Journal of Helminthology (2005) **79**, 159–167 DOI: 10.1079/JOH2005281

Dynamics and predicted decline of *Anguillicola crassus* infection in European eels, *Anguilla anguilla*, in Neusiedler See, Austria

M. Schabuss[1,3]*, C.R. Kennedy[2], R. Konecny[1,5], B. Grillitsch[3], W. Reckendorfer[1], F. Schiemer[1] and A. Herzig[4]

[1]Institute of Ecology and Conservation Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria: [2]Department of Biological Sciences, University of Exeter, Exeter, EX4 4PS, UK: [3]Aquatic Ecotoxicology, Department of Natural Sciences, University of Veterinary Medicine Vienna, Veterinärplatz 1, 1210 Vienna, Austria: [4]Biological Station Illmitz, 7142 Illmitz, Austria: [5]Umweltbundesamt, Spittelauer Lände 5, 1090 Vienna, Austria

Abstract

The eel population in Neusiedler See has been maintained by regular massive stocking since 1958. After the establishment of the National Park Neusiedler See-Seewinkel in 1993, eel stocking was prohibited and the population, together with the specific parasites of eels, was predicted to decline to extinction within 10 years. This investigation was undertaken to document the decline and extinction of the *Anguillicola crassus* population in eels. From 1994 to 2001, 720 eels were collected from two sites in the lake. Prevalence and abundance of *A. crassus* were lower in spring than in summer and autumn and larger eels harboured more parasites than smaller ones. Neither year of study nor sampling site were correlated with parasite infection levels. No significant trend in the population parameters of *A. crassus* was detected over the 8 years of the survey. This suggested that there had been no significant decline in the eel population. This suggestion was confirmed by investigations of the fishery, which also found evidence of regular illegal stocking. The stability of the *A. crassus* population over the past decade seems to reflect the lack of change in eel population density. No mass mortalities of eels occurred over the period despite the many similarities between Neusiedler See and Lake Balaton in Hungary. Differences in eel size, eel diet and the lack of large-scale insecticide use are discussed as possible explanations for the absence of eel mass mortalities in Neusiedler See.

Introduction

Since the appearance of the exotic eel swimbladder nematode *Anguillicola crassus* Kuwahara, Niimi & Itagaki, 1974 in Europe in the early 1980s (Paggi *et al.*, 1982; Neumann, 1985; Peters & Hartmann, 1986) along with imported Japanese eels, *Anguilla japonica* (Kennedy & Fitch, 1990; Køie, 1991), a number of publications have documented arrival, spread and population increase in their country or locality in view of its pathogenic potential (Kennedy & Fitch, 1990; Køie, 1991; Moravec, 1992; Molnar *et al.*, 1993; Würtz *et al.*, 1998; Barus *et al.*, 1999; Lefebvre *et al.*, 2002a,b; Audenaert *et al.*, 2003). Some authors have also focused on regulation and stability of *A. crassus* populations (Ashworth, 1994; Haenen *et al.*, 1994; Ashworth, 1995; Ashworth & Kennedy, 1999).

The first record of *A. crassus* in Austria in 1987 (M. Rydlo, unpublished) came from the sub-alpine lake Mondsee (federal district Upper Austria). From the lowland lake

*Fax: 00431250774690
E-mail: Michael.Schabuss@vu-wien.ac.at

Neusiedler See (federal district Burgenland), this parasite was first recorded in 1988 (Konecny & Wais, 1993; Herzig *et al.*, 1994). As the eel fishery was of major economic value in this lake, great concern about this parasite arose in view of its reported impact on the eel population in the nearby Lake Balaton (Hungary), which resembles the Neusiedler See in many biotic and abiotic characters. Just one year after it was first recorded in Lake Balaton in 1990 (Csaba *et al.*, 1991; Szekely *et al.*, 1991), *A. crassus,* in combination with additional adverse factors, such as low water oxygen content and high water temperatures and secondary bacterial infections (Bekesi *et al.*, 1997), caused a mass mortality of eels in Lake Balaton in 1991 (Molnar *et al.*, 1991), 1992 (Molnar *et al.*, 1994) and 1995 (Balint *et al.*, 1997; Barus *et al.*, 1999).

