, Queensland, Victoria and Northern Territory (Simpson et al. 2002). In 2009, the NSW Government released five million native fish and trout. Victorian Government stocking averaged 1.3 million native fish and trout for three years to 2009. The enormous scope of stocking was further emphasised by Crook and Thurston (2009); in the MDB alone, more than 60 million native fish were stocked over 30 years. The vast majority were released to support recreational fishing (policy which, while not always well guided or ecologically sound, proves enduringly expedient for politicians and fisheries executives). In Queensland's Wet Tropics Region, Burrows (2004) noted that 2 million native fish, from up to 36 species, were stocked for fishing enhancement. Fish stocking and escapes from farm dams and aquaculture have translocated numerous native species and stocks (Ayres and Clunie 2010), threatening adverse consequences.

Anglers tend unrealistically to regard fish stocking as the solution for fisheries problems; as a 0panacea. Pouring young fish into waterways seems a quick-fix technological solution and a way to enhance recreational opportunities (Phillips 2003; Halverson 2010). Regrettably, the stocking panacea concept often diverts remedial action from challenging problems like species invasions, habitat degradation, biodiversity impacts, disease or overfishing. Managers confronting environmental or fisheries problems may propose stocking as an easier alternative to proper solutions. But real costs and likely benefits need to be analysed. Research knowledge on the long-term trajectories of stocking programs, and their benefits and costs, is very sparse (Davies et al. 1988; Hutchison et al. 2006; Halverson 2010). Furthermore, the easy response to problems – stocking more hatchery fish – may prove hard to resist for managers and politicians, with little motivation to fund studies to assess real outcomes.

Regrettably, hatchery fish can display low fitness, behavioural problems and poor viability through genetic and developmental issues associated with hatchery selection (Phillips 2003; Rowland and Tully 2004). These deficiencies often remain cryptic, but realisation is growing that there is greater benefit in promoting management of wild stocks, rather than depending on hatchery releases (Phillips 2003; Halverson 2010; Chapter 12).

Distribution patterns

The evidence of native fish redistribution collated by Ayres and Clunie (2010), identified 28 families and 76 species that have been translocated. Many translocations occurred through the 1970s–1990s, mainly in eastern and southeastern regions, some going unrecorded. Plainly, the natural patterns of species' and genotypic distributions have been extensively shuffled and blurred (Burrows 2004; Closs et al. 2004; Olden et al. 2008). Most translocations have been in Queensland (41 species), followed by Victoria (18), South Australia (14), New South Wales (11), Tasmania and the Australian Capital Territory (9), Western Australia (3) and Northern Territory (1). Advances in fish propagation preceded understanding of accompanying ecological issues (Phillips 2003). Isolated stocks and unrecognised genetic differences existed (Keenan et al. 1997; MDBC 2003; Ansell and Jackson 2007). But agencies' recent translocation policies and regulation of stocking (Phillips 2003; Simpson et al. 2002; Chapter 12) restrict introductions and growth in the problem may be declining.

As to alien species, Table 2 highlights state-by-state differences, with Queensland (29 species) then Victoria (19), New South Wales (18), Western Australia (12), Tasmania and Northern Territory (8) and South Australia (7). As noted, alien fish established in southern waters through colonial development much earlier than in the tropics and sub-tropics. Aquarium fish are predominantly warm-water species (McNee 2002; Corfield et al. 2008); the industry developed relatively late, after population centres expanded northwards, and alien species introductions shifted towards tropical zones. The distributions of 30 aquarium fishes mapped by Corfield et al. (2008) revealed species clusters around population centres, implicating human activity as the main vector for spread, and requiring public information programs. At least 16 species are established near Townsville, 10 near Brisbane, five near Cairns, four near Darwin, four near Sydney and three near Canberra (Lintermans 2004; Corfield et al. 2008). Conversely, the spread of aquarium fishes to remote areas is limited (Arthington and McKenzie 1997; Bomford and Glover 2004; Corfield et al. 2008), with an obvious biogeographic pattern in the distribution of drainage regions that have remained free of alien fish (and probably translocated fish also) (Chapter 2). Twelve of the 14 drainages apparently free of non-indigenous fish are located in the far north, in the Kimberley and Northern geographic provinces (Figure XX - MAPS). Southwards, only the arid, remote and thinly populated Bulloo-Bancannia Basin and the Western Plateau have not been invaded.

Complex factors set these patterns, including European settlement, human population density, environmental change and climatic regime. Ecologists have long accepted that fish invasions are associated with ecological disruption (Harris and Silveira 1999; Kennard et al. 2005; Davies et al. 2010). The extent to which that association reflects cause-and-effect varies with particular cases; there are many confounding influences (see later). Because disruption is usually associated with human settlement, populous areas are good indicators of the occurrence of non-indigenous fish (Arthington and McKenzie1997; Olden et al. 2008).

The discrete, linear nature of riverine habitats is critical in shaping the biogeography of freshwater fish, unlike distributions of marine or terrestrial species. Although some alien species (tilapia, trout, carp, gambusia) are more-or-less euryhaline, there is scant evidence of these species making coastal movements to new drainages. This partly reflects limitations of available survey data but, despite the vector of big freshwater plumes spreading seawards in floods, such inter-basin travel seems rare. Non-indigenous fish tend to remain within their established drainage until human activity moves them (Rahel 2007; Olden et al. 2008).

Many alien fishes, and some natives too, have been able to exploit the altered environments of reservoirs and other changed freshwater systems. Many rivers’ lotic, fluctuating conditions are replaced by the lentic, relatively stable habitats of impoundments, reservoirs, weir-pools and farm dams. Redfin, carp, tilapia, trout and gambusia have all flourished in impoundments with suitable thermal conditions, whereas several of these fishes are not highly rheophilic and do not cope well in faster-flowing water. Lentic conditions also sustain altered trophic structures, often dominated by autotrophic sources producing plankton-rich systems and supporting abundant smaller, planktivorous fish and invertebrates. Thermal stratification in deep storages provides temperature refugia at depth for fish approaching their upper tolerance limits (Phillips 2001), facilitating their persistence and spread.

Thumbnail case studies

Knowledge of the status, history and effects of alien fish in Australia remains patchy. But case studies can illustrate these details, at least for several important species. Thumbnail outlines (redfin, gambusia, brown trout, tilapia, carp), with key references, exemplify many alien species. Drainage region codes refer to Map XX.

Redfin *Perca fluviatilis* Linnaeus, 1758

(Redfin perch, English perch, European perch, Eurasian perch)

(DRAWING ex McDowall 1996)

Native of Eurasia, introduced to Tasmania from England in 1862. Widely distributed through cooler waters of southern Australia: Regions: MDB, TAS, SWWA, SEN, SWV, SEV, SAG. Northward distribution limited by upper thermal tolerance of 31°C.

Prefers still and slow-flowing waters, especially with abundant vegetation, where egg strands are laid in spring. High fecundity and flexibility to spawn when very small can produce abundant, stunted populations.

Moderate-sized, colourful, schooling fish. Macrophagic predator, <400–450 mm and <1–2 kg. Diet: fish, crustaceans, molluscs and insects. Significant predator and competitor of native fish. Populations often structured by cannibalism. Vector of Epizootic Haemopoietic Necrosis Virus, which is acutely fatal or pathogenic to various native fish. Associated with trophic cascades (see later).

Popular recreational species in some areas, good eating qualities. Range expansion through deliberate introductions, hatchery contamination and bait-bucket transfers. May not have reached potential southerly range, may contract southward through climate change. Noxious in some states.

Literature: Roughley 1951; Weatherley and Lake 1967; Cadwallader and Backhouse 1983; Langdon 1989, 1990; McDowall 1996; Allen et al. 2002; Morgan et al. 2002; Ludgate and Closs 2003; Simon and Townsend 2003; Rowe et al. 2008; Ansell and Jackson 2007; Wilson et al. 2005; Wilson et al. 2008; Froese and Pauly 2010.

Gambusia, *Gambusia holbrooki* (Girard, 1859)

(Eastern gambusia, mosquitofish, topminnow)

(DRAWING ex McDowall 1996)

Native to rivers flowing into Gulf of Mexico. Probably introduced in 1920s for aquaria, later widely released for mosquito control. Distributed through much of Australia, especially near populous areas: Regions: NEQ, BURD, FITZ, SEQ, NEN, SEN, MDB, SEV, SWV, SAG, TORR, SWWA, TAS, NT.

Prefers warm shallows in still and slow-flowing, fresh or brackish waters, tolerates variable water quality. Often in near-surface shoals. Extremely eurythermic – survives under ice, tolerates <44°C. Sexually dimorphic, viviparous, <35–60 mm. Microphagic predator, eats larvae, eggs, small invertebrates.

