

Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences

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SUMMARY

1. Invaders can influence freshwater systems at the individual, population, community and ecosystem levels. Some of these impacts may be subtle or not easily predicted but they may be critical to understanding more obvious changes. Despite this, studies of impacts of freshwater invaders at several levels of ecological organisation are rare. Most commonly reported are changes in the distribution or abundance of populations after invasion, whereas documentation of impacts on ecosystem functioning, such as energy and nutrient flux, is rare.
2. Unlike most invaders, salmonids have been studied at multiple ecological levels. These fish can cause trophic cascades that result in increased algal biomass and production and are responsible for changes to energy and nutrient flux in both streams and lakes. The mechanisms behind these changes are different in the two systems and only become evident when information at the individual and population levels are considered. In streams, salmonids can alter invertebrate behaviour that suppresses grazing of periphyton. In lakes, salmonid feeding behaviour can stimulate phytoplankton by shunting nutrients from the littoral to the pelagic zone.
3. Simultaneous study at several ecological levels should yield a fuller understanding of the mechanisms underlying impacts of invading animals and plants, providing a sounder basis for predicting the impacts of freshwater invasive species. Species traits of the invaders that may be associated with particularly profound impacts include: a method of resource acquisition formerly lacking in the invaded system, a broad feeding niche that links previously unlinked ecosystem compartments, a feeding relationship 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.

Keywords: community, invasion, lakes, population, *Salmo trutta*, streams

Introduction

In recent decades the threat of biological invaders has gained prominence and much effort has been focused on predicting which species are likely to be invasive or why potential invaders succeed or fail (e.g. Moyle & Light, 1996; Kolar & Lodge, 2001). This paper focuses

on equally important questions that concern invaders that do become successfully established; what are the impacts of successful invaders and can these be predicted? The effects of invaders vary from undetectable to dramatic. Particularly striking examples of freshwater invaders that have changed the nature of whole communities include the Nile perch [*Lates nilotica* (L)] in Lake Victoria, East Africa (Kaufman, 1992; Goldschmidt, Witte & Wannink, 1993), opossum shrimps [*Mysis relicta* (Lovén)] in Flathead Lake, North America (Spencer, McLelland & Stanford, 1991) and

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zebra mussels [*Dreissena polymorpha* (Pallas)] in the rivers and Great Lakes of North America (Strayer *et al.*, 1999; Nalepa & Schloesser, 1993, Ricciardi 2003).

Reports of reduced abundance or extirpation of native species by invaders are common; however, invasive species can have effects at multiple ecological levels (Mack *et al.*, 2000). At the level of individual organisms, invaders may alter the behaviour of native species, influencing habitat use and foraging. At the population level, invaders may induce changes in the abundance or distribution of other species. At the community level, invaders may alter both direct and indirect interactions among populations and even induce trophic cascades. Finally, at the ecosystem level, invaders may change the pathways and magnitude of movements of energy and nutrients. When we discuss ecosystem-level consequences, we deal specifically with impacts of invaders on the ecosystem processes relating to energy and nutrient flux.

The primary aim of this review is to examine the impacts of salmonid invaders at multiple levels of ecological organisation in streams and lakes. Studies reporting information about the impacts of invaders at the ecosystem level have been relatively rare (Vitousek, 1990), but are becoming more common (note many recent studies cited in this review). Simultaneous investigations of impacts at all ecological levels are even rarer. However, multilevel data are available from a number of investigations of salmonid invaders in lakes and streams around the world and we will focus on these as case studies that emphasise the value of the multilevel approach for understanding the mechanism of invader impact. In addition, we seek generalisations about the impacts of a range of freshwater invaders, including invertebrates, amphibians, fish and plants, at the individual, population, community and ecosystem levels of ecological organisation. A particularly powerful way to uncover the role that species play in ecosystems is to remove or add them. In the final section of this review we show how invasions provide a body of natural experiments that are relevant to the fundamental ecological question of what species do in ecosystems.

Individual level

Freshwater invaders have altered the behaviour of natives, generally through predation or competition. Behavioural responses to salmonid invaders in lakes

