

## Parasite communities in eels of the Island of Reunion (Indian Ocean): a lesson in parasite introduction

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**Abstract** Eel populations from the small rivers on the Island of Reunion (French Overseas Department in the Indian Ocean) were investigated with respect to the occurrence and abundance of helminths during the autumn of 2005. The native species *Anguilla marmorata* ( $n=80$ ), *Anguilla bicolor* ( $n=23$ ), and *Anguilla mossambica* ( $n=15$ ) were studied. Six species of helminths were identified, four of them having a definitely nonnative status. Furthermore,

unidentified intra-intestinal juvenile cestodes and extra-intestinal encapsulated anisakid nematode larvae were present in a few eels. We found that the invasive swim bladder nematode *Anguillicoloides (Anguillicola) crassus* had been introduced into the island. Six specimens were collected, four from *A. marmorata*, one from *A. bicolor* and one from *A. mossambica*. The maximum intensity of infection was two worms. The other helminths also showed a low abundance. These species were the monogenean gill worms *Pseudodactylogyrus anguillae* and *Pseudodactylogyrus bini* and the intestinal parasites *Bothriocephalus claviceps* (Cestodes), *Paraquimperia africana* (Nematodes), and the acanthocephalan *Acanthocephalus reunionensis* Warner, Sasal, and Taraschewski, 2007. The latter species, found as intra-intestinal immatures, is thought to utilize amphibians as required hosts; its status, introduced or native, could not be determined. *P. africana* was described from *A. mossambica* in South Africa and has not been recorded outside Africa. The other species are known from populations of European and American eels. However, *A. crassus* and the two *Pseudodactylogyrus* species originate from East Asia, where they are indigenous parasites of *Anguilla japonica*. Both an assignment test based on seven specific microsatellite loci and subsequent sequencing of mitochondrial haplotypes of a partial fragment of cytochrome c oxidase 1 strongly suggest that the *A. crassus* may originated around the Baltic Sea. According to the results presented here, populations of the indigenous eel species from Reunion can be considered to harbor extremely isolationist alien parasite communities. Our findings support the hypothesis that during the present time of global biological change, invasion by a nonnative species into a target island is more likely to reflect the political affiliation of the colonized environment and the pathways of trade and tourism than geographic proximity between donor and recipient areas or other natural circumstances.

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## Introduction

Theoretical considerations on the structure of animal communities, including parasites, on islands and their continuous supplementation by new species arriving from adjacent continents have long been considered under the premise that the processes involved are governed by nature. According to the “colonization time hypothesis,” the helminth species richness in a fish host on an island is related to the time since the respective host arrived (Rohde 1989; Guégan and Kennedy 1993).

Natural invasions and colonization of islands have always taken place, but since humans have begun increasingly and dramatically to alter the earth, the vast opportunities for anthropochore transport have accelerated and reinforced this phenomenon, making island environments very vulnerable to exotic invaders (Taraschewski 2006).

For the indigenous freshwater fishes of tropical oceanic islands, a characteristic pattern can be determined: species belonging to the families Gobiidae, Eleotridae, Kuhliidae, Anguillidae, and a few others dominate the species poor communities. These fishes have an amphidromous or catadromous mode of life (Tesch 2003; Font 2007; Froese and Pauly 2007). The native or endemic species share their habitats with varying numbers of introduced species, belonging to families such as the Poeciliidae (guppy, sword-tail, platy etc.), Cichlidae (tilapia, Nile tilapia etc.), and Cyprinidae (common carp, grass carp etc.).

The anguillid genus *Anguilla* Shaw, 1803 comprises 15 species with different distributional ranges (Watanabe 2000; Aoyama et al. 2001; Tesch 2003). Due to their catadromous biology combined with a pronounced migratory behavior, eels are typical elements of the native fish fauna of rivers and lakes of marine islands in many geographical regions (Froese and Pauly 2007). Along the Southwest Indian Ocean, four species have been identified: *Anguilla bicolor* McClelland, 1844, *Anguilla marmorata* Quoy and Gaimard, 1824, *A. mossambica* (Peters, 1852) and *Anguilla nebulosa labiata* (Peters, 1852; Tesch 2003; Keith et al. 2006). For Reunion Island, a recent study revealed that *A. marmorata* is the most abundant eel species, *A. mossambica* and *A. bicolor* being less frequently caught. *A. nebulosa labiata* is considered to be very rare (Robinet et al. 2007).