The eel fishery in Neusiedler See, like that in Lake Balaton, is based on allochtonous populations and has been maintained by regular massive stocking since 1958 (Herzig *et al.*, 1994). Since the establishment of the transboundary national park Neusiedler See–Seewinkel between Austria and Hungary in 1993, stocking of eel has been prohibited. The eel population was therefore predicted to decline and was expected to become extinct within 10 years (Herzig *et al.*, 1994). One could therefore also predict a concomitant decline in the *A. crassus* population. This provided a unique opportunity to document the decline and probable extinction of an *A. crassus* population and to compare events in Neusiedler See with those in Lake Balaton.

Materials and methods

The Neusiedler See (47°45′N 16°48′E) is the biggest, westernmost steppe lake in Europe. The basin of this shallow, eutrophic lake covers an area of 321 km^2 across the Austrian-Hungarian border. The mean depth of the lake is 1.2 m and the water temperatures can reach more than 30°C during summer. A dense reed belt (*Phragmites communis*) encircles the lake and covers more than 50% of the lake area (180 km^2). The conductivity in the reed belt lies in the range between 2000 and 4000 μS and the salinity can reach 2 g l^{-1} (Wolfram *et al.*, 2001; Herzig *et al.*, 2002).

Eels were collected by electrofishing in the course of an ecological investigation of the fishery of the reed belt (Wolfram *et al.*, 2001) at two different sampling areas, located about 5 km apart from each other: in the bay of Illmitz and in the national park area in the southern part of the lake (fig. 1).

Wherever possible, samples were taken at least once a year at both localities, but as sampling had to fit into the fishery ecological investigation it was more frequent in some years at one sampling area (1995 and 1996 in Illmitz, 1997 and 1998 in the southern area) whereas no samples were taken in others (1999 and 2000). Sampling spanned a period of 8 years from 1994 to 2001 and a total of 19 samples were taken. Sampling was normally restricted to spring, summer and autumn as the freezing of the lake rendered electrofishing impossible in winter.

Eels were transported to the laboratory alive and their weight (± 0.1 g) and length (± 0.1 cm) were recorded. Weight and length data for all eels were used to calculate

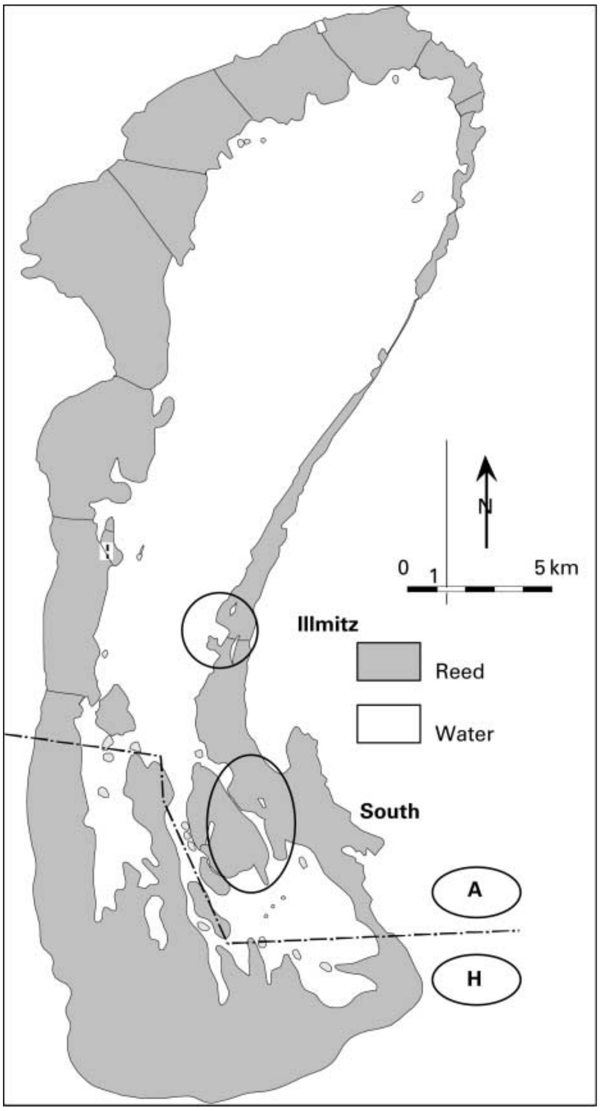

Fig. 1. Eel sampling areas in Neusiedler See, Austria (after Wolfram *et al.*, 2001). A, Austria; H, Hungary.

