Chapter 11
Invasion of exotic species: Lessons for GMOs?

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Introduction

A number of species that have never occurred in a particular ecosystem may be extremely well adapted to living there. However, the species pool in any ecosystem is restricted by the limitations in species to migrate. Nowadays, as humans increasingly travel and, even more importantly, have their cargo moved from coast to coast, and between continents, quantities of stowaways are also carried. From a captive situation such as in a ballast water tank, or being slipped in through customs by a tourist, some of the translocated exotic species start to thrive after escaping into a new environment. When exotic species expand their territory in new environments at the expense of native species, they are called *invasive* species. The introduction of exotic species may be intended (i.e. bringing reptiles, birds and ornamental flowers into a new environment for specific purposes) or not intended (micro-organisms, spores, eggs, insects, small animals, seeds, etc.). Both groups are challenging to manage.

The introduction of exotic species (non-GM) is ranked as the second most important factor in all large-scale environmental problems. Habitat destruction is ranked as number one; chemical pollution is ranked third and climate change, fourth (Sandlund et al. 1999). Introduced exotic species leads us in the direction of a 'recombination ecology' or a 'global biological homogenisation' (Enserink 1999), with a consecutive loss of native biodiversity. The introduction of (non-GM) exotic species has been going on for a long time, and as usual, we might have something to learn from past experiences.

In this chapter, I present two case studies of introduced exotic species to discuss some of the similarities and differences between non-GM and GM exotic species. I argue that GMOs form a sub-group of the exotic species (Box 11.1). As all exotic species, GMOs may be introduced into recipient ecosystems, they may have secondary spread and they may become invasive. A comparative analysis of similarities and differences may provide valuable insights; as a common starting point, we should all agree that we have to lean on models as long as the empirical data are not (yet) available. This is the case because GM species have not been used extensively in nature for more than a decade. Yet, general Invasion Biology can tell us that the major ecosystem effects will not (or will rarely) be visible within this time frame.

Box 11.1
In Latin, *exoticus* means 'from the outside'. Exotic species (also called alien, non-native, non-indigenous) are species that are observed in ecosystems where they do not naturally belong. This means that they never had the ability to spread by their own means, i.e. by natural migration. By this definition, all GMOs are exotic because they cannot fulfil any criteria of natural migration (from the laboratory), neither can GMOs be said to have a natural evolutionary background, as opposed to native species. Thus, GMOs are modified and introduced by humans.

Case study I: The invasion of vendace in northern Norway

Vendace (*Coregonus albula*), is a highly specialized zooplanktivore fish species with a natural distribution that does not include the northern parts of Norway, Sweden or Finland. However, in the 1960s the species was introduced into tributaries of Lake Inari, Northern Finland (Mutenia & Salonen 1992). In Lake Inari, vendace reached a high population density during the second half of the 1980s (Mutenia & Ahonen 1990), then subsequently swam downstream into the Pasvik watercourse in Norway, where it was recorded in the upstream part for the first time in 1989 (Amundsen et al. 1999). By the early 1990s, the vendace invaded the whole Pasvik watercourse (Fig. 11.1).