The Japanese eel (*Anguilla japonica* Temminck and Schlegel), the European eel (*Anguilla anguilla* (Linnaeus)) and to a lesser extent the American eel (*A. rostrata* (Lesueur)) have been intensively studied due to their great economic importance, but much less is known about the species occurring around the Indian Ocean (Tesch 2003). The same is apparent for the parasites of eels.

Within the last 25 years, several helminths of the Japanese eel attained a huge interest after colonizing Europe, North Africa, and finally North America, where the two recipient host species *A. anguilla* and *A. rostrata* turned out to be highly susceptible and vulnerable, especially with respect to infections by the swim bladder nematode *Anguillicoloides* (*Anguillicola*) *crassus* (see Kirk 2003; Knopf 2006; Taraschewski 2006; The parasite was named *Anguillicola crassus* until it was recently transferred to the genus *Anguillicoloides* by Moravec (2006). In contrast, for long, there were no reports on alien parasites having invaded populations of the eel species occurring around the Indian Ocean (Taraschewski et al. 2005), but, recently, the East Asian monogenean *Pseudodactylogyrus anguillae* (Yin & Sproston, 1948) has been recorded from juvenile *A. mossambica* in South Africa (Christison and Baker 2007).

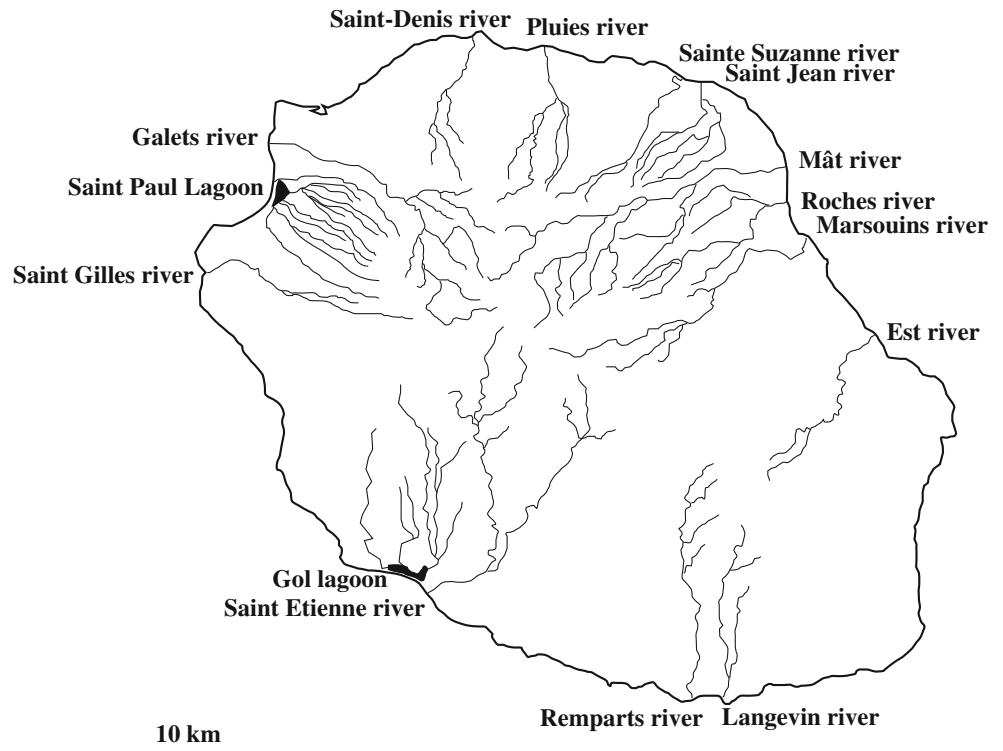
In the present survey, we investigate for the first time the macroparasite community of the three common eel species of Reunion Island. The parasites of *A. marmorata* and of *A. bicolor* have not as yet been surveyed. Moreover, it was the aim of this work to estimate the origin of the introduced swim bladder nematode and consider this introduction in the light of global change.

