

Hosts and parasites as aliens

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Abstract

Over the past decades, various free-living animals (hosts) and their parasites have invaded recipient areas in which they had not previously occurred, thus gaining the status of aliens or exotics. In general this happened to a low extent for hundreds of years. With variable frequency, invasions have been followed by the dispersal and establishment of non-indigenous species, whether host or parasite. In the literature thus far, colonizations by both hosts and parasites have not been treated and reviewed together, although both are usually interwoven in various ways. As to those factors permitting invasive success and colonization strength, various hypotheses have been put forward depending on the scientific background of respective authors and on the conspicuousness of certain invasions. Researchers who have tried to analyse characteristic developmental patterns, the speed of dispersal or the degree of genetic divergence in populations of alien species have come to different conclusions. Among parasitologists, the applied aspects of parasite invasions, such as the negative effects on economically important hosts, have long been at the centre of interest. In this contribution, invasions by hosts as well as parasites are considered comparatively, revealing many similarities and a few differences. Two helminths, the liver fluke, *Fasciola hepatica*, of cattle and sheep and the swimbladder nematode, *Anguillicola crassus*, of eels are shown to be useful as model parasites for the study of animal invasions and environmental global change. Introductions of *F. hepatica* have been associated with imports of cattle or other grazing animals. In various target areas, susceptible lymnaeid snails serving as intermediate hosts were either naturally present and/or were introduced from the donor continent of the parasite (Europe) and/or from other regions which were not within the original range of the parasite, partly reflecting progressive stages of a global biota change. In several introduced areas, *F. hepatica* co-occurs with native or exotic populations of the congeneric *F. gigantica*, with thus far unknown implications. Over the fluke's extended range, in addition to domestic stock animals, wild native or naturalized mammals can also serve as final hosts. Indigenous and displaced populations of *F. hepatica*, however, have not yet been studied comparatively from an evolutionary perspective. *A. crassus*, from the Far East, has invaded three continents, without the previous naturalization of its natural host *Anguilla japonica*, by switching to the respective indigenous eel species. Local entomostrac crustaceans serve as susceptible intermediate hosts. The novel final hosts turned out to be naive in respect to the introduced nematode with far reaching consequences for the parasite's morphology (size), abundance and pathogenicity. Comparative infection experiments with Japanese and European eels yielded many differences in the

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hosts' immune defence, mirroring coevolution versus an abrupt host switch associated with the introduction of the helminth. In other associations of native hosts and invasive parasites, the elevated pathogenicity of the parasite seems to result from other deficiencies such as a lack of anti-parasitic behaviour of the naïve host compared to the donor host which displays distinct behavioural patterns, keeping the abundance of the parasite low. From the small amount of available literature, it can be concluded that the adaptation of certain populations of the novel host to the alien parasite takes several decades to a century or more. Summarizing all we know about hosts and parasites as aliens, tentative patterns and principles can be figured out, but individual case studies teach us that generalizations should be avoided.

Free-living animals: characteristics of successful invasions

Over the past 200 years, during which time humans have drastically altered the earth, many plants and animals have become displaced as side effects of human activities. Others have been deliberately introduced to new areas or have expanded their distributions following the anthropogenic breakdown of biogeographic barriers. For free-living animals ('hosts' in parasitological terms), the literature on invasions is vast, widely scattered and of uneven quality, making quantitative analyses difficult. Nevertheless, a few tentative rules characterizing the patterns and processes of successful invasions and establishments have already been summarized for vertebrates in the 1980s (Brown, 1989; Ehrlich, 1989), for example: (i) many good invaders have the ability to tolerate a wide range of physical conditions, i.e. they have a broad ecological amplitude; (ii) being native to a relatively stressful, harsh environment seems to be characteristic of a good invader; (iii) species that inhabit disturbed environments, and those closely associated with humans, are most successful in invading man-made habitats; (iv) a successful invasion is often enhanced by habitat similarity between source and target areas; (v) invading exotics tend to be more successful if native species do not occupy similar niches; (vi) isolated environments with a low diversity of native species, for example Hawaii, tend to be most susceptible to invasion; (vii) successful invaders which tend to be natives of continents and extensive, non-isolated habitats on continents usually do not derive from Australia, New Zealand or Polynesia; and (viii) most vertebrate invaders are closely associated with humans, have a high abundance in their native range, as well as short generation times.

In the 1990s, the interest in animal invasions was challenged by a range of extensions of crustaceans, bivalves and other invertebrates from the area north of the Black and Caspian Seas (Ponto-Caspian). Three frameworks, namely the historic, vulnerability and propagule pressure models for understanding free-living species' (hosts') invasions were elaborated, mainly based on studies of invertebrates (see Sakai *et al.*, 2001; Reid & Orlova, 2002), but these three hypotheses are not mutually exclusive. The historical model hypothesizes that a combination of life history

characteristics, such as the ability to alternate between parthenogenesis and gametogenesis, predisposes certain species to greater success than others. Species in which isolated individuals can self-fertilize are generally good colonists. Characteristics common to successful colonists across taxa include r-selected life histories (pioneer habit, short generation time, high fecundity and high growth rates) and the ability to shift between r- and K-selected strategies. The vulnerability model identifies attributes that are thought to render certain ecosystems vulnerable to invading allochthonous species. The propagule pressure model is based on the frequency and quantity of a colonizer's propagule input into an ecosystem. This hypothesis is based on the anthropogenic establishment of invasion corridors facilitating the long-distance dispersal of species between the source and destination areas. Examples of vertebrate colonizations support the propagule pressure model. North America's most successful invading birds, the European starling and the house sparrow, both became invasive only after repeated introductions (Ehrlich, 1989).

Bij de Vaate *et al.* (2002) described three major invasion routes of 24 Ponto-Caspian macroinvertebrates into the Baltic Sea and/or the Rhine basin, while Reid & Orlova (2002) analysed the colonization success of Ponto-Caspian invaders in the Baltic and Great Lakes of North America. The latter authors found elements of all three invasion model frameworks in the conspicuous success of the Ponto-Caspian aliens. They suggested that the long and complex geological history of the Ponto-Caspian basins resulted in the evolution of diverse modern faunal assemblages with wide adaptive capacities and high phenotypic variability. In contrast, the recipient areas are geologically young. The Baltic is poor in biodiversity while the Great Lakes have a relatively high species diversity in some faunal groups (Reid & Orlova, 2002). Interestingly, in Western Europe native as well as exotic species (of American and even of Ponto-Caspian origin) have been eliminated following the later arrival of very strong Ponto-Caspian invaders (Dick & Platvoet, 2000; Van der Velde *et al.*, 2000; Devin *et al.*, 2004), as also happened to native invertebrates in North America (Ricciardi *et al.*, 1998; Dermott, 1998; Ricciardi & MacIsaac, 2000).

Do invading and successfully establishing alien species, derived from certain donor areas have definable genetic characteristics? According to Lee (2002), the evolutionary genetics of invading species remains

relatively unexplored. A recent hypothesis suggests that the invasion success of many species depends more on their ability to respond to natural selection than on a broad physiological tolerance or plasticity, which are commonly considered to explain such success, but in the view of Lee (2002) often fail upon close examination. High levels of 'additive genetic variance', providing the main substrate for selection, are thought to be essential for invasion success. In addition to other factors, a small number of particular genes can have a profound impact on colonizing ability. Among two species of South American ants, success in the USA is apparently dependent on a single modified gene affecting the ability of workers to recognize queens and to down-regulate their numbers. In the novel area, this self-recognition was lost, leading to large and densely set polygyne colonies which had a negative impact on native ant populations (see Lee, 2002).

We do not know whether the genomes of the Ponto-Caspian migrators possess high levels of additive genetic variance or whether they can respond quickly to natural selection in the target environment. However, the most successful Ponto-Caspian crustacean invader, *Dikerogammarus villosus*, has been analysed for its biological traits by Van der Velde *et al.* (2000), Kley & Maier (2003) and Devin *et al.* (2004). This species can be classified as r-selected, but an option to shift between r- and K-strategies has not been observed (compare Sakai *et al.*, 2001; Reid & Orlova, 2002). *D. villosus* is larger than the indigenous gammarids of the recipient Rhine river system for instance, which should be disadvantageous in terms of predation by fish. However, most sections of these rivers resemble canals with banks stabilized by piled rocks creating a crevice system in which only eels are capable of preying on gammarids (see Thielen, 2005). Thus, the alien crustacean does not seem to be handicapped by its size in large parts of its colonized range. Furthermore, *D. villosus* shows more rapid growth than native members of its family and reaches sexual maturity earlier. Reproduction is recorded throughout the year with peaks in spring and summer, and clutch sizes are larger than in native gammarids. In contrast to the latter species, which reduce their reproduction during the summer when their major food substrate (deciduous leaves) is hardly available, *D. villosus* maintains large clutch sizes during the summer. This seems to correspond with its ability for carnivorous feeding. Thus, due to the shorter generation time, higher fecundity and also to its ability to prey on other gammarids (Dick & Platvoet, 2000), it can cause the complete extinction of its indigenous competitors (Devin *et al.*, 2004; Thielen, 2005). Certain other invaders with sympatric occurrence in the donor area (Ponto-Caspian), for example *Echinogammarus ischnus*, are able to coexist with this dominant crustacean in its colonized range (Kley & Maier, 2003).

Drifts of species often show a conspicuous unidirectional pattern. A vast number of Red Sea fish and invertebrates have colonized the Mediterranean after the inauguration of the Suez Canal while only a few Mediterranean species have successfully established in the Red Sea (Por, 1978; Galil & Zenetos, 2002).

In the Eastern Mediterranean, cases have been described in which autochthonous species have been wholly outcompeted and displaced by invaders.

Furthermore, certain colonizers have been superior in interactive, bathymetric habitat segregation; i.e. native species have had to move into deeper and cooler waters. However, as part of this invasive meltdown (*sensu* Simberloff & von Holle, 1999) competitive interactions between the invaders themselves have also become apparent (Galil & Zenetos, 2002).

Characteristics of successful parasite invasions

When considering parasites, colonization by exotic species has been viewed from medical, veterinary and other applied view points, and it is only recently that researchers have begun to ask questions as to why certain host species and regions are exposed or vulnerable to parasitic invasions while others are less affected. The literature on invasive parasites and hosts colonized by them is less voluminous than for free-living organisms. Nevertheless, tentative rules characterizing the circumstances leading to a successful invasion can often be determined more clearly than those extrapolated from colonizations by free-living organisms, since interactions between a colonized host and its novel parasite often resemble the conditions in a microcosm experiment.

Usually, it is not the availability of vacant niches in the new habitat which seems to be the decisive factor, as postulated for invasions by free-living organisms (Brown, 1989; Ehrlich, 1989), but rather the presence of a suitable habitat itself, i.e. a susceptible host. In the case of parasites with a heteroxenic life cycle, two or more suitable hosts have to be available in the recipient territory. Often, if one species serving as a susceptible intermediate or final host is already present then the introduction of a single species can be the prerequisite for a successful parasite invasion. The American euryhaline amphipod *Gammarus tigrinus*, serving as the sole intermediate host for the acanthocephalan *Paratenuisentis ambiguus* in the North American east coast, was naturalized into the German River Weser in 1957 to replace the indigenous amphipod fauna. These gammarids had become extinct following pollution from potassium mines. About 25 years later, invasion by the acanthocephalan occurred. A susceptible target final host (*Anguilla anguilla*) congeneric with the source final host (*A. rostrata*) was naturally present in the river (Taraschewski *et al.*, 1987).

During the 1990s, both exotics had spread into the river Rhine, dominating the amphipod fauna (*G. tigrinus*) and the intestinal helminth community of local eels (*P. ambiguus*), respectively (Sures & Streit, 2001). However, after the inauguration of the (Rhine)-Main-Danube Canal, *D. villosus* colonized the river Rhine and eradicated the inferior competitor *G. tigrinus* (Dick & Platvoet, 2000). As a consequence, *P. ambiguus* lost its status as the dominant intestinal helminth of its final host, and from 2001 it has no longer been recorded in eels investigated from that river (Thielen, 2005). This sequence of events, i.e. the intentional introduction of an exotic host, the subsequent accidental introduction of its parasite, and the final disappearance of both due to the anthropogenic breakdown of a biogeographic barrier, documents the fate of an alien parasite with high host specificity, totally dependent

on the availability of its sole intermediate host species. Within the infracommunities of *G. tigrinus*, no competitive interactions of *P. ambiguus* with other parasites negatively affecting the acanthocephalan seemed to exist, and, thus, the abundance of the parasite in the final host appears to be regulated by the density of its sole intermediate host (Thielen, 2005).

As a second tentative rule parasites with low host specificity (corresponding to the 'habitat specificity' of free-living organisms) and with simple life cycles (no necessity for several shifts from one distinct host to another) are better colonizers than species with more specific requirements. The liver fluke *Fasciola hepatica*, which lacks a distinct second intermediate host (Andrews, 1999), has established in many overseas populations (table 1), while the smaller liver fluke *Dicrocoelium dendriticum*, dependent on specific ants as second intermediate hosts, has not become transcontinentally displaced (no literature available).

