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Occurrence of *Anguillicola crassus* (Nematoda: Dracunculoidea) in Japanese eels *Anguilla japonica* from a river and an aquaculture unit in SW Taiwan

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ABSTRACT: The infection by swimbladder nematodes of the genus *Anguillicola* (Dracunculoidea: Anguillicolidae) was examined in 2 populations of the Japanese eel *Anguilla japonica* in SW Taiwan. Wild eels from the Kao-Ping river were compared with cultured eels from an adjacent aquaculture unit. Only the cosmopolitan species *Anguillicola crassus* was present. Among wild eels, prevalence of infection varied between 21 and 62%, and mean intensity between 1.7 and 2.7 for adult worms. Similar intensity values (1.3 to 2.8) were recorded for the larvae. In cultured eels, prevalence as well as mean intensities were higher. In the cultured hosts, mean larval intensities exceeded those of adult worms 2-fold, and maximum larval intensities were 4- to 5-fold higher than in eels from the river. In cultured eels, dead larvae were also more abundant than in wild eels. We conclude that infrapopulations of *A. crassus* in Japanese eels are regulated by the defense system of this host, intraspecific density-dependent regulation being less likely as the major regulatory mechanism. No influence of the parasite on eel condition was found in either wild or cultured eels, indicating a low or moderate pathogenic effect of *A. crassus* on this host. This study shows that *A. crassus* is moderately common in cultured and wild Japanese eels in Taiwan, where the parasite is endemic.

KEY WORDS: *Anguillicola crassus* · *Anguilla japonica* · Swimbladder · Taiwan · Aquaculture

INTRODUCTION

Anguillicola crassus Kuwahara, Niimi & Itagaki, 1974, is an endemic swimbladder parasite of the Japanese eel *Anguilla japonica* in East Asia (Kuwahara et al. 1974, Nagasawa et al. 1994). The parasite has successfully spread to Europe, North Africa and North America, where it has attained high prevalence and intensities within populations of the European eel *A. anguilla* and the American eel *A. rostrata*, respectively (Neumann 1985, Taraschewski et al. 1987, Køie 1988, Moravec & Taraschewski 1988, Moravec 1992, Johnson et al. 1995, Fries et al. 1996, Maamouri et al. 1999, Sures et al. 1999b, Kirk 2003). The parasite was obviously introduced to Europe with live-eel imports from Taiwan to the German harbor of Bremerhaven (see Koops & Hartmann 1989, Køie 1991).

In Europe, this alien parasite has created interest among ichthyoparasitologists and individuals involved in fisheries and aquaculture because of its high pathogenicity in the economically important European eel, which had not coevolved with the parasite (Boon et al. 1990, Van Banning & Haenen 1990, Molnár 1993, 1994, Hartmann 1989, Molnár et al. 1993, 1995, Würtz et al. 1996, 1998, Knopf et al. 1998, Kelly et al. 2000, Würtz & Taraschewski 2000, Kirk 2003).

According to the available literature, the European and the Asian populations of *Anguillicola crassus* seem to differ in several aspects of their life-cycle and their host–parasite relations. In Asia as well as in Europe different copepods and ostracods are known to act as intermediate hosts (Hirose et al. 1976, De Charleroi et al. 1990, Kennedy & Fitch 1990, Thomas 1993, Moravec & Konecny 1994, Nagasawa et al. 1994, Ooi et

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al. 1997, Kirk et al. 2000a,b, Moravec et al. 2005). However, transmission via paratenic hosts has not been described from Asia, whereas in Europe various species of fishes as well as amphibians and even larvae of aquatic insects have been found to carry L_3 (and partly L_4) -larvae in their viscera or their swimbladders (Haenen & van Banning 1990, Thomas & Ollevier 1992, Moravec & Konecny 1994, Székely 1994, Moravec & Škoríková 1998, Sures et al. 1999a). These differences might be due to the more intensive research activity related to *A. crassus* in Europe in comparison to Asia. However, parallel laboratory infections with *A. japonica* and *A. anguilla* have revealed a more severe host reaction directed against *A. crassus* in Japanese eels than in European eels (Nielsen & Buchmann 1997, Nielsen 1999, Knopf & Mahnke 2004).