## Materials and methods

The volcanic island of Reunion is situated in the Western Indian Ocean about 1,600 km east of Africa, about 800 km east of Madagascar, and about 160 km southwest of the island of Mauritius. Reunion, politically belonging to France, has a length of about 70 km and a width of about 50 km (Fig. 1).

Eels were collected by electrofishing in the main rivers of the island during September 2005. These small, swiftly flowing streams can be seen in Fig. 1. Altogether, 118 eels (80 *A. marmorata*, 23 *A. bicolor* and 15 *A. mossambica*) were collected (Table 1). The fishes were brought to the laboratory in oxygenated tanks and were killed by decapitation prior to dissection and parasitological examination. These were performed by the first two authors of this communication. Eel species identification was done following Ege (1939), considering the coloration of the back and the ratio between the anterior end of the anal (LA) and the dorsal (LD) fins and total body length (TL; ratio = [(LA - LD) / TL] × 100). This ratio is particularly important for small fishes or when coloration is not clear enough. It allows differentiation between short-fin species (ratio < 2% for *A. bicolor bicolor*) and long-fin species (ratio > 14% for *A. marmorata*, < 14% for *A. nebulosa labiata* and around 14% for *A. mossambica*; Ege 1939; Tesch 2003). Specimens belonging to *A. marmorata* from

**Fig. 1** Map of the Reunion Island with the sampled rivers. 165×128 mm (600×600 DPI)



about 15 cm in length have a well-marked marbled dark brown-greenish coloration. All eels were measured to the nearest millimeter (total length in centimeter) and weighed to the nearest gram (empty weight in grams). The gills and digestive tract were removed and examined under a binocular-dissecting microscope for parasites. The swim bladders were opened and inspected for adult helminths with overhead light. Worm larvae inside the swim bladder wall were sought in squash-prepared tissue. The parasites collected were fixed according to different procedures prior to their identification: nematodes in 70% alcohol, cestodes were relaxed overnight in chilled tap water followed by adaptive frequency allocation and 40% buffered formalin, acanthocephalans were also relaxed overnight in chilled tap

water followed by 5% formalin, monogeneans were fixed under a microscopic slide with Malmberg fluid. The two monogeneans *P. anguillae* and *P. bini* were differentiated up to species level for five specimens of *A. mossambica*. For the other eels infected by these gill worms, we did not distinguish between the two species.

To trace the most likely geographic origin of the specimens of the invasive nematode *A. crassus*, a population genetic approach was applied. Whole DNA was extracted (Bruford et al. 1992) and gel-quantified. First, seven dinucleotide microsatellite markers were amplified as described (Wielgoss et al. 2007). Genotypes were analyzed and size-called by ABI's Genescan and Genotyper softwares (vers. 4), respectively. A statistical evaluation was performed in GENECLASS2 (Piry et al. 2004) in order to assign individuals to previously sampled invasive and endemic populations ( $n=490$ ) using two different Bayesian models (Rannala and Mountain 1997; Baudouin and Lebrun 2000). A Monte Carlo resampling algorithm of Paetkau et al. (2004) simulated 10,000 random individuals which were compared to real data using the default  $\alpha$ -value of 0.01. The higher the relative likelihood of stemming from a given population, the higher the assigned match score in percent by GENECLASS2. Thus, a 99% score is considered very highly likely if statistically different from chance assignment. Because DNA extracted from one individual (REU101) was found to be severely degraded, typing for this sample was limited to only a few markers. Second, a part of 552 bp of the mitochondrial gene

**Table 1** Sample size of the eels from the rivers and lagoons of the Reunion Island which were dissected (compare Fig. 1)

River	<i>Anguilla bicolor</i>	<i>Anguilla marmorata</i>	<i>Anguilla mossambica</i>
Saint Jean River	14	12	9
Roches River	5	15	6
Saint Gilles River	4	14	0
Remparts River	0	21	0
Marsouins River	0	13	0
Gol Lagoon	0	3	0
Saint Paul Lagoon	0	1	0
Mât River	0	1	0
Total	23	80	15

cytochrome c oxidase subunit I (COI) was directly sequenced from the amplicon using the recommended polymerase chain reaction protocol for universal invertebrate primers HCO2198 and LCO1490 (Folmer et al. 1994). Sequence data for mitochondrial haplotypes were integrated into a large dataset consisting of 419 specimens from invasive and endemic *A. crassus* populations and were analyzed under maximum parsimony criteria to infer a haplotype network in TCS version 1.20 (Clement et al. 2000).