The fish communities in the lakes of the Pasvik watercourse were originally dominated by whitefish (*Coregonus lavaretus*). The gradual downstream expansion of vendace in the Pasvik watercourse has facilitated a study of the mechanisms of ecological interactions in a large scale 'natural experiment', comparing several levels in the food web over 15 years.
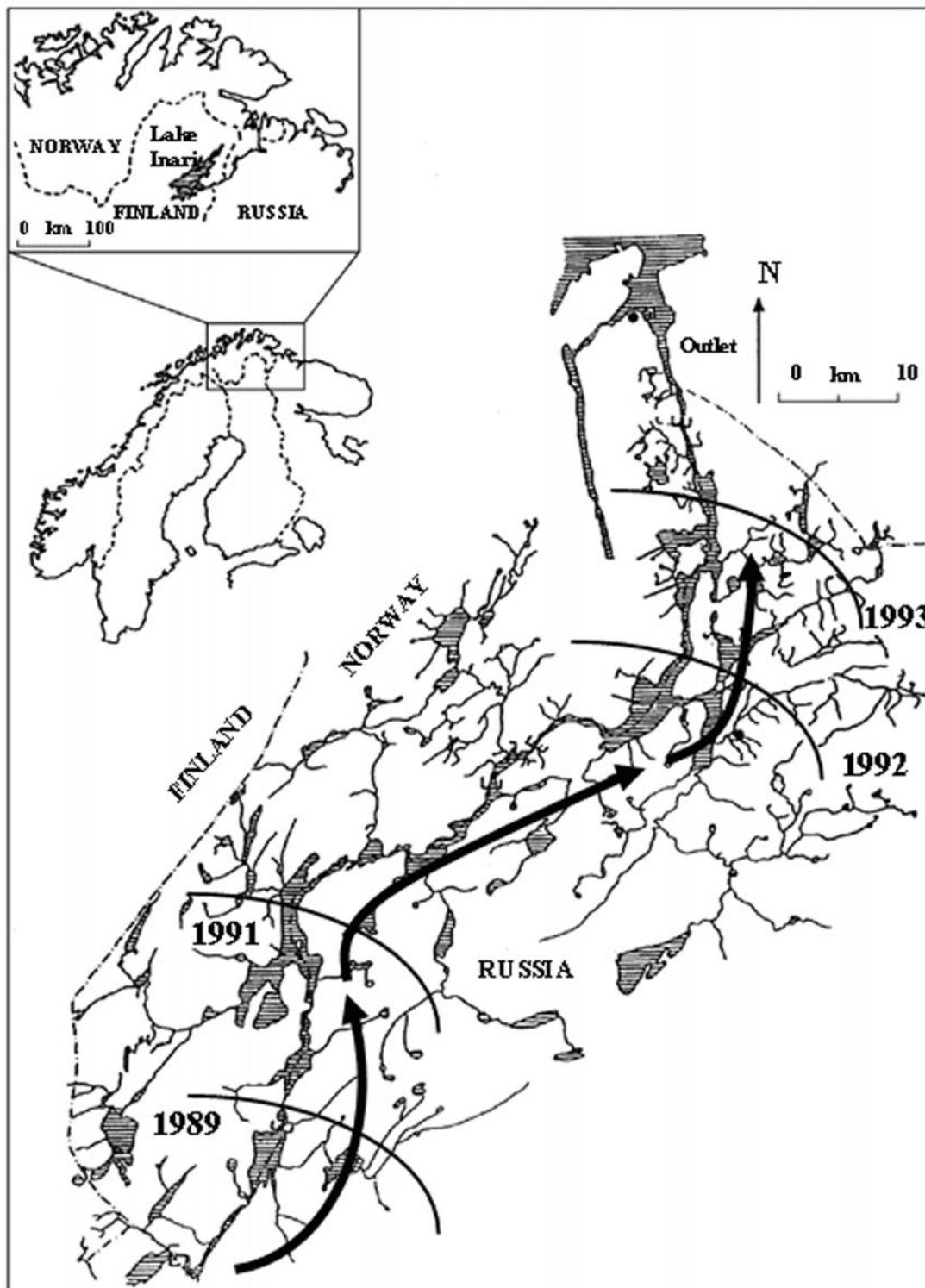
Figure 11.1. Map of the Pasvik watercourse. Arrows show the direction of the vendace invasion and arcs show the year of the first observation.