the condition factor according to the formula: *total weight/(total length)* ^{3} **100* (Bagenal & Tesch, 1978). Eels were killed by decapitation, dissected, sexed by examination of the gonads (80% of eels were sexed) and the swimbladders removed. Specimens of *A. crassus* were removed from the swimbladder lumen and the swimbladder wall was searched for larvae and examined for gross morphological changes (thickening and lesions) using a stereomicroscope with magnifications from 20 × to 60 × . Except in the years 1994 and 1995 (5 of a total of 19 samples), all *A. crassus* specimens were assigned to the two ages classes, i.e. adult and non-adult (including third and fourth stage larvae) worms according to Moravec & Taraschewski (1988). Furthermore, the intestines of all eels were examined for helminth parasites using standard methods (see Schabuss *et al.*, 1997). Data on intestinal helminths of the eel population will be presented in a separate paper.

Table 1. Length (L), weight (W) and condition factor (cf) of eels from the two sampling areas in Neusiedler See, Austria.

	Illmitz ($n = 424$)			South ($n = 296$)		
	L (cm)	W (g)	cf	L (cm)	W (g)	cf
Minimum	10.5	1.7	0.10	16	4	0.10
Maximum	82	947	0.27	73	750	0.22
Mean ± SD	39.8 ± 10.5	119 ± 107	0.15 ± 0.03	43.2 ± 9.3	141 ± 105	0.15 ± 0.02

n, number of eels examined.

In order to describe the parasite population structure, the terms prevalence, mean intensity and mean abundance were used according to Bush *et al.* (1997). The variance to mean ratio of parasite abundance was calculated to provide an index of the degree of dispersion of *A. crassus* in its host. The effects of sampling site, year, season and host length on prevalence, mean intensity and abundance were explored with an analysis of variance (ANOVA, general linear model procedure available in SPSS 10.0). Sampling site (Illmitz, South), year (1994, 1995, 1996, 1997, 1998 and 2001), season (spring, summer, autumn) and size class (<20, <30, <40, <50, <60 and > 60 cm) were entered as categorical predictors and individual host length (L) and sex as a covariate. Significance was accepted for $P \leq 0.05$.

Results

The total lengths, weights and condition factors of eels caught in the years between 1994 and 2001 are shown in table 1. The number of eels per sample ranged from 5 to 68 (mean 37.9 ± 14.4 SD). A total of 424 eels was caught in the bay of Illmitz and 296 specimens in the southern area respectively. There was no significant difference between the length frequency and condition factor of eels from the two sampling areas, but significant differences ($P \leq 0.001$) in length and condition factor were found between the years of the study. The average length of eels increased slightly from 1994 to 2001.

During the 8-year study, a total of 720 eels was examined with a total of 1545 *A. crassus* (all stages) found in the lumen and walls of the swimbladder. The prevalence, mean intensity and abundance of adult, non-adult and all developmental stages of *A. crassus* pooled over all sampling dates and both sampling areas are shown in table 2.

The results of the general linear model are presented in table 3. The season of sampling had a pronounced influence on the prevalence and abundance of *A. crassus*. The total length of eels had significant effects on the prevalence, mean intensity and abundance. In contrast, the year of the investigation and the sampling site had no effect on infection levels.

The prevalence, mean intensity and abundance of *A. crassus* (all stages) at each sampling site in Neusiedler See are shown in fig. 2. Prevalence values ranged from a minimum of 40% in April 1996 to a maximum of 82% in August 1997. The lowest mean number of *A. crassus* per infected host and the lowest abundance were found in April 1996 and the highest mean intensity and abundance were observed in May 2001. As there were no significant differences in terms of prevalence, mean intensity and abundance between the two sampling areas, data from the two sites were pooled for further analyses. Seasonal patterns, however, were found in the prevalence and abundance of infection. The prevalence was significantly lower in the spring compared to the summer ($P \leq 0.001$) and autumn ($P \leq 0.01$) and the abundance was significantly lower in the spring compared to the summer ($P \leq 0.001$) and autumn ($P \leq 0.05$). The mean intensity did not change significantly between seasons.

The distribution of *A. crassus* in eels from Neusiedler See displayed a negative binominal distribution in the

Table 2. Prevalence, mean intensity (± SD), infection range per eel and mean abundance (± SD) of adult, non-adult and all *Anguillicola crassus* stages in all 720 examined eels in Neusiedler See, Austria (pooled data over all sampling dates and both sampling areas).