The present study is the first report on *Anguillicola crassus* in wild and cultured populations of Japanese eels in Taiwan. Our aim was to study population structures of *A. crassus* in its Asian heartland and compare them with those described from Germany and Europe, where this invasive species has established a dense mesh of huge metapopulations over the last 20 yr. Furthermore, our investigation was also meant to have practical relevance. Eel farming hFas become a prosperous industry in Taiwan, China and other east and southeast Asian countries (Lee et al. 2003a, b). The aquaculture plants are run with *A. japonica* and other Asian or non-Asian eel species (Ooi et al. 1996, 1999, Shin & Chen 2000, Chang et al. 2002). Unfortunately, these eel farms do not publish their experiences with *A. crassus*, and so the otherwise well-organized fishery management in Asia still depends on published data collected from Japanese eel farms more than 25 yr ago (Egusa 1979).

MATERIALS AND METHODS

Wild eels were collected from the Kao-Ping River in SW Taiwan from December 2000 to March 2003. The sampling locations and the methods of eel capture have been described in detail by Tzeng et al. (2002). Farm eels were purchased from 2 ponds of an aquaculture system at Bu-Dai in SW Taiwan in February and March 2003. In the years 2000 to 2002, live eels were transported to the laboratory, killed by decapitation, and deep-frozen until parasitological examination. In the year 2003, eels were investigated in fresh condition.

The length and weight of the eels were measured to the nearest 1.0 mm and 0.1 g, respectively. The sex of each eel was determined according to external morphology and visual examination of the gonads. The developmental stage of the fish was classified as either a yellow or silver eel according to skin and fin coloration, eye diameter and gonad development (Pankhurst 1982, Han et al. 2003). The condition (c- or corpulence-factor) of the eels was calculated as described by Schäperclaus (1990).

The adult parasites were removed from the swimbladder lumen of the eels by forceps; their species, sex and number were recorded. The walls of the swimbladders were checked for larval stages (L_3 and L_4) by squash preparation using 2 Perspex plates. In accordance with the results of Blanc et al. (1992), all larvae with a body length >1.5 mm were considered Stage L_4 larvae. The prevalence, mean intensity and abundance of the parasites in the eels were calculated as described by Bush et al. (1997). Additionally, we also counted encapsulated dead larvae and adults or remnants of both stages, but without determining the sex.

For taxonomic studies, adult worms were cleaned carefully with distilled water and then fixed and stored in 70 % alcohol until morphometrical investigation. We measured the following features: length/width of body, length/width of oesophagus, length/width of buccal capsule and number of peribuccal teeth. Ratios of length and width of the body, oesophagus and buccal capsule were calculated.

For statistical analysis of the infection ($p \leq 0.05$) and condition ($p \leq 0.01$) data, a Mann-Whitney *U*-test was employed. Spearmans correlation coefficient was used to determine the correlations between the different parameters (Sachs 1992). All results were checked for outliers according to the outlier test $n \cdot SD > 4$, $p < 0.05$.

RESULTS

Eel data

Sex, developmental stage, body length, weight and condition of the investigated Japanese eels are summarized in Table 1. The sex ratios of the eels were skewed towards females in wild eels but towards males in cultured eels, similarly to results from previous studies eels in Taiwan (Tzeng et al. 1995, 2002).

The cultured eels had higher C-factors than the wild eels sampled in spring 2003, which could indicate that the availability of food or temperature are more favorable under culture conditions than in the river.

Identification and measurement of *Anguillicola crassus*

All adult nematodes collected from the lumen of the swimbladders of all wild and cultured Japanese eels were identified as *Anguillicola crassus* Kuwahara, Niimi & Itagaki, 1974, using the key of Moravec & Tara-

Table 1. *Anguilla japonica*. Percentage of females and silver eels in samples, and mean (±SD) weight, length and condition factor of all eels examined (including males). R: river, C: cultured eels