During this period the vendace proved to be a keystone species (i.e. a strongly interacting species in the food web – see Figure 11.2 for a community overview), with effects on at least three trophic levels:
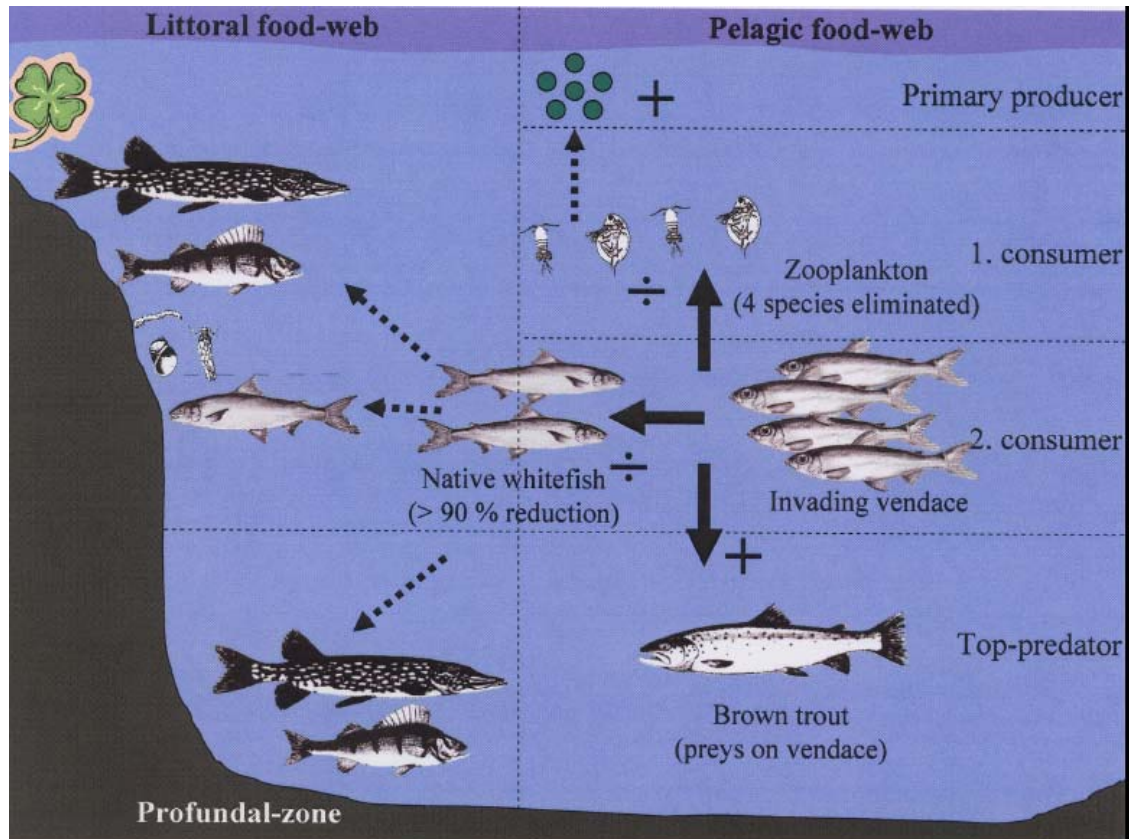

Figure 11.2. Community overview of direct (bold arrows) and indirect effects (dashed arrows) of the invading vendace into the food web of the Pasvik watercourse.

1) As a *predator*, vendace has grazed down the zooplankton community, eliminating the four largest species of zooplankton between 1991 and 1998. In addition, a reduction of body sizes within cladoceran species and a shift towards smaller species in the zooplankton community was observed. These results represent a strong 'top-down' regulation that may limit the food resources of other zooplanktivore fish species. Studies of predation effects on zooplankton communities are usually based on comparisons between water bodies in which a fish predator is present or absent (Brooks & Dodson 1965; Hall et al. 1976). Such studies can be done experimentally or when a predator invades a new area, and may reveal how ecological interactions work, e.g. how exotic species (or GMOs) may alter native ecosystems.

2) As a *competitor*, vendace has competed with the native whitefish for pelagic food resources, the zooplankton. This interaction has lead to a more than 90% reduction in the density of the whitefish. Subsequent to a biological invasion, the processes of interspecific competition, rather than its steady-state outcome, can be studied in the receiving ecosystem (Simberloff 1981; Pimm 1989; Ross 1991). Introduced exotic species thus provide large-scale 'natural experiments' where ecological theory (e.g. competition) may be tested empirically. Biological invasions may also provide unique long-term recording of empirical data (Bøhn et al. 2004). By definition, two

species compete when they negatively affect each other by consuming, or controlling access to, a limited resource (Keddy 1989). Low resource availability and high niche overlap make competition more likely (Giller 1984; Wootton 1998). Interspecific competition may, for one or more of the species involved, lead to altered resource utilization, to reduced density, or ultimately to competitive exclusion and extinction (Gause 1934; Hardin 1960).