and streams have been documented for both fish and invertebrates. In New Zealand streams, introduced brown trout [*Salmo trutta* (L)] change the diurnal activity and microhabitat selection of invertebrate prey, particularly those taxa that feed on periphytic algae on the surfaces of rocks on the streambed. Mayflies [*Nesameletus ornatus* (Eaton)] from streams containing brown trout are more active during the night than mayflies from streams with only native fish (McIntosh & Townsend, 1994). Mayflies (*Deleatidium* spp.) also tend to spend less time on the surfaces of rocks in streams when brown trout are present as compared with streams with native fish or no fish (McIntosh & Townsend, 1996). Diehl *et al.* (2000) found mayflies (*Baetis* spp.) exposed to brown trout also spent less time on the surfaces of rocks. Further, brown trout alter diurnal drift patterns of invertebrates, reducing the propensity to drift of some mayflies (*Deleatidium*) and increasing night drift of other taxa including snails [*Potamopyrgus antipodarum* (Gray)] and caddisflies [*Olinga feredayi* (McLachlan) and *Aoteapsyche colonica* (McLachlan)] (Williams, 2000). Baetid mayflies [*Baetis caelestis* (Allen & Murvosh)] also increase their night drift in the presence of rainbow trout [*Onchorhynchus mykiss* (Walbaum)] (Douglas, Forrester & Cooper, 1994). The altered behaviours demonstrated by the invertebrates in invaded streams result from exposure to invaders that differ in their predation strategy from native fish. For example, brown trout are strong visual predators that feed primarily during the day whereas native fish in New Zealand streams (*Galaxias*) use mechanical cues to find prey and feed during the day and night (McIntosh & Townsend, 1995b). When changes in microhabitat selection and diurnal activity do occur, they can translate into altered foraging patterns by invertebrates. For example, by comparing the amount of chlorophyll *a* in mayfly guts during night and day, McIntosh & Townsend (1995a) showed mayflies (*Deleatidium*) in trout streams fed primarily at night whereas mayflies in streams with native fish fed during both day and night.

As in streams, salmonids introduced to lakes alter prey behaviour. In high-altitude European lakes that were previously fishless but now contain introduced brook char (*Salvelinus fontinalis* Mitchell), copepod (*Cyclops abyssorum taticus* Kozminski), densities have a near-bottom maximum. This pattern is not typically seen in lakes which remain fishless (Gliwicz & Rowan,

1984). The same near-bottom maximum was most pronounced at midday in a lake stocked with brown trout (Gliwicz & Rowan, 1984). These distributional patterns are a result of visual predation by trout and the depth distribution of the fish, which they were rarely found in deep water. Restriction of copepods to deeper water is likely to influence their foraging success, but this does not appear to have been measured. The ability of *C. a. tataricus* to alter its depth distribution has allowed it to persist in lakes stocked with salmonids, from which other zooplankton species have disappeared (Gliwicz & Rowan, 1984).

Invasive salmonids can also restrict native fish (Walser, Belk & Shizawa, 1999; McIntosh *et al.*, 1992) and amphibians (Tyler *et al.*, 1998) to less preferred microhabitats. As with invertebrates, this change in behaviour can translate to reduced feeding activity and success. For example, native fish in New Zealand streams exhibit fewer successful predation attempts in the presence of brown trout (Edge, Townsend & Cowl, 1993). In North American streams, introduced brook char (*S. fontinalis*) change microhabitat selection, foraging rates and reaction distances of native bull charr [*S. confluentus* (Suckley)] (Nakano *et al.*, 1998). Non-salmonid invaders may also cause diet shifts in native species. For example, native lake trout [*S. namaycush* (Walbaum)] shift their diets towards zooplankton from littoral fish in the presence of invading bass [*Micropterus dolomieu* (Lacepède) and *Ambloplites rupestris* (Rafinesque)] (Vander Zanden, Cassleman & Rasmussen, 1999). Red-legged frogs [*Rana aurora* (Baird & Girard)] alter their microhabitat use and foraging in response to introduced bullfrogs [*R. catesbeiana* (Shaw)], smallmouth bass (*M. dolomieu*) and mosquitofish [*Gambusia affinis* (Baird & Girard)] (Lawler *et al.*, 1999; Kiesecker & Blaustein, 1997).

Population level

Extirpations, reductions in abundance, and altered distributions of native species have been commonly reported as a result of invasions. Population-level impacts have been documented after introductions of amphibians (Lawler *et al.*, 1999), crustaceans (Spencer *et al.*, 1991; Yan & Pawson, 1997; Lodge *et al.*, 2000), fish (Kaufman, 1992), molluscs (Strayer *et al.*, 1999), and plants (Boylen, Eichler & Madsen, 1999). Invading salmonids have reduced both the abundance and distribution of native fish and invertebrates, a pattern