Locality/ date	n	Percentage Females	Silver	Weight (g)	Lenght (cm)	C-factor
R/ Dec 2000	14	50	43	385.2 ± 168.2	62.0 ± 6.3	0.15 ± 0.02
R/ Mar 2001	20	100	10	289.4 ± 125.5	58.4 ± 7.8	0.14 ± 0.01
R/ Jun 2001	20	75	0	229.4 ± 66.5	52.0 ± 4.3	0.16 ± 0.02
R/ Sep 2001	21	86	0	178.0 ± 46.1	51.4 ± 4.4	0.13 ± 0.01
R/ Aug 2002	20	78	0	205.3 ± 138.2	49.8 ± 9.0	0.15 ± 0.02
R/ Mar 2003	73	82	0	136.5 ± 176.1	43.8 ± 11.5	0.12 ± 0.02
C/ Feb 2003	25	4	0	248.0 ± 49.6	53.9 ± 3.0	0.16 ± 0.01
C/ Mar 2003	46	15	0	237.3 ± 26.7	54.8 ± 2.4	0.14 ± 0.02

Table 2. *Anguillicola crassus*. Morphometric features of parasites from wild (n = 168) and cultured (n = 71) Japanese eels *Anguilla japonica*. Data for all seasons combined. ♂:male; ♀: female

Characteristic	Sex	Culture (♂=7; ♀=8) min.–max.	$\bar{x}$ ± SD	River (♂=71; ♀=47) min–max	$\bar{x}$ ± SD
No. of teeth	♂	22 – 28	25.4 ± 2.4	18 – 33	24.1 ± 3.0
	♀	24 – 30	27.1 ± 2.1	20 – 30	23.7 ± 2.1
Dry weight	♂	0.0 – 0.3	0.1 ± 0.1	0.0 – 2.6	0.4 ± 0.5
	♀	0.0 – 2.2	0.6 ± 0.9	0.0 – 20.8	4.1 ± 4.9
Body length (mm)	♂	5.83 – 9.01	7.1 ± 1.4	2.29 – 23.21	9.4 ± 3.8
	♀	3.3 – 19.7	9.0 ± 5.9	4.54 – 31.45	16.6 ± 7.7
width (mm)	♂	0.24 – 0.52	0.3 ± 0.1	0.14 – 1.55	0.6 ± 0.3
	♀	0.22 – 1.30	0.6 ± 0.4	0.21 – 3.59	1.5 ± 0.9
length:width	♂	17.2–25.0	21.1 ± 3.0	9.3 – 36.1	16.6 ± 4.4
	♀	13.9 – 21.2	16.6 ± 2.5	7.5 – 26.2	12.9 ± 4.3
Oesophagus length (µm)	♂	495 – 653	611.0 ± 58.1	361 – 871	621.5 ± 85.3
	♀	540 – 921	682.5 ± 140.7	554 – 1040	781.6 ± 118.1
width (µm)	♂	119 – 198	160.5 ± 26.6	69 – 248	167.9 ± 42.6
	♀	119 – 287	177.6 ± 61.7	129 – 347	218.2 ± 54.2
length:width	♂	3.3 – 4.3	3.9 ± 0.4	2.7 – 6.5	3.9 ± 0.8
	♀	3.2 – 5.3	4.0 ± 0.7	2.7 – 5.0	3.7 ± 0.5
Buccal capsule length (µm)	♂	18 – 22	19.8 ± 1.7	13 – 22	18.3 ± 2.2
	♀	14 – 24	20.7 ± 3.3	15 – 24	19.9 ± 1.8
width (µm)	♂	46 – 60	51.8 ± 5.4	38 – 61	48.2 ± 5.3
	♀	45 – 69	60.9 ± 7.7	39 – 69	53.1 ± 5.6
width:length	♂	2.1 – 3.2	2.6 ± 0.3	2.2 – 3.3	2.6 ± 0.2
	♀	2.8 – 3.3	3.0 ± 0.2	2.3 – 3.2	2.7 ± 0.2

schewski (1988). *A. globiceps* Yamaguti, 1935 was not found in any of the eels investigated. The morphological features of 133 specimens are summarized in Table 2.