3) As a *prey*, vendace has become the most important prey species for the dominant pelagic predator, the brown trout. This means that the feeding behaviour of the brown trout has changed and that vendace replaces the whitefish as the link between the zooplankton and the top predators. In general, the impact of predation on a prey community depends on the habitat-specific density of different predators, and their prey selectivity. When a new prey species is invading, an altered size- and species-selection of prey may be expected directly in the predators. In addition, indirect effects, acting through e.g. competition between prey species in the food web, may change growth rates and thus also the timing of new activities (ontogenetical niche shifts), thereby changing the overall outcome in the community. The trade-off between food acquisition and predator avoidance is a major determinant for the habitat choice of animals (Pyke 1984; Stephens & Krebs 1986). When size-selective predators are present, this trade-off discriminates between age- or size-classes in a prey population, and between species within a prey community (Werner et al. 1983; Persson 1988; Hambright et al. 1991; L'abee-Lund et al. 1993; Brabrand & Faafeng 1993).

There are important links between the different effects that vendace contributes to, and the different components of the food web after its invasion. Altering one level in a food web necessarily impacts the other levels, so that the total effect will depend on a number of indirect effects, in addition to the direct effects. As with the vendace fish invader, direct effects have been observed on three trophic levels (zooplankton, zooplanktivore fish and top-predators). The indirect effects are harder to track and follow. The case study of the vendace shows that invasions have case-specific effects that are extremely difficult to predict.

Ecosystem or food-web effects are difficult to study, interpret and understand due to high complexity. Furthermore, only a very few examples of ecosystem changes due to the impact of exotic species have been studied *during* the period of change, and no researchers at all would pretend to fully understand which mechanisms were responsible for the effects shown, even though the scientific discipline of Invasion Biology has 50–100 years of active research to acknowledge. This situation will not become easier with introduced GM species.

Case study II: Rabbits in Australia

The second case study concerns rabbits in Australia, a case that will be familiar to most readers. In 1859 Thomas Austin imported 24 rabbits from England to Victoria: 'The introduction of a few rabbits could do little harm and might provide a touch of home, in addition to a spot of hunting'[1]. Twenty years later, in 1879, there was still a focus on the advantages of introducing exotic species: 'All birds and animals may be introduced as shall afford sport and amusement without doing injury to the Agriculturist and Gardner' (Strahan 1992).

However, by 1890 the situation was very different from what had been imagined. Farmers had to abandon their properties in the face of rabbit plagues in some places. The view of reality and the focus had shifted from a positive potential to a dramatic pest. In the following decades the rabbits, in combination with sheep and cattle, grazed down Australian landscapes. Plants and trees, which

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[1] http://www.agric.wa.gov.au/programs/app/barrier/history.htm

keep the surface of the soil intact with their roots, were grazed down and removed, and severe dust storms appeared. Entire homesteads were buried by dust, people died from being buried in dust storms, communities had to reorganize on semi-arid land. There were also adverse health effects, such as blindness. All of this exemplifies indirect and unintended ecosystem effects. Rabbit control through means of shooting, trapping, poisoning, and fencing has proven to be ineffective on a large scale. In 1951, a virus disease (myxomatosis) was introduced to the rabbits in Australia. This reduced the numbers of rabbits from ~600 million to ~100 million in a couple of years. Later, this kind of control turned out to be complicated by the evolution of resistance, resulting in a continuous 'arms race' between rabbits and scientists. Immediately after the introduction of myxomatosis, a return of endangered plant species was observed. The rabbits are estimated to have cost Australian agriculture approximately USD 300 million per year (at least 2% of all agricultural production). The total costs to the nation are twice as high, USD 600 million dollars per year, according to the Australian CSIRO (Commonwealth Scientific and Industrial Research Organisation[2]).

High densities of rabbits still inhabit the southern part of the whole continent and Australia continually struggles with soil erosion. This is the number one environmental issue facing the country, due to overgrazing by rabbits and other feral species. The cost of lost productivity due to loss of land is incalculable.

Lessons from introduced species – similarities and differences between non-GM and GM exotic species?