Range expansion through introductions for mosquito control and bait-bucket transfers. Little value in controlling mosquitoes, probably detrimental through impacts on native mosquito predators. Range in Australia may be increasing, this could continue in response to new mosquito-borne diseases. Adaptable to degraded habitats.

A major threat to biodiversity through aggressive predation and competition, even against larger fish. Large habitat and/or dietary niche overlaps with many native fish. Implicated in threatened status of fish and frogs. Noxious species.

Literature: Cadwallader and Backhouse 1983; Lloyd 1990; Pen and Potter 1991; Arthington 1991; McDowall 1996; Ivantsoff and Aarn 1999; Allen et al. 2002; Wilson et al. 2005; Rowe et al. 2008; MacDonald and Tonkin 2008; Pyke 2008; Reynolds 2009; Gambusia Control Homepage 2010; Froese and Pauly 2010.

Brown trout, *Salmo trutta* Linnaeus, 1758

(DRAWING JH)

Native to Europe, reached Tasmania 1864, widely released for angling in cooler mainland waters. Distributed through many streams and impoundments, above 600 m ASL northwards, down to sea level in Tasmania. Regions: NEN, SEN, NTAS, STAS, SWWA, SWV, SEV, MDB, SAG.

Medium-large bodied, <900 mm, <14 kg. Macrophagic predator, eats insects, crustaceans, fish. Requires good water quality <23-25°C and fluvial gravels for spawning. Anadromous Tasmanian population. Has reached potential range in Australia, probably declining through climate change.

Implicated in threatened status of several galaxiids and two frog species through predation and competition. Habitat and/or dietary niche overlaps with upland native fish. May cause trophic cascades.

One of the world’s most important angling species, good eating qualities, sustains major economic activity in many areas.

Literature: Roughley 1951; Weatherley and Lake 1965; Scott and Crossman 1973; Tilzey 1976; 1977; Jackson and Williams 1980; Cadwallader and Backhouse 1983; Crowl et al. 1992; Cadwallader 1996; Townsend 1996; McDowall 1996, 2006; Threatened Species Section 2006; Froese and Pauly 2010; Brinsley 2011.

Tilapia, *Oreochromis mossambicus* (Peters, 1852)

(Mozambique tilapia, Mozambique mouth-brooder)

(DRAWING – JH)

Native to East Africa, introduced for food in Asia, Papua New Guinea, elsewhere in tropics. In Australian aquaria since 1977. Spreading through illegal introductions, distribution patchy but expanding near northern population centres. Successful, vagile invader in all countries where it is introduced. Has not reached potential range, may increase through climate change; threatens MDB, Gulf drainage and warm coastal rivers. Regions: SEV, SEQ, NEQ, BURD, PILB.

Prefers warm, slow-flowing streams, lakes and impoundments, especially vegetated, fresh–brackish sites. Euryhaline, tolerates poor water quality. Wide temperature tolerance: 8–42°C. Medium-sized, schooling fish <350 mm, <1100 g. Adaptable macrophagic omnivore, adults herbivorous, piscivorous and/or detritivorous, phenotypic and dietary plasticity. Fecund mouthbrooder. Hybridizes with other cichlids.

Major threat to biodiversity. Noxious species. Affects other fish by habitat modification, predation, competition for space and food, disrupting spawning. Good eating quality, valuable aquaculture species, provides important animal protein and food security in developing countries.

Literature: Cadwallader and Backhouse 1983; Arthington 1991; Pollard 1990; 1991; McDowall 1996; Allen et al. 2002; Canonico et al. 2005; Ansell and Jackson 2007; Doupé and Burrows 2008; Doupé et al. 2009a, 2009b; Froese and Pauly 2010; Doupé and Knott 2010.

Common carp, *Cyprinus carpio* Linnaeus, 1758

(Carp, European carp, koi carp, mirror carp)

(DRAWING ex McDowall 1996)

Native to Asia, now established in all continents except Antarctica; world’s most widely distributed freshwater fish. Ornamental strains introduced in 1850s, 1878. Spreading rapidly after ‘Boolara’ strain introduced in 1961, plus escapes of ornamental koi strain.

Widespread distribution in southern Australia. Successful, vagile invader in all countries where it has been introduced, has not reached potential range. Regions: MDB, NEN, SEQ, SEN, SEV, SWV, NTAS, STAS, SAG, TORR, SWWA.

Prefers still or slower-flowing streams, lakes and impoundments, especially well-vegetated, fresh–brackish sites. Tolerates poor water quality. Large bodied, <80 cm, <10 kg. Omnivore/detritivore, dietary plasticity. Zooplanktivory can promote algal blooms through trophic cascade. Potamodromous spring spawning migration to vegetated wetlands; extremely fecund. Population recruitment from floodplains. Hybridizes with goldfish, strains are interbreeding, hybrids may increase fitness. Noxious species.

Major threat to biodiversity. Generally reviled, declared noxious in all States. Valued as food in Europe and Asia, where an important aquaculture species. Ornamental koi valued by aquarists. Commercial fishery in SEV. Encouraging progress towards integrated control, and recombinant genetic techniques for eradication.

Literature: Roughley 1951; Scott and Crossman 1973; Shearer and Mulley 1978; Hume et al. 1983; Fletcher et al. 1985; Roberts et al. 1995; Roberts and Tilzey 1996; McDowall 1996; Harris and Gehrke 1997; Roberts and Ebner 1997; King et al. 1997; Robertson et al. 1997; Davis et al. 1999; Koehn et al. 2000; Schiller and Harris 2001; Stuart and Jones 2002; Khan et al. 2003; Koehn 2004; Brown and Walker 2004; Brown et al. 2005; Smith 2005; Driver et al. 2005a, 2005b; Stuart and Jones 2006; Ansell and Jackson 2007; Gilligan and Rayner 2007; Thresher 2008; Bax and Thresher 2009; Jones and Stuart 2009; Haynes et al. 2009; Froese and Pauly 2010; Gehrke et al. 2010.

Fish invasion ecology

Fish from elsewhere must overcome many challenges to invade a new environment. Predation, nutrition, reproduction, dispersal and environmental tolerances are key challenges. Each of these may take precedence at particular points in the rolling, repetitive sequence of invasion stages that unfolds as a new species inserts itself into the existing aquatic community. Mark Davis's (2009) book *Invasion Biology* details these invasion stages, which include introduction, establishment, naturalization, dispersal, population distribution, and invasive spread as definable points in an ongoing series of cyclical iterations. The two processes that are fundamental to successful invasion of a species are establishment and dispersal. Both of these operate at the individual level, but ultimately lead to the persistence and spread of populations and meta-populations (Figure 2) (Davis 2009). Davis provides a thoughtful review of this flourishing field of biology.

(FIGURE 2 NEAR HERE)

Establishment

To become established, enough individuals must survive long enough to reproduce. The parameters determining whether individuals succeed are the mortality rate and the introduced species' numerical strength. Mortality will be a complex function of time, existing 'enemies' (predators, parasites, diseases), food availability, water quality and other habitat variables, particularly sheltering cover (Weatherley 1972; Gulland 1977; Wooton 1991). Abiotic environmental factors are most critical in determining the outcome of aquatic invasions (Moyle and Light 1996b; Bomford and Glover 2004), suggesting that if abiotic conditions suit an invader, establishment is likely, regardless of other biota already present. The new fish must find enough food, avoid being eaten and exploit habitat conditions within its preferences or tolerances for long enough to breed. The numerical strength parameter is expressed as propagule pressure, which is the product of the number of individuals at each introduction event times the number of events. Invasions are more likely to succeed after multiple introductions of many individuals, with cumulatively increasing propagule pressure (Figure 3) (Rahel 2002; Davis 2009; Strayer 2010). In reviewing risk assessments for exotic fish, Bomford and Glover (2004) found that about 50% of reported fish species introductions resulted in new populations establishing, and that releases of large numbers of fish at different times and places increased the probability. They found that, worldwide, all species with more than 10 introductions had established at least one alien population, especially when the climate in the new area closely matched that of their source. Examples of different outcomes in Australia include the rapid invasions of trout introduced in thousands on multiple occasions to cool habitats. At the opposite extreme are the threatened species like trout cod, whose establishment remains problematic even after many large-scale conservation releases (Douglas et al. 1994; Lintermans 2007). Behavioural and physiological attributes involved in the biotic and abiotic interactions that decide invasion outcomes are discussed below.