that has been particularly well documented in Australasia (see review in Cowl, Townsend & McIntosh, 1992). In a study of the Taieri River system, New Zealand, Townsend & Cowl (1991) found that native fish and invading trout rarely co-occurred and that native fish were generally found only in streams above waterfalls that restrict the upstream movement of trout. Trout predation and competitive exclusion of native fish from favourable habitats may both be responsible for the fragmented distribution of native fish (Cowl *et al.*, 1992; McIntosh, 2000). There are cases, however, where trout and native fish coexist. McIntosh (2000) found that trout and natives could coexist where trout were small (<150 mm fork length), possibly because smaller trout are less effective predators or competitors. Townsend & Cowl (1991) found sympatric trout and native fish in streams that had unstable beds. In these streams, densities of both native fish and trout were typically lower than in streams where they were allopatric. Density of native fish [*Galaxias truttaceus* (Valenciennes)] was also reduced in Tasmanian streams in the presence of brown trout (Ault & White, 1994). In other Australian streams, native fish [*Galaxias olidus* (Günther)] were able to persist in intermittent streams with trout because of the native's tolerance of stream conditions during dry periods (Closs & Lake, 1996). In this case, upstream distribution of trout was constrained by drying, rather than waterfalls. Distributional changes of natives occur in invaded lakes as well. In North American lakes, lake trout (*S. namaycush*) limit the distribution of bull trout (*S. confluentus*), apparently by predation (Donald & Alger, 1993). In Banff National Park, Canada, bull trout have persisted in lakes stocked only with *Oncorhynchus* spp. but have been eliminated from lakes stocked with lake trout and brook trout (Schindler, 2000). Bull trout and lake trout coexist in one lake, possibly because of the size of the lake and complexity of surrounding streams (Schindler, 2000).

Salmonid invaders also generally reduce invertebrate abundance and distribution. In experimental channels in New Zealand, Flecker & Townsend (1994) found large invertebrates were relatively rare in the presence of brown trout and insect density and biomass was generally lowest in trout channels. In some cases, impacts are sufficient to extirpate populations, changing the regional distributions of native species. The distributions of native crayfish in some

New Zealand streams were negatively correlated with the presence of brown trout (Usio & Townsend, 2000; Whitmore *et al.*, 2000). Introduced trout in lakes may eliminate or reduce the abundance of large bodied benthic and planktonic invertebrates (Bradford *et al.*, 1998; Carlisle & Hawkins, 1998; McNaught *et al.*, 1999; Parker *et al.* 2001). Rainbow trout (*O. mykiss*) introduction led to declines in *Chaoborus* and *Daphnia* abundance, but caused increases in abundance of the cladoceran *Holopedium*, rotifers and other small-bodied species (Carpenter & Kitchell, 1993). Likely explanations for increases in small species include reduced predation by *Chaoborus* or reduced competition with other larger species (Carpenter & Kitchell, 1993).

The effects of size-selective predation may also be reflected in changes to the size class structure of prey in invaded systems. Huryn (1998) found that the average individual size of most large invertebrate taxa was smaller in a brown trout stream as compared to a nearby stream with native galaxiid fish. Similarly, invading zooplankton (*Bythotrephes cederstroemi* (Schoedler)) in a North American lake extirpated or reduced the abundance of small zooplankton taxa, leading to an increase in abundance of larger taxa that were presumably resistant to predation (Yan & Pawson, 1997).

A more subtle impact of introduced salmonids is damage caused by genetic introgression with native fish. Introgression can increase the likelihood of extinction by reducing fitness and the ability of populations to adapt to changing conditions (Allendorf & Leary, 1988). In North America, cutthroat trout (*Salmo clarki* (Girard)) (Allendorf & Leary, 1988), Apache trout (*O. apache* (Miller)) and Gila trout (*O. gilae* (Miller)) (Dowling & Childs, 1992) have undergone extensive hybridisation with invading rainbow trout (*O. mykiss*). Stocking of conspecifics can also result in introgression and loss of genetic information; hybridisation occurs between hatchery and wild populations of salmonids, including brown trout (Hansen *et al.*, 2001) and brook trout (*S. fontinalis*) (Hayes *et al.*, 1996).

Community level

While introduced species clearly cause direct impacts on prey or competitors, they may also indirectly alter interactions within communities, sometimes resulting in trophic cascades. A variety of experiments have

shown that introduced salmonids can indirectly increase algal biomass (Flecker & Townsend, 1994; McIntosh & Townsend, 1996; Diehl *et al.*, 2000; Nyström *et al.*, 2001). In stream channel experiments, Flecker & Townsend (1994) showed algal biomass was higher in channels with brown trout than channels with native fish or no fish. In their experiment, trout reduced invertebrate grazer biomass, apparently releasing algae from top-down regulation by grazers. In similar experiments, McIntosh & Townsend (1996) found higher algal biomass in trout channels but no decline in grazer abundance; however, they did find invertebrate grazing activity was lower in the presence of trout. In stream channel experiments in North America, Diehl *et al.* (2000) showed a similar brown trout-induced increase in algal biomass was due primarily to changes in invertebrate behaviour. Algal assemblage composition can also be different in the presence of trout. In a comparison of streams with native fish and invasive trout, Biggs *et al.* (2000) found that algal assemblages in trout streams were dominated by erect taxa that are more susceptible to grazing. Presumably, the relaxation of grazing pressure allowed the erect taxa to flourish in trout streams, whereas in streams with native fish erect taxa were rapidly consumed. Thus, it appears that trout can indirectly regulate algal abundance and community composition in streams by altering both grazer abundance and grazer foraging behaviour.