Not all exotic species establish after introduction. In fact, the 'tens rule' (Williamson 1996) states that approximately ten per cent of all introduced species succeed in establishment. Further, approximately ten per cent of the established species become pests. This means that approximately one per cent of all introduced exotic species have some sort of serious negative consequences in the receiving ecosystem.

The 'tens rule' may be difficult to apply directly over to GM exotic species. One reason for this is that fitness-relevant traits, such as growth rate or resistance to a limiting factor (predators, parasites, diseases), are often directly modified. This is discussed later in the chapter. Exotic species (both non-GM and GM) can be divided into two categories: i) those that need support, e.g. by agricultural means such as ploughing, fertilizer, etc. in order to survive, and ii) those that are free ranging and would be readily spread into the environment. The distinction is not always clear. We should remember that all agricultural fields are also part of the 'ecological theatre' in which the 'evolutionary play' is continuously being played (Lövei 2001). Many agricultural plants are also used in areas where the same species, or close relatives, live in the surrounding environment. As all GM organisms have been defined as exotic, the issues of co-existence and horizontal gene transfer between closely related species will fall under the umbrella of Invasion Biology. However, there is no parallel to this issue from classical Invasion Biology. This chapter thus deals mainly with exotic species that have the ability to spread into the environment.

Similarity – Introductions are followed by secondary spread (invasions)

The spread of exotic species, whether they are GM or not, occurs in at least two stages: the first is the active transport made by humans (the introduction). This stage is often unintentional and beyond human control, e.g. in ballast water in ships, in GM-contaminated seeds of maize, etc. The second stage is the secondary spread made by the species itself (spread of pollen,

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[2]http://www.csiro.au/communication/rabbits/qa2.htm

microorganisms, running animals, and swimming fish belong to this category). The latter stage is completely beyond human control, but depends on the rate of spread of the exotic species and its ability to establish in still further environments. The vendace invasion serves as an example of how these two stages of spread may be separated in time by several decades.

Similarity – Unintended ecosystem effects after long time delays
Both of the aforementioned case studies show that the sum of ecological harm comes from direct and indirect effects over an extended period of time. For the vendace, the time delay between the first introduction and the observed ecosystem changes (in the Norwegian part of the watercourse) was approximately 35–40 years, due both to the secondary spread of the species and the building up of consequences through linked ecological interactions, i.e. competition from the invading vendace forced the native whitefish to change habitat, and in the new habitat a high density of predators fed on the small-sized and relegated whitefish individuals. For the rabbits in Australia, a time delay of approximately 20–30 years occurred before people realized that the rabbits represented an irreversible large-scale plague.

The time lag before effects are observed is an important but difficult fact to handle in decision making. A major difficulty with political decision making is to tackle the trade-off between rapid profit and long-term negative consequences. This is a matter relevant to most environmental problems. However, for biological pollution, i.e. reproducing organisms that may be increasingly harmful over time, there are, in addition, risks of inaction. Here, action means that society acts to prevent the introduction of a potentially harmful species, or eradicates it early in the process of establishment. As one prominent invasion biologist Daniel Simberloff (2003) puts it: 'because of their population growth and dispersal abilities, introduced species are one target of resource management at which it is often better to shoot first and ask questions later'.

Unfortunately, many examples from Invasion Biology show a shift from the expectation of progress and benefit, due to the introduction of an exotic species, to the realization of the spread of a growing pest. This is regularly a one-way shift. Biological pests hardly ever shift back to beneficial species but instead last for the unforeseeable future (for example, this is the case with the rabbits in Australia). Whereas it may be completely natural to have a naïve first attitude to what is new and unknown, we should realize that risks and the harm of self-replicating biological organisms are not like any other 'invention'. A 'successful' invasive species cannot be taken back, and the harm to the receiving ecosystem regularly increases over time. Therefore, all biological material should be treated with precaution and humility.

Similarity – huge resources are needed to understand and study complex ecological interactions
To rightly evaluate the ecosystem consequences of an exotic species a long-term perspective is necessary. Often it will also be necessary to follow the consequences on several trophic levels, which necessitates a diverse competence. Further, the complex structure of food webs makes studies difficult and sometimes inconclusive, especially in species-rich ecosystems. As an example, the amount of resources required to study the vendace invasion, in a fairly detailed manner through a period of change, is quite considerable. People included in this 15 year long study include, from Norway, one university professor, two PhD students, seven Masters students and one university field course over five years. In addition, there have been seven Russian and three Finish researchers involved in the study. An estimate of the financial input adds up to approximately USD 1 million. Large samples of fish (15,000) and zooplankton (50,000) have been necessary to reach conclusions on the ecosystem changes.