Prevalence and intensity of *Anguillicola crassus* infection

Quantitative data on the swimbladder nematodes are presented in Table 3. Eels from the river had a lower prevalence (P) of *Anguillicola crassus* (P_{max} = 62%) than cultured eels (P_{max} = 88 %) The intensity of larval ($p < 0.01$) and adult worms ($p < 0.05$) in the wild eels collected in early 2003 was significantly lower than in the cultured eels. The most striking differences were the mean larval intensities and especially the maximum larval number per eel (Table 3).

We classified 4 groups of eels harboring dead *Anguillicola crassus*: (1) no dead; (2) 1 to 10 dead; (3) 11 to 20 dead; (4) > 20 dead; (Fig. 1). The frequency distribution of dead *Anguillicola crassus* differed significantly between wild and cultured eels. We found dead *A. crassus* in 22% of the wild eels, whereas 56% of the cultured eels harbored at least 1 dead nematode (Fig. 1).

Seasonal occurrence of *Anguillicola crassus* infection

The prevalence of infection with *Anguillicola crassus* in wild eels was somewhat lower in the winter sample (December) than in the other seasons (Table 3), but the mean intensity of larval and adult *A. crassus* did not differ significantly among seasons except between September 2001 compared to December 2000 ($p < 0.05$). No comparison could be made for cultured eels since these were only available for 1 season.

Frequency distribution of *Anguillicola crassus* infection

The frequency distribution of adult and larval *Anguillicola crassus* per eel was calculated for wild and cultured eels, and approached a negative binomial distribution in the wild eel population, indicating a high degree of overdispersion (Fig. 2). In cultured eels, the extent of over dispersion was more pronounced, corresponding with the overall higher prevalence of infection in the cultured eels.

Condition factor of eels

We could not detect any significant difference in condition between uninfected and infected eels, either in the river or in the aquaculture population (Fig. 3).

Table 3: *Anguilla japonica* infected with *Anguillicola crassus*. Prevalence (P), abundance (A) and mean intensity (MI) of parasites in wild (R) and of cultured (C) eels

Locality/ date	P %	A $\bar{x}$ ± SE	Mean intensities (larvae) $\bar{x}$ ± SE	max.	(adults) $\bar{x}$ ± SE	max	larvae + adults $\bar{x}$ ± SE	max.
R/ Dec 2000	21	0.7 ± 0.5	2 ± 0	2	2.7 ± 1.7	6	3.3 ± 1.5	6
R/ Mar 2001	55	1.1 ± 0.4	1.3 ± 0.3	2	1.8 ± 0.5	6	2 ± 0.6	8
R/ Jun 2001	60	1.2 ± 0.3	1.3 ± 0.2	2	1.7 ± 0.3	6	2 ± 0.4	8
R/ Sep 2001	62	2.0 ± 0.8	2.8 ± 1.0	5	2.6 ± 0.9	12	3.2 ± 1.2	17
R/ Aug 2002	60	2.1 ± 0.9	2.7 ± 1.0	8	2.6 ± 0.9	9	3.5 ± 1.3	17
R/ Mar 2003[a]	51	1.2 ± 0.2	2.8 ± 1.0	12	1.7 ± 0.2	4	2.3 ± 0.4	12
C/ Feb 2003	88	6.7 ± 2.9	6.8 ± 3.4	64	2.9 ± 0.6	10	7.6 ± 3.2	73
C/ Mar 2003	65	4.4 ± 1.3	5.4 ± 2.2	42	2.9 ± 0.6	9	6.7 ± 1.8	47

[a]In March 2003, 1 eel did not fit statistically (n·sigma = 8.44, p = 0) and was omitted from the table. We detected 157 larval stages and 1 adult female in its swimbladder. It is likely that this fish had escaped from an aquaculture farm

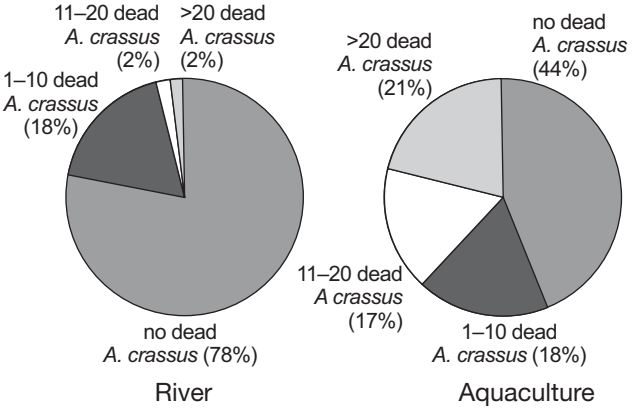

Fig. 1. *Anguilla japonica* infected with *Anguillicola crassus*. Frequency distribution of dead parasites (larvae and adults) found in wild (n = 168) and cultured (n = 71) Japanese eels