Nyström *et al.* (2001) demonstrated a trout-induced trophic cascade in ponds, where rainbow trout reduced biomass and activity of grazing snails, resulting in higher algal biomass. Trout have also initiated trophic cascades in North American lakes that have been historically fishless. By examining fossil pigments, Leavitt *et al.* (1994) documented a four to six-fold increase in algal biomass in lakes stocked with trout. While the reduction in planktonic and benthic grazers are likely to have influenced the phytoplankton, Leavitt *et al.* (1994) suggest that enhanced P recycling by fish was important in increasing phytoplankton abundance. In a more recent survey of similar mountain lakes in the Sierra Nevada, U.S.A., Schindler, Knapp & Leavitt (2001) found that trout introduction led to an increase in algal production that was sustained for as long as trout were present. Enhanced phosphorus regeneration by fish was again implicated as the cause of the trophic cascade.

Trophic cascades may also be caused by non-salmonid invaders. Bass [*Micropterus salmoides* (Lacépède)] and northern pike [*Esox lucius* (L)] in lakes (Carpenter & Kitchell, 1993 and Elser *et al.*, 2000, respectively), signal crayfish [*Pacifastacus leniusculus* (Dana)] in ponds (Nyström, Bronmark & Graneli, 1999), and rusty crayfish [*Orconectes rusticus* (Girard)] in streams (Charlebois & Lamberti, 1996) all cause increases in primary producers by reducing grazer abundance. Introduced opossum shrimp (*M. relicta*) in Flathead Lake, U.S.A., had little impact on primary producers but initiated a trophic cascade to higher trophic levels by removing a key food item (herbivorous zooplankton species) used by kokanee salmon [*Onchorhynchus nerka* (Walbaum)] (Spencer *et al.*, 1991). Interestingly, salmon have not been able to use opossum shrimp as a food source because the shrimp spend daylight hours deep in the lake where salmon do not feed.

Invaders do not always initiate trophic cascades in invaded systems. The lack of impact of opossum shrimp on primary production in Flathead Lake, U.S.A., has been attributed to nutrient limitation of phytoplankton rather than grazer limitation (Spencer & Ellis, 1998). Similarly, Parker *et al.* (2001) removed non-native trout from a small lake in Canada and found little evidence of a trout-induced trophic cascade. Several factors may be responsible for the lack of an effect, including nutrient limitation, low temperature, and the presence of omnivores in the lake (Parker *et al.*, 2001).

Ecosystem level

As compared with the individual, population and community levels, documented changes to ecosystem processes are rare. This probably reflects a lack of measurement of ecosystem processes by researchers rather than a lack of impact on these processes (Vitousek, 1990). There is some evidence that introduced trout can significantly change energy and nutrient flux in streams. As previously noted, invasion by brown trout caused a trophic cascade leading to increased algal biomass in New Zealand streams. Huryn (1998) pursued the consequences of this cascade at the ecosystem level by compiling comprehensive production/consumption budgets for two neighbouring streams: one with invading brown trout and one with native galaxiids. He found annual net

primary production was six times higher in the stream with brown trout and secondary production by grazing invertebrates in the trout stream was 1.5 times that in the galaxiid stream. In the trout stream, grazers consumed only about 21% of primary production and trout consumed nearly all the annual invertebrate production. In contrast, in the stream with native galaxiids, grazing invertebrates consumed 75% of the primary production and galaxiids only consumed about 18% of prey production. These differences represent substantial changes in the pathways of energy flux in the streams.

Recent comparison of other trout and galaxiid streams has shown that trout streams can be more retentive of nitrogen than galaxiid streams (K. S. Simon and C. R. Townsend, unpublished data). This result is not surprising given the higher algal biomass and primary production typically seen in trout streams (Huryn, 1998). Altered nutrient cycling has also been demonstrated in lakes. As previously noted, trout introduced to fishless lakes enhance phosphorus recycling to the pelagic from the littoral zone (Leavitt *et al.*, 1994; Schindler *et al.*, 2001). The magnitude of phosphorus regeneration in lakes in the Sierra Nevada's was roughly equivalent to atmospheric phosphorus deposition to the lake, representing a significant increase in the availability of P to primary producers (Schindler *et al.*, 2001).