Similarity – Irreversibility

Some of the human impacts on natural ecosystems are possible to reverse, meaning that stopping unwanted development, like chemical pollution, may lead to a restoration of the system. Even though it is correct to say that ecosystems never return exactly to their original state (since all living systems continue to evolve) they may return more or less to their pre-disturbed state or quality. Examples of reversible impact factors include DDT, acid precipitation, nuclear emissions, organic and inorganic pollutants, etc. When it comes to spread of living organisms, we may learn a lesson from Invasion Biology: Invasive species may be eliminated just after their introduction only under some (unlikely) specific conditions. And it is almost impossible to get rid of them later.

By the same token, GMOs that often carry single or multiple enhanced fitness traits will have a huge evolutionary potential if spread into the environment. Hence, they must be considered as potentially irreversible elements of the future environment and evolution. What this will ultimately mean, e.g. for ecosystem interactions and biodiversity, is open to speculation. The environment and the ecosystems function on a level of complexity that we rarely can cope with in terms of precise scientific understanding. When, in addition, we know that introduced invasive species represent irreversible events, we should act with precaution.

Difference – Public invisibility

An important difference between introduced (non-GM) exotic species and GMOs in the environment is the public invisibility of GMOs. Humans are terrestrial mammals and it is easy for us to recognize and react to introduced exotic species and their effects: we are able to see rabbits, dust storms, plant eradications, and exotic fish species. In contrast, the public will not be able to distinguish a GM from a non-GM organism in the environment. No outside examination will reveal the modified genetic origin of a maize plant, a tilapia or salmon fish as they will look more or less identical. The same is true for hybrids between GM- and non-GM organisms. Furthermore, microorganisms and naked DNA are invisible (to the human eye). The invisibility of GMOs, or the difficulty in easily distinguishing them from conventional organisms, is causing huge difficulties for handling and management, and has triggered a resource-demanding enterprise in tracing and controlling GMOs.

Difference – Scale of introduction

GMOs are intended for industrial production, which means they will be introduced on a large scale and on a continuous basis (e.g. for fish farming). In contrast, non-GM exotic species are usually introduced without purpose in small numbers e.g. in ballast water tanks in ships.

Difference – GMOs often have modified fitness parameters

I will now go into some more detail, by using examples, about specific traits that are modified in GMOs: increased resistance to controlling factors and enhanced growth. What do these traits mean in nature?

GMOs with increased physiological tolerances, or GMOs that are able to resist predators, parasites or any kind of disease are expected to perform better in nature, simply because stress from factors in the environment are released. Resistance to controlling factors implies increased survival. GMOs may thus reduce grazing, predation, parasites, diseases, and other cues in the environment. Whereas these may be valuable traits in a contained system, we have to remember that both agriculture and aquaculture represent open systems that interact with neighbouring ecosystems. We should therefore evaluate the potential invasiveness of GMOs on a case-by-case basis. Increased tolerance or resistance represents an expansion of the fundamental niche of a species, which likely leads to an expansion of its geographical distribution (increased spread).

This is due to the fact that limiting environmental factors, both biotic and abiotic, restrict the distribution of organisms. An expansion of the fundamental niche of a species is also expected to influence the species' ecological role through increased competitive ability within its natural geographical range.

For example, GM fish are often modified to have increased growth, usually resulting also in a larger maximum size, by inserting growth hormone genes. The effect of introducing growth hormone genes can be remarkable; transgenic coho salmon have been shown to be eleven times heavier (on average) compared to control fish over a period of fourteen months (Tymchuk et al. 2005). Growth is a fundamental fitness trait that is linked to a number of species interactions in food webs. High growth rates and large size may translate to strong competitive ability and increased predation on lower trophic levels. Transgenic coho salmon are shown to outgrow non-transgenic salmon when food availability is low, as is usual in nature, and also to invariably contribute to the dominating individuals in competition trials with non-transgenic individuals (Devlin et al. 2004). Altered growth also means altered ecological interactions with most other species. This is well known from studies of fish. Fish have indeterminate growth, meaning that the adult size is flexible and not fixed. This fact is already taken advantage of by GM techniques, as we have seen.