In most cases, the success or failure of a parasite in a recipient area does not seem to be decided at the parasite-community level. Most parasite communities studied are isolationist, i.e. non-interactive. In isolationist infracommunities, competition between the parasite species should play a minor role (Esch *et al.*, 1990; Poulin, 1998). In certain cases, however, competitive exclusion may be involved (see below: *Boophilus decoloratus* vs. *B. microplus*), being postulated to be important in determining the success of many free-living colonizers. In addition, the physical environment of the invaded area (other than inside the host) may prevent successful establishment of an alien parasite, even though susceptible final and intermediate hosts are present. *Fasciola hepatica*, for instance, has not established in Iceland, where the mean temperature does not exceed 10°C for 10 months of the year. Accordingly, the liver fluke would have to overwinter in the snail, *Lymnaea truncatula*, to complete one developmental cycle. *Lymnaea truncatula*, however, lives for just 12–14 months, so that the transmission of the invasive fluke is unlikely under such a temperature regime (Torgerson & Claxton, 1999).

Spread of hosts and parasites following invasion

After the invasion and establishment of a host or parasite in a new area, it is unlikely that it will remain localized. After the establishment of a viable, self-sustaining population, the subsequent stage of a species' colonization is usually its spread or dispersal throughout the area (hosts) or within either the distributional range of a susceptible native host or the novel range of a recently invaded exotic host (parasites).

Recent theoretical work has shown that invasive spread is a much more complex process than classical models had suggested because long range dispersal events can have a large influence on the rate of range expansion through time (Hastings *et al.*, 2005). The authors of the latter review believe that the key to understanding dispersal is measuring human transport by cars, trucks or boats. Island-hopping invaders, for instance, hitching a ride with tourists (Chown & Gaston, 2000) benefit from such human aid. Nevertheless,

Kinlan & Hastings (2005) have compiled literature data on post-introduction spread rates of some marine and terrestrial exotic species revealing considerably different speeds, as can be seen from the following examples: *Carcinus maenas* (crab) 173 km year⁻¹, *Littorina littorea* (periwinkle) 42 km year⁻¹, *Mytilus galloprovincialis* (mussel) 115 km year⁻¹, *Sturnus vulgaris* (starling) 200 km year⁻¹, *Bubulcus ibis* (cattle egret) 800 km year⁻¹. The freshwater crayfish *Orconectes rusticus* has been recorded to spread just 0.7 km year⁻¹ (Wilson *et al.*, 2004). As to the parasites, the spatial epidemiology of the invasive honeybee mite *Varroa destructor* (= *V. jacobsoni*, see Andersen & Trueman, 2000; Solignac *et al.*, 2005) has been investigated among honeybee apiaries in the greater Auckland area of New Zealand. The odds of finding *Varroa* was highest in apiaries in the area surrounding transport and storage facilities in the vicinity of Auckland International Airport and it was calculated that the maximum rate of local spread of the mite was about 12 km year⁻¹ associated with beekeeper-assisted movements of infected bee hives (Stevenson *et al.*, 2005). Under different circumstances and for other host-parasite associations, however, the dispersal of the introduced parasite can proceed in greater jumps and thus more rapidly.

A 'lag period' between local establishment and spread can often be observed. In the literature, this phenomenon is discussed with respect to exponential growth of the new population (being the lag phase in an exponential population growth curve), and to the stochastic extinction of propagules delaying the onset of dispersal. In addition, the genome of the propagule may first have to undergo adaptive evolutionary change in the novel environment (see Sakai *et al.*, 2001). For parasites, lag times have not yet been documented or discussed.

After the eel-specific East Asian swimbladder nematode *Anguillicola crassus* was introduced into Europe around 1982, or shortly before, via imports of live eels from Taiwan to a German harbour at the river Weser, it showed a high dispersal ability and colonized populations of the European eel throughout the continent in less than 10 years. Populations on the western edge of Europe were reached after 10 years in Portugal or 16 years in Ireland (Kirk, 2003). The parasite was recorded from rivers and lakes along the North African coast starting in the 1990s (El Hilali *et al.*, 1996; Maamouri *et al.*, 1999; Rahhou *et al.*, 2001). The first record from North America was from 1995 (Johnson *et al.*, 1995). Barse *et al.* (2001) documented the rapid dispersal of the invader in populations of the American eel. From Texas, where *A. crassus* was introduced to North America, evidence is available revealing that no lag period occurred (Johnson *et al.*, 1995). Furthermore, as postulated by Hastings *et al.* (2005), the spread of *A. crassus* was facilitated by anthropochore transfers. After the parasite had invaded England, the dispersal followed the routes of the lorries by which eels were distributed for stocking purposes. Resting points of lorry-drivers, where they exchanged the maintenance water of the eels, could be identified as the stepping stones in the dispersal of the exotic nematode (Kennedy & Fitch, 1990).

Table 1. Intermediate hosts of *Fasciola hepatica* in selected geographical regions and countries.

Region	Snail hosts	Status of the host	Status of the parasite	References
Europe and the Middle East	<i>Lymnaea (Galba) truncatula</i> <i>L. (G.) glabra</i> <i>L. (Stagnicola) occulta</i> <i>L. (S.) palustris</i> and others	Native Native Native Native	Native	Torgerson & Claxton (1999), Rondelaud <i>et al.</i> (2001), Bargues <i>et al.</i> (2003), Moghaddam <i>et al.</i> (2004)
North Africa (Maghreb)	<i>L. truncatula</i>	Native?	Native?	Jabbour-Zahab <i>et al.</i> (1997), Mekroud <i>et al.</i> (2004), Belfaiza <i>et al.</i> (2004)
USA and Mexico	<i>L. (Fossaria) bulimoides</i> <i>L. (Pseudosuccinea) columella</i> <i>L. (F.) modicella</i> <i>L. (F.) caperata</i> <i>L. (F.) humilis</i> and others	Native Native Native Native Native	Exotic	Hubendick (1951), McKown & Ridley (1995), Dunkel <i>et al.</i> (1996), Rognlie <i>et al.</i> (1996), Cruz-Mendoza <i>et al.</i> (2004)
Cuba, Caribbean area	<i>L. (Fossaria) cubensis</i> <i>L. columella</i>	Native Native	Exotic	Hubendick (1951), Jabbour-Zahab <i>et al.</i> (1997), Vigo <i>et al.</i> (2000), Gutiérrez <i>et al.</i> (2003a,b), Canete <i>et al.</i> (2004)
Bolivia, Peru, (Altiplano), Argentina (Patagonia)	<i>L. truncatula</i> <i>L. viatrix</i> (= <i>L. viator</i> = <i>L. truncatula</i> ?)	Exotic ? ?	Exotic	Hubendick (1951), Jabbour-Zahab <i>et al.</i> (1997), Meunier <i>et al.</i> (2001), Kleimann <i>et al.</i> (2004)
Brazil, North-east Argentina	<i>L. columella</i>	Exotic	Exotic	Pereira de Souza <i>et al.</i> (2002), Coelho & Lima (2003), Prepelitchi <i>et al.</i> (2003), Kleimann <i>et al.</i> (2004)
East Africa	<i>L. truncatula</i>	Exotic	Exotic	Malone <i>et al.</i> (1998)
South Africa	<i>L. truncatula</i> <i>L. columella</i>	Exotic Exotic	Exotic	De Kock <i>et al.</i> (1989, 2003)
Australia, New Zealand	<i>L. (Austropeplea) tomentosa</i> <i>L. columella</i> <i>L. (Fossaria) viridis</i> (= <i>F. ollula</i>)	Native Exotic Exotic	Exotic	Ponder (1975), Harris & Charleston (1976), Boray (1978), Baldock & Arthur (1985), Boray <i>et al.</i> (1985), Faull (1987), See: Cowie (1997), Mayberry & Casey (2000), Muirson (2004)

Differential colonization success, co-existence and competitive exclusion of related parasite species

The rapid spread of *A. crassus* is in contrast to the failure to spread of the congeneric swimbladder nematode *A. novaezelandiae*, which was introduced into a lake near Rome in Italy, apparently along with a stock of *Anguilla australis* from New Zealand (Paggi *et al.*, 1982; Moravec & Taraschewski, 1988). In 1988, high prevalences (80%) and intensities of infection (1 to 27, mean 11) were recorded from its novel host *Anguilla anguilla* in the lake (Moravec *et al.*, 1994), but the parasite remained localized.

In 1993, the strong disperser *A. crassus* was found to have invaded the European lake habitat of *A. novaezelandiae*. In this year, its abundance was already double that of *A. novaezelandiae* (prevalence 47% vs. 21%, mean intensity: 4 vs. 2). The latter species had dropped in abundance compared to 1988, and, interestingly, based on morphological determination, no mixed infections were recorded (Moravec *et al.*, 1994). Unfortunately, the

phenomenon was not followed up in the subsequent years. In 2004 all swimbladder nematodes collected from eels of the lake belonged to the species *A. crassus* based on morphological as well as allozyme investigations (Münderle, 2005).

The fate of the two *Anguillicola* species in Europe shows that transcontinental displacement of species by humans can be followed by successful establishment in one habitat (in this case by both species) and by strong (*A. crassus* from Asia) or weak (*A. novaezelandiae* from New Zealand) dispersal. Furthermore, the weak disperser was also inferior judging by the observed competitive exclusion. In contrast, the two monogeneans *Pseudodactylogyrus anguillae* and *P. bini* co-occur as alien parasites in populations of the European eel, even at the infracommunity level (Buchmann *et al.*, 1987; Dzika, 1999). Obviously, these two sympatrically occurring parasites of the Japanese eel had already achieved coexistence during their coevolution with the Japanese eel and with each other prior to their coinvasion in Europe. According to Morand *et al.* (2002) intra- and interspecific competition

is apparently absent among monogeneans. Species richness seems to be more due to the host characteristics than to parasite interactions.

The ecology of the two *Anguillicola* species that were introduced to Europe reveals more interesting links to the tentative lists of Brown (1989) and Ehrlich (1989). Except for the fact that both parasites have a narrow final host specificity (only hosts of the genus *Anguilla* are susceptible (Moravec & Taraschewski, 1988), in experimental infections, *A. crassus* failed to mature in the congrid eel *Ariosoma balearicum* (Sures *et al.*, 1999)), the strong invader *A. crassus* can persist under a wide range of temperatures and other ecological factors. It can maintain its life cycle under natural conditions in southern Scandinavia (Mo & Steinen, 1994; Wickström *et al.*, 1998) as well as in North Africa (El Hilali *et al.*, 1996; Maamouri *et al.*, 1999) and it is very abundant and reproduces under fully tropical conditions in aquaculture of the Japanese eel in Thailand where its host, *Anguilla japonica*, does not occur naturally (H. Taraschewski *et al.*, unpublished). In Asia as well as in its colonized areas, *A. crassus* occurs in lake and river systems, even under the impact of heavy pollution, and in aquaculture (Münderle *et al.*, 2006). In addition to fresh water, *A. crassus* parasitizes eel populations in brackish waters, and its second stage larvae (L2) are relatively euryhaline (Reimer *et al.*, 1994; Hahlbeck, 1996; Kirk *et al.*, 2000a). A range of copepods and ostracods may serve as intermediate hosts (Kirk, 2003; Moravec *et al.*, 2005), with the option of including various paratenic hosts (Moravec & Škorikova, 1998; Sures *et al.*, 1999). The poor colonizer *A. novaezelandiae* has been little studied in these terms (Moravec *et al.*, 1994), but comparing the occurrence of this species in New Zealand (Lefebvre *et al.*, 2004a) to that of the strong colonizer *A. crassus* in its Asian homelands (Nagasawa *et al.*, 1994; Münderle *et al.*, 2006), *A. novaezelandiae* is less abundant in populations of its indigenous host than *A. crassus*. In Taiwan, the suspected source environment of displaced *A. crassus* (Koops & Hartmann, 1989), this species has

turned out to be almost as abundant as in many European eel populations (compare the tentative list of Brown (1989) and Ehrlich (1989)). The low abundance of *A. novaezelandiae* resembles the epidemiology of *Anguillicola papernai* in its indigenous African host *Anguilla mossambica* (Taraschewski *et al.*, 2005), and it might well happen that both *Anguillicola* species will become extinct after a prospective introduction of *A. crassus* into the native distributional areas of these conspecifics (see table 2).

Thus far, it remains unclear why *A. crassus* is more abundant in Taiwanese populations of *Anguilla japonica* than *A. novaezelandiae* in New Zealand and *A. papernai* in South Africa, and why it is a stronger disperser and competitor than *A. novaezelandiae*.

We can only speculate on the spread and competitive capacity of *A. papernai*. In laboratory experiments, this species successfully reproduced in the European eel *A. anguilla* (Taraschewski *et al.*, 2005). Thus far, no comparable data on the genetic variability of these three *Anguillicola* species are available, but European, American and East Asian populations of *A. crassus* were studied by random amplified polymorphic DNA-polymerase chain reaction (RAPD-PCR) and compared to reference samples of *A. papernai* from South Africa and *A. australiensis* from northeast Australia. The latter species did not colonize, although it showed rather high prevalences (around 50%) in its native range (Kennedy, 1994). Interestingly, less diagnostic DNA-fragments could be detected from *A. crassus* than from the two congeners. In contrast, *A. crassus* displayed a higher degree of polymorphism than the two non-invasive species, at least in its introduced range (D. Lehmann & H. Taraschewski, unpublished). However, in this study only a few samples of *A. papernai* and *A. australiensis* were available. More genetic investigations on many populations of *Anguillicola* species other than *A. crassus* are needed. Interestingly, comparing the two *Anguillicola* species which were introduced into Europe, the weak disperser and competitor came from the remote

Table 2. Host–parasite associations of species of *Anguillicola* (see Moravec & Taraschewski, 1988).