(FIGURE 3 NEAR HERE)

Population spread

Having become established, individuals in the new population must disperse and the population must spread to consolidate its invasion if it is to persist as a metapopulation. This will require spawning and recruitment of new individuals to generate new propagule pressure, with iterations of the establishment process, then their dispersal to other parts of the drainage system through successive cycles (Figure 2). The eventual spatial extent of spread will be influenced by structural barriers, (catchment boundaries, waterfalls, dams), or by physical and chemical barriers including temperature, hydraulics or solute concentrations (dissolved oxygen, salinity). Dynamical models are needed for predictions and analyses; even in 5–10 y periods, invasive species populations can increase by orders of magnitude (Keller et al. 2009), and useful lessons from epidemiology are applicable to invasive species. Different traits (longevity, tolerances, migratory behaviour, *r* or *K*-selection strategies) become important at different stages in the invasion process, and Keller et al. (2009) reported trait-based statistical techniques for predicting the success of future introductions, and risk assessments. A species' capacity to transit from introduction to eventual community integration is enhanced if it enters an environment where it is freed from attack by its natural enemies (diseases, parasites, adapted competitors and predators). The exceptional robustness of eucalypt trees in many parts of the world where they have been propagated from seed, or the success of introduced trout bred from transported eggs, attest to the potential strength of this enemy release phenomenon.

Metapopulation development

At the longest timescales, invasion success hinges on evolutionary processes (Vermeij 1996; Mooney and Cleland 2001; Davis 2009). Two factors determine the capacity of new species to adapt to environmental variations like seasonality, climate change, arrival of other invaders, or evolving adaptations among enemies. These factors are the species' innate behavioural and physiological flexibility, and its genetic diversity. Carp, for example, show exceptional plasticity, successfully penetrating extremely diverse communities, habitats and geography worldwide. Carp in Australia give interesting clues: the two early strains (Prospect, Yanco) established small local populations but failed to spread (Shearer and Mulley 1978; Davis et al. 1999). But when Boolara strain and then koi imports escaped into the wild, populations boomed in a highly dynamic invasion (Hume et al. 1983; Roberts and Ebner 1997; Haynes et al. 2009). Presumably, the early strains lacked both genetic variability and phenotypic plasticity, but these attributes became powerfully obvious with the later introductions. Redfin also show phenotypic plasticity in response to population density, with sexual maturity at small size producing superabundant, stunted populations structured by cannibalism. Alternatively, shrinkages of geographic and altitudinal distributions of cool-water fishes like redfin, trout and tench, which suffered genetic bottlenecks through introduction of small numbers of fish on few occasions (Weatherley and Lake 1967), and show limited capacity to evolve, are predictable through climate warming. Notwithstanding low genetic diversity, brown trout show plasticity and are highly adaptable to various cool environments.

Additionally, top-level native predators (cormorants, pelicans, herons, cod, bass, eels, golden perch) may be evolving new foraging behaviours and shifting their prey preference towards superabundant carp. This factor, together with drought, is probably implicated in slumping carp numbers through 2000–2010. Social learning (Duffy et al. 2009), where animals learn by observing others, is another adaptation in receiving communities that is likely to modify invaders' success. Additional factors could include declining resource availability and arrival of new pathogens with new invaders. Over time, multiple adaptations and changes among species' enemies are reflected in the irruption and decline cycle experienced by many invaders; rapid establishment and spread leading to abundant populations that then regress over long periods to lower abundances and community integration (Strayer et al. 2006; Davis 2009).

Habitat invasibility

The invasibility, or susceptibility of an environment to establishment of new species (or new genotypes), is commonly invoked as a key to non-indigenous species' successes (Arthington and McKenzie 1997; Phillips 2003; Davis 2009). Invasibility participates in complex interactions also involving propagule pressure, species' attributes and stochastic events to control the outcome of any introduction. Droughts and floods, river regulation, catchment land use, or changes in existing aquatic communities can all modify invasibility. Thus invasibility is subject to environmental variation in both the biotic and abiotic arenas, it fluctuates over time, and is specific to particular invading animals. Striking examples of increased invasibility occur where dams discharge cold, hypolimnetic water into naturally warm rivers; native communities are often profoundly affected, and replaced by cold-tolerant trout, redfin or carp. This scenario played out on the Mitta Mitta River (Phillips 2001; Todd et al. 2005), the Macquarie River (Roberts and Tilzey 1996) and elsewhere. Highly invasible environments are also found near urban centres, where degraded habitats and suppressed native fish communities combine with frequent introductions of ornamental fish (Arthington and McKenzie 1997; Rowe et al. 2008).

Recurrent ecological disasters in the Murray River provide potent examples of sudden changes in invasibility. Flooding often follows droughts, with impacts compounded by altered flow regimes. Vast quantities of accumulated organic detritus and leachate may then be washed into stream channels, de-oxygenating water and causing blackwater events over hundreds of kilometres (MDBA 2011; NSW I&I 2011). Carp, which spawn abundantly in floodwaters and tolerate poor-quality water, can recruit in enormous numbers, whereas most native fish, unable to survive these conditions (McNeil and Closs 2007), may suffer great mortalities (MDBA 2011; NSW I&I 2011). These events damage the native community's resistance and resilience, re-setting the stage for intense renewal of carp invasion.

At an opposite extreme of invasibility, in the arid-zone rivers of the Lake Eyre Basin (LEB), alien species' abundances decrease relative to native species when large floods occur (Costelloe et al. 2010), suggesting the enormously variable hydrological regimes and native-dominated communities of LEB rivers resist establishment and proliferation of alien fish. Waterbodies that experience extremes of other environmental variables (stream velocity, thermal regime, connectivity, water quality) are also likely to have lower invasibility because the array of potential invaders is less likely to include species able to cope with those extremes. Few non-indigenous species are found in isolated mound springs, hypersaline estuaries like the Murray River's Coorong, or turbulent headwater streams.

Events in the natural cycle of environmental variation (bushfires, storms, floods, droughts, climatic cycles) are ecological disturbances that shape the structure of natural aquatic communities. Human-induced impacts (eroding catchments, drained wetlands, polluted streams, disrupted flows, instream barriers, species introductions) add to the range and severity of these disturbances, which may be 'pulse', 'ramp' or 'press', depending on their temporal pattern (Connell 1978; Reice et al. 1990). The term 'disturbed' is often loosely invoked to describe conditions better classified as environmentally degraded. Freshwater systems are particularly prone to the imposition of multiple sources of stress, both natural and human-induced. Interactions among multiple stressors in freshwaters are highly complex, and disentangling their effects is difficult (Ormerod et al. 2010), especially when compounded by new challenges like climate change and species invasions. Alien fish are often seen as both a symptom and a cause of river degradation. In southeast Queensland rivers, for instance, variation in alien fish indices is strongly related to human-induced degradation of stream and catchment condition (Kennard et al. 2005).

In a seminal paper, Connell (1978) questioned the value of equilibrium theory in ecology and developed the intermediate-disturbance hypothesis to describe the influence natural disturbances have on community structure. Using data from rainforests and coral reefs, he showed that biotic communities experiencing disturbance at either very high frequency or very low frequency were much less diverse than communities disturbed at intermediate frequencies. Similarly, severe disturbances produced greater subsequent diversity than small. This phenomenon is explained by the effect of periodic disturbance in reducing the abundance of dominant, over-populous species and allowing the re-emergence of naturally low-abundance, specialist species that may be less successful competitors, and which can exploit temporary increases in available resources of habitat or nutrients. Local communities can thus be kept in a non-equilibrial state with high diversity. Presumably, these intermediately disturbed communities may be colonised by either non-indigenous or indigenous species if they are present and suitably adapted to the new opportunities. This corresponds with Davis's (2009) conclusion that the same processes affecting invasibility are driving diversity.

Invasibility, biological diversity and river health

There are parallels among the concepts of freshwater invasibility, biological diversity and river health; all respond to ecological degradation and all are emergent properties of the system rather than its constituents. River health in the MDB was assessed by Davies et al. (2010) using measures of condition of themes (Hydrology, Fish, Macroinvertebrates and, subsequently, Vegetation and Physical Form) to represent functional and structural links among ecosystem components, biophysical condition and human interventions. Alien and native species occurrence, abundance and biomass in riverine communities provided nativeness metrics in the Fish Theme that were concordant with other metrics and themes. The Index of Biotic Integrity (Karr et al. 1986; Harris and Silveira 1999) employs similar data on non-indigenous species to assess the condition of freshwater ecosystems.

Does good river health promise low invasibility? Certainly, the contrary can be true – poor health (e.g. urban streams, blackwater events) can favour invasions, but only by suitably adapted species (e.g. gambusia, guppies, carp) – trout are rare in stormwater drains. A postulated relationship between community diversity and invasibility presupposes that increased species richness should increase resistance to invasion because the system's resources would be more fully utilised, with fewer niches available, in speciose environments. This diversity–invasibility hypothesis, which arises from traditional niche theory, has little evidence to support it and there are many shortcomings (Davis 2009; Bomford and Glover 2004). Many plant studies show positive, not negative, relationships between numbers of native and non-native species. Others have concluded that species composition is more important than richness, and biological resistance of native fish fauna has not been found to be an important factor mediating fish invasion (Moyle and Light 1996a; Kennard et al. 2005). Processes operating at larger scales, such as propagule pressure, may overwhelm processes at the local level, such as competition for resources or release from enemies, which might potentially modify invasibility. Diversity at either species or functional levels has not been shown to be a reliable predictor of invasibility under natural conditions at any spatial scale (Davis 2009).