## Results

A total of eight helminth species were found in the eel species investigated, six of these could be identified, while two species, occurring as intra- or extra-intestinal juveniles, remained unidentified (Table 2).

We encountered the gill monogeneans *P. anguillae* Yin and Sproston, 1948 and *P. bini* Kikuchi, 1929. These parasites commonly occurred in *A. mossambica*, rarely in *A. marmorata*, and were not found in *A. bicolor*. In *A. mossambica*, they reached intensities of up to 30 worms (Table 2). For five specimens of this eel species, specific identification was done. *P. anguillae* was far more abundant (90% of the worms) than *P. bini*.

The swim bladder inhabiting nematode *Anguillicoloides crassus* (Kuwahara, Niimii, and Itagaki, 1974) was detected in all three native eel species, its prevalence ranging from 4% to 8%. Intensity did not exceed two worms (Table 2). No eggs with L2-larvae were found in the lumen of the swim bladders, which might reflect the fact that just one eel (*A. marmorata*) contained two worms belonging to the same sex. *A. crassus* is recorded for the first time from these three *Anguilla* species (see Taraschewski 2006).

Inside the gut, three identifiable helminths were found, the most prevalent being *Paraquimperia africana* Moravec et al. 2000 occurring in about 20% of the available *A. marmorata*. *A. mossambica* was less frequently infected, whereas *A. bicolor* did not harbor this parasite. Intensity

was equally low in both hosts. *A. marmorata* is a new host record for this parasite (see Moravec et al. 2000).

The acanthocephalan *Acanthocephalus reunionensis* Smales et al. 2007 occurred as a satellite or as a rare species (*A. marmorata*). In *A. mossambica*, it reached intensities of up to six individuals comprising female as well as male specimens. However, even when both sexes were present, no gravid females were encountered. This is the first record of this spiny-headed worm for all three eel species (see Smales et al. 2007).

*Bothriocephalus claviceps* (Goetze, 1782) was a rare parasite of *A. marmorata* in this study, being demonstrated in this host for the first time (see Taraschewski 2006).

The unidentified intra-intestinal immature cestodes and encapsulated extra-intestinal nematode larvae were only found in *A. marmorata* (Table 2).

Double infections of two different species of helminths appeared in nine eels and triple infections in one. Two of the five eels infected with *A. crassus* also showed another helminth infection.

*A. marmorata* occurred in all sampled waters; conversely, the other two eels were more abundant in two or three rivers at the east coast of the island and almost restricted to these places.

For all host species, the average weight and the mean length were comparably low, very large eels being absent from the samples (Table 3; compare Tesch 2003).

The available data are insufficient and too scattered (in terms of abundance and prevalence) for a statistical evaluation of overdispersion and size class aggregation of the parasites in their host populations.

Three of the helminth species detected in the indigenous eels of Reunion are native parasites of the Japanese eel *A. japonica* (*P. anguillae*, *P. bini*, *A. crassus*) and one (*B. claviceps*) of the two Atlantic eels (*Anguilla anguilla* and *A. rostrata*; see Taraschewski 2006). In contrast, *P. africanus* seems to be native in the East African region where it has been recorded from *A. mossambica* (see Moravec et al. 2000). The status of *A. reunionensis* remains doubtful (Smales et al. 2007).

**Table 2** Prevalence and intensity (min–max) of the parasites species found in the collected eels from Reunion Island

Species	<i>Anguilla marmorata</i>	<i>Anguilla bicolor</i>	<i>Anguilla mossambica</i>
<i>n</i>	80	23	15
<i>Pseudodactylogyrus</i> spp. ( <i>P. anguillae</i> and <i>P. bini</i> )	2.5% (1)	0	60% (1–30)
<i>Anguillicoloides crassus</i>	3.8% (1–2)	7.7% (1)	6.7% (1)
<i>Paraquimperia africana</i>	21.3% (1–2)	0	13.3% (1–2)
<i>Acanthocephalus reunionensis</i>	1.3% (1)	13.0% (1–4)	20% (1–6)
<i>Bothriocephalus claviceps</i>	2.5% (1–2)	0	0
Unidentified intra-intestinal cestode larvae	7.5% (1–3)	0	0
Unidentified extra-intestinal nematode larvae	10% (1–12)	0	0