Parasite species	Geographic region	Eel species, population	References
<i>Anguillicola crassus</i>	East Asia	<i>Anguilla japonica</i> (wild and cultivated) <i>A. anguilla</i> cultivated <i>A. rostrata</i> cultivated	Egusa (1979), Nagasawa <i>et al.</i> (1994), Ooi <i>et al.</i> (1996)
after its displacement	Europe, North Africa, North America	<i>A. anguilla</i> (wild and cultivated) <i>A. rostrata</i> (wild and cultivated)	El Hilali <i>et al.</i> (1996), Barse <i>et al.</i> (2001), Kirk (2003), Münderle <i>et al.</i> (2006)
<i>Anguillicola globiceps</i> little studied	East Asia	<i>A. japonica</i>	Nagasawa <i>et al.</i> (1994)
<i>Anguillicola australiensis</i>	Australia, (New Zealand ?)	<i>A. reinhardtii</i>	Kennedy (1994)
<i>Anguillicola novaezelandiae</i> after its displacement	Australia, New Zealand Italy (no permanent establishment)	<i>A. australis</i> (<i>A. dieffenbachii</i> ?) <i>A. anguilla</i>	Moravec & Rohde (1992), Moravec <i>et al.</i> (1994), Lefebvre <i>et al.</i> (2004b)
<i>Anguillicola papernai</i> laboratory infections	South Africa (Europe)	<i>A. mossambica</i> (<i>A. anguilla</i>)	Taraschewski <i>et al.</i> (2005)

territory of New Zealand, while *A. crassus* originated from East Asia, a non-isolated area of a huge continent (cf. Brown, 1989; Ehrlich, 1989). For macroparasites of fish, East Asia is the source area of several strikingly successful invaders, such as the cestodes *Bothriocephalus acheilognathi* (Boomker *et al.*, 1980; Scholz & Di Cave, 1992; Cribb *et al.*, 1997; Choudhury *et al.*, 2004) and *Khawia sinensis* (Williams & Sutherland, 1981; Chubb & Yeomans, 1995), the monogeneans *Pseudodactylogyrus anguillae* and *P. bini* (Buchmann *et al.*, 1987; Hayward *et al.*, 2001a) and the copepods *Lernaea cyprinacea* (Hall, 1983; Kennedy, 1993; Robinson & Avenant-Oldewage, 1996; Goodwin, 1999; Durham *et al.*, 2002; Carnevia & Speranza, 2003) and *Neogergasilus japonicus* (Mugridge *et al.*, 1982; Hudson & Bowen, 2002) each of which have colonized several continents.

For some reason, the fish (and other host taxa?) of East Asia seem to be a stressful, harsh environment (cf. Brown, 1989) making their parasites very successful colonizers of novel hosts, animal communities and areas vulnerable to invasions.

However, the successful expansion of East Asian fish macroparasites seems to be based on additional factors. All of the above species are associated with cyprinids or anguillids (Blanc, 2001), and among these fishes, several species have a very high commercial value (*Cyprinus carpio*, *Ctenopharyngodon idella*, *Anguilla* spp.) and are subject to globally organized trade (see: www.fishbase.org).

Do invasive hosts and parasites depend on vacant niches in their target environment?

All tentative rules considered above on the success or failure of invasive free-living animals also seems to apply to parasites, except that the community and niche structure of parasites within target hosts, in most cases, seems to play a less important role than for free-living animals in their complex habitats. However, competitive interactions between hosts may affect the parasites, as already mentioned for the non-permanent colonization success of *Paratenuisentis ambiguus* in the river Rhine. This insight has been utilized in different eradication campaigns directed against parasites. For instance, the Asian prosobranch *Melanoides tuberculata* has been naturalized in Brazil and the Caribbean area where it has successfully eliminated *Biomphalaria glabrata* and *B. straminea*, the native intermediate hosts of *Schistosoma mansoni* (Pointier & Giboda, 1999; Guimaraes *et al.*, 2001).

As to the likelihood that a native species will be outcompeted and eliminated by an exotic invader with similar niche requirements, more research is needed, although, from 1990 onwards, researchers have become increasingly aware of highly competitive, aggressive invaders such as *Dikerothymus villosus*, *Dreissena polymorpha*, *Melanoides tuberculata*, several ant species and mallard ducks *Anas platyrhynchos*, for instance, which do not depend on vacant niches in areas they colonize (Nalepa & Schloesser 1993; Dick & Platvoet, 2000; Sakai *et al.*, 2001; Falcon *et al.*, 2003). In Lake Victoria (East Africa), the Nile perch *Oreochromis niloticus*, introduced in the 1950s, first had a lag period

with low population densities over many years, but then it boomed in abundance causing the extinction of about 200 of approximately 400 endemic cichlid species in the lake (see Sakai *et al.*, 2001).

Well documented examples of the negative impact of exotic parasites on their native competitors are rare. But *A. crassus*, considered above, and *Khawia sinensis*, for instance, seem to have the potential for displacing other parasites from their microhabitats. On the European scale, the East Asian caryophyllid *Khawia sinensis* has been observed to out-compete the indigenous *Caryophyllaeus fimbriceps* in the intestine of carp (see Scholz, 1989). Thus, among invasive parasites highly competitive species also seem to exist, but, likely due to a different niche structure of the recipient parasite communities, fewer cases of out-competition are known than from free-living organisms. For example, the indigenous sub-Saharan African cattle tick *Boophilus decoloratus* is being rapidly and completely displaced by the colonizing Asian congeneric *B. microplus* in regions where both ticks co-occur (Tonnesen *et al.*, 2004). Only under certain climatic conditions does the alien parasite fail to display its competitive advantage (Sutherst, 2001). Everywhere else the indigenous species is out-competed by a higher reproduction rate due to more blood engorgement of the invasive parasite (Estrada-Peña, 2002) combined with the sterility of hybrid progeny. Virgin females of both *B. decoloratus* and *B. microplus*, when experimentally mated with males of the other species, subsequently produced sterile eggs (Spickett & Malan, 1978). The phenomenon of hybrid sterility more adversely affecting the species with lower reproductive rate deserves further investigation.

Interestingly, we know about cases in which (against the main directions of the respective species drift) fish parasites of European origin have become established in East Asia where they coexist with a native congeneric species. Apparently, *Bothriocephalus claviceps*, a cestode, known from the European and the American eel, invaded Japan (Scholz *et al.*, 2004), although the Japanese eel hosts the indigenous congeneric intestinal dweller *B. anguillae*. Now, both parasites seem to have a sympatric status in Japan, but the preliminary findings of Scholz *et al.* (2004) are now supplemented by additional data. Furthermore, the monogenean *Gyrodactylus anguillae*, obviously a native parasite of the European eel, has recently been recorded from the respective indigenous eel species of Japan, Australia (two species) and North America (see Hayward *et al.*, 2001b).

Considering all these findings and hypotheses, the subject 'hosts and parasites as aliens' comprises many facets, and one should be careful in defining general rules in terms of, for example, the biological traits or the genome of the parasites or the speed or direction of their dispersal. In addition, it is obvious that many observations and much data related to this subject have been collected under a practical scope and not 'with an independent eye': 'The predominant concern with free-living introduced species, for researchers as for conservationists and resource managers, is with the potential damage they may inflict on native species' (Simberloff & von Holle, 1999); and for parasites, researchers have been eager to document various

aspects of a negative impact of exotic parasites on economically important wild or cultivated native hosts of the colonized area (for *A. crassus* see Würtz & Taraschewski, 2000; Kirk, 2003; Gollock *et al.*, 2004, 2005a,b; Münderle *et al.*, 2004), and not on native or other introduced parasitic species. Nevertheless, for the mutual dependence or independence of host and parasite arrival and establishment certain patterns can be determined.

Host–parasite co- or each independent invasion

The modes of colonization by free-living organisms (hosts) and parasites are usually or often interwoven and, thus, should not be treated separately. The arrival and dispersal of a certain host species can be the cause of a parasite's establishment (or its disappearance) and, on the other hand, the loss of its native parasites might encourage an invasive host's colonization success by increasing its competitive abilities. The following four patterns of host parasite associations can be determined:

1. While colonizing novel areas, hosts may lose the parasites of their source area. This may be linked with the small size of the host's founder population not permitting parasite establishment (cf. Anderson & May, 1991; Sakai *et al.*, 2001). According to the parasite escape hypothesis, a host may profit from this favourable situation, attaining higher population densities and greater individual sizes in the colonized areas compared to the conspecifics in their native range (Torchin *et al.*, 2001, 2002), as postulated for instance for the globally introduced European green crab *Carcinus maenas*. In the European source area, body size and biomass are negatively correlated with the prevalence of castrating parasites and the crabs generally remain smaller than in introduced regions. The new non-European populations are less affected by parasites and their members grow to larger sizes than in Europe. In contrast, limb loss, an estimator of predation, is not significantly lower than in non-European populations. These data suggest that the invasion success of green crabs is related to the reduced negative impact of parasites on the dynamics of crab populations in the non-native range (Torchin *et al.*, 2001). However, observations from the Red Sea invasive crab *Charybdis longicollis* do not support the parasite escape hypothesis. Its first record in the Mediterranean was in 1959. In the 1980s, it formed as much as 70% of the benthic biomass on sandy-silt bottoms off the Israeli coast. In 1992 its native erythrean sacculinid rhizocephalan *Heterosaccus dollfusi* was recorded for the first time in the Mediterranean. This spread quickly and reached a high prevalence (Haifa Bay: 77% in 1995). But although infected female and male crabs became castrated and were altered in growth, phenotype and behaviour by the parasite, no noticeable reduction in the densities of the host populations could be detected (Galil & Zenetos, 2002). In addition, for other conspicuously successful invasive free-living aquatic species like *Dikerogammarus villosus* and *Dreissena polymorpha*, there is no indication that the presence or absence of parasites is a decisive factor regulating their populations. In the non-parasitological

literature other evolutionary releases, such as the lack of respective predators in the colonized environment, are considered relevant factors in determining colonization success (Lee, 2002; Schlaepfer *et al.*, 2005).

Introduced hosts that did not bring their native parasites may become colonized by parasites of related hosts in the recipient area, like the American cane toad *Bufo marinus*, which in Australia only harbours local endoparasites (Barton, 1997). However, in its Australian range cane toads do not have local ectoparasites (Lampo & Baylis, 1996), which might have to do with its toxins. Other toad species with similar toxins to which local blood-sucking ectoparasites might be adapted, do not exist in Australia (see Schlaepfer *et al.*, 2005).

Often, parasites from the source area of displaced hosts follow their hosts, however, usually with a delay of one or several decades. The first record of the acanthocephalan *Paratenuisentis ambiguus* in the German river Weser occurred about 25 years after the introduction of its intermediate host *Gammarus tigrinus* (Taraschewski *et al.*, 1987), similarly to the host–parasite pair *Charybdis longicollis/Heterosaccus dollfusi* in the eastern Mediterranean (Galil & Zenetos, 2002). On the Hawaii archipelago, however, the most isolated of all terrestrial habitats on earth, it took 100 years from the appearance of the mosquito vector until the first epizootics of bird malaria were recorded (Van Riper *et al.*, 1986).

2. A host may establish in a colonized area together with a parasite, with or without a lag time of the latter. The parasite remains associated with its host and does not include hosts from the new territory in its host range. In Germany, the American racoon-specific ascarid *Baylisascaris procyonis* became abundant in alien populations of its host (Grey, 1998). In the USA a small number of infections occur in dogs and visceral larvae are known from wild vertebrates as well as from humans (Sorvillo *et al.*, 2002; Bowman *et al.*, 2005; Gavin *et al.*, 2005) which has not been recorded in Germany to date.
3. Host and parasite coinvide but, due to the low host-specificity of the parasite, it successfully colonizes populations of novel hosts, native or introduced, in the recipient area. The East Asian tapeworm *Bothriocephalus acheilognathi* attained its global distribution through intercontinental introductions of carp and grass carp, but many other species of fish in target communities turned out to be susceptible hosts (Brouder & Hoffnagle, 1997; Dove *et al.*, 1997).
4. Parasites colonize a target region without their hosts. Japanese eels (*A. japonica*) are not cultivated in Europe and have not been stocked in European waters. Nevertheless, two species of gill monogeneans and the swimbladder nematode *A. crassus* have invaded Europe as previously discussed.

Invasion models 3 and 4 are, however, difficult to distinguish because infected exotic hosts are often temporarily stored or cultivated in the recipient area without becoming naturalized. Furthermore, the introduction of a parasite can follow model 1 with a time lag with respect to the intermediate host, and models 3 or 4, for instance, for the final host (*Paratenuisentis ambiguus*, Taraschewski *et al.*, 1987). For invasion and establishment

according to models 3 and 4, potential host species that are within the host range of the invaders have to be available. A few parasites such as *Ichthyophthirius multifiliis* and *Ichthyobodo necator*, with a very low host specificity and monoxenic life cycles, attained a global distribution so early and quickly that the modes and pathways of their invasions and spread can no longer be documented (Schäperclaus, 1979). Accordingly, they are not listed as alien species in any respective reviews.