What makes a successful invader?

Species with narrow physiological tolerances (temperature, salinity, dissolved oxygen, turbidity, water velocity) account for most introductions that fail to establish populations. Physiological constraints in environmental variables often limit establishment of non-indigenous fishes (Kolar and Lodge 2001). Furthermore, different sets of attributes – physiological and otherwise – may influence species' transitions between separate stages (introduction, establishment, spread, integration) of the invasion (Marchetti et al. 2004). To predict characteristics of future successful invaders, Marchetti et al. (2004) modelled quantitative profiles of invasive species' characteristics, showing suites of variables that were important in predicting three steps in the invasion process: establishment (parental care, physiological tolerance), spread (lifespan, distance from nearest native source, trophic status) and abundance (maximum size, physiological tolerance, distance from nearest native source). Longer lifespan, higher physiological tolerances and smaller native ranges favoured successful establishment. Descriptive studies of invading species' biological characteristics have dominated past research, but may not expose underlying mechanisms, some of which may be as simple as the number of propagules introduced, or prior invasion success elsewhere. These two mechanisms, representing human interest in a species, predict establishment success and may mask underlying biological characteristics (Marchetti et al. 2004).

Australian experience with fish invasions reinforces lessons from elsewhere, with the history and ecology of salmonids (Weatherley and Lake 1967; Tilzey 1980; Fletcher 1986;), cyprinids (Koehn 2004; Smith 2005), poeciliids and cichlids (McKay 1977; Corfield et al. 2008), and the percid redfin (Weatherley and Lake 1967; Morgan et al. 2002), having been recorded. Together with overseas studies, these reports portray the suites of characteristics that can increase success rates among introduced species. Fish that appeal to humans are likely to have been introduced widely, often, and in substantial numbers. The great success of brown and rainbow trout, goldfish, gambusia, tilapia, redfin and carp, each of which has been widely promoted by human activity, are telling examples. Extensive translocation of angling species like golden perch, Murray cod, silver perch, Australian bass and freshwater catfish similarly stems from these native species' popularity.

Water quality variables provide some filtering of non-indigenous fish. Australia's latitudinal range, from cool-temperate Tasmania to the tropical north, supports many patterns of thermal preference, and only eurythermal species like goldfish, carp and gambusia extend across broad latitudinal ranges. These same three species show similarly great capacity to prosper in waters whose dissolved oxygen concentrations fall to levels uninhabitable by most fish (McNeil and Closs 2007). A few others including tilapia, guppies and brown trout thrive in saline waters, unlike most freshwater species. Species' tolerances are summarised by McDowall (1996); Allen et al. (2002) and Froese and Pauly (2010).

Water velocity also limits non-indigenous fish. While lowland and slopes-region rivers generally have less-than-challenging velocities, fish with the modest swimming ability of guppies, gambusia or redfin are precluded from swifter upland streams in which they might otherwise penetrate native communities. Even carp, which are powerful swimmers, have limited success in headwater streams, as their few spawning 'hotspots' that drive recruitment are in distant lowland reaches (Gilligan and Rayner 2007) or impoundments, and often separated by barriers. Nevertheless, generally broad tolerances for water velocity, temperature, salinity, dissolved oxygen, and probably other water-quality variables, characterize many invasive fishes, enabling their success in diverse habitats and across wide distributions.

Major variations in hydrological cycles characterise Australian freshwater systems (Williams 1980; DeDeckker and Williams 1986; Boulton and Brock 1999), the most variable of Earth's river systems (Puckridge et al. 1998). Larger native fish have evolved reproductive strategies to cope with this great variation, exploiting booming resources of food and nursery habitats in occasional floods to breed abundantly (Harris 1988; Schiller and Harris 2001; King et al. 2003). These opportunists have evolved considerable longevity, with larger body size and a 'wait-and-see' strategy for coping with drier cycles (e.g. Australian bass, silver perch, golden perch, Murray cod longevity >20 y) (Chapters 7 and 8). Many (not all) current alien species have reproductive patterns evolved in environments that are much more predictable; so their spawning tends to be seasonally regular. Carp are an exception and it is likely that their great longevity and ability to recruit abundantly in flooded wetlands have contributed to the strength of their invasion (Koehn 2004; Smith 2005; Gilligan and Rayner 2007).

Relatively few larger Australian freshwater fish are predominantly herbivorous. They include two mullets (striped mullet *Mugil cephalus* and freshwater mullet *Myxus petardi* are properly classed as catadromous freshwater species) and bony herring *Nematalosa erebi* (McDowall 1996). Bony herring are a true keystone species, converting plant material, mainly filamentous algae and biofilms, into abundant fish flesh without any intervening transformation by invertebrate grazers. They underpin the trophic structure of tropical, subtropical and warm-temperate fish communities (Chapter 6). Abundant resources of aquatic plant material with limited native competition for this resource probably contributed to the success of tilapia, carp and goldfish, which can also process plants and detritus.

In recommending study of invaders at several ecological levels, Simon and Townsend (2003) listed traits of invaders associated with particularly profound impacts: a method of resource acquisition formerly lacking in the invaded system, a broad feeding niche linking previously unlinked ecosystem compartments, feeding relationships with negative consequences for native strong interactors, physiological traits that enhance resource transformation and lead to high biomass, and behavioural or demographic traits that provide high resistance or resilience in the face of natural disturbances. Carp demonstrate how well the simultaneous expression of all these characteristics empowers an invader.

The patterns illustrated by carp and other alien fish indicate that successful invaders are likely to be long-lived ecological generalists, adaptable to a wide variety of foods and physiologically tolerant. They are usually favoured by humans, so that a key determinant of success – propagule pressure – is at high level.

Impacts of non-indigenous fishes

Lakes and streams are among the ecosystems most modified by species invasions. Environmental, economic and social impacts may follow fish introductions, as well as species enrichment, (Davis 2009; Keller et al. 2009; Strayer 2010). An extreme example followed the 1950s introduction to Africa's Lake Victoria of the predaceous Nile perch (*Lates niloticus*), leading to the biggest modern vertebrate extinction known, over 200 endemic fish going extinct within a few decades (Kolar and Lodge 2001; GISP 2004), with disastrous impacts on human communities. This history derailed attempts to introduce Nile perch to Australia to replace declining barramundi (Williams 1982).

Movements of species, facilitated by commerce and transport, have increased species richness worldwide, even though most transported species fail to establish, and only small proportions of newly established species become pests (Mooney and Cleland 2001). But numbers accumulate over time; many countries now have 20% or more alien species in their flora. New Zealand has as many alien plant species as there are natives. Where invaders do succeed, they often integrate without species extirpations into existing communities, even in extreme cases like California's San Joachim estuary, where 60% of the 50 species present were non-indigenous (Moyle and Light 1996b). New assemblages come to resemble co-evolved communities, both structurally and functionally. Where extirpations do occur, they mostly result from piscivore introductions, perhaps because affected prey are not adapted to the new predator's behavioural traits. This probably explains trout's impact on galaxiids, which previously experienced lower predation pressure.

So, while invasions have often been implicated in declining biodiversity and habitat degradation, most alien fish introductions either failed to establish in the wild, or else integrated into existing communities with little ecological harm. But there is limited knowledge about the array of ecological, economic and evolutionary impacts of species invasions and some Australian cases have been much more damaging. This is a topic needing more research and better understanding. Because invaders' impacts are poorly understood it is quite inappropriate to equate lack of data with a conclusion of 'no impact' (Leprieur et al. 2009). Because of the potentially large associated risks, a precautionary approach is the only appropriate course.

Impacts occur through both biotic and abiotic interactions (Table 4). But many impact reports are correlative or anecdotal because of the difficulty of establishing causal relationships and through confounding of fish introductions by habitat degradation (Bomford and Glover 2004; Rowe et al. 2008). One of the most regrettable results of the trend towards homogenization of Australia's fish fauna through non-indigenous species has been the loss of native communities' unique character (Chapter 10). Introductions have changed freshwater biogeography, with increased faunal similarity among primary drainages, particularly those suffering most human-mediated environmental changes (Olden et al. 2008).