**Table 3** Mean weights (empty weight in grams  $\pm$  SE), lengths (total lengths in cm  $\pm$  SE) and range of LA–LD ratio (min–max in %) of the dissected eels

Species	<i>Anguilla bicolor</i>	<i>Anguilla marmorata</i>	<i>Anguilla mossambica</i>
Mean weight	41.8 $\pm$ 41.4	58.6 $\pm$ 61.9	34.6 $\pm$ 22.9
Mean total length	31.0 $\pm$ 9.0	29.4 $\pm$ 8.6	25.8 $\pm$ 6.4
LA–LD ratio	0–3.4	10.8–22.1	12.1–16.6

The six specimens of *A. crassus* were subjected to a molecular analysis in order to trace their geographic origin (Table 4). Overall, DNA quality was acceptable and only DNA extracted from one individual (REU101) was found to be severely degraded. Consequently, microsatellite typing for this sample was limited to only a few markers (three out of seven). The remainder of the specimens could be more accurately typed for at least five microsatellite markers. For all but one individual (REU115), a partial sequence of 552 bp of the mitochondrial locus CO1 could be unambiguously determined for both strands.

Based on GENECLASS2, Rannala and Mountain's (1997) Bayesian method (RMB) retrieved assignments of consistently high confidence (up to 99.997%), with nine out of 12 assignments being significant (Table 4). On the contrary, Baudouin and Lebrun's (2000) Bayesian method could not match this accuracy, though the population assignments were almost identical. Considering invasive populations only using RMB, individuals were assigned to the Northeastern European population, which includes the Baltic Sea (OER, ALA) and Ireland (SHA). To provide more confidence, a haplotype network based on the mitochondrial CO1 locus was considered and as a result,

50% of the samples shared an extremely seldom private haplotype, which is found only in the Baltic population of Aland (ALA). The remainder did not allow for exclusion of any locations except that from Northern America (STJ).

## Discussion

This work presents the first parasite survey of fishes from Reunion Island. The parasite communities of the four species of eels from eight neighboring biotopes reveal a remarkably high species richness (eight species), coinciding with a low degree of dominance of the single parasite species. No core species exist; instead, the helminths in all hosts either occur as satellite or as rare species. Only in *A. mossambica* do *Pseudodactylogyrus* spp. reach a prevalence of more than 50%; but, here, we combined the two species *P. anguillae* and *P. bini*.

Moreover, except for this host–parasite association, the intensities of all parasites are less than about ten and, thus, rather low.

This is in contrast to results from a comparable study on *A. mossambica* from small rivers of the Eastern Cape on the Southern African mainland where only four (native) helminths occurred. A dominant core species showing prevalences of 70–100% and intensities partly of more than 50 worms was present there: the stomach-dwelling nematode *Heliconema longissimum* (see Taraschewski et al. 2005). This species is also widely distributed in populations of various anguilliform hosts in Asia and Australia (Moravec et al. 2006, 2007) but was absent in eels from Reunion Island. Furthermore, the intestinal nematode *P. africana*, also recorded from Reunion in the present study,

**Table 4** Assignment of individual nematode specimens from Réunion to known European and American subpopulations according to log Likelihood ranking

Individuals	# loci	Microsatellites											mtDNA	Proposed Origin	
		Rannala and Mountain (1997)						Baudouin and Lebrun (2000)							
		Colonies			+Endemic			Colonies			+Endemic				
		Pop	Score (%)	P	Pop	Score (%)	P	Pop	SCORE (%)	P	Pop	SCORE (%)			P
REU44a	6	SHA	88.861	0.018	KAO	99.997	0.0269	ORI	60.271	0.003	KAO	28.416	0.001	ALA	Ireland
REU44b	5	OER	99.105	0.085	KAO	99.989	0.2649	OER	55.970	0.008	KAO	80.234	0.108	ALA	Baltic
REU113	7	OER	99.982	0.008	YAM	99.346	0.0034	OER	64.709	0.000	YAM	90.395	0.001	ALA	Baltic
REU115	7	ALA	96.692	0.011	MIK1	99.998	0.132	ALA	69.785	0.009	MIK1	64.201	0.240	–	Baltic
REU131	7	ALA	94.673	0.030	MIK2	95.552	0.0003	ALA	49.554	0.009	MIK2	86.123	0.000	all	Baltic
REU101	3	OER	91.834	0.221	KAO	45.254	0.1158	OER	64.672	0.296	OER	27.210	0.121	not US	Baltic

Bold probability values (*P*) indicate significant relationship between assigned and proposed population of origin ( $\alpha > 0.01$ ) using 10,000 simulated samples according to Paetkau et al. (2004).