DISCUSSION

The investigated populations of the Japanese eel *Anguilla japonica* in Taiwan harbored only 1 species of swimbladder nematode, *Anguillicola crassus*. This parasite has been recorded from East Asia within the central distributional range of *A. japonica.* The respective data from Japan, Korea and China have been reviewed by Nagasawa et al. (1994). *Anguillicola globiceps*, another swimbladder nematode occuring in Japanese eels, was not found in the present study. This latter parasite, originally described by Yamaguti (1935) from Japan, differs in several morphological features (oesophagus, buccal capsule, number of peribuccal teeth) from all other congeneric species (Moravec & Taraschewski 1988), and is thus easily distinguishable from *A. crassus*. Nevertheless, in many reports from Japan, China and Taiwan, *A. crassus* and *A. globiceps* were not properly differentiated (see Kuo 1994, Nagasawa et al. 1994). Thus, due to lack of recent data, the distribution of these 2 species in East Asia is uncertain.

The pattern of seasonal occurrence of *Anguillicola crassus* described herein corresponds with reports for cultured Japanese eels in Japan (Egusa et al. 1969), with a lower prevalence in late winter and spring (February to April) than in summer (June to August). Decreased prevalence in winter was also noted in eels from Pusan, Korea (Kim et al. 1989). This could arise from, several factors such as lower availability of copepods during the cold or dry season in East Asia (November to April). During the rainy season, which begins in subtropical East Asia in May (Yen et al. 1990), the eels become more active (Tesch 1999).

The frequency of adult and larval nematodes approaches a negativly binominal distribution in wild

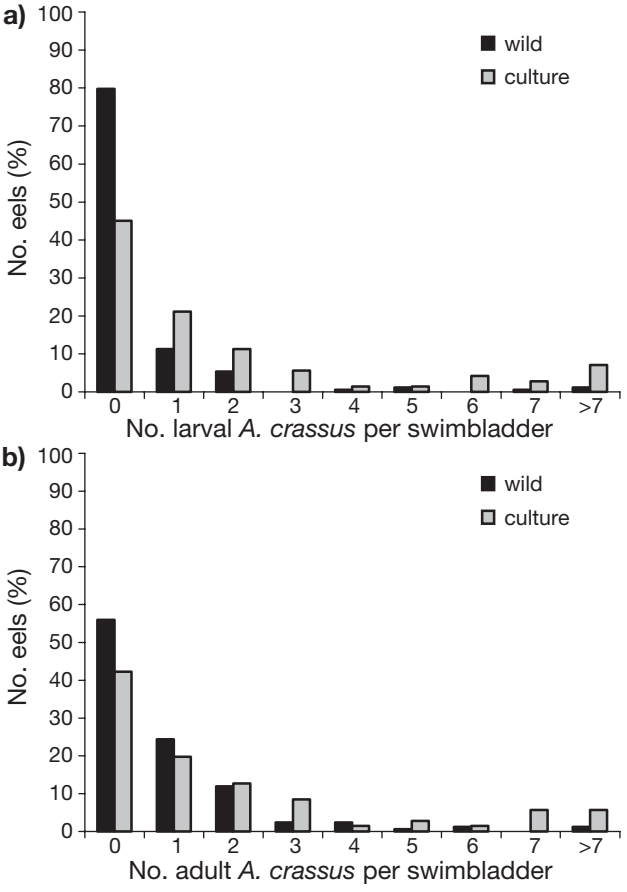

Fig. 2. *Aguilla japonica* infected with *Anguillicola crassus*. Observed frequency distribution of (a) larval and (b) adult parasites in wild (n = 168) and in cultured (n = 71)