Widespread fish stocking with both alien and native species poses several threats to wild native populations (Table 4) (Clunie et al. 2002; Phillips 2003; Gillanders et al. 2006). Translocated natives may produce impacts comparable to those of alien fish, with species displacement, loss of genetic stocks, or introductions of parasites and diseases. The threats prompted agencies to develop guidelines for hatchery and stocking operations, despite data limitations (Phillips 2003;

Ansell and Jackson 2007; Chapter 12). Objective data on impacts of alien fish are in short supply and pest potential is difficult to assess (Bomford and Glover 2004; Corfield et al. 2008). Data used for risk assessments are often anecdotal, speculative and based on limited observation, and invasiveness is not necessarily a useful trait for defining the potential impacts of fish. Assessing the risk of a fish becoming a pest should be based on traits related to its impacts on native biota, subsequently supported by its invasive potential (Corfield et al. 2008). The contrasting histories of destructive carp and (apparently) relatively benign goldfish in Australian waters illustrate extreme differences in environmental impacts of superficially similar alien species. Furthermore, the impacts of alien species are often synergistic to those of other stressors: 'Exotic species might be a primary cause for decline, a contributing factor for a species already in trouble, the final nail in the coffin or merely a bouquet at the funeral' (Corfield et al. 2008: page 56). Establishing the relative contribution of non-indigenous species to declines or extinctions is a daunting task and closer examination of case histories is required to determine species' roles.

Bomford and Glover (2004) developed a model to provide a simple, quantitative method for ranking the risks associated with new fish, using the resources of Fishbase (Froese and Pauly 2010) for inputs. Fishbase is a valuable, comprehensive resource, but nevertheless reflects limitations and inadequacies of available data; for example, carp are described as '... never known to dominate the environment', a comment that, in Australia, could not be further from the truth.

Predation and competition

Invading fishes may occupy places at any consumer level of food webs, from herbivores and detritivores to top predators. Table 4 and Thumbnail case studies (above) summarise the mechanisms and impacts of these changes. With the outstanding exceptions of carp and goldfish, most of the important invaders have been largely carnivorous. This applies to translocated native species, as well as to the aliens. But large or small, translocated or alien, invading fishes play diverse roles in ecological modifications. Removal of redfin from New Zealand ponds resulted in marked changes in prey fish (common bullies *Gobiomorphus cotidianus*) (Ludgate and Closs 2003). Contrastingly, Wilson et al. (2008) found redfin removal from South Australian stream pools did not change abundance of similar prey (flathead gudgeon *Philypnodon grandiceps*) but did alter gudgeons' microhabitat use. Predator–prey interactions are species- and habitat-specific, also varying with ontogenetic stages (Stoffels and Humphries 2003).

Rainbow and brown trout introductions around the world have often been detrimental to native fish, with population declines and even extinctions. Species displacement and fragmentation also have occurred in Australasia (Tilzey 1976; Jackson and Williams 1980; Crowl et al. 1992). Fortunately, trout strongly overlap the ranges of relatively few native fishes, mainly Galaxiidae, Anguillidae and Gadopsidae plus Australian grayling *Prototroctes maraena*, trout cod and Macquarie perch. Many such overlaps occur in Tasmania; mainland trout habitats are at higher altitudes and inhabited by fewer natives, notably mountain galaxias, eels and blackfish *Gadopsis marmoratus* and *G. bispinosus*. These species remain **sympatric** with trout in many areas (Harris and Gehrke 1997; Davies et al. 2008), although mountain galaxias require structural cover like macrophytes or broad shallows to maintain populations. In streams lacking cover, galaxiids become restricted to upper headwaters less accessible to trout, and populations become fragmented (Lintermans 2000; Green 2008). These interactions are dynamic; dry periods and warm temperatures displace trout, allowing recovery of native populations (Closs and Lake 1996), significantly for climate-change predictions. In the enlarged Lake Pedder in Tasmania following hydropower development, a combination of the predatory impact of brown trout, habitat degradation and, importantly, competition and predation by translocated climbing galaxias, led to the precipitate decline and ‘extinct in the wild’ status of Pedder galaxias (Threatened Species Section 2006). Trout predation on other small fishes would undoubtedly occur where ranges overlap. One key such area is near the lower altitudinal distribution of trout (around 600 m) in eastern MDB tributaries where endangered trout cod and Macquarie perch cling to existence. Trout are often only one of multiple stressors, with effects confounded by land use changes and habitat degradation (Cadwallader 1996; Erskine and Harris 2004), but their predation and competition have deleteriously affected some native fish populations. Research is needed to tease out the impacts of habitat change versus alien species impacts and, especially, to evaluate interactions between the two (Ormerod et al. 2010).

Diminutive gambusia are important predators and aggressive competitors, preying on young fish, amphibians and invertebrates (Lloyd 1990; Arthington 1991; MacDonald and Tonkin 2008). Impacts reducing the abundance and distribution of many small and larger native fishes and frogs have been attributed to gambusia, through fin nipping, competition for prey and predation of young (Rowe et al. 2008). Undoubtedly, some of the other 32 escapees from the aquarium industry (Table 2) will be having comparable impacts, but these pose large knowledge gaps.

Tilapia have great dietary plasticity (Ansell and Jackson 2007; Froese and Pauly 2010) and may prey on fish (Doupé et al. 1999a; Doupé and Knott 2010), as well as being highly successful competitors for space, spawning areas and food. Despite their value as a source of protein and human food security, Canonico et al. (2005) considered tilapia cannot continue to be introduced without further damaging native species and biodiversity. Their impacts elsewhere, their popularity among some Asian and Islander cultures, and the risk of spread, especially into the MDB and Gulf rivers combine to place tilapia at the top of lists of threatening invasive species (Ansell and Jackson 2007; Doupé and Burrows 2008).

(TABLE 4 NEAR HERE)

Food-web changes

Ecological communities are complex networks of interacting carnivores, herbivores and plants. Impacts through different mechanisms and at different levels of ecological organization (individual, population, community, ecosystem) can alter nutrient and energy flux in streams and in lakes (Simon and Townsend 2003). As well as the numerical effects of predators consuming prey, trophic cascades may occur, in which animals at high trophic levels may deplete those in the level below, thus releasing the next lower level from consumptive control. These include the indirect, top-down effects of carnivores on plants, mediated through predation on herbivores (Polis et al. 2000; Townsend 1996) (Table 4), for example when populations of herbivorous fish or grazing macroinvertebrates are reduced or restricted to less-preferred microhabitats or suboptimal foraging in the presence of predators. Predator-avoidance behaviour, with prey employing adaptive foraging strategies to reduce predation risk, can reduce the impacts of herbivorous prey on plants, thus driving trophic cascades leading to plant overgrowth (Schmitz et al. 2004). The presence of trout and galaxiids in a stream may lead to mayfly larvae seeking refuge, thus reducing their grazing impact on attached algae (McIntosh and Townsend 1996). Although such anti-predator strategies may reduce mortality from predation, sub-lethal impacts can still occur, as when the presence of brown trout caused golden galaxias (*G. auratus*) to change its use of open-water habitat, reducing feeding opportunities (Stuart-Smith et al. 2008).

Fish may trigger trophic cascades culminating in nuisance blooms of cyanobacteria by preying on grazing zooplankton, or promote blooms by altering availability of nutrients and light (Gehrke and Harris 1994). Cyanobacterial blooms have caused extensive environmental, economic and social disruption in Australia. Carp contribute to these 'bottom-up', food-web modifying pathways by preying on zooplankton when young, by excreting nutrients from dense, high-biomass populations, by re-suspending sediments and by damaging macrophytes (Gehrke and Harris 1994; King et al. 1997). Predator manipulation has been the basis of management strategies to control trophic cascades and reduce these algal blooms in lentic waterbodies (Gehrke et al. 2010), and its effectiveness in controlled environments has been demonstrated by enclosure/exclusion experiments (Khan et al. 2003; Schmitz et al. 2004).

Parasites and diseases

Through isolation across the disjunction of Wallace's Line, and lacking most of the world's freshwater fish families, Australia's native fish fauna remained free of many of the world's parasites and diseases. The fish are therefore vulnerable to introduced pathogens because they lack specific resistances (Lymbery et al. 2010). The 8–10 million ornamental fish imported to Australia each year pose a particular, but insufficiently documented hazard of disease introduction (McNee 2002). Although quarantine stringency has improved, there have been many disease incursions and establishment of viral, bacterial, fungal, protozoan and metazoan pathogens from ornamental fish: quarantine protection has proved inadequate (Whittington and Chong 2007). Disease incursions will continue and exotic pathogens will become established unless research and monitoring are improved, guidelines are revised and the numbers of species and sources are dramatically reduced.