Phylogenetic aspects of species introductions

Blanc (2001) presented an incomplete list of almost 100 parasites and pathogens of fish that have been introduced to Europe. These predominantly originated from East Asia, however, by splitting up their recipient hosts to the family level, interesting phylogenetic links have become apparent. The majority of cyprinid and anguillid (*A. anguilla*) parasites are of Asian descent, whereas most salmonid parasites have North America as their source area. All introduced parasites of the Centrarchidae come from America, following their hosts according to invasion models 1 and 2. The probability that a certain potential host in a target area becomes colonized is dependent on the number of related host species in potential source zoogeographical areas. A region with a large number of related hosts has a greater potential to function as a donor territory for potential invasive parasites than that with few related hosts and thus related parasites. But with respect to the abundance of North American salmonid parasites in Europe, imports of rainbow trout, an outstanding item of aquacultural interest, might be the predominant causative mechanism. On the other hand, the likelihood that certain host taxa will become colonized by exotic parasites from a certain geographic region is influenced by the radiation and species richness of the parasite taxa involved. Unlike the scheme of Blanc (2001), the European eel was colonized by the North American eoacanthocephalan *Paratenuisentis ambiguus* (see above). Unlike Europe, Eoacanthocephala have undergone conspicuous speciation and radiation in North America (Amin, 1985), so many candidates for displacement were available from this taxon. In addition, carp, a European cyprinid fish that was colonized by the North American caryophyllid *Atractolytocestus huronensis* (Oros *et al.*, 2004) for instance, does not fit into the pattern of Blanc (2001).

The general question now arises as to how parasite communities of wild animals are assembled during evolutionary times. Paterson & Gray (1997) analysed the ectoparasite communities of seabirds (fig. 1) which are rich in species and show the same very extended distributional ranges as their hosts (see Poulin, 1998). These communities are thus already globalized by nature and are little affected by anthropogenic displacements. The authors concluded that the communities were formed by the following four evolutionary factors namely host–parasite cospeciation (but a host speciation does not have to be accompanied by a parasite speciation (Paterson & Banks, 2001), host-switching, sorting events like a

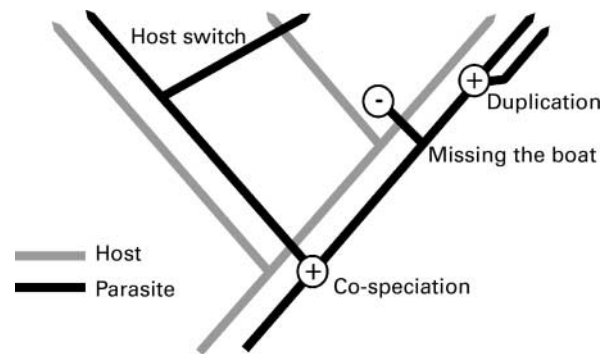


Fig. 1. Four categories of evolutionary events in a host–parasite association. (From Paterson & Gray, 1997.)

parasite ‘missing the boat’ (extinction) and intra-host speciation (duplication) of the parasite.

For parasites of freshwater fish, for instance, the situation is different. The respective component communities are often very habitat specific and unsaturated with a low community richness (see Esch *et al.*, 1990; Poulin, 1998). Such host–parasite associations are vulnerable to parasite invasions such as those documented for eels of the river Rhine (Thielen, 2005). These have been colonized by several alien helminths which extended their distributional range without an expansion of their native hosts. Thus, a new evolutionary factor driving the formation of parasite communities can be determined, i.e. sudden host colonization (switch) by allopatric parasites utilizing human transport or in other words ‘catching the speed boat’. If we consider the eel-specific helminth species as being part of the component communities of eels along the river Rhine (Thielen, 2005), the importance of this novel evolutionary factor becomes obvious.

Paraquimperia tenerrima

The European eel shares this nematode with the American eel *Anguilla rostrata* (Moravec, 1994). Its precursor probably coevolved with the ancestor of the two closely related (Lehmann *et al.*, 2000) Atlantic species *A. anguilla* and *A. rostrata*, but has not yet split into two species like the host. *Anguilla mossambica*, the African longfin eel, which is considered to belong to the same clade/species group as the two Atlantic eel species (Tsukamoto & Aoyama, 1998; Aoyama *et al.*, 2001) is the host of the congeneric *P. africana* (Moravec *et al.*, 2000) suggesting that *P. tenerrima* in the two Atlantic eel species has followed the coevolution mode.

Bothriocephalus claviceps

This cestode is also shared by the two Atlantic eel species (Cone *et al.*, 1993; Sures & Streit, 2001). But although congeneric species parasitize the Japanese eel (Scholz *et al.*, 2004) it is difficult to judge whether this intestinal helminth has coevolved with Atlantic eels in the same way as *P. tenerrima* since the genus *Bothriocephalus* is not eel-specific (Scholz *et al.*, 2004). Furthermore, from

1922 *A. rostrata* has been repeatedly introduced into Europe for stocking purposes (Tesch, 1999), so that it is not impossible that *B. claviceps* as well as *P. tenerrima* colonized *A. anguilla* during the last century, *A. rostrata* being the donor host.

Paratenuisentis ambiguus

This eoacanthocephalan obviously evolved as a parasite of the American eel *A. rostrata* by performing a slow and gradual host switch from some sympatric fish species to *A. rostrata*. Later on it colonized the European eel *A. anguilla* (Taraschewski *et al.*, 1987).

Anguillicola crassus

The genus *Anguillicola* must have evolved in the Indo-Pacific region where most of the 15 recent species of the genus *Anguilla* occur (Aoyama *et al.*, 2001; Lin *et al.*, 2001; Watanabe *et al.*, 2005). When the precursor of *A. anguilla* and *A. rostrata* settled in the area which is now the North Atlantic around 20 million years ago (Lehmann *et al.*, 2000; Lin *et al.*, 2000), its swimbladder parasite (presumably it had one) was lost due to some sorting event. Four other eel species of Indo-Pacific distribution are known to host *Anguillicola* species (table 2), suggesting a host–parasite coevolution of this nematode genus. *A. crassus*, which has recently colonized the European eel, seems to have undergone coevolution with the Japanese eel *A. japonica* (Moravec & Taraschewski, 1988) and then caught the speed boat to the North Atlantic.

Pseudodactylogyrus

The two monogeneans *P. anguillae* and *P. bini* obviously coevolved with the Japanese eel. As for *A. crassus*, the Japanese eel was the source host for these invasive monogeneans (Buchmann *et al.*, 1987). Although we do not know whether their ancestor performed an intrahost duplication it is likely that it did so. Concerning the monogeneans, findings are available suggesting that all three modes of speciation considered above have occurred. Regarding the *Dactylogyrus* species sampled from 19 fish species in Europe it appears that in this genus diversification mainly resulted from intrahost speciation events (Simkova *et al.*, 2004). In contrast, in the genus *Gyrodactylus* host switch seems to have happened more commonly (Zietara & Lumme, 2002; Huyse *et al.*, 2003; Meinila *et al.*, 2004). Gutierrez (2001) studied six species of monogeneans belonging to three genera of the gills of a catfish in Rio de la Plata and hypothesized that co-speciation was the predominant mode of diversification.

Any further specific helminths infecting populations of the European eel in the river Rhine are not worth treating in this context because too little is known about them (Thielen, 2005). For all alien helminths of the European eel in the river Rhine, forming the majority of eel-specific helminths there, the target host is a congener of allopatric donor hosts.

Within a very few years, *A. anguilla* has become the required host of all these parasites in their European range without having passed through a coevolutionary

phase. The novel host–parasite relationship following an abrupt anthropogenically initiated host switch to a naive recipient host and often associated with elevated pathogenicity (see below) is one of the most interesting aspects of global biological change and is a challenging field for future research.

Well-investigated model invasive parasites

The subjects of invasions of hosts and areas by parasites and of how parasite communities in and on their hosts are shaped in times of global homogenization of biota are complex, as documented above. Two highly successful invasive parasites that have been investigated in various respects, will now be considered. They differ in their modes of invasion, their host–parasite interactions and in the perspectives of future research related to hosts and parasites of aliens.

Fasciola hepatica

Life cycle in the native and novel ranges

As a pathogenic parasite of cattle and sheep, the common temperate liver fluke *Fasciola hepatica* is of great economic importance, and many applied aspects of its host–parasite relations (Behm & Sangster, 1999; Fairweather & Boray, 1999; Mulcahy *et al.*, 1999) and its metabolism (Tielens, 1999) are well investigated. It has been widely distributed in its natural range, the Palaearctic Region, since historical times (Torgerson & Claxton, 1999), although its spread within this area to non-continental territories or to North Africa (see table 1) remains unclear. Within this native range, a domestic life cycle with cattle and sheep (Torgerson & Claxton, 1999), sylvatic cycles either with cervids and wild boar (Shimalov & Shimalov, 2000; Priemer, 2001) or lagomorphs and/or rodents (Mas-Coma *et al.*, 1988; Rondelaud *et al.*, 2001) and a synanthropic cycle with rats as final hosts (Ménard *et al.*, 2000; Valero *et al.*, 2002) can be differentiated. These life cycles seem to be interconnected to different extents. Interestingly, in a study by Rondelaud *et al.* (2001), in addition to the two native lagomorphs, the European hare and the rabbit, an introduced lagomorph from North America, *Sylvilagus floridanus*, was also infected in captures from French watercress beds, with prevalences for the three lagomorph species being 39%, 42% and 25% respectively. However, due to its more aquaphilic habitat preference, another alien host, the nutria *Myocastor coypus* may play a greater role in the sylvatic transmission of the fluke in its European range (Ménard *et al.*, 2000; Vignoles *et al.*, 2004).

In Europe and in the temperate part of the Middle East and North Africa, *Lymnaea truncatula* is the principal snail host, but in certain areas other lymnaeids, such as members of the *Stagnicola* type group, may serve as additional or even as major intermediate hosts (see table 1).

Meanwhile, *F. hepatica* has attained a global distribution using cattle and other domestic ruminants, originally deriving from the Palaearctic region (Torgerson & Claxton, 1999), and native wild animals such as kangaroos, wombats and possums (Spratt & Presidente, 1981), or rodents (Fuentes *et al.*, 1997) as final hosts. Cases among

wild exotic mammals from the colonized environment have also been detected (Viggers & Spratt, 1995; Kleinmann *et al.*, 2004). Finally, in parts of its introduced range, humans are frequently infected as accidental hosts (Mas-Coma *et al.*, 1999), or even serve as major final hosts in the life cycle of the liver fluke. Between Lake Titicaca and the Bolivian capital, prevalences of 40%, locally approaching 100%, have been recorded from the human population (Esteban *et al.*, 1999). As to the pathogenicity of *F. hepatica*, no differences between final hosts of the native occurrence compared to those serving as such in the colonized environment can be determined. Within the entire distributional range no populations of cattle or sheep exist that have been bred towards a low susceptibility with respect to the liver fluke and thus these hosts are subjected to a high pathogenic impact (Behm & Sangster, 1999). Wild mammals (and humans: see Mas-Coma *et al.*, 1999), too, suffer from this pathogenic parasite which does not seem to affect alien hosts more severely than the native European ones (Viggers & Spratt, 1995; Priemer, 2001).

In most introduction areas, propagules of the invasive fluke have most likely repeatedly invaded their target areas with cattle or sheep via trade routes from countries within the original or the progressively extending range of the parasite (compare the propagule pressure model). After such events, the geographic spread within the new continent or island seems to occur in jumps (saltative dispersion) with long or short distance spread via pasture animals loaded on trucks. In addition, one should assume that anthropogenic dispersion is supplemented by a smoothly expanding range with continuous propagation through wild animals.

As for the intermediate hosts, the establishment of alien populations of *F. hepatica* shows five different models of establishment and host–parasite associations (table 1), namely:

1. Indigenous lymnaeids from the recipient area, forming wide nets of populations, are acquired as susceptible hosts (example: USA).
2. A colonization of the target area by the Palaearctic host *Lymnaea truncatula* preceded the arrival and dispersal of the fluke (Bolivia).
3. A susceptible lymnaeid of exotic origin had spread within the recipient territory prior to the invasion of the parasite (Brazil).
4. Two non-indigenous lymnaeids are utilized as intermediate hosts, one of them being *L. truncatula* (South Africa). In South Africa, the colonization of *L. truncatula* must have taken place prior to the invasion of the parasite during the European settlement, while the invasion of *L. columella* seems to have occurred recently (table 1).
5. An indigenous lymnaeid as well as alien relatives, other than *L. truncatula*, and of non-Palaearctic origin, serve as intermediate hosts (Australia). In Australia, the colonization by the allocthonous snail species (table 1) occurred after establishment of the parasite.

Additional sequences and combinations of colonizations by intermediate hosts and by the parasite may have occurred. Following models 1, 4 and 5, the parasite should benefit from the double-bind or multiple-bind

transmission associated with the use of two or more fairly common intermediate hosts, gaining a higher abundance and distribution associated with an elevated ecological plasticity, and, possibly, an increased genetic divergence than in areas with just one transmission pathway (Boray *et al.*, 1985; Canete *et al.*, 2004).