The perch shown in Fig. 11.3 has three more or less separate and different ecological roles as the size of the fish changes (perch have ontogenetic niche shifts). Small perch eat mainly zooplankton in the pelagic habitat, while medium-sized perch eat benthic invertebrates and large perch are piscivorous. In nature, this means that perch functions as three different species in practice. A GM fish experiencing rapid growth would in nature potentially alter such fine-tuned evolutionary equilibria.
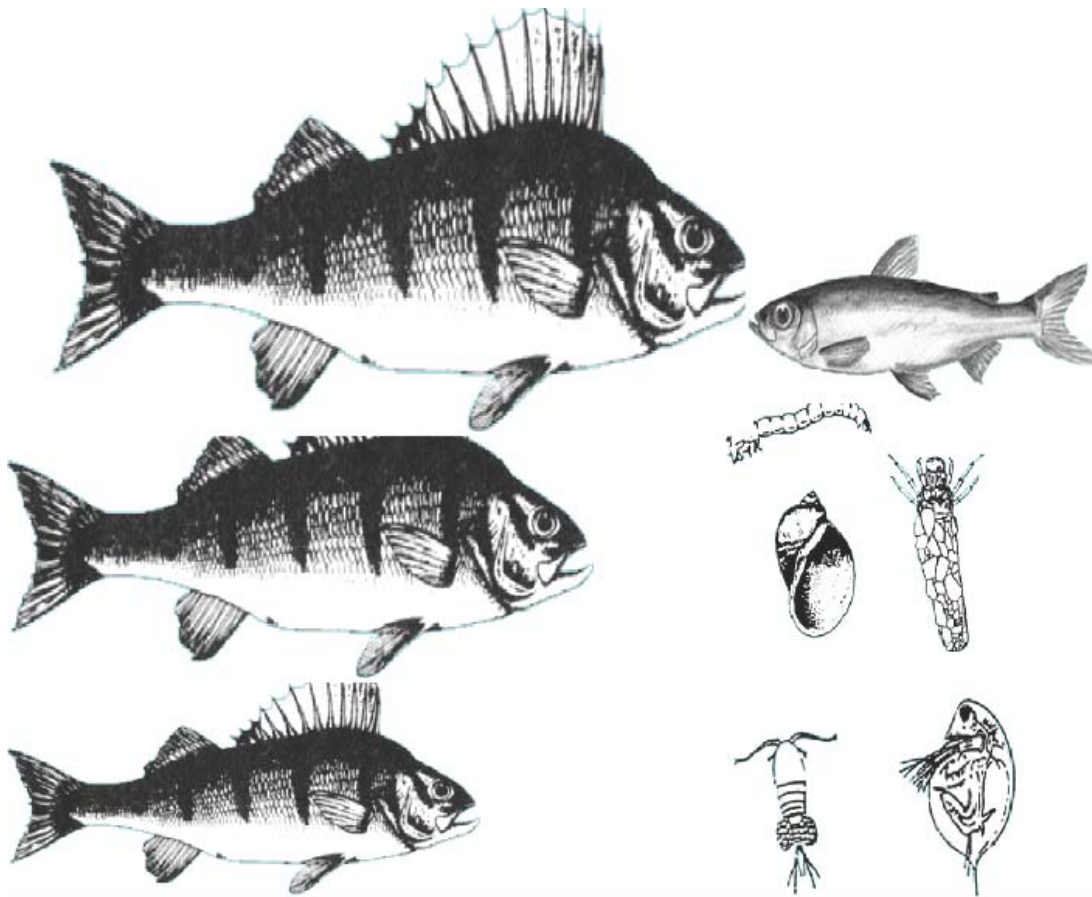
Figure 11.3. Ontogenetic niche shift in perch (Perca fluviatilis).