Impacts of non-salmonid invaders on ecosystem processes have also been documented. Elser *et al.* (2000) experimentally added northern pike to a Canadian lake and induced a trophic cascade. The cascade was accompanied by increases in dissolved inorganic nitrogen and a reduction in the residence time of carbon, nitrogen and phosphorus in the water column. Zebra mussels (*D. polymorpha*) in lakes enhance recycling of nitrogen and phosphorus and increase the flux of carbon to the benthos (Gardner *et al.*, 1995; Arnott & Vanni, 1996; Klerks *et al.*, 1996). With their massive filtering potential, the mussels use large amounts of suspended organic matter, shunting carbon to the benthos and releasing mineralised nitrogen and phosphorus back to the water column. Likewise in streams, invasive asiatic clams [*Corbicula fluminea* (Müller)] enhance carbon flux to the benthos through their high filtration rates (Hakencamp & Palmer, 1999). Plants can also cause changes to nutrient cycling. With its high P demand, purple loosestrife [*Lythrum salicaria* (L)], another invasive

wetland plant in North America, accelerates P turnover [twice that of native cattail, *Typha angustifolia* (L)], leading to low porewater nutrient concentrations (Templer, Findlay & Wigand, 1998). In freshwater marshes, common reed [*Phragmites australis* (Cav.) Trin. ex Steud.], which is invasive in North America, achieves a high biomass and consequently sequesters nitrogen, possibly reducing nitrogen availability to other organisms (Templer *et al.*, 1998). However, such changes to nitrogen availability do not necessarily have large effects in an ecosystem. For example, Findlay, Dye & Kuehn (2002) found little difference in microbial biomass and production associated with detritus of native cattail (*T. angustifolia*) or common reed.

What species do in ecosystems – lessons from successful freshwater invaders

Examination of the impacts of salmonid invaders demonstrates that invaders can cause changes at multiple ecological levels. In both streams and lakes, salmonids can induce trophic cascades. The mechanisms for these impacts, however, are quite different in the two habitats. In streams, salmonids initiate cascades at the individual and population level by reducing grazer activity and biomass, respectively. In lakes, salmonids initiate cascades at the ecosystem level by enhancing nutrient exchange among ecosystem compartments. Clearly, if we are going to predict what invaders will do in invaded ecosystems, we need to understand exactly what role these invaders will play.

Species traits of invaders that influence the size of their impact

At the most basic level, invaders can be expected to exert a stronger impact on ecosystems if they are capable of building high densities and biomasses and, in cases where they replace an ecologically equivalent native species, where they can develop a higher biomass than the native. This is because a higher density or biomass can be expected to translate into a higher energy and nutrient demand. Species traits that play a role in determining achievable density or biomass are both physiological and demographic. In the New Zealand streams discussed earlier, brown trout characteristically achieve higher biomasses than

the native galaxiid fish they replace (Townsend *in press*). Perhaps trout are more efficient energy converters, having higher consumption, assimilation or net growth efficiencies than the natives. In addition, or alternatively, brown trout may recruit more successfully or be subject to lower interyear class mortality, or be more resistant to dislodgement during spates or other disturbances, or be quicker to recolonise afterwards (more resilient). While evidence is lacking for most of these features, trout consumption efficiency (proportion of available prey that is consumed) is higher and recruitment and year-class structure is less variable than for galaxiids (A. D. Huryn, personal communication). Similarly, rusty crayfish (*O. rusticus*) have a higher per capita feeding rate than the crayfish they displace in North American streams (Olsen *et al.*, 1991).

The ability to achieve a high biomass and dominant role in the community is a general characteristic of invaders that have profound ecosystem impacts, including fish, crayfish and bivalves in both lakes and rivers (see above). An exception are pathogens and some parasites, which can have strong effects at a relatively low biomass. Knowledge of the achievable biomass of a potential invader should aid in the prediction of likely ecosystem impacts. It needs to be remembered that a species may be capable of achieving a higher biomass in non-native locations if it is introduced without a full complement of specific parasites, pathogens and enemies. Thus, Boustead (1982) reported that brown trout in New Zealand are associated with only 17 parasites compared with 63 in the United Kingdom, while McDowall (1990) noted that the New Zealand fauna lacks a top-level piscivore. Invaders that achieve a large individual size may be capable of maintaining a high biomass because of a lower vulnerability to predation, as suggested for the rusty crayfish (Charlebois & Lamberti, 1996).

Invaders that affect strong interactors in native communities

Some invaders cause direct ecosystem impacts because their modes of resource acquisition generate or dramatically enhance particular energy and nutrient pathways. Thus, zebra mussels and Asiatic clams increase the flux of carbon to the benthos of lakes and streams (Ricciardi, 2003). While this resource-acquisition function is not novel in the native communities,

the magnitude of the flux is. In their study of the Asiatic clam in a sandy stream, Hakenkamp & Palmer (1999) reported that this invader is the only filter-feeding species there that also feeds on deposits. In a terrestrial environment, Vitousek (1990) also noted that ecosystem impacts often derive from unique resource-acquisition strategies, citing the case of the invasion of a nitrogen-poor volcanic region by the nitrogen fixing tree, *Myrica faya* (Aiton).

In most cases, however, ecosystem impacts occur because an invader establishes trophic relationships with negative consequences for native species, which themselves interact strongly with others. These indirect consequences can be generated from the bottom up by invasions of plants, or top down by carnivores or in either direction by invasions of species feeding at intermediate levels (Fig. 1). Consequences might also derive from detritivorous invaders that affect the dead organic matter component of the ecosystem (Fig. 1).