Due to the lack of a widely distributed susceptible snail host, *F. hepatica* shows a markedly discontinuous distributional pattern in certain colonized areas. In East Africa, *L. truncatula* only occurs above 1200 m where the temperature requirements of this Palaearctic gastropod are met (Malone *et al.*, 1998). In southern Africa, *L. truncatula* is also limited to mountainous landscapes such as Lesotho (De Kock *et al.*, 2003). Although already present in South Africa (De Kock *et al.*, 1989), the dispersal of the highly invasive *Lymnaea columella* has not been investigated over the last few years. Under tropical conditions, such as those prevailing in Cuba or Brazil, this susceptible, recently acquired snail host of *F. hepatica* has achieved high abundances (Pereira de Souza *et al.*, 2002; Canete *et al.*, 2004), and one should assume that it will soon do the same in large parts of Africa.

Genetic divergence of invasive intermediate hosts, the Red Queen hypothesis

In the Bolivian Altiplano, allocthonous populations of *L. truncatula* persist at an altitude of about 4000 m under intense UV radiation (Meunier *et al.*, 2001). In addition to high prevalences of the castrating parasite *F. hepatica* (Graczyk & Fried, 1999), this situation should create a marked evolutionary pressure. The invasive dipteran *Drosophila subobscura* showed a rapid morphological response to altitude following its introduction to North America from Europe, and one should assume that this coincided with an increase in genetic divergence (see Lee, 2002). In principle, highly dispersive species with a rapid range expansion are thought to display a large amount of gene flow leading to elevated genetic diversity (Sakai *et al.*, 2001). However, populations of *L. truncatula* from the Andes do not conform to this hypothesis. Jabbour-Zahab *et al.* (1997) conducted genetic studies on these snails using isoenzymes and detected the absence of within snail population polymorphism. A few years later, Meunier *et al.* (2001) studied specimens of *L. truncatula* from 13 Altiplano populations at six polymorphic loci, and specimens from 12 populations in France, Spain, Portugal and Morocco served as reference samples. In the Old World, low levels of polymorphism existed within and between snail populations. In contrast, in Bolivia only a single multilocus genotype could be detected. This remarkable result corresponds with data from other invasive gastropods. *Biomphalaria pfeifferi*, the intermediate host of *Schistosoma mansoni* in sub-Saharan Africa (Morgan *et al.*, 2001), in Madagascar exhibited only two microsatellite genotypes (Charbonnel *et al.*, 2002). Finally, perhaps the most successful disperser of all freshwater snails, *Melanooides tuberculata*, was shown to form genetic clones, associated with phenotypic morphs, which do not merge into a single invasive population in the introduced range. A single clone can invade an extensive area (Falcon *et al.*, 2003). In its Asian home range, *M. tuberculata* hosts a diverse community of trematodes which partly

followed their host to colonized territories in the Americas (Scholz *et al.*, 2001).

The low genetic divergence of the three invasive molluscs is associated with hermaphroditic reproduction, mainly by selfing. The option of self-fertilization is a feature of a good colonist, but with respect to ability to respond to natural selection pressures due to climatic conditions or trematodes, for instance, one should expect that parthenogenesis and gametogenesis would alternate, at least after a successful invasion (see above: the historical model). According to Sakai *et al.* (2001) reduced genetic diversity can have two consequences. First, inbreeding depression may limit population growth and lower the probability that the population will persist. Second, reduced genetic divergence will limit the ability of the population to evolve. So why do the three snail hosts *L. truncatula*, *B. pfeifferi* and *M. tuberculata* not conform to the Red Queen hypothesis in the 'mutual arms race' between host and parasite, as, for example, *Potamopyrgus antipodarum* seems to do? In New Zealand, the native range of the latter invasive prosobranch, it was found to undergo parthenogenic reproduction in biotopes with low trematode pressure, and to show sexual recombination in others that have a high prevalence of (castrating) trematodes (Lively, 2001). In several populations of *M. tuberculata*, the low frequency of fertile males, indicative of sexual reproduction, was not correlated with the prevalence of trematodes (Ben Ami & Heller, 2005).

Nevertheless, a novel snail host of *F. hepatica* has been shown to differ in its susceptibility to the introduced parasite. Cuban populations of *Lymnaea (Pseudosuccinea) columella* were studied by three different techniques. Of 21 enzyme loci analysed, none exhibited either within or between sample variation. This absence of enzyme polymorphism supports the assumption of selfing as the dominant reproductive system in this hermaphroditic host species. Conversely, RAPD profiles displayed clear differences between susceptible and resistant isolates for 17 of 26 primers tested, while no within group variation was detected. DNA-ITS sequence analyses for both snail categories showed only two bases that differed between groups at 0.17% variation confirming that susceptible and resistant snails belong to the same species (Gutiérrez *et al.*, 2003a,b). Similar results on the same host species were obtained by Calienes *et al.* (2004). In both studies, the resistance status was correlated with phenotypic features. Jabbour-Zahab *et al.* (1997) conducted a genetic study using starch gel electrophoresis on populations of two novel hosts of *F. hepatica*, *Lymnaea viatrix* from the northern Bolivian Altiplano and *L. cubensis* from Venezuela, Guadeloupe, Cuba and the Dominican Republic, and compared these to populations of the traditional host *L. truncatula* from France, Portugal and Morocco. They identified a western genotypic group comprising samples of *L. cubensis* and an eastern genotypic group based on samples of *L. truncatula* from Europe. Surprisingly, samples that were considered to belong to *L. viatrix* showed no genetic divergence from the Portuguese sample. Thus it is possible that *L. viatrix* (= *L. viator*, see Hubendick, 1951) is of European origin and even conspecific with *L. truncatula* (see table 1).

The genetics and biological traits of various intermediate hosts of *F. hepatica* deserve further investigation in order to address many open questions, for example: how do resistant strains evolve, if the respective snail host reproduces by selfing? Do they derive from different introductions? In a study by Gutiérrez *et al.* (2003a), more than 80% of *L. columella* from Cuban isolates were susceptible to *F. hepatica*, while other isolates were not. What happens if propagules belonging to one or the other genotype repeatedly invade a recipient ecosystem (compare above: the propagule pressure model)? Will one genotype achieve a selective advantage in the target area if the parasite is present or if it is not, and will the balance change following the introduction of the parasite? These are questions that need to be addressed.

Co-occurrence and genetic divergence of Fasciola spp., hybridization of displaced parasites

As for the genetic divergence of *F. hepatica*, the situation is no less complex than for its snail host. Worms within one population may be provided with a different set of chromosomes, furthermore, the novel sympatric occurrence of *F. hepatica* and *F. gigantica* may complicate the interpretation of results (see below). Morozova *et al.* (2004) investigated the haplotype frequency and the polymorphism of fragments of the ND1 and CO1 mitochondrial genes of worms from different, distant sites within the former Soviet Union, and Itagaki *et al.* (2001) studied the sequence of these genes in triploid worms of *Fasciola* spp. in Japan. Thus far, neither these molecular trials nor laboratory studies on life-cycle traits or the phenotypic variation of flukes from the original and from the introduced range, reveal any patterns or allow any conclusions. Vignoles *et al.* (2004) found that four strains of *F. hepatica* originating from France differed in morphological and life-cycle features in experimentally infected *L. truncatula*. However, the results of such laboratory life-cycle trials have to be treated with caution, since the developmental patterns of *F. hepatica* in intermediate hosts may be modified by various environmental factors (Belfaiza *et al.*, 2004; Rondelaud *et al.*, 2004). Valero *et al.* (1999) conducted morphological measurements on adult worms and their eggs from sheep in the Bolivian Altiplano and from the lowlands of Spain. Only slight allometric differences were apparent. Due to this paucity of data, it is not known whether *F. hepatica* shows a reduced genetic diversity in its novel range due to a bottleneck at the time of colonization as described from the parasitic mite *Varroa destructor* (Solignac *et al.*, 2005) or whether it performs 'speciation attempts' in its introduced range as described for *Echinococcus granulosus* (Thompson & Lymbery, 1987).

A challenging field of future research might be the sympatric occurrence of *F. hepatica* and *F. gigantica* in the 'post-globalized' world. Formerly, the distributional ranges of these two congeners seem to have been confined to the temperate Palaearctic (*F. hepatica*) and to the tropical Oriental Region (*F. gigantica*), but now an increasing number of papers document a geographical overlap of both species (see Lotfy & Hillyer, 2003). In East Africa, the two trematodes have a narrow distributional transitional zone between 1200 and 1800 m altitude, i.e.

F. hepatica: above 1200 m, *F. gigantica*: below 1800 m (Malone *et al.*, 1998), and they will probably retain only partly overlapping habitat preferences as long as *L. columella* has not colonized the lowlands of East Africa enabling *F. hepatica* to descend to a lower altitude. At present, the likelihood that both fasciolids co-occur in the liver of host individuals is still limited. A similar situation is found in an Iranian region on the Caspian Sea where three species of lymnaeids have been found, *Lymnaea (Stagniola) palustris*, a secondary intermediate host of *F. hepatica*, *L. (G.) truncatula*, the major snail host of this fluke (table 1) as well as *Radix gedrosiana*, a member of the *Radix (Lymnaea) auricularia* complex transmitting *F. gigantica*. In this landscape, the distributional overlap of *G. truncatula* and *R. gedrosiana* also corresponds to the co-occurrence of the two fasciolids (Moghaddam *et al.*, 2004). On the other hand, in laboratory studies recognized intermediate hosts of one of the two congeners were shown to permit patent infections by the other. Snails, for instance belonging to a *L. truncatula* strain, were susceptible to *F. gigantica* from Madagascar and highly susceptible to *F. gigantica* strains originating from China and Egypt (Dar *et al.*, 2003a,b, 2004). Such findings, which should be treated with caution, demonstrate that the epidemiological consequences of fasciolid introductions might be unpredictable.

The morphological distinction between *F. hepatica* and *F. gigantica* has traditionally been difficult, partly due to host-mediated modifications (Akahane *et al.*, 1970). In parallel, however, the genetic classification of worm isolates by molecular tools has progressed (Hashimoto *et al.*, 1997; Itagaki *et al.*, 2001). According to Marcilla *et al.* (2002), a simple PCR-restriction fragment length polymorphism assay using the common restriction enzymes Ava II and Dra II is safe for distinguishing both fasciolids. The sequence showed a few nucleotide differences between the two congeners but no intraspecific variation within either species. Using eight other restriction enzymes, Itagaki *et al.* (2001) identified eight of 70 triploid Japanese worms as belonging to the '*F. gigantica* type', the remaining 62 were categorized as *F. hepatica* type. In other molecular studies, fasciolid specimens from Japan had, in most cases, been identified as *F. gigantica* (Hashimoto *et al.*, 1997) and, interestingly, using different molecular tools natural hybridization has been claimed (Agatsuma *et al.*, 2000). In addition, Chinese workers have suggested that intermediate genotypes between both invaders occur (Huang *et al.*, 2004), and Lotfy & Hillyer (2003) discuss additional cases in which worms were suspected to be hybrids of both liver flukes.

Further scientific evidence is needed to show where and under what circumstances natural hybridization between *F. hepatica* and *F. gigantica* occurs, whether hybrids are fertile and, if so, whether they backcross to one or both parental populations (introgression), and finally, whether one species is 'genetically assimilated' by the other. Among free-living invaders (hosts) for instance, mallard ducks in colonized environments were shown to have 'genetically taken over' (endangered) duck species which became increasingly mallard-like in appearance (see Rhymer & Simberloff, 1996). This phenomenon is

also known from non-vertebrate invaders such as freshwater crayfish (Perry *et al.*, 2001; Wilson *et al.*, 2004), but no comparable data are available from invasive parasites. However, we know of another mode of displacement of a native parasite species by an exotic through hybridization. Hybrid sterility combined with a faster population growth of the invasive species seems to be the reason for the disappearance of the tick *Boophilus decoloratus* in areas in which the alien competitor *B. microplus* has become established (Estrada-Peña, 2002).

Invaders may benefit from hybridization with native species leading to fertile offspring and introgression by gaining additional genetic variability as discussed with respect to free-living animals (Lee, 2002; Wilson *et al.*, 2004). An interesting case with parasite involvement supporting this hypothesis has been described from honeybees in their new range.

As early as the 16th century, the European honeybee, *Apis mellifera*, was introduced into North America where it partly attained a feral status (Kraus & Page, 1995). In the neotropics, however, the climatic conditions were not suitable for this species and so the possibilities for producing honey were limited. Thus, attempts were undertaken to cross *A. mellifera* with the African honeybee *A. (mellifera) scutellata*. Such hybrids escaped from a laboratory in Brazil and dispersed. Introgression with populations of *A. mellifera* progressively occurred, leading to 'africanized' hybrids. The process of 'africanization' quickly spread because africanized queens attain maturity earlier than non-africanized queens and are thus more likely to pass on their genes than their non-hybrid competitors. Meanwhile, the africanization process has reached as far as the southern USA (Dietz & Vergara, 1995). This hybridization coincides with an elevated aggressiveness and an overall fitness gain, and interestingly, also with an increased defensive capacity against the invasive East Asian bee mite *Varroa destructor* (= *V. jacobsoni*) (Guzmán-Nuova *et al.*, 1999; Andersen & Trueman, 2000; Solignac *et al.*, 2005) which has decimated many feral colonies of *A. mellifera* in its introduced range (Kraus & Page, 1995; Guerra *et al.*, 2000).