REU Reunion island, SHA Shannon, Ireland, OER Oeresund, Baltic, ALA Aland, Baltic, KAO Kao-Ping, Taiwan, YAM Yamagushi, Japan, MIK Mikawa Bay, Japan, ORI Oria, East Atlantic

reached prevalences of between 50% and about 65% and mean intensities of up to 15 worms in the eels from the African mainland. Interestingly, in that study, no monogeneans were found on the gills of the eels, but *P. anguillae* was recently detected (Christison and Baker 2007). Most populations of the two Atlantic eel species (*A. anguilla* and *A. rostrata*) were free of gill-dwelling monogeneans prior to the arrival of the East Asian parasites, *P. anguillae* and *P. bini* (Kikuchi, 1929; see Taraschewski 2006). In these two eel species, the microhabitat of the swim bladder was also unoccupied until the early 1980s when the invasive nematode *A. crassus* colonized Europe and, during the 1990s, North America (Kirk 2003). According to Kennedy and Guégan (1996), eels are generally considered to harbor species poor component—and infrapopulations with many vacant niches. Nevertheless, in tropical mainland Northern Australia, populations of *Anguilla reinhardtii* with conspicuously diverse parasite communities have been described (Kennedy 1994).

According to Esch et al. (1988), two categories of fish parasitic helminths are recognized in terms of parasite colonization: autogenic species which mature in fish and allogenic species which mature in vertebrates other than fish and have a greater colonization potential and ability than the ones using freshwater fishes as final hosts. This hypothesis is supported by the findings of a survey on macroparasites of sticklebacks (Gasterosteidae) on Sable Island situated about 250 km east of the Canadian Atlantic coast in which five allogenic and two autogenic species (*Gyrodactylus canadensis* Hanek and Threlfall, 1969 and *Thersitina gasterostei* Pagenstecher, 1861) were recorded (Marcogliese 1992). On Hawaii, the few native or endemic freshwater fish species reflected an extreme ecological isolation with respect to their parasite communities. Prior to the introduction of exotic freshwater fishes and parasites, they only carried infections with allogenic parasites maturing in gulls and marine mammals (Font 1998). Meanwhile, autogenic as well as allogenic nonnative parasites show a higher diversity and are more widely distributed among the native and introduced fishes of Hawaiian streams than the native allogenic ones using the fish as intermediate hosts (Font 2007).

Among the alien parasites of Hawaiian stream fishes are the cosmopolitan cestode *Bothriocephalus acheilognathi* of Asian origin as well as the hirudinean *Myzobdella lugubris* Leidy, 1851, which is an autochthonic species of the Southern USA. Thus far, however, none of the introduced parasites has been traced back to its geographic origin (Font 2007).

Our findings from Reunion resemble the situation described for native endemic Hawaiian gobiids, although the species richness of exotic autogenic parasites recorded from the eels in our study is even higher. Both examples of oceanic islands reveal that in the present times of global

change, colonization of islands by parasites does not depend on an island's distance to the respective mainland or its size, but reflects the territory's political affiliation, the prevailing routes of trade, and other anthropogenic features.

As to the occurrence of *A. crassus* in Reunion, the genetic information seems strong enough to rule out North American and Southwestern European origins. When including mitochondrial DNA, the most likely scenario is an introduction of eels from Northern European countries, with the Baltic Sea being the best candidate. Populations from the Baltic Sea display very high heterozygosities and are genetically more diverse as compared to Atlantic or Mediterranean populations (Wielgoss et al. 2007). This makes such a brackish, cool water body a huge reservoir for dispersal. The 50% frequency of the private haplotype shared only with specimens from Åland (ÅLA) makes a single secondary spread of European origin more likely than an independent and mixed import from Asian source populations from both Japan and Taiwan, as suggested by microsatellite data including these samples. An alternative explanation may be that a yet unsampled Northern European location gave rise to the small population found in Reunion, thus, giving more weight to the Asian signals in the Bayesian analysis, which founded both the European and American invasive samples a mere 30 years ago.