	Adult	Non-adult	All stages
Total no. of parasites	460	697	1545
Prevalence (%)	32.11	51.01	62.64
Mean intensity (± SD)	2.63 ± 2.38	2.51 ± 2.33	3.43 ± 3.44
Intensity range	1–16	1–16	1–24
Mean abundance (± SD)	0.84 ± 1.82	1.28 ± 2.08	2.15 ± 3.18

Table 3. The effects of site, year, season and host length on the prevalence, intensity and abundance of *Anguillicola crassus* in eels using a general linear model (ANOVA tests).

Effect	df	χ^2	P
Prevalence			
Site	1	0.00	0.98
Year	5	0.16	0.60
Season	2	1.93	<0.001
Host length	1	1.24	<0.05
Intensity			
Site	1	38.02	0.07
Year	5	9.97	0.51
Season	2	5.84	0.60
Host length	1	146.43	<0.001
Abundance			
Site	1	29.45	0.08
Year	5	12.44	0.27
Season	2	37.61	<0.05
Host length	1	193.70	<0.001

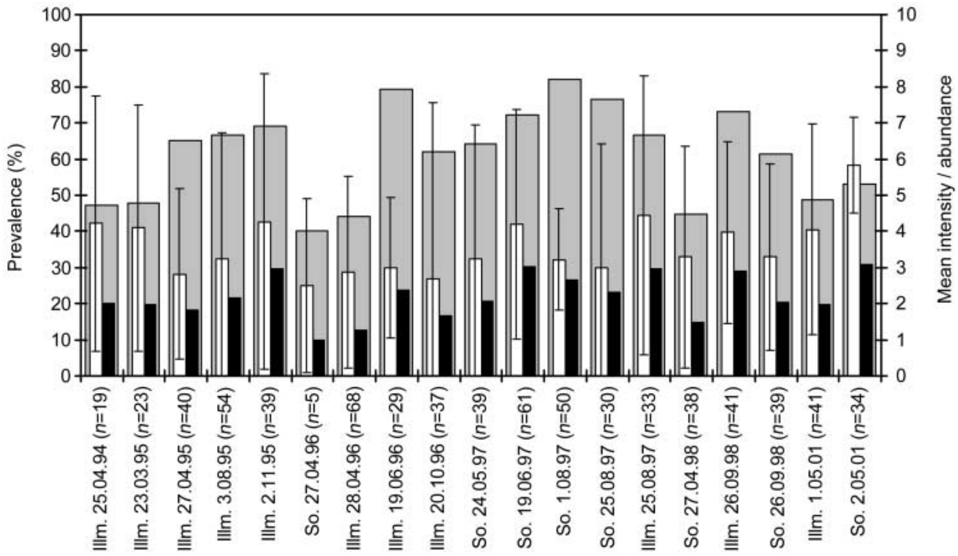

Fig. 2. Prevalence % (■), mean intensity (□) (± SD) and abundance (■) of *Anguillicola crassus* (all stages) in each sample in Neusiedler See, Austria. Illm., Illmitz; So., southern part of the lake; *n*, number of eels examined.

years from 1994 until 2001. The variance to mean ratio was > 1, indicating overdispersion. The majority of eels were either uninfected or with low numbers of *A. crassus* (37% of eels uninfected; 52% with 1–5 parasites), while a small number was heavily infected (fig. 3). No significant difference in the frequency distribution of *A. crassus* (all stages) between the two sampling areas was found ($P \leq 0.65$).

All size classes of eel were infected with *A. crassus* (fig. 4). The smallest infected eel was 10.5 cm long. The prevalence was significantly correlated ($P \leq 0.05$) with the total length of eels, but no significant differences were found between size classes. The mean intensity and abundance of *A. crassus* were significantly correlated ($P \leq 0.001$) with body length of eels, and larger eels ($>$50 cm) harboured significantly more nematodes than smaller ones. Eels in the size class 50–59 cm had a significantly higher abundance than eels in size classes 20–49 cm ($P \leq 0.01$), 30–39 cm ($P \leq 0.001$) and 40–49 cm ($P \leq 0.05$), and a significantly higher mean intensity than eels in the size class 30–39 cm ($P \leq 0.001$).