For studies on the potential hybridization of displaced congeneric parasites, the two fasciolids *F. hepatica* and *F. gigantica* could be a promising pair of species. Due to their economic importance the data collected should also be of interest to veterinarian parasitologists.

Anguillicola crassus

Synanthropic status, ecological characteristics

From the late 1960s, elvers of the European eel (*A. anguilla*) were imported into Japan in increasing quantities to satisfy the demands of the eel aquaculture industry (Egusa, 1979). Juveniles of the Japanese eel (*A. japonica*) were no longer available in sufficient numbers (Tesch, 1999, 2000). In the 1970s, the import of *A. anguilla* elvers decreased because it became apparent that European congeners responded sensitively to infections by indigenous parasites of Japanese eels, such as *Pseudodactylogyrus* spp. and the swimbladder nematode *Anguillicola crassus*. The latter parasite occurred in 10–40% of cultured Japanese eels with an 'intensity of 1–3, occasionally attaining up to 20 adult worms'. In

contrast, in European eels cultivated in Japan the prevalence often reached up to 100% and high numbers of worms were usually found per eel (Egusa, 1979). This high abundance in the introduced host was accompanied by a conspicuous pathogenicity (Egusa, 1979). The Japanese fisheries biologist Egusa seemed to have realistically assessed the dimensions in his observations claiming 'Precautions should be taken to prevent the introduction of these parasites to Europe' (Egusa, 1979). Only about 3 years later, however, *A. crassus* was detected in the German river Weser (Neumann, 1985) at the mouth of which a fish processing industry is located. This followed repeated imports of live eels from Taiwan and New Zealand over several proceeding years (Koops & Hartmann, 1989).

When Egusa's warning appeared in 1979, the two monogeneans *Pseudodactylogyrus bini* and *P. anguillae* had already invaded Europe, probably via imports of live Japanese eels from the eastern part of the former Soviet Union to an eel aquaculture plant in the Kaliningrad region (formerly German Königsberg) near the Baltic coast (Golovin, 1977 in Buchmann *et al.*, 1987). But most likely their dispersal in the recipient continent resulted from introductions in the 1980s (Buchmann *et al.*, 1987), probably using the same invasion corridors and pathways as *A. crassus*.

In the USA, *A. crassus* was first located in an eel aquaculture in Texas in 1995 after this production facility had stocked its ponds with eel elvers of unknown identity and origin purchased from US east coast suppliers (Johnson *et al.*, 1995). Its spread from Texas northeastwards was followed by Barse & Secor (1999). At about the same time as *A. crassus* appeared in North America, a detrimental effect of the parasite on cultured American eels *A. rostrata* was reported from a fish farm in Taiwan (Ooi *et al.*, 1996). For the two invasive dactylogyrids, the Texan eel farm apparently did not serve as the entry point for the invasion. In the mid 1990s, *P. anguillae* had already been recorded on the island of Nova Scotia (Canada) and in South Carolina, later, both invasive gill worms (*P. anguillae*, *P. bini*) were found at different localities within the USA (Cone & Marcogliese, 1995; Hayward *et al.*, 2001a). At present, various pilot projects to cultivate eels are in preparation or have already commenced, for instance in the region of eastern and southern Africa and around Madagascar (various personal communications), where four eel (*Anguilla*) species co-occur (see Skelton, 1993; Aoyama *et al.*, 2001). Thus, it is rather likely that *A. crassus* and the two pseudodactylogyrids will achieve a further extension of their distributional ranges or have done so already. Any attempts to farm eels will be accompanied by inter-continental and small range transport of live juvenile and/or adult eels, infected with non-indigenous invasive parasites. According to Watanabe *et al.* (2005), 15 species of freshwater eels of the genus *Anguilla* are recognized. Most species occur in Asia where aquaculture is of major economic importance (Tesch, 1999, 2000, see also www.fishbase.org).

Furthermore, huge quantities of eels of different species, live elvers as well as processed eels, are transported across the globe. For eels and especially

elvers, Hong Kong is the established trade centre (Tesch, 1999, see: www.info.gov.hk/censtatd/). Elvers of *Anguilla anguilla* were shown to have the potential of harbouring larvae of *A. crassus*, which can mould to the adult stage after the host has reached a suitable size (Nimeth *et al.*, 2000). In 1996/97, 65% of elvers of the European eel caught on the west coast of Europe were bought by Chinese companies to stock the immense eel aquaculture programme in China (Kuhlmann, 1997). While eel farming increasingly flourishes in China, it has recently become less important first in Japan and then in Taiwan (Lee *et al.*, 2003), being an extremely dynamic and unpredictable branch (Tesch, 1999; Ciccotti & Fontanelle, 2000), and even Italian eel production, for long the number one in Europe, has entered into a sudden crisis (Ciccotti & Fontanelle, 2000; E. Ciccotti personal communication). In addition to cheap energy and labour, the availability of reasonably priced elvers seems to be a major factor creating instability in the global eel-producing industry (Kuhlmann, 1997; Ciccotti & Fontana, 2000), but newcomers in eel culture still become established on the market (see for instance: Savvidis, 1999; Appelbaum & Hurvitz, 2000; Kim & Lee, 2000). Despite their high commercial value, any attempts at the artificial fertilization and hatching of eels has failed, and thus, the dependence on catching free-living elvers (the prices of which steadily increase, see Kuhlmann, 1997) and their trade has remained (Tesch, 1999). For farmed European eels, *A. crassus* is no more the economic threat, as reported from Japan in the 1970s (Egusa, 1979) and Europe in the 1980s (Liewes & Schaminee-Main, 1987; Van Banning & Haenen, 1990; Kamstra, 1991), due to progress in chemotherapy (Taraschewski *et al.*, 1988; Hartmann, 1989; Geets *et al.*, 1992).

But eels are not just displaced for aquaculture purposes. In Europe as well as in East Asia, the stocking of feral eel populations (*A. anguilla* and/or *A. japonica*) using elvers or young of the year purchased from salesmen is still customarily conducted on a large scale (Tesch, 1999, 2000), and also landlocked waters are stocked (see Schabuss *et al.*, 2005). In Japan, European eels are used for stocking rivers where *A. japonica* is rare (Aoyama *et al.*, 2000). Such alien fish reach the sexually maturing silver phase and perform their downstream spawning migration at the same time as native Japanese eels do so, raising concerns about the potential impact of interbreeding between both species (Miyai *et al.*, 2004).

Thus, the degree of synanthropism and globalization imposed on eels reaches almost that of the major final domestic hosts of *F. hepatica*. In both cases the commercial utilization of the final hosts seems to be the major driving force in the jump dispersal of the respective parasites. In contrast to *F. hepatica*, however, no intermediate host of *A. crassus* needed to be introduced to certain environments prior to its successful establishment of the parasite. This was due to the nematode's acceptance of various copepod and ostracod species, which inhabit fresh or brackish water or even the sea, as intermediate hosts (Moravec & Konecny, 1994; Moravec *et al.*, 2005), such as *Eurytemora affinis*, a common calanoid copepod of the European estuarine environment (Kirk, 2003). Furthermore, of the almost 40 species of fish acting as paratenic

hosts, those inhabiting brackish waters like the Baltic Sea, especially gobiids, sticklebacks and percids, seem to play a major role in the transmission of the parasite. In members of these fish families, *A. crassus* develops up to the fourth stage larva (L4) or even to a pre-adult stage with a low degree of encapsulation by the host (Sures *et al.*, 2001; Kirk, 2003). Within and around the Baltic, the spread of *A. crassus* is thought to have been propagated by migratory eels (Reimer *et al.*, 1994) favoured by the broad range of salinities that L2 (the developmental stage that is in direct contact with the host's environment) can tolerate. At 10°C, L2 retain their infectivity to intermediate hosts for up to 80 days in pure fresh water, 21 days in 50% seawater and up to 8 days in 100% sea water (Kirk, 2003). This euryhaline behaviour of *A. crassus* resembles the broad salinity tolerance known from the highly invasive Ponto-Caspian invertebrates treated above (see Sakai *et al.*, 2001, Reid & Orlova, 2002).

Host–parasite relations in native compared to colonized hosts

In terms of life cycles, no obvious differences comparing the parasite's native to its introduced range are apparent, except that the occurrence and use of paratenic hosts are not known from East Asia (Nagasawa *et al.*, 1994; Kirk, 2003). This may be due to the paucity of investigations dedicated to the parasite in its indigenous range (see Munderle *et al.*, 2006). As to the host–parasite interactions in the native final host compared to the recipient host *Anguilla anguilla*, striking differences, which have as yet not been described in more detail from any other pair of hosts (donor vs. target), are apparent. In laboratory trials, European eels as well as Japanese eels were infected with 30 L3 of *A. crassus* (of European origin) per host individual and kept under equal conditions for 98 days. By the end of this period in Japanese eels about 60% of the inoculated worms were recovered as dead larvae encapsulated in the swimbladder wall. In contrast, the European eels did not contain any dead larvae in the wall of their swimbladder. Thus, adult worms recovered were less abundant in the Asian source host compared to the European eel. Furthermore, in Japanese eels, female as well as male worms gained several times less weight during the experiment than conspecifics that had matured in European eels (compare fig. 2). Accordingly, in its novel host, *A. anguilla*, the parasite achieved a higher survival and a higher reproduction rate than in its native host (Knopf & Mahnke, 2004). These experimental data correspond to various previously gathered field data from Europe and East Asia (see below) and to recent findings from Taiwan. Munderle *et al.* (2006) investigated wild Japanese eels from a river and cultured conspecifics from an eel farm in Taiwan, captured during different seasons. In the river, the prevalence of adult worms varied between 21 and 62% with mean intensities ranging from 1.7 to 2.7. In aquaculture, prevalence as well as mean intensity were higher (65–88%, 2.9 worms per swimbladder). The overall maximum intensity of adult parasites was 12. Interestingly, the aquaculture eels, which were exposed to a higher infection pressure than the wild eels, harboured about tenfold more dead encapsulated

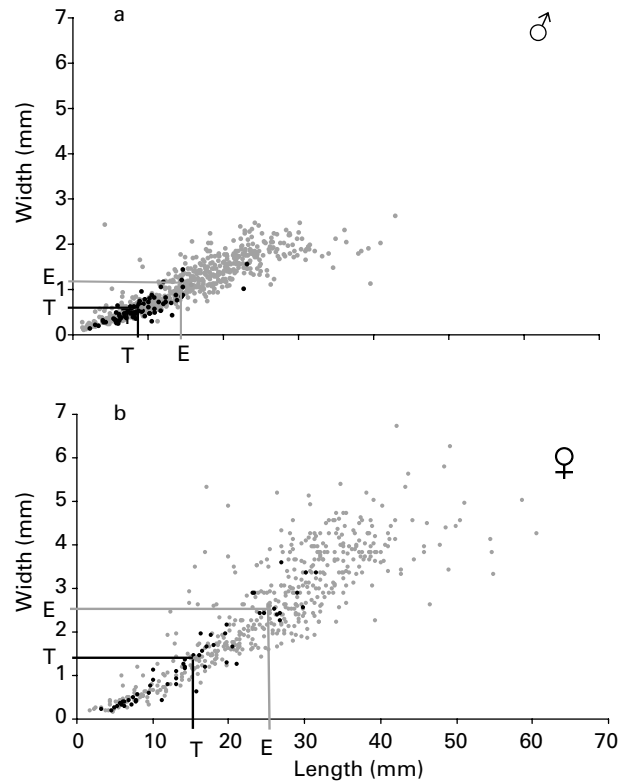


Fig. 2. Body sizes of male (a) and female (b) *Anguillicola crassus* sampled throughout Europe (E) (♂, $n = 596$; ♀, $n = 506$; 17 populations) from 2002–2004 versus Taiwan (T) (♂, $n = 77$; ♀, $n = 55$; two populations) from 2000–2003; black/grey lines, mean values. (From Munderle, 2005.)

larvae in the wall of their swimbladders than the latter host individuals. Furthermore, Munderle (2005) showed that worms from Taiwan collected from naturally infected *A. japonica* were considerably smaller than individuals from European parasite populations (fig. 2).

From the results of both investigations (Knopf & Mahnke, 2004; Munderle *et al.*, 2006) it can be concluded that infrapopulations of *A. crassus* in *A. japonica* are regulated by a concomitant immunity which is parasite density-dependent while those parasitizing European eels are not. In field studies on European eels, dead larvae have also occasionally been detected (Molnár, 1994; Würtz *et al.*, 1998; Audenaert *et al.*, 2003), but it is not clear whether they were eliminated by the host or just encapsulated after death. Obviously, the defence of this host is not directed against the larvae of the parasite, as can be also seen from electron-microscopic studies by Würtz & Taraschewski (2000), revealing that the histotropic larvae did not create a severe cellular reaction. The leucocytes gathering around the larvae seemed to be attracted rather to cellular debris resulting from the parasite's movements. Furthermore, no antibody response directed against the larvae of *A. crassus* inside the

tissue of the swimbladder could be demonstrated in the European eel by means of enzyme-linked immunosorbent assay (ELISA) (Haenen *et al.*, 1996; Knopf *et al.*, 2000a,b) (fig. 3). This is surprising since the larvae are in direct contact with the tissue and the blood of the host, and in their anterior tip they produce a trypsin-like histolytic enzyme which they seem to excrete during their migration from the gut lumen into the swimbladder wall, and which they probably also utilize during their histotropic phase inside the wall (Polzer & Taraschewski, 1993). According to Knopf *et al.* (2000a,b), European eels reveal a certain antibody response against *A. crassus* which is elicited by adult worm antigens and not those of the larvae (fig. 3). In preliminary trials with European eels these antibodies, however, did not seem to affect secondary infections (Knopf *et al.*, 2000a). Unfortunately, no parallel experiments were conducted with experimentally infected Japanese eels, but Nielsen & Buchmann (1997) demonstrated that the antibody response directed against adult *A. crassus* (against intraperitoneally injected cuticular antigens) was stronger in Japanese eels than in European eels.