By reducing the biomass of efficient grazers (e.g. *Cladocera* in lakes, insect nymphs in streams), salmonid invaders (I_1 in Fig. 1) permit the build up of greater biomass and enhance production of algae in both lakes and streams (direct impact on grazers I_2 and indirect impact on plants I_4). In this way, patterns

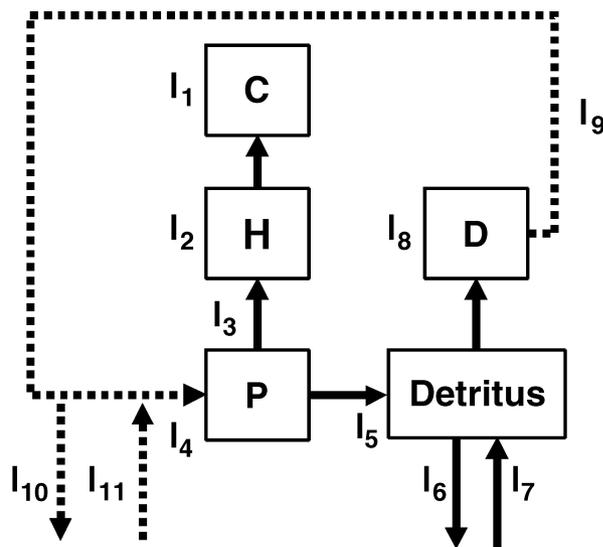


Fig. 1 Conceptual diagram of potential impacts of invaders (I_1 to I_{11}) on ecosystem compartments and links among compartments. P: plants; H: herbivores; C: carnivores; D: detritivores. Solid lines indicate transfers of organic matter. Dashed lines indicate pathways of inorganic nutrients.

of energy and nutrient flux may be altered dramatically. In the case of the New Zealand streams, brown trout also reduce the per capita amount of grazing performed by surviving herbivores (I_3). This occurs because of the novel feeding strategy of brown trout, adding weight to the general argument that ecosystem impacts will often be associated with novel resource-acquisition strategies.

The ability of carnivorous invaders to generate a trophic cascade depends on the responsiveness of herbivores and plants in the food chain. The relevant herbivores in both streams and lakes are highly vulnerable to predation and the algae, with their short generation times, can respond rapidly and dramatically. Where herbivores are less vulnerable (because of intrinsic properties or the availability of refugia in a heterogeneous environment) or plants less responsive, ecosystem consequences of an invading carnivore are likely to be muted. Moreover, Riley *et al.* (in press) have noted that at higher ambient nutrient concentrations the trout-induced cascade in New Zealand streams is obscured because differential grazing pressure is insufficient to induce observable differences in algal biomass. In oligotrophic lakes, nutrient limitation of phytoplankton appears to override the top-down effect caused by invasive fish (e.g. Parker *et al.*, 2001).

Plant invasions in freshwater ecosystems (I_4) include some dramatic examples of weedy macrophytes that may blanket whole lakes, such as Eurasian watermilfoil (*Myriophyllum spicatum* L) (Madsen *et al.*, 1991; Boylen *et al.*, 1999), Canadian pondweed [*Elodea canadensis* (Michx.)], and *Lagarosiphon major* (Ridley) (Wells, De-Winton & Clayton, 1997); these plants have inevitable though usually unmeasured ecosystem consequences. Similarly, riparian trees can impact on every aspect of stream ecosystem function, via shading (reducing incident light, lowering temperature), hydrological changes, and the input of large amounts of dead plant matter (I_7) (Townsend & Riley, 1999). For example, invasion of salt cedar (*Tamarix* spp.) in arid zones of the U.S.A. and Australia has led to altered stream hydrology and geomorphology, and changes to flood frequency and severity (Tickner *et al.*, 2001). This parallels invasions in terrestrial settings where introduced plants can alter disturbance frequency and intensity, particularly by enhancing or suppressing the probability of fire or by increasing or decreasing soil erosion (Mack & D'Antonio, 1998;

Mack, D'Antonio & Ley, 2001). In addition, *Tamarix* is associated with a significant lowering of the water table (Tickner *et al.*, 2001). The importance of nutrients in groundwater exchange for productivity of desert streams is well known (Valett *et al.*, 1994) and it is likely that invasion by *Tamarix* will alter nutrient (I_{9-11}) and energy flux in these streams. Invading emergent macrophytes can also alter nutrient flux patterns (Templer *et al.*, 1998). Invading plants can thus influence ecosystem functioning through effects on nutrient cycling (I_9) and nutrient import from groundwater (I_{11}). They can also be expected to have effects that propagate up through the food web (I_3) or via changes to the rate of production of dead organic matter (I_5).