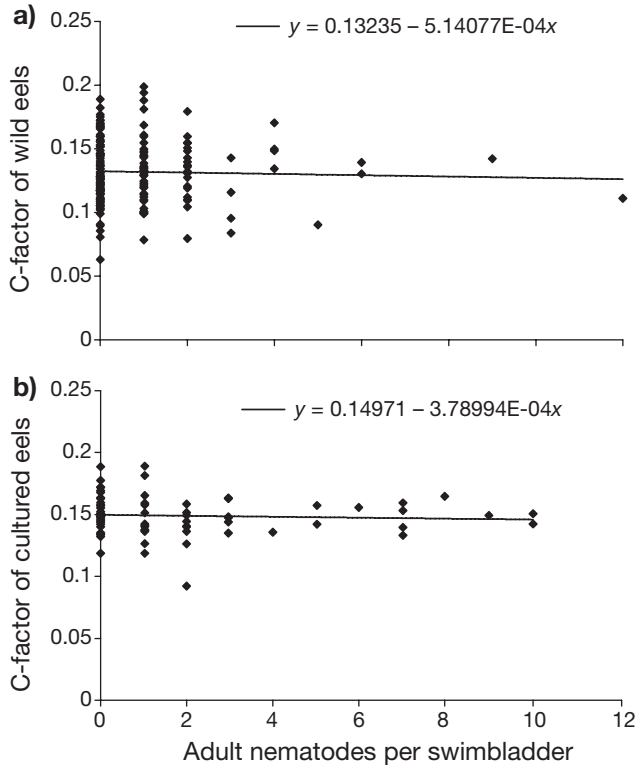

Fig. 3. *Aguilla japonica* infected with *Anguillicola crassus*. Condition factor (c-factor) of (a) wild (n = 168) and (b) cultured (n = 71) Japanese eels as a function of infection intensity (adult parasites)

and cultured eels, revealing a high degree of overdispersion. This is characteristic of macroparasite infections in hosts (Anderson & May 1978, Shaw & Dobson 1995) and thus expected. Experimental infection of European eels with *Anguillicola crassus* revealed that a few hosts were responders in terms of antibody production, while others showed almost no reaction (Knopf et al. 2000a, b). Probably, Japanese eels (which have a stronger defense against *A. crassus* than European eels: Knopf & Mahnke 2004) also differ markedly in their response. This heterogeneity might be the major causative mechanism behind the observed aggregation.

The results of our study, revealing prevalence rates of 21 to 88%, contrast with data from Japan, where lower prevalences (10 to 40 %) of *Anguillicola crassus* have been described from wild and pond-reared Japanese eels (Moravec 1994). The river eels from Kao-Ping had a maximum prevalence of 62%, which is within the range of data for European eels in Europe. Sures & Streit (2001) reported 94% of eels examined from the river Rhine in Germany to be infected with *A. crassus*, whereas very low prevalences (6.7 to 8.9%) were reported for the Butroe river in Spain (Gallastegi et al. 2002). These data show that infection rates of Japanese as well as European eels can vary extremely between different habitats, obviously reflecting various ecological characteristics such as the availability of intermediate and/or paratenic hosts and the population density of the hosts. Nevertheless, the prevalence of 80 to 100% recorded for Europe (Kirk 2003) are unknown for East Asia (Moravec 1994, Nagasawa et al. 1994). The same applies to the intensity of infection (Kirk 2003): 30 yr after arrival of the parasites, eels in the river Rhine still harbor more than twice as many adult *A. crassus* (Sures & Streit 2001) than Japanese eels in the Kao-Ping river.

Data on other host–parasite systems involving a native host and its indigenous *Anguillicola* species indicate lower abundances than in our study. From different populations of the Australian eel *Anguilla australis* in New Zealand Lefebvre et al. (2004) reported, very low prevalence (<12 %) and mean intensity infected with *Anguillicola novaezelandiae* (1 to 2 nematodes infected eel^{-1}). Taraschewski et al. (2005) detected similar low prevalence and intensity of *A. papernai* in *Anguilla mossambica* in South Africa. These observations suggest that *A. crassus* has very efficient modes of transmission and persistence, not only in recently adapted hosts such as the European eel, but also in its natural (East Asian) final and intermediate hosts. In Europe it quickly colonized the continent, whereas *A. novaezelandiae* introduced into a lake in Italy failed to spread, and finally disappeared (Paggi et al. 1982, Moravec et al. 1994).