In laboratory studies with European eels, *A. crassus* showed a mode of intraspecific density regulation. Fourth stage larvae inside the swimbladder arrested in their further development (invasion of the swimbladder lumen after the final moult) if the host harboured a huge infrapopulation of adult worms (Ashworth & Kennedy, 1999), but again no parallel studies were conducted with Japanese eels which is also true for the observed developmental arrest induced by low temperatures (Knopf *et al.*, 1998). In *A. japonica* density-dependent regulation of the parasite might be hidden behind the severe concomitant immunity found in this host.

Another interesting observation is available from the European eel. Larvae of *A. crassus* inside the swimbladder wall of experimentally infected host individuals elicited a significant increase in blood serum levels of the stress hormone cortisol, whereas the endocrine response was no longer detectable when worms became adults (Sures *et al.*, 2001). Since high, long-term elevations of stress hormones lead to an impairment of the host's immune system, the upregulation of cortisol in the infected eels might be triggered by the parasite (Sures *et al.*, 2001). One is tempted to assume that this response does not occur in the Japanese eel, but, thus far, this remains pure speculation.

Abundance of A. crassus in populations of the European eel with pathological implications

The different susceptibility to infections by *A. crassus* in the European eel compared to the Japanese eel, as discussed above, seems to be the major factor leading to a markedly higher abundance of the parasite in Europe than in East Asia. In the following, the parasite larvae inside the swimbladder wall are no longer considered since most authors did not include these stages in their worm counts. Some 30 years after the arrival of this invasive parasite, infected European eel in the river Rhine still harbour more than twice as many *A. crassus* adults in their swimbladder (Sures & Streit, 2001) than

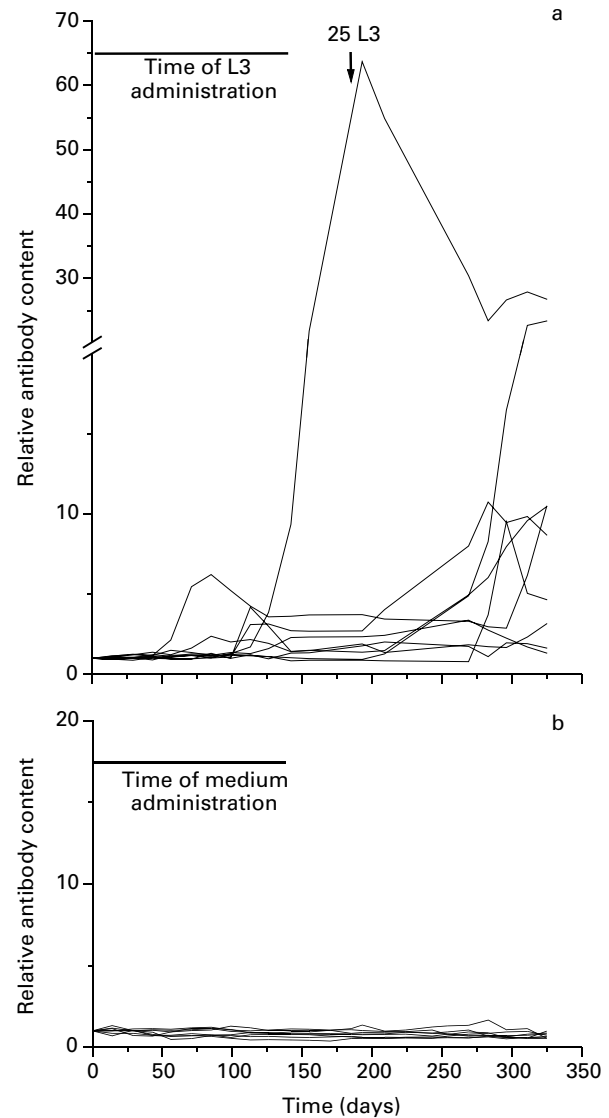


Fig. 3. (a) Course of the antibody response in nine individual eels *Anguilla anguilla* orally administered twice a week with 3 third stage larvae (L3) for 140 days and 25 L3 at day 185 as measured by ELISA using a crude antigen from the body wall of adult *Anguillicola crassus*. The graphs show the antibody content relative to the start of the experiment. During the first 60–80 days p.i., when only larvae were present in the swimbladder wall, the antibody levels did not rise. Very similar results were obtained when the experiments were conducted with larval antigens (not shown here). b) Course of the antibody response in nine individual eels *Anguilla anguilla* in the control group; orally administered with RPMI-1640 medium twice a week over 140 days as measured by ELISA using a crude antigen from the body wall of adult *Anguillicola crassus*. The graphs show the antibody content relative to the start of the experiment. (From Knopf *et al.*, 2000a.)

Japanese eels in a comparable river in Taiwan (Münderle *et al.*, 2006). According to Nagasawa *et al.* (1994) reviewing previous field observations from East Asia, the difference in mean intensities between Europe

and East Asia are even more pronounced, and prevalence rates of 80% or more, as reported from Europe (see Kirk, 2003), are unknown from populations of the Japanese eel (Nagasawa *et al.*, 1994). In the first years after *A. crassus* colonizes a population of *Anguilla anguilla*, the prevalences usually increase rapidly from one year to the next (Taraschewski *et al.*, 1988; Wickström *et al.*, 1998) with mean intensities of more than ten adult worms and maximum values of 40 to even more than 200 worms crowding inside the lumen of the organ that normally is filled with gas (Taraschewski *et al.*, 1988; Kirk, 2003; Knopf, 2006). Hahlbeck (1996) recorded 220 worms from a silver eel of the coastal Baltic Sea.

After about five years, such high maximum intensities are no longer attained and mean intensities fluctuate around three to seven adult nematodes per eel (Ashworth & Kennedy, 1999; Kirk, 2003). These values may remain stable (Lefèbvre & Crivelli, 2004; Schabuss *et al.*, 2005) but other authors have presented data revealing that the mean intensities were further decreasing (Haenen *et al.*, 1994; Audenaert *et al.*, 2003). For prevalence, in all long-term studies, stable levels of 60–90% or more were consistently recorded from many European waters (Kirk, 2003). This corresponds with analyses by Anderson & May (1991) postulating that the mean and the maximum intensity of infection are more relevant parameters in describing trends in epidemiology than the prevalence rate. The reasons for the decline in intensity after the establishment of the parasite *A. crassus* in a population of European eel are still unknown. It may result from parasite-induced alterations in the swimbladder (fig. 4) such as a conspicuous thickening of its wall combined with cauliflower-like proliferation of the endothelium, submersion of the formerly superficially located blood vessels and the appearance of inflammatory spots (fig. 4). Such swimbladder tissue seems to be a less suitable microhabitat for L3. Furthermore, the host's blood vessels (the adult parasites feed on blood; Polzer & Taraschewski, 1993) seem to be less accessible to the worms (see Van Banning & Haenen, 1990; Molnár *et al.*, 1993, 1995; Würtz & Taraschewski, 2000; Lefèbvre *et al.*, 2002). After the initial colonization phase with very high parasite intensities, most eels of the respective populations should possess pathologically altered hydrostatic organs (see Lefèbvre *et al.*, 2002). The swimbladder wall of Japanese eels infected by *A. crassus* has not yet been investigated histologically, but naked eye inspections of naturally infected hosts (Münderle *et al.*, 2006) support the assumption that the tissue response of the swimbladder wall is much less conspicuous than in the European eel, resulting from the lower abundance of the parasite in the respective eel populations. The altered structure of the European eel's swimbladder wall (Würtz & Taraschewski, 2000), resulting from present or previous infections by *A. crassus* (see Lefèbvre *et al.*, 2002), appears to be a general response of an anguilliform fish against a dense infrapopulation of a helminth in its hydrostatic organ, as can be concluded from a histological study of swimbladders of *Muraenesox cinereus* infected with the trematode *Aerobiotrema muraenesocis* (Yamada *et al.*, 2001).

Anguillicola spp. and other introduced parasites: how do the colonized hosts adapt to them?

Data are available from three host–parasite associations for the occurrence of other *Anguillicola* species in their native host range (cf. table 2). These parasites have either not been invasive (*A. australiensis*, *A. papernai*) or have failed in spreading after a jump-invasion (*A. novaezelandiae*). The recorded prevalence and mean intensities were lower than those recorded from the invasive congener *A. crassus* in East Asia and considerably lower than those known from the European range of the latter species (Kennedy, 1994; Lefèbvre *et al.*, 2004b; Taraschewski *et al.*, 2005; Münderle *et al.*, 2006). These data support the hypothesis that a successful colonizer shows a comparably high abundance in its native range (cf. Brown, 1989; Ehrlich, 1989).

Furthermore, the assumption of a successful invasion being associated with high levels of genetic divergence (see Lee, 2002) seems to be supported by studies on *A. crassus*. D. Lehmann & H. Taraschewski (unpublished data) conducted RAPD–PCR investigations with 15 decamer primers on *A. crassus* from 14 populations in Europe, the USA and Japan. Samples of *A. australiensis* from Queensland and *A. papernai* from South Africa served as references. *Anguillicola crassus* had the lowest number of species-specific diagnostic markers and *A. papernai* the highest. Only one population specific marker was detected for *A. crassus* in Europe in worms from the eel population of the river Sousa in Portugal. All individuals of the remaining populations could not be distinguished by any specific markers. Thus, no closed population clusters with significant bootstrap values are present in phenograms.

Interestingly, after the colonization of a new continent (a new host), the genetic polymorphism displayed by *A. crassus* did not reveal a bottleneck effect as one might expect. Instead, the mean degree of polymorphism increased after each colonization (Japan 63.1%, Europe 70.1%, USA 83.6%). These findings correspond well with the larger size (fig. 2), higher survival and fecundity and the greater abundance of *A. crassus* in the individuals and populations of the European eel compared to the Japanese eel (*A. rostrata*, the American eel, has not been sufficiently studied) discussed above. Obviously, the target host *A. anguilla* did not have time to evolve a defence strategy against its novel parasite. Thus, the switch from the stressful, harsh environment (cf. Brown, 1989; Ehrlich, 1989) prevailing in the Japanese eel to the 'land of plenty', provided by the naive new host has coincided with a gain of genetic divergence. In contrast, the bee mite *Varroa destructor*, a native parasite of the Asian honeybee *Apis cerana*, has lost genetic diversity when it colonized populations of the Western honeybee *A. mellifera* (Solignac *et al.*, 2005).

Whether the pathological changes caused by *A. crassus* in the colonized host are caused by the blood-sucking activity of the adult worms, that form larger infra-populations than in the native host, by their excretions, by the migratory L3 and L4 inside the swimbladder wall or by L2 discharged by adult females, erroneously invading the wall tissue and/or by other factors remains controversial (Haenen *et al.*, 1989; Molnár *et al.*, 1993, 1995; Würtz & Taraschewski,