Asian fish tapeworm, *Bothriocephalus*, is a pathogenic new parasite in Australia that is not host-specific. Usually associated with carp and gambusia, it has crossed into at least one native fish (Dove et al. 1997) and threatens other native fauna (Henderson 2009). Four new monogenean tapeworms have been introduced with alien ornamental fish (Dove and Ernst 1998). At least two new pathogenic parasites were introduced to Western Australia by alien fishes (Lymbery et al. 2010), together with the copepod parasite, *Lernaea cyprinacea*. Epizootic haematopoietic necrosis virus (EHNV) is a virulent iridovirus, probably endemic to Australia, which causes severe mortalities in redfin and may also be carried by rainbow trout (Whittington et al. 2010). EHNV is an indiscriminate pathogen, with at least 10 native (Macquarie perch, silver perch, mountain galaxias, Murray cod, golden perch, Australian bass) and alien species experimentally susceptible to infection. Aquarium gouramis carried gourami iridovirus that caused 90% losses among farmed Murray cod (Whittington and Chong 2007). Goldfish ulcer disease, a bacterial infection introduced with goldfish (Humphrey and Ashburner 1993), caused outbreaks among roach and silver perch as well as goldfish, and threatened the Atlantic salmon aquaculture industry. Many other pathogens have been imported with ornamental fish, highlighting disease risks associated with the trade (Whittington and Chong 2007).

Nodaviruses have caused high mortalities in freshwater and marine fish hatcheries. Nodavirus infecting Australian bass in hatcheries, and threatening to cause disease among wild fish, led to curtailment of stocking plans and compulsory screening of all hatchery bass (Frances et al. 2005). The outbreaks emphasize the hazards of distributing mass-propagated fish and the need for intensive control of hatchery operations and stocking procedures (Whittington et al. 2010). Viral encephalopathy and retinopathy is virulent in barramundi and at least seven other freshwater fish are naturally or experimentally susceptible (AGDAFF 2008); mortalities generate concern over barramundi farming outside the species' natural range. One of the biggest risks associated with the global movement of species is the introduction of non-native infectious agents (Gozlan et al. 2010) and intensive monitoring and control are imperative.

Making-over the environment to suit

Carp (and perhaps tilapia) are unique among Australia's non-indigenous fish, succeeding as ecosystem engineers, changing aquatic environments to the disadvantage of enemies, while also employing the more-usual strategies of invaders. Habitat disruption is the ultimate weapon in the carp armoury. Most native competitors and predators lack carp's tolerances, so that impacts from benthivorous feeding, sediment resuspension, nutrient loading and loss of attached aquatic plants combine to disrupt ecological adaptations that sustain native communities. Interference competition seems unavoidable in the face of dense schools of big carp, and their removal can rehabilitate zooplankton and native fish (Gehrke et al. 2010). Huge reproductive potential together with schooling behaviour can overwhelm predators, especially in degraded ecosystems where predators are few. Predation on the eggs of freshwater catfish and other nesting species is suspected (presenting a worthwhile research opportunity). Even carp's role as vectors for parasites like the copepod ectoparasite *Lernaea,* or the Asian fish tapeworm *Bothriocephalus* (Dove et al. 1997), which are pathogenic for native fish, disadvantages natives and further reduces their effectiveness as carp competitors and enemies.

With water quality tolerance, large body size, considerable longevity (<38 y), high reproductive potential (fecundity <$2X10^6$), rapid maturity (1–2 y), short generation interval (2–4 y), schooling behaviour, powerful migration and barrier-leaping ability, plus great dietary flexibility focused near the bottom of food webs, carp are superbly adapted invaders. Adaptations and phenotypic plasticity enable them to thrive in degraded habitats. Dams and weirs provide refuge from high-flow mortalities (Driver et al. 2005a); more alien fishes live in regulated than unregulated rivers (Gehrke and Harris 2001). Coldwater pollution below dams similarly favours carp (Roberts and Tilzey 1996; Phillips 2001) while displacing native fish (Todd et al. 2005). In much of the MDB carp represent >90% of total fish biomass. Populations reach densities >1,000 carp/ha, with biomass densities >3,000 kg/ha (Harris and Gehrke 1997). Vast numbers of rotting carp foul the shorelines of wetlands evaporating in drought. In the Sustainable Rivers Audit Davies et al. (2008; 2010) also found carp were overwhelmingly dominant (87% of alien fish biomass, 58% of total fish biomass). Carp continue to expand their geographic and altitudinal range; climate matching shows the species' potential distribution includes all Australian fresh waters (Koehn 2004).

Given the values accorded carp (historically, at least) for angling, food and ornament, and with high propagule pressure through repeated introductions of multiple genotypes, it is not surprising they have so dominated freshwater environments and continue to spread. As Koehn (2004) emphasised, carp are not just another alien species in Australia, they are in a class of their own, demanding concerted national efforts to manage their drastic effects.

Longer-term impacts

Dissolving biogeographic barriers and species movements have evolutionary consequences, with potentially dramatic changes in selection, evolutionary responses and shifts in the behaviour and traits of both invading species and invaded communities. Evolutionary processes can increase, decrease or qualitatively change the impacts of an invader through time (Vermeij 1996; Strayer et al. 2006), requiring a long-term view. Direct consequences have included extraordinarily rapid adaptations of new species clines in new environments, sometimes as swiftly as 20 years, as well as evolution of new **polyploid** species from intrusion of invaders into native populations (Mooney and Cleland 2001). There are examples of invasive species altering the evolutionary pathway of native species by competitive exclusion, niche displacement, hybridisation, introgression, predation, and ultimately extinction. Invaders themselves evolve in response to their interactions with natives, as well as in response to new abiotic environments created through human interventions (Mooney and Cleland 2001; Davis 2009). Evolving adaptations of existing predators, together with responses to climate variations, may be implicated in recent declines in Australian carp populations, suggesting research opportunities in carp population dynamics.

Homogenization mostly increases biodiversity, at least in the short-to-medium term and at local scales, because establishment of non-indigenous species outpaces extirpation of natives (Rahel 2002). But there are important exceptions, where non-indigenous species have had devastating impacts on endemic species, as with Nile perch in Lake Victoria. Furthermore, increases in species-level biodiversity may be offset by lost genetic diversity.

Fish may hybridize readily. Low-level introgression occurs naturally among closely related species and is an important source of genetic variation, but becomes a conservation concern when human disturbances (species introductions, habitat modification, overexploitation) increase its prevalence (Schwartz and Beheregaray 2008). Isolating mechanisms preventing hybridization between species may break down following population declines (Rowe et al. 2008), sometimes producing rapid evolution. Native species' fitness can be reduced following hybridization, even threatening extinction, especially when large numbers of introduced individuals swamp relict native populations (Mooney and Cleland 2001; Phillips 2003). Because there are few family-level taxonomic overlaps (Table 1), hybridization between alien and native Australian species is less of a risk than it is between translocated and indigenous native species. But hybridization has occurred between alien species (carp and goldfish, tilapia species (McDowall 1996)) and may enhance their adaptation to local environments, producing more-vigorous pests. Increased genetic variation and hybrid vigour with enhanced fitness probably drove the explosive spread of carp following introductions of new Boolara and koi strains amongst the long-stable Prospect and Yanco strains (Davis et al. 1999; Haynes et al. 2009).

With translocated hatchery fish, insidious threats may result from reduced genetic diversity, loss of co-evolved adaptations to specific habitats, or swamping of indigenous populations through competitive displacement, hybridization and introgression (Phillips 2003; Rowland and Tully 2004). Genetic homogenization through hatchery stockings risks obscuring genetic structuring at population level, thus closing a window into the evolution of biogeographical boundaries. Interbreeding with conspecifics or hybridization with congenerics following hatchery stocking are risks that particularly affect the genetic integrity and fitness of native species in degraded environments or relict populations (Phillips 2003). Both Murray cod and trout cod parental lineages were lost following their introduction to Cataract Dam, outside their native distributions (Harris and Dixon 1986); the population now comprises only fertile hybrids. Hybrids of Australian bass and estuary perch *Macquaria colonorum* have also been identified in eastern Victoria (Schwartz and Beheregaray 2008), where the species' ranges overlap. Many individuals (<46%) were detected, with hybrid fertility and backcrossing. Significantly, some of the samples came from hatchery broodfish and stocking programs, and putative bass have previously been stocked repeatedly. Parent populations could be extirpated, either through outbreeding depression or replacement by hybrids, and genetic screening of hatchery broodstock is needed (Schwartz and Beheregaray 2008).