An example of an impact of herbivory (I_2) comes from zebra mussels, which are capable of removing a large fraction of phytoplankton (measured as a reduction in chlorophyll *a* concentration) in lake water (I_4), particularly in oligotrophic settings (Gardner *et al.*, 1995). Crayfish are also capable of exerting an influence through herbivory. For example, Lodge *et al.* (1994) reported a reduction in surface area of macrophytes in a northern Wisconsin lake in the presence of *O. rusticus*. However, crayfish are highly omnivorous, feeding on plants, animals and dead organic matter, so their consequences can be subtle and manifold, both in the grazing (I_{1-4}) and detritivory ($I_{5,8}$) parts of the food web. Thus, Nyström *et al.* (2001) showed in enclosure experiments that the invading *P. leniusculus* (Dana) had weak negative effects on predatory invertebrates, strong negative effects on herbivores, a negative impact on macrophytes but a positive effect on periphyton, probably because reduced grazing by snails more than counteracted any direct grazing effect of crayfish on periphyton. Others have commented that trophic cascades are less likely to be observed where conditions favour inter-trophic level feeding (McNaught *et al.*, 1999), but omnivores can create trophic cascades if they are less efficient at consuming the resources of their prey than at consuming the prey themselves. Finally, it is worth noting that several invaders may be present in the same system. If these are functionally very similar, the outcomes may not be very different from a single invasion of one of the species. If multiple invaders are functionally distinct, the ecosystem outcomes may simply be additive. Where two non-interacting predators have strong but different effects on the same

species, as described by Nyström *et al.* (2001) for crayfish (*P. leniusculus*) and rainbow trout (*Onchorhynchus mykiss*), their combined effects seem to reflect responses to the more effective predator. In situations where the invaders themselves interact, or where prey respond to one predator in a way that makes them more vulnerable to the other (Kiesecker & Blaustein, 1997), the outcomes will be particularly difficult to predict.

Invaders that build or break links between ecosystem compartments

Most ecosystems contain compartments that can be more or less distinct in their functioning. For example, there may be stronger interactions among species within than between the pelagic, littoral and benthic compartments of lakes. The same may be true in streams of high order but the distinction is less strong in small tributaries. Fig. 1 illustrates a single compartment (e.g. the pelagic zone of a lake); when compartments are linked by the action of certain species, the effects can be visualised in terms of inputs and outputs of nutrients ($I_{10,11}$) or dead organic matter ($I_{6,7}$) or both.

Invaders with a particularly broad feeding niche may strongly link compartments that were previously unlinked or only weakly linked, and thus have particularly powerful ecosystem consequences. Trout introduced to lakes can create new links between benthic and pelagic compartments by feeding on benthic or littoral invertebrates and excreting P to the pelagic compartment (I_{11}), resulting in increased primary productivity of the pelagic compartment. This effect reinforces any trophic cascade that the trout generate in the pelagic zone by depleting cladoceran grazers ($I_{2,4}$). The magnitude of nutrients shifted from the littoral compartment, compared with all other inputs to the pelagic zone, will determine the influence the fish have in the latter (Schindler & Eby, 1997).

Trout invaders in streams usually include a component of terrestrial invertebrates in their diet (Edwards & Hury, 1995). If this is more substantial than that previously taken by displaced native species, the invader may be responsible for more strongly linking the benthic community with a 'pelagic' ecosystem compartment (I_7). However, this may not generally amount to a substantial change. For

example, Edwards & Huryn (1996) calculated that terrestrial prey accounted for only about 5% of total prey consumption by brown trout in a New Zealand stream, although for certain age classes and in certain seasons this value increased to 20% or more. On the other hand, by reducing grazing activity and promoting algal production, not all of which is eaten alive, the trout are responsible for a net downstream displacement of dead organic matter (sloughed off algal cells). This enhancement of the flux of dead organic matter to detritivores downstream (I_6) can be considered a further example of an invader altering the linkage between ecosystem compartments.

Bivalves that invade streams (Asiatic clams – Hakenkamp & Palmer, 1999) and lakes (zebra mussels – Gardner *et al.*, 1995; Arnott & Vanni, 1996; Klerks *et al.*, 1996; Makarewicz, Bertram & Lewis, 2000; Ricciardi, 2003) profoundly influence the flux of energy and nutrients to (and from) the benthos by filtering out a large proportion of phytoplankton and suspended dead organic matter from the open water (increasing links I_7 and I_{11}). For example, zebra mussels have been reported to remove up to 30% of total suspended matter from the pelagic compartment to the benthos per day (Klerks *et al.*, 1996) and, consequently, to be responsible for substantial increases to dissolved fractions of nutrients in western Lake Erie (Makarewicz *et al.*, 2000).