Higher growth rates may also affect behavioural and life history traits in fish. High growth rates may also be likely to increase the fecundity and the maximum swimming speed; the fish may mature earlier and become more dominant on spawning grounds. However, the viability of GM fish may be lower compared to non-GM fish. The transgenic Japanese medaka, expressing growth hormones, studied by Howard et al. (2004), may serve as an example. The GM fish was 83% heavier and the males mated three times more compared to the non-GM males. However, the GM offspring survival was 30% lower than the non-GM offspring. The sum of these differences (as demonstrated in a mathematical model) leads to two interesting effects. The first is that due to more mating, the GM fish will take over the population, and secondly, due to the lower offspring survival, the population goes to extinction (Howard 2004). The phenomenon of being invaded by malfunctioning individuals is called a 'Trojan Gene Effect'.

Also with plants, the introduced transgene may increase the fitness of the organism in the environment: transgenic Bt-sunflowers, expressing Bt-toxin that reduces grazing by insects, are shown to hybridize with unmodified sunflowers in the environment (Snow et al. 2003). The hybrids also express Bt-toxin (at a lower level). In areas where insects graze on the sunflowers, the hybrids are shown to be superior seed producers, with up to 55% more seeds (Snow et al. 2003). Under these conditions, GM sunflowers would gradually spread into wild populations and take over due to higher fitness. According to Snow (2002), 'It is currently impossible to prevent gene flow between sexually compatible species in the same area. Pollen and seeds disperse too

easily and too far to make containment practical. This makes the need for environmental studies all the more urgent'.

To sum up the adaptive value of many transgenic organisms, many or all affected traits have short-term positive fitness consequences: higher growth rates, increased disease resistance, reduced age at maturation, higher number of offspring, expanded environmental tolerance. Thus, the traits that are advantageous for industrial production are strongly overlapping with what makes a species invasive in nature. There may be metabolic or other costs involved in producing these transgenic traits, and these should be studied under controlled and contained conditions. However, to extrapolate data from the laboratory to complex ecosystems is extremely difficult, also because many organisms (e.g. fish) behave differently in the laboratory as compared to in nature (due to genotype by environment interactions) (Devlin et al. 2004). A summary of similarities and differences between non-GM and GM species is given in Table 11.1.

Table 11.1. Summary of similarities and differences between non-GM and GM exotic species.

	Similarity	**Difference**
Introductions followed by invasions	Both have secondary spread (invasions).	
Ecosystem effects after long time delays	Effects often appear several decades after introduction.	
Huge resources needed to understand complex ecological interactions	To evaluate ecosystem consequences of exotic species, long-term studies on several trophic levels may be required.	
Irreversibility	After release, exotic species (whether GM or non-GM) can rarely be eliminated from the environment.	
Public invisibility		Whereas non-GM exotic species often are easily recognized, GMOs will often not be distinguished from a non-GM organism in the environment – they will look identical.
Scale of introduction		Whereas many GMOs intended for industrial production will be released on a large-scale, non-GM exotics are mostly released unintentionally and on a small-scale.
Modified fitness-parameters		GMOs have a number of traits that may be altered towards higher fitness. Advantageous traits for industrial production overlap with what makes a species invasive.

Conclusion

From Invasion Biology we have learned that a minority of introduced species have caused huge ecological and economic problems, after time lags of decades. A rather naïve and short-sighted perspective has prevailed in the history of humankind; species have been introduced with a focus on profit, and not on their potential damage. For a long time, however, the introduction of exotic species was limited by the poor ability of humans to travel across large distances. Recently, this ability has been dramatically increased, and many well-adapted exotic species (invasive species) have caused large-scale ecological harm to native biodiversity. Unfortunately, we may *not* have learned the most important lessons of Invasion Biology and may end up in the same situation again, with unwanted introductions of exotic GM species. Many exotic GM species even have fitness advantages compared to species in the natural environment. The performance of these should be thoroughly tested in contained semi-natural conditions to explore their potential invasiveness. The pressure to commercialize GMOs should not be at the cost of thorough independent scientific testing (Fig. 11.4), nor at a scale relevant for foodwebs and ecosystems.

Figure 11.4. Technology seems to be running ahead and risk assessment and risk management are dragged passively behind.

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