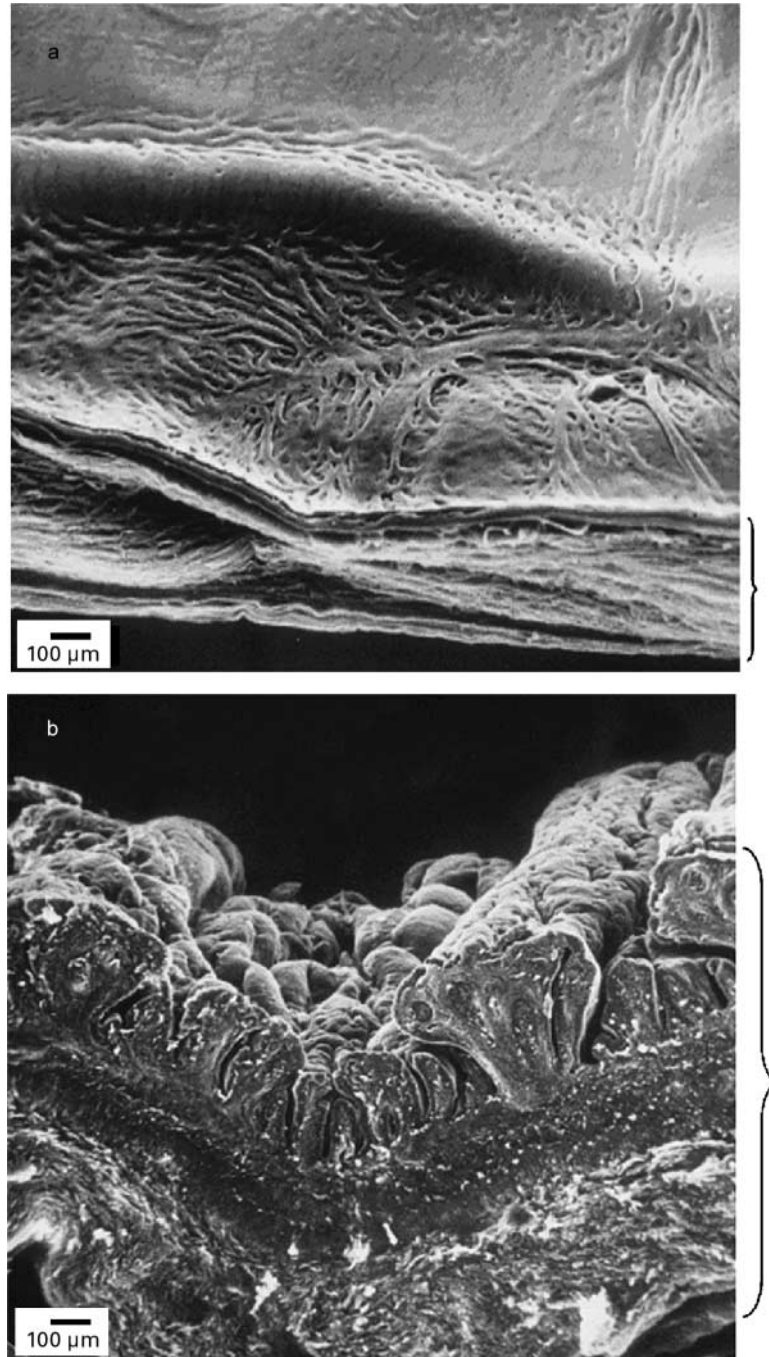


Fig. 4. Scanning electron micrographs of two sectioned swimbladders of the European eel cut open by a scapellum, viewed onto the inner surface of the organ. (a) Wall of an uninfected swimbladder; the smooth inner surface shows only longitudinally arranged elevations marking the underlying blood vessels. (b) Wall of a heavily infected, thickened swimbladder. The epithelium is characterized by large folds and cauliflower-like proliferation. Brackets: diameter of the swimbladder wall (same magnification). (From Würtz & Taraschewski, 2000)

2000). Other changes coinciding with infections of *A. crassus* in *Anguilla anguilla*, and eel mortalities connected with high intensities and adverse cofactors are discussed by Kirk 2003 and Gollock *et al.*, 2004, 2005a,b.

Obviously, as an effect of a pathologically thickened and inflamed swimbladder wall, the gas secretion, i.e. the function of this hydrostatic organ, becomes disturbed as reflected by reduced O₂ content depending on the density of the parasite's infrapopulations (Würtz *et al.*, 1996).

Accordingly, several authors have discussed whether the spawning migration of infected individuals of the European eel to the Sargasso Sea, which is mostly performed at depths of several hundred metres (Tesch, 1999), might be impaired by a thickened dysfunctional swimbladder wall resulting from an actual and/or previous infection by *A. crassus*. In their view, this might explain the decreasing abundance of elvers and adult eels throughout Europe (for this literature see M nderle *et al.*, 2004). However, a thorough evaluation of the literature reveals that the density of all eel species under intensive human management (*A. japonica*, *A. anguilla*, *A. rostrata*) have been declining over the last 30 years, irrespective of the arrival (Europe, North America) or persistence (East Asia) of *A. crassus* (Tzeng *et al.*, 1995; Tesch, 1999, 2000; Haro *et al.*, 2000; Stone, 2003).

In laboratory trials, the parasite can survive for up to 6 months in eels maintained in sea water (Kirk *et al.*, 2000b), but migrating silver eels approaching their spawning ground have been little investigated for infection levels (see Hahlbeck, 1996) and not in respect to the structure and function of their swimbladder. Furthermore, many questions on the spawning migration still remained unsolved (Tesch, 1999; Wirth & Bernatchez, 2001). M nderle *et al.* (2004) could not detect any differences in swimming performance against a current between uninfected and naturally infected European eels, but the experiments were not conducted under the pressures prevailing at 400 or 600 m depths, and thus far we do not have any information on the time and long-distance migration behaviour of uninfected and infected eels. One may speculate that infected eels reach the spawning ground but with a delay in arrival and depleted energy reserves so that they are less likely to achieve reproductive success than the uninfected conspecifics. This assumption is supported by considerations of Gollock *et al.* (2004) according to which glucose mobilization and utilization is increased in *Anguillicola*-infected eels as a result of the metabolic strain of harbouring a blood-feeding parasite and that the glucose turnover is further elevated by stressors. When the mature silver eels of *Anguilla anguilla* gather in the mating grounds at several hundred metres depth (Tesch, 1999), there should be little opportunity for antiparasitic sexual mate choice based on optical cues (see Milinski, 1994) selecting good genes suitable for achieving a low susceptibility status for *A. crassus*. But selection based on a different arrival parameter for eels should be feasible. Wirth & Bernatchez (2001) detected that European eels from the North Atlantic, the Baltic Sea and the Mediterranean Sea show a pattern of genetic differentiation. This implies that non-random mating and restricted gene flow among eels of different geographic origin takes place in the Sargasso Sea, refuting the hypothesis of panmixia. The authors consider it most likely that a temporal delay between the arrival of adult eels from different latitudes at the common breeding site causes the genetic differentiation.

A rise in antibodies directed against *A. crassus* in European eels shows considerable variance (fig. 3): responders as well as non-responders can be differentiated (Knopf *et al.*, 2000a) and the degree of divergence revealed in antibody response probably

also exists for other parameters in the eel's defence system. Due to the high abundance of *A. crassus* throughout almost the entire distributional range of *Anguilla anguilla* (see Kirk, 2003), genes that permit concomitant immunity to the parasite could well be selected and easily dispersible even if a slight geographic segregation of arrival at the spawning ground exists. Under these conditions, the adaptation of the naive host to the novel parasite might proceed in a number of decades. *Anguilla japonica* obviously spawns near seamounts in the Mariana Ridge. Synchronized spawning takes place periodically from April to November once a month during new moon (Ishikawa *et al.*, 2001; Tsukamoto *et al.*, 2003) and other Pacific eel species seem to conform to the new moon hypothesis (Sugeha *et al.*, 2001). Under these circumstances, genes useful in the defence against swimbladder nematodes may have been selected.

Data from other novel host–parasite associations reveal that the modes of host adaptation leading to resistance or low pathogenicity can differ. When American rainbow trout (*Oncorhynchus mykiss*) were introduced into Europe by the end of the 19th century, they responded very sensitively to whirling disease caused by the myxosporean *Myxobolus cerebralis*. In contrast, the native host *Salmo trutta* showed few pathological symptoms (Hedrick *et al.*, 2003). After the invasion of North America by *M. cerebralis* in the 1960s, significant declines in populations of rainbow trout and other indigenous salmonids became apparent (Hedrick *et al.*, 2003). In North America, even today no population of native salmonids adapted to this exotic parasite has been discovered, but according to the (somewhat controversial) literature it appears that certain populations are on the way to achieving a status of low susceptibility (Thompson *et al.*, 1999; Hedrick *et al.*, 2001; Ryce *et al.*, 2001).

In Germany, however, one wild self-maintaining population of rainbow trout was detected which, about 110–120 years after its first contact with the disease agent, proved to be virtually resistant against the parasite. Laboratory progeny of these fish did not develop clinical signs of whirling disease (in the target age group) after experimental infection (El-Matbouli *et al.*, 2005). Probably the resistance status of this introduced host population will remain geographically isolated for a longer period as rainbow trout do not gather at a single mating ground. Interestingly, in North America a spatial variance in the severity of the disease in rainbow trout populations became apparent. This turned out to be correlated with a different local composition and predominance of certain genotypes of *Tubifex tubifex* serving as the oligochaete host of the parasite (Kerans *et al.*, 2004; Beauchamp *et al.*, 2005).

In this case, it becomes apparent that host–parasite adaptation is a complex process involving the intermediate hosts (salmonids), the final hosts (the invasive, cosmopolitan oligochaete *T. tubifex*) and the parasite itself. Concerning *Anguillicola crassus* we do not have any information about differences in susceptibility to the parasite of the crustacean intermediate hosts in Europe compared to those of the Asian source area.

The host–parasite relations of a monoxenic invasive parasite have been well investigated. The mite *Varroa destructor* originally infecting hive bees in East Asia and

now in many parts of the globe has achieved a huge scientific interest. In the Asian bee *Apis cerana* the mites invade drone and worker brood cells, but reproduce only in drone cells, most of the infected worker brood is removed from the hive and bees also remove mites from their bodies. In the naïve host *Apis mellifera* the parasite reproduces in drone as well as in worker cells and the hygienic and grooming behaviour of the workers is comparatively low (Boot *et al.*, 1999).

Following the parasite's introduction, populations of the western honeybee *A. mellifera* were significantly harmed. In California, 75% of 208 colonies of feral honeybees became extinct during the spread of the exotic parasite between 1990 and 1993 (Kraus & Page, 1995). In other parts of America, however, africanized hybrid bees (see above) proved to be little affected (Mondragón *et al.*, 2005). According to studies of Guzmán-Novoa *et al.* (1999) in Mexico, the brood of hybrid *A. mellifera* is half as attractive to the mites as that of non-hybrid bees. Furthermore, in hives of hybrid bees the removal of infected brood is four times higher and workers are more efficient in grooming. In experiments by Guerra *et al.* (2000), the ability to remove an artificially infected brood was tested among bees with different degrees of africanization. Insects apparently africanized for several generations deriving from a wild swarm in Brazil were compared with the progeny of non-africanized *A. mellifera* from the USA and from a Brazilian island where non-africanized bees had been exposed to *Varroa* infections (without treatment) for more than 12 years, as well as first generation non-africanized/africanized hybrids. Only bees africanized for several generations were highly efficient at displaying removal behaviour. About twice as many infected broods were cleaned by them compared to the first generation hybrids (51% vs. 25%), or to the non-africanized bees that had been under selective pressure by the parasite for more than a decade (61% vs. 35%). In Europe, where africanized bees do not exist, thus far no genotype of the domestic bee with low susceptibility to *V. destructor* has been bred.

In this novel host-parasite association we know that resistance is based on behavioural and other differences determining whether a genotype of bee is susceptible to the parasite or not. In contrast to *Varroa destructor*, for *M. cerebralis* the resistance mechanism is thus far completely unknown, and for *A. crassus*, it is likely that major causative mechanisms behind concomitant immunity in the Japanese eel will be described in the near future.

Anguillicola crassus and *Fasciola hepatica*: successful but different invasive species

In summary, it can be concluded that both *A. crassus* and *F. hepatica* are typical strong invaders showing most abilities that are thought to characterize successful free-living invaders. For *A. crassus* which colonized its recipient areas without its final or intermediate hosts, invasion and dispersal are not linked to any host introductions. In contrast, in each invaded territory colonization by the liver fluke is interwoven with that of the final and partly of the intermediate hosts in a

specific pattern. *Anguillicola crassus* seems to be the best investigated invasive helminth in terms of host parasite interactions in the novel final host, allowing general conclusions on several aspects of the subject hosts and parasites as aliens. *F. hepatica* did not perform a host switch with respect to its major final hosts in its introduced range. Here the interactions with newly acquired intermediate hosts are respective research items. Further comparative considerations include:

1. The L2 of *A. crassus* can tolerate a wide range of physiological conditions and is rather unspecific in its choice of intermediate hosts. For *F. hepatica*, intermediate host specificity is narrow, but several susceptible hosts such as *Lymnaea columella* are highly invasive.
2. The life cycle of *A. crassus* is rather simple with various options for intermediate and paratenic hosts. Compared to other digeneans, *F. hepatica* also has a simple (abbreviated) life cycle.
3. The final hosts (donor as well as target hosts) of both parasites show close association with humans, although eels are wild animals. The parasites' spread has been based on human transport to a large extent.
4. For *A. crassus*, novel final hosts are subjected to a high abundance and pathogenicity of the parasite due to a lack of co-evolution. In contrast, the major final hosts of *F. hepatica* are the same in the parasite's native range as in the introduced range. These domestic animals have been bred with the aim of producing milk and meat and are incapable of performing concomitant immunity. Also, wild native and exotic additional hosts within the distributional range of the parasite are unlikely to have undergone co-evolution with the parasite and accordingly suffer from a high pathogenicity. Host-parasite relations in the parasite's source environment compared to its target area is a promising field of research and here questions of evolutionary ecology and biological global change can be studied under rather defined conditions, as in a microcosm experiment.
5. The indigenous host of the swimbladder nematode *A. japonica* seems to be a 'stressful harsh environment' in which the parasite is regulated by the host. In the naïve host *A. anguilla*, the parasite is not markedly regulated by the host and achieves a larger size, better growth, higher survival and greater fecundity than in the donor host. For *F. hepatica* such differences cannot be determined.
6. In the colonized hosts (and continents) *A. crassus* has attained a higher genetic divergence than in the source host and continent, but these findings are still preliminary. The liver fluke has not been investigated in this respect.

This review on hosts and parasites as aliens is intended to create interest in parasites among scientific workers concerned with invasions of free-living animals and environmental global change. On the other hand, parasitologists should benefit in their future research from information on invasions and colonizations by host animals. These aspects of the same subject should not be considered independently. Finally, it is noteworthy that 50% or more of all animals on earth exhibit a parasitic mode of life (Poulin, 2001).

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