Social and economic effects

The memories of older Lachlan River residents were recorded using oral-history techniques to capture their knowledge of historical changes in the river (Roberts and Sainty 1996). Their perceptions dwelt on the disappearance of aquatic plants, the loss of water clarity and the invasion of carp hordes. Pervasive environmental degradation is emerging as an underlying cause of reduced human wellbeing and emotional health among rural communities (Rowe et al. 2008). Horwitz et al. (2001: p253) argued that the biodiversity of inland waters and human health are linked: 'Biodiversity, and its endemic features, contribute to a person's attachment to a particular place and become part of a person's identity. Loss, destruction or change in a location has the potential to affect an individual's psychological well-being and challenge a community's identity and image of itself.' Aboriginal communities suffer cultural impacts when their connections with native fish, which formed an important part of traditional lifestyle and social interactions, are lost to environmental degradation and replacement by alien species (Rowe et al. 2008).

The National Recreational and Indigenous Fishing Survey (Henry and Lyle 2003) provided comprehensive statistics on fish catch, effort, species composition, and profiles of anglers and their expenditure. They found 19.5% of people over 5 y fished annually, spending about 20.6 million days fishing, about 20% of which were in freshwater, and harvesting 2.1 million carp and 1.3 million redfin, among other fish. Estimated expenditure on services and items totalled $1.8 billion.

Invasive species are a side effect of trade that often proceeds to grim and (usually) irreversible outcomes, such as the disastrous, continuing spread of zebra mussels and quagga mussels *Dreissena* spp. through North America. Alien species in the USA grew exponentially over 150 y, with a strong correlation with the importation of goods (Keller et al. 2009). In 2001, non-indigenous species annually caused estimated economic losses of US$137 billion in the USA (Kolar and Lodge 2001). With numbers increasing rapidly through globalization, non-indigenous species are now among leading global threats to biodiversity and ecosystem function (Strayer et al. 2006). The costs of invasive species should not be assessed only in dollars, positive and negative values assigned to invasive species should be informed by financial, scientific, social and ethical considerations. Analytical approaches to the impacts and dynamics of invasive species were assessed by Keller et al. (2009), showing the utility of combining ecological and economic models in addressing management questions.

In the USA, 50,000 alien plant and animal species present at the end of the millennium caused environmental damage and losses totalling approximately US$137 billion annually (Pimentel et al. 2000) and 42% of listed threatened species were at risk primarily because of non-indigenous species. These costs offset the benefits of alien species (food crops, livestock), which provided >98% of the US food system at an annual value of $800 billion. In Australia, the costs of non-indigenous fish, including lost ecosystem services, declining fisheries, social impacts, reduced water quality and control costs are poorly documented, if at all (Koehn and Mackenzie 2004), inviting research analysis.

Compensatory economic benefits accompany non-indigenous fish; values have been identified (GISP 2004; Rowe et al. 2008 Gozlan et al. 2010) recognizing the same species that damage ecosystems may also produce social and economic benefits. Non-indigenous fish may provide benefits through recreational fisheries or aquaculture and food security (Cadwallader 1996; Rowe et al. 2008; Halverson 2010), but those species that prove harmful can have major adverse impacts (Pimentel et al. 2000; Rowe et al. 2008; Keller et al. 2009). Gozlan et al. (2010) argued that the general consensus that non-indigenous fish species have overall negative economic effects is misconceived. There are direct, positive and negative, social and economic effects (revenue, food security versus control costs, loss of biodiversity) and also indirect effects (wider benefits to society versus loss of ecosystem goods and services). Some 17% of the world’s finfish production is derived from non-indigenous species, but there are few data on other costs and benefits of fish introductions (Gozlan et al. 2010). So invasions can either increase or decrease ecosystem populations or materials, and can provide both benefits and costs to humans (Strayer et al. 2006).

In Australian, clear benefits from deliberate fish introductions include the recreational, social and economic values of trout fisheries plus fisheries for hatchery-bred native species in rivers and – especially – in impoundments (Simpson et al. 2002; Ansell and Jackson 2007). Aquaculture with trout, silver perch and barramundi is also economically significant. Among Victorians, at least, there is appreciation for redfin, which may be offset against associated impacts (Rowe et al. 2008). Rowe et al. (2008) provided multidisciplinary insights to the environmental, social and economic impacts of non-indigenous fish and pest species in Australia, using social impact assessment and cost-benefit analyses based on six alien species (gambusia, redfin, roach, tench, streaked goby, yellowfin goby). Better estimates are needed of the values of ecosystem services provided by intact, biodiverse inland waters so these values can be properly factored into cost-benefit assessments.

Pest control and eradication

Research efforts towards controlling pest fish were spurred by impacts of carp on rural communities, by evidence of gambusia’s role in frog declines, by the flood of aquarium imports and by the invasive spread of tilapia. States and the Commonwealth have gazetted regulatory controls and pest species classifications (Chapter 12) to manage the problems, and native fish translocations are better controlled. The Invasive Animals Cooperative Research Centre (IA CRC) (http://www.invasiveanimals.com) estimates that invasive terrestrial and freshwater vertebrates cost Australasia at least $720 million annually, and is studying advanced tools and strategies for integrated pest management of carp and other pest fish. Groundbreaking programs in the IA CRC providing career options for students include development of genetic technologies, biocides, pheromone-assisted trapping and environmental manipulation. The ‘daughterless’ program is a radical concept using recombinant methods targeted initially at carp and gambusia (Thresher 2007, 2008; Bax and Thresher 2009). It aims to manipulate fish genotypes to produce heritable constructs that bias gender ratios towards male progeny without reducing fitness, thus driving population fertility downwards. It offers hope as the first long-term, sustainable tool for control and possible eradication of pest animals.

More-direct tools are also emerging. Williams carp-separation cages being installed in fishways (Stuart and Jones 2002; Stuart 2008) exploit carp’s propensity for leaping over barriers to separate them from native fishes which, except for a few (mullets, spangled perch), rarely leap. Separated carp are harvested. Carp populations recruit from floodplain wetlands (Smith 2005; Gilligan and Rayner 2007), and flow manipulations and innovative trapping techniques enable them to be targeted at these sites (Stuart and Jones 2006). Trapping large-scale upstream dispersals of adult and young-of–the-year carp as they pass through fishways provides another powerful tool (Stuart and Jones 2002; Stuart 2008). Carp eradication is being attempted in two Tasmanian lakes (http://www.ifs.tas.gov.au/ifs), using containment, intensive multi-gear fishing, sterile ‘Judas carp’ and barrier netting. Eradication has succeeded in Lake Crescent, with dramatic reductions in Lake Sorell.

The values of fish from elsewhere

Australian attitudes to fish from elsewhere range widely. There is general loathing for carp; hobbyists’ enthusiasm for ornamentals in aquaria; anglers’ and aquaculturists’ great affection for trout; appreciation for redfin in some regions (hostility in others); general ignorance about gambusia and tilapia, and even more so about weatherloach, gobies, platys, tench, roach, etc. Issues stemming from native fish translocations are seldom recognized in the general community, and the pre-eminent value of wild stocks over hatchery fish has yet to become widely known. Each of these positions motivates polarized community groups and there is neither a strong consensus (except about carp) nor a broad understanding of the issues. Similarly, there is no consensus on what constitutes a pest fish. Apart again from carp, plus the few other species gazetted as pests (aquarium escapees, redfin), this perception depends on the background and affiliations of individuals and varies widely across the community.

Fishing is one of very few modern-day activities that allow people to express their innate hunter-gatherer biology. This fundamental human characteristic is suppressed in modern, sedentary, post-agricultural communities. In Australia recreational fishing is highly valued, with community involvement rates of about 20%, frequently targeting trout, redfin, or native species like silver perch, golden perch, Murray cod, barramundi or Australian bass. A big but unquantified proportion of exploited native species comprises hatchery-bred, translocated fish. These alien and translocated species play important roles in the wellbeing of Australians. Community benefits accrue from recreational fishing, which enhances people's ability to experience natural environments, contributes to personal health and wellbeing and is a stress-relieving emotional outlet, especially in rural communities, that is important for mental health (Horwitz et al. 2001; Rowe et al. 2003). The National Recreational and Indigenous Fishing Survey (Henry and Lyle 2003) reinforced these views, documenting psychological, environmental and social benefits and showing that non-catch motives (to relax and unwind, to be outdoors, for solitude, to be with friends and family) were rated higher than catch-related motives (food, competition, sport). Aboriginal people have strong cultural and spiritual values associated with native fish (Rowe et al. 2008) and displacement by alien species may impact on cultural heritage, beliefs and community values. Fishing is an invaluable component of the cultural lifestyle of Aboriginal communities and is connected to the traditional responsibilities of land management and kinship (Henry and Lyle 2003), maintaining social networks for these communities.

In recreational fisheries management, there is a need to dispel the 'stocking panacea' concept among anglers and managers (Phillips 2003; Havorsen 2010) and to replace it with an evidence-based understanding of potential benefits and the financial and ecological costs of fish stocking programs. Further interdisciplinary studies of the economic, social and ecological aspects of recreational fishing would be valuable.