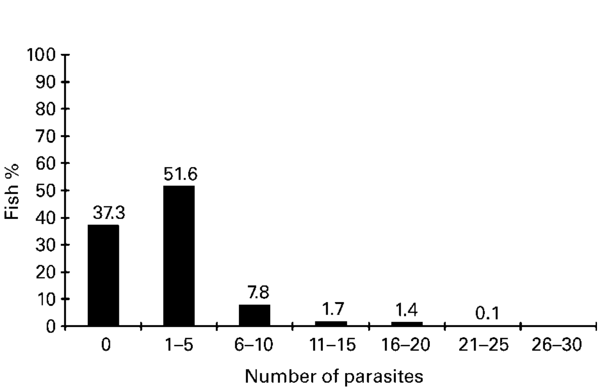

Fig. 3. Frequency distribution of *Anguillicola crassus* (all stages) in 720 eels in Neusiedler See, Austria.

Pooled data of the prevalence, mean intensity and abundance of all *A. crassus* stages in eels of Neusiedler See calculated for each year are shown in fig. 5. As there was no significant difference in the prevalence, mean intensity and abundance between the years of the study, the infection level of *A. crassus* remained constant throughout the 8 years of investigation.

No correlation between the sex of eels and prevalence ($P \leq 0.92$), mean intensity ($P \leq 0.94$) and abundance ($P \leq 0.43$) of *A. crassus* was found.

Discussion

The most important factors correlated with *A. crassus* infections in eels in Neusiedler See were the season of sampling and the length of eels. The infection was lower in the spring in terms of prevalence and abundance than in the summer and autumn, and larger eels ($>$50 cm) harboured more parasites than smaller ones. The year of study and the sampling site showed no significant correlation with parasite infection. No particular trend in the development of the infection with *A. crassus* could be detected during the 8-year study period.

Adult nematodes were found at each sampling date and season (ranging from March to November) throughout the investigation, but nevertheless a seasonal pattern in prevalence and abundance of *A. crassus* was evident. Although previous investigations have not detected any seasonality (Kennedy & Fitch, 1990; Thomas & Ollivier, 1992; Molnar *et al.*, 1994; Würtz *et al.*, 1998), some authors (Benajiba *et al.*, 1994; Hartmann, 1994; Palikova & Navratil, 2001; Lefebvre *et al.*, 2002a) have noted temporal patterns in *A. crassus* infections. Hartmann (1994) and Palikova & Navratil (2001) found increased prevalences and intensities during the summer, whereas Lefebvre *et al.* (2002a) noticed biannual peaks in early summer and late winter in a 4-year survey of eels in the Rhone River delta. These biannual peaks support the existence of a 6-month life

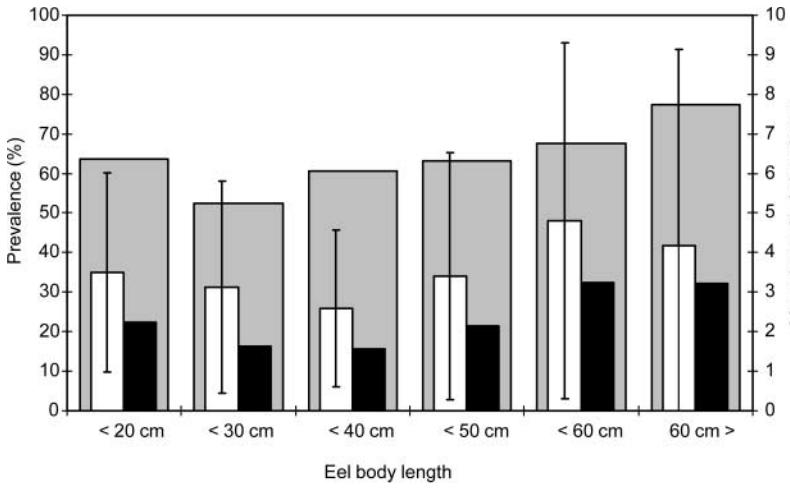

Fig. 4. The relationship between prevalence % (■), mean intensity (□) (± SD) and abundance (■) of *Anguillicola crassus* (all stages) and eel body length.