Other invaders, by impacting key native species, may be responsible for severing (or reducing the strength of) links between ecosystem compartments. For example, Vander Zanden *et al.* (1999) used stable isotope analysis to unravel changes to the food-web relationships of lake trout [*Salvelinus namaycush* (Waldbaum)] in Canadian lakes resulting from the invasion of smallmouth bass (*M. dolomieu*) and rock bass (*A. rupestris*). The invaders were responsible for substantial declines in the abundance of littoral fish, upon which lake trout preyed, and this resulted in a shift in the diet of lake trout towards zooplankton in the pelagic compartment and reduced dependence on the littoral compartment (tending to sever link I_{11} in Fig. 1, assuming that the figure concerns the pelagic zone). A further dramatic example is provided by the invasion of Nile perch in Lake Victoria, where it has been responsible for the destruction of the majority of endemic haplochromine cichlid fish populations (Goldschmidt *et al.*, 1993). Approximately 80% of the haplochromine biomass consisted of cichlids that fed

in the lake's thick layer of detritus (Kaufman, 1992). Current anoxic conditions in the deep water of the lake, and other physico-chemical changes, may be due in part to a decoupling of the recycling capacity of the lake caused by Nile perch (Kaufman, 1992) (tending to sever link I_{11} if Fig. 1 represents the pelagic zone).

In some cases, invaders may simultaneously create and break links between compartments. We previously noted that salmonid invaders may link benthic and pelagic compartments in Canadian lakes. In some fishless Canadian lakes, native gammarid amphipods also link benthic and pelagic compartments by ingesting P from sediments and excreting it in the pelagic zone (Wilhelm, Hudson & Schindler, 1999). Gammarids are absent from some Canadian lakes stocked with trout and salmonids are known to eliminate gammarids from European lakes (Parker *et al.*, 2001). In lakes where gammarids have been removed by invaders, an existing link between benthic and pelagic compartments may be replaced by a new link through the invader. The net result of the invasion will probably depend on the magnitude of the broken and new P fluxes between compartments.

Evolution of invader impacts

It is important to remember that the ecology of invaders and native species are not immutable; natural selection may act on one or both and alter the overall impact of the invasion. Introduced predators may have particularly strong effects on native prey that do not recognise or respond appropriately to the invader (Shave, Townsend & Cowl, 1994; Kiesecker & Blaustein, 1997; Nyström *et al.*, 2001). However, as a result of a strong novel selection pressure, prey may evolve to become less vulnerable; the fixed nocturnal behaviour of nymphs of the mayfly, *N. ornatus*, in trout streams, but not in streams containing native galaxiid fish, illustrates how the nature of the interaction might change with time. We note that other taxa, such as *Deleatidium* in New Zealand streams, do not exhibit a fixed behavioural response to invaders. More research is needed to clarify if evolutionary change of natives in response to invaders is truly important.

A common outcome of invasions by fish is introgression with native species (e.g. Allendorf & Leary, 1988). The hybrids may have less profound ecosystem

effects than would the pure-bred invader. However, impacts may still be substantial if the hybrids are particularly vigorous and/or they inherit characteristics from the invader such as those described above.

Conclusion

Changes caused by freshwater invaders can be complex and there are consequences of invasion at all levels of ecological organisation. These impacts are diverse, ranging from subtle changes in individual behaviour to altered nutrient and energy fluxes in ecosystems. While invaders operate at multiple ecological levels, researchers rarely study invasions at each level. This is unfortunate because information about responses at several levels of organisation will be required to fully understand the range of impacts observed. For example, knowledge of behavioural changes by grazing invertebrates is needed to understand the alterations to nutrient and carbon cycling observed in streams invaded by brown trout. We see a clear need for simultaneous measurement of invader impacts at multiple ecological levels in invaded systems. Such work needs to be done across taxonomic groups of invaders to strengthen our ability to generalise about invader impacts.

Multi-level study of invasions will not only help clarify how invaders change ecosystems but may also help us predict which invaders are most likely to have strong consequences at the ecosystem level. Considerable effort has been aimed at predicting invaders and their consequences, and although our ability to do so has generally been poor (Lodge, 1993; Mack *et al.*, 2000) it appears to be improving (Kolar & Lodge, 2001; Ricciardi, 2003). Those invasive taxa that have caused changes at the ecosystem level in freshwaters tend to possess novel ways of resource acquisition (e.g. trout in lakes and streams), to differ greatly from natives in their resource demands or turnover rates (e.g. zebra mussels and purple loostrife, respectively), or to impact key native species that are themselves important in nutrient and energy fluxes (e.g. Nile perch). Most of these invaders achieve high biomass and cause ecosystem consequences as a result of their enhanced demand for, or production of, energy and nutrients. Knowledge of the mechanism and magnitude of acquisition and use of energy and nutrients by an invader will aid in predicting its likely impacts. Some notable freshwater invaders have caused eco-

system-level changes by building, breaking or enhancing links between ecosystem compartments. Thus, useful predictions about the consequences of freshwater invaders will also require a sound understanding of the host ecosystem so we can point to likely effects on links among ecosystem compartments.

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