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


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 & Konceny 1994, Nagasawa et al. 1994, Ooi et
either a yellow or silver eel according to skin and developmental stage of the fish was classified as Anguillicola

phology and visual examination of the gonads. 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

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-
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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 overdispersion 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 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

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

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. M: male; F: female

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Sex</th>
<th>Culture (n=71; f=8)</th>
<th>River (n=71; f=47)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of teeth</td>
<td>M</td>
<td>22–28</td>
<td>25.4 ± 2.4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.0–0.3</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td>Dry weight</td>
<td>M</td>
<td>0.0–2.2</td>
<td>0.6 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.0–2.2</td>
<td>0.6 ± 0.9</td>
</tr>
<tr>
<td>Body length (mm)</td>
<td>M</td>
<td>5.83–9.01</td>
<td>7.1 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.3–19.7</td>
<td>9.0 ± 5.9</td>
</tr>
<tr>
<td>width (mm)</td>
<td>M</td>
<td>0.24–0.52</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.22–1.30</td>
<td>0.6 ± 0.4</td>
</tr>
<tr>
<td>length:width</td>
<td>M</td>
<td>17.2–25.0</td>
<td>21.1 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>13.9–21.2</td>
<td>16.6 ± 2.5</td>
</tr>
<tr>
<td>Oesophagus length (µm)</td>
<td>M</td>
<td>495–653</td>
<td>611.0 ± 58.1</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>540–921</td>
<td>682.5 ± 140.7</td>
</tr>
<tr>
<td>width (µm)</td>
<td>M</td>
<td>119–198</td>
<td>160.5 ± 26.6</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>119–287</td>
<td>177.6 ± 61.7</td>
</tr>
<tr>
<td>length:width</td>
<td>M</td>
<td>3.3–4.3</td>
<td>3.9 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.2–5.3</td>
<td>4.0 ± 0.7</td>
</tr>
<tr>
<td>Buccal capsule length (µm)</td>
<td>M</td>
<td>18–22</td>
<td>19.8 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>14–24</td>
<td>20.7 ± 3.3</td>
</tr>
<tr>
<td>width (µm)</td>
<td>M</td>
<td>46–60</td>
<td>51.8 ± 5.4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>45–69</td>
<td>60.9 ± 7.7</td>
</tr>
<tr>
<td>width:length</td>
<td>M</td>
<td>2.1–3.2</td>
<td>2.6 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2.8–3.3</td>
<td>3.0 ± 0.2</td>
</tr>
</tbody>
</table>
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 occurring 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 negatively binominal distribution in wild

<table>
<thead>
<tr>
<th>Locality/ date</th>
<th>P</th>
<th>A</th>
<th>Mean intensities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>±SE</td>
<td>(larvae)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>±SE max.</td>
<td>±SE max.</td>
</tr>
<tr>
<td>R/ Dec 2000</td>
<td>21</td>
<td>0.7 ± 0.5</td>
<td>2 ± 0</td>
</tr>
<tr>
<td>R/ Mar 2001</td>
<td>55</td>
<td>1.1 ± 0.4</td>
<td>1.3 ± 0.3</td>
</tr>
<tr>
<td>R/ Jun 2001</td>
<td>60</td>
<td>1.2 ± 0.3</td>
<td>1.3 ± 0.2</td>
</tr>
<tr>
<td>R/ Sep 2001</td>
<td>62</td>
<td>2.0 ± 0.8</td>
<td>2.8 ± 1.0</td>
</tr>
<tr>
<td>R/ Aug 2002</td>
<td>60</td>
<td>2.1 ± 0.9</td>
<td>2.7 ± 1.0</td>
</tr>
<tr>
<td>R/ Mar 2003</td>
<td>51</td>
<td>1.2 ± 0.2</td>
<td>2.8 ± 1.0</td>
</tr>
<tr>
<td>C/ Feb 2003</td>
<td>88</td>
<td>6.7 ± 2.9</td>
<td>6.8 ± 3.4</td>
</tr>
<tr>
<td>C/ Mar 2003</td>
<td>65</td>
<td>4.4 ± 1.3</td>
<td>5.4 ± 2.2</td>
</tr>
</tbody>
</table>

*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.

![Graph](image1.png)

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.

![Graph](image2.png)

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