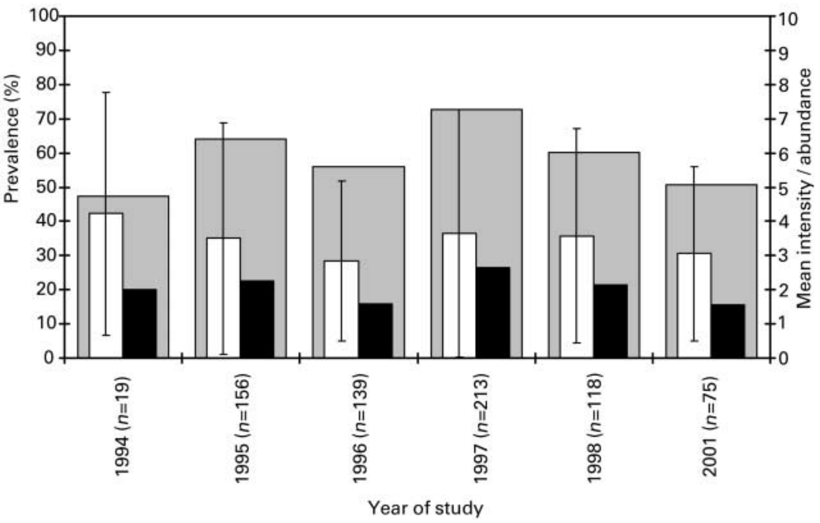

Fig. 5. Prevalence % (■), mean intensity (□) (± SD) and abundance (■) of *Anguillicola crassus* in eels in Neusiedler See, Austria from 1994 to 2001. *n*, number of eels examined.

cycle for *A. crassus* (Thomas & Ollevier, 1993). As winter sampling in Neusiedler See was impossible due to freezing of the lake, the hypothesis of a 6-month life cycle could not be tested. Low temperatures retard development from third- to fourth- stage larvae, although viability is maintained (Knopf *et al.*, 1998) and eels do not feed during the winter period (Barus *et al.*, 1996). Consequently, new *A. crassus* infections are confined to warmer months of the year (Kennedy & Fitch, 1990) and, in contrast to the warm Mediterranean lagoons (Benajiba *et al.*, 1994; Lefebvre *et al.*, 2002a), a second peak of infection in late winter seems to be unlikely in Neusiedler See.

In the present study, a significant correlation was found between parasite infection and body length of eels. As reported in other studies, larger eels harboured more parasites than smaller ones (Möller *et al.*, 1991; Thomas & Ollevier, 1992; Molnar *et al.*, 1994; Barus *et al.*, 1996; Lefebvre *et al.*, 2002a,b; Audenaert *et al.*, 2003). Such an accumulation of parasites in larger eels is explained by a longer exposure time of older (=larger) eels to the parasite, a larger host area (body size) for parasite establishment, a higher consumption of infected prey with increasing host size and a differential efficiency of the parasite transmission between intermediate and paratenic hosts (Lefebvre *et al.*, 2002a). Eels are believed to become more piscivorous with increasing size (Tesch, 1977), but they do show great trophic opportunism (Moravec & Skorikova, 1998) and Kennedy *et al.* (1992) showed that adult eels also ingest zooplankton. Thomas & Ollevier (1992) report that crustacean intermediate hosts serve as the source of infection for smaller eels, whilst larger eels mainly acquire infection by preying on paratenic hosts. Gut analyses showed that eels in Neusiedler See mainly feed on aquatic insects (>50% of the food items throughout the year consist of Odonata, Coleoptera, Ephemeroptera and Trichoptera) and on *Asellus aquaticus,* especially in the spring, whereas zooplankton and fish are of minor importance (Herzig *et al.*, 1994; Wolfram *et al.*, 2001). Eels become piscivorous in Neusiedler See at a size larger than 50 cm. As there are few eels in Neusiedler See with a body length over 50 cm (Herzig *et al.*, 1994; Wolfram *et al.*, 2001; Wolfram & Mikschi, 2003), fish as paratenic hosts may play a minor role in the transmission of the nematode compared with other water bodies (Pazooki & Szekely, 1994; Szekely, 1994, 1995, 1996; Rolbiecky, 2002). Food analyses of eels by Herzig *et al.* (1994) showed a relatively high proportion of gastropods in the eel diet (10–40% of the gut contents), and as snails are known to act as paratenic hosts for *A. crassus* (Moravec, 1996), they may represent, next to aquatic insect larvae (Moravec & Skorikova, 1998), an important source of parasite infection in