As Halverson (2010) described, in his fascinating exposé: *An Entirely Synthetic Fish: How Rainbow Trout Beguiled America and Overran the World*, outdoor pursuits driven by angling play a powerful role in the emotional and physical wellbeing of individuals. Public policy underpinnings of rainbow trout aquaculture in the USA in the 1870s were explicitly motivated by concerns, even then, that people were losing their contacts with the natural world and the long-term implication was decline into 'a less bold and spirited nation'. The extraordinarily successful breeding and distribution programs that followed established recreational fisheries for *O. mykiss* in every continent except Antarctica. In Australia, negative consequences of trout invasion vary: threatened galaxiids in Tasmania and Victoria, suppressed macroinvertebrates and trophic cascades in many places, adverse interactions with Macquarie perch or trout cod in the subalpine zone, fragmentation of mountain galaxias populations. The ecological severity of these consequences also varies, ranging from a threat of extinction of two or more galaxiid species, through to relatively minor changes requiring intensive surveys for detection, and all stages in between. Some comfort rests in knowledge that trout have been introduced to every suitable habitat over 150 years; they have reached their potential range and are probably contracting. Their impacts have long since been felt and it is hard to conceive of any new impacts that might appear.

Unlike other alien species, trout are valued in Australia, providing substantial economic and social benefits and widely considered desirable (Karolak 2006). High-quality habitats, abundance and rapid growth, edibility, physical appeal, fish-farming adaptability, and special angling quality make salmonids a prized group generating an enormous literature. Many freshwater scientists and managers are anglers, often with backgrounds in trout fishing. Early fishing involvement provides experience in natural environments, bringing appreciation for watery places and things that live in them. Such favoured upbringing contrasts starkly with that of many modern city-dwellers who are increasingly alienated from the natural world. Fishing can produce this affinity with nature whether aimed at native or alien species, but salmonids play a special part in induction to the planet's natural systems. In an ideal world, perhaps, wild native stocks might provide these values, but the realities of entrenched environmental changes, plus the well-established status of trout all indicate this is unrealistic.

So the values accorded to fish from elsewhere vary greatly. Each must be judged on its merits, and with the best evidence at hand. Economic and social benefits must be weighed against realized and potential damage. This is a complex task, sometimes difficult to approach objectively and usually clouded by inadequate knowledge. Many topics invite research to build the knowledge of alien and translocated fishes' impacts, and to weigh their problems and benefits.

Conclusions

Freshwater biota, like the climate, have been in flux through geological time, with invasions, extinctions and evolution continually at play long before humans intervened, leading some people to pose the 'So what?' question to such issues as biotic homogenization or climate change. The planet has experienced many of these changes before, so why worry now? One response to this is that the rates of change of atmospheric constituents and of biotic compositions are far greater than ever before experienced. Furthermore, the changes are occurring within a global context of profoundly altered natural systems, and natural resistance and resilience to change are in decline. 'Changes in resistance and resilience are fundamental drivers leading to what has been described as a crisis in biodiversity. The spatial patterning, structure, and functioning of most of the ecosystems of the world have been altered by the activities of humankind. ... humans have purposefully and inadvertently moved biological material across barriers that ... have separated the unique biotic realms of the continental land masses. We are now developing a whole new cosmopolitan assemblage of organisms across the surface of the Earth with large consequences not only for the functioning of ecosystems but also for the future evolutionary trajectory of life' (Mooney and Cleland 2001: p5450).

Various ecological impacts have followed fish invasions and the severity of their impacts covers a long continuum, from the habitat and water-quality degradation of carp, the competitive impacts of gambusia and tilapia, through the community disruption of predators like redfin and trout, to the poorly understood effects of invading aquarium fish like goldfish, weatherloach or guppies. Then there are the genetic and evolutionary implications of translocated native species. Scientific concern is growing over the poorer quality of hatchery fish compared to wild stock, with low fitness and reduced viability stemming from trait selection and adverse behavioural adaptations in hatcheries (Phillips 2003; Rowland and Tully 2004; Halverson 2010). The population impacts of liberating great numbers of low-quality, propagated native fish among relict wild conspecifics are little-known and present an important knowledge gap and research opportunity.

In another complex set of interactions, human modifications of ecosystems (water-resource management) combine with natural disturbance (flooding, drought) to exacerbate ecological disasters like blackwater events (MDBA 2011; NSW I&I 2011). Blackwater is a natural occurrence and a resilient fish community could recover in time. But multiple structural and functional changes have been imposed on river ecosystems (flow alteration, migration barriers, coldwater pollution, catchment damage, etc.) and tipped the balance towards dominance by carp gambusia and other alien pests, and have profoundly impacted on native communities' capacity to recover (MDBC 2003). Destructive interplays between natural disturbance and human modification of ecosystems confront society and scientists with challenging questions: is it realistic to aim for control or even eradication of alien pest fish? How much change is needed in the ways that ecosystems have been managed before their resources and services are secure and usage patterns are sustainable?

Much alien species literature is opinion-based, rather than set in the context of comprehensive empirical data, and large gaps in objective information have been stressed (Arthington and McKenzie 1997, Koehn and Mackenzie 2004; Leprieur et al. 2009), noting the challenges, cost and long-term commitment associated with the necessary studies. Divergent opinions about the impacts of non-indigenous fish in Australia stem from these shortages of objective evidence (Lintermans 2004; Doupé and Knott 2010) and the consequential need to infer impact through evidence from distinctly different ecosystems elsewhere (Bomford and Glover 2004; Corfield et al. 2008). And most invasions lack any obvious impacts. Partly because of this lack of evidence, the sharp philosophical divides that characterize perceptions about impacts of alien fish in Australia are often based more on value judgements than on objective data. At one polarized extreme of debates lies the nativism paradigm (Davis 2009), wherein native species are regarded as inherently more desirable than non-indigenous species. Non-indigenous becomes synonymous for pests. Opposing views arise from those who point to social or economic benefits of some non-indigenous species. Salmonids are obvious examples, so too are the translocated native angling species.

Although manipulating ecosystems can never be considered risk free, for risk management the economic values of species should be combined with their associated level of ecological risk (Gozlan et al. 2010). Benefits of non-indigenous freshwater fish in Australia are recognizable and broadly quantifiable. Recreational fishing is important socially and economically. Non-indigenous fish have bolstered its value and have some indirect value for environmental management. Aquaculture supplies seafood to large markets. Both aspects make significant contributions to the quality of life for Australians. Regrettably, the ecological costs of native fish translocations remain uncertain and, in some cases, possibly escalating. Some translocations may cause particular impacts that rival or even exceed those of many alien species.

With very few exceptions, perhaps only in the tantalizing glimmer of hope that effective control or even eradication of carp, gambusia or tilapia might become feasible (Thresher 2008; Bax and Thresher 2009; IA CRC), invasions by non-indigenous fish are mostly irreversible. Some of their impacts may be ameliorated by reducing the compounding, habitat-mediated effects of other stressors, or by more-stringent regulation of fish stocking. But alien species in general are here to stay, and some capacities for native species to evolve in the face of environmental change have been permanently lost through translocation. Given the limited knowledge so far available, there may yet be further unpleasant news about non-indigenous species' effects, and many knowledge gaps remain. The one clear lesson is that species introductions overall have harmed biodiversity and ecosystem services, and this experience should drive future management. But at least a precautionary approach to importation and distribution of fish species is emerging, with efforts to define and manage threatening processes and to highlight risky species. Decisions about aquarium fish imports, distribution of angling species and allocation of resources for control measures are the responsibility of the community's representatives; scientists' role is to provide and convey the best knowledge, so that representatives may make wise decisions about managing their responsibilities and the community's assets.

What should we conclude? Fish from elsewhere have changed forever the character of Australian freshwater ecology. This has occurred alongside profound changes to the abiotic condition of freshwater systems through land and water use. Some unique and important ecological attributes have been irrevocably damaged. Impacts in some cases (carp, tilapia, gambusia, aquarium fish) are continuing on an uncertain but damaging trajectory and there are only limited prospects of their reversal through species eradication or control. The risks of native species translocation have neither been thoroughly elucidated, nor yet satisfactorily controlled. And, as Closs et al. (2004, p.189) poignantly noted, one of the saddest aspects of the homogenization of the global fauna is that 'With each new introduction, somewhere different becomes just a little more like everywhere else.' The irreplaceable treasure of biodiversity is being constantly chipped away, despite our moral and legal obligations. Against this gloomy summary are some brighter points. In a fast-changing environment, we must accept that most or all of the various kinds of non-indigenous fish are here to stay, and a few have undeniable values that contribute to the quality of Australian lives, albeit at a cost to the integrity of freshwater environments.