Comparison of the 2 sampling areas in the present study revealed interesting differences in the host parasite interaction. The higher prevalence and intensity of infection in the cultured eels is probably related to the higher density of the final host (eel). In addition, intermediate hosts (copepods) seem to be sufficiently available in culture. Under aquaculture conditions, the high infection pressure is reflected by the 2-fold higher intensity of larvae compared to adults. Furthermore, the maximum larvae intensity was many times higher in cultured eels than in the eels from the river, where larvae and adults occurred at about the same intensity levels. However, mortality of the parasites in the cultured eels was considerably higher than in river eels. Thus, it appears that in the Japanese eel the infrapopulations of the parasite regulate themselves in a density dependent fashion or (more likely) become regulated by the immune system of this host (concomitant immunity).

In our field study on *Anguilla japonica* and its parasite *Anguillicola crassus*, high infection pressure was accompanied by high mortality among the parasites, obviously arising from the host's immune response to parasite-density pressure. Apparently, this host has evolved effective mechanisms for parasite recognition

and defense during a long host-parasite coevolution. In the European eel, this has not been the case. Knopf & Mahnke (2004) conducted comparative experimental infection of *A. anguilla* and *A. japonica* with *A. crassus*. In the Japanese eel, the recovery rates of the parasites were lower, their mortality higher and their individual weight lower than in the European eel. Knopf et al. (2000a,b) reported that the specific humoral immune response of European eels against *A. crassus* was characterized by a late onset and mainly directed against antigens in the body wall of adult nematodes. In comparison with European eels, Japanese eels showed an enhanced humoral immune response against antigens of *A. crassus* (Nielsen & Buchmann 1997, Nielsen 1999), which might partly explain the differences in susceptibility between the 2 eel species.

We do not know whether the different survival rates of *Anguillicola crassus* in the 2 eel species is connected with the differential rise in antibodies, or whether the antibodies are just 'markers'. Nevertheless, the different host parasite relations, leading to different cellular alterations of the swimbladder-wall (Würtz & Taraschewski 2000), are obviously connected with the different abundance and pathogenicity of the parasite in populations of the Japanese compared to the European eel.

The western part of Taiwan is still one of the fastest developing industrial zones of the world. However, it has no legislative restrictions on pollution (Chi 1994, Tsai et al. 2003). The consequences of rapid economic growth are nowadays ascertainable. The Kao-Ping River basin is not only the largest and most intensively used river in Taiwan, it is also heavily polluted (Kao et al. 2003). Livestock wastewater from hog farms, as well as municipal, domestic and industrial sewage represent the main sources of water pollution (Kao et al. 2003). Under these circumstances, it is surprising that sufficient suitable copepods are available to allow sufficient transmission of *Anguillicola crassus* to achieve the high prevalence (approx. 50%) and intensity (~2 adult worms per infected eel) reported here. Thus, our results support the hypothesis that *A. crassus* is a generalist which can persist under various environmental conditions.

Our findings show that *Anguillicola crassus* is still present in eel aquaculture in East Asia. In Bu-Dai aquaculture, no losses of eels associated with infection by *A. crassus* are known and the condition-factors calculated herein do not support high pathogenicity in the Japanese eel. Obviously the parasite is not a major problem in aquaculture systems based on the indigenous eel species *Anguilla japonica*. Thus far, all economic losses of cultured eels have occurred only when European (Egusa 1979) or American (Ooi et al. 1996) eels were involved as hosts. Accordingly *A. crassus* is not a major target in aquacultures with *A. japonica*. However, many countries in South and Southeast Asia, Oceania and Africa (South Africa, Moçambique, Madagascar, Réunion) are presently running pilot projects on establishing eel farms with local or imported eels (H. Taraschewski unpubl.). These projects should pay special attention to preventing the further spread of *A. crassus*.

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