Frenot et al. (2005) reviewed the literature on alien microbes, fungi, plants, and animals occurring on most of the sub-Antarctic islands which are under the administration of France or Britain, as well as parts of the Antarctic continent. They found that the large majority of aliens are European in origin. In the present case, the introduced species also came from Europe, although most are of East Asian origin.

On the island of Reunion, we identified two fish farms as well as a supermarket where European eels were temporarily kept alive. It is, then, highly probable that some European eels may have escaped from a fish tank or pool, leading to the spread of its exotic parasites. The geographic origin of *A. crassus* in Reunion followed up in this study reveals a degree of globalization which has not yet reached its climax. If this was the case, European and Japanese eels would have been imported from China, where gigantic eel aquacultures have been built up out-competing the formerly successful eel farming first in Japan and then in Taiwan (see Taraschewski 2006).

In its native host *A. japonica* and its natural distributional range, *A. crassus* reveals a moderate abundance and a low degree of pathogenicity. Conversely, in populations of European and the American eels, the prevalence and intensity are significantly higher which coincides with a substantially increased size of parasite individuals and conspicuous pathogenicity. This difference seems to result from a lack of adaptation between host and parasite in the

novel Atlantic hosts, which do not develop a concomitant immunity like the well-adapted natural host (Würtz and Taraschewski 2000; Lefebvre et al. 2002, 2004; Knopf 2006; Munderle et al. 2006; Taraschewski 2006).

One should assume that the invasion of *A. crassus* (and parts of the other nonnative eel parasites encountered on Reunion) will be followed or is already being followed by its spread and establishment in the eel populations of Mauritius, Madagascar, as well as South and East Africa. However, the eel species occurring in this region should not be as naive as *A. anguilla* and *A. rostrata* with respect to their defense against the swim bladder nematode because they occur together with *Anguillicoloides papernai* Moravec and Taraschewski, 1988 which, however thus far, has only been recorded from *A. mossambica* in South Africa (Taraschewski et al. 2005). Thus, it is doubtful whether *A. crassus* will attain the same conspicuous speed of dispersal, high abundance, and pathogenicity as described from Europe in its novel African range. In Europe, it first appeared around 1982 in Germany, and then colonized most populations of the European eel throughout the continent in less than 10 years before it finally reached Ireland after 16 years (Kirk 2003). Its spread was largely facilitated by anthropogenic transfers. After the parasite had invaded England, its dispersal followed the routes taken by the lorries transporting eels for stocking purposes. The resting points of the 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 and Fitch 1990).

As for the two invasive monogeneans encountered in the native eels of Reunion, the host species should be completely naive because they obviously did not have previous contact with dactylogyrids and perhaps with other monogeneans as well. Both *Pseudodactylogyrus* species are very successful colonizers (Buchmann et al. 1987; Hayward et al. 2001) and, thus, the very recent first record of *P. anguillae* from *A. mossambica* kept in a fish pond in South Africa (Christison and Baker 2007) is not surprising.

The low abundance of all helminths species recorded from eels of Reunion, introduced as well as autochthonic (*P. africana*), appears to result from the ecological conditions prevailing within the swift, small rivers with their low diversity of invertebrates potentially serving as intermediate hosts. Even in Europe, where the prevalence of *A. crassus* in *A. anguilla* ranges around 60–90%, streams revealed a lower abundance of this copepod- and ostracod-transmitted parasite than lake biotopes (Munderle 2005).

Summarizing, there is currently an increasingly globalized world fisheries industry. Isolated oceanic islands may show a higher parasite species richness for the same host species from the adjacent continent if the island is affiliated with a country which is more developed and has a higher rate of trade than the respective mainland. For the eels of Reunion,

we found an assemblage of native and introduced species with global players which have East Asia as their source area, being the dominating element. Thus, the hypotheses related to island colonization, which were elaborated 30 or more years ago (MacArthur and Wilson 1967) at a time when the large scale international displacement of species had not yet become a major ecological phenomenon, no longer fit the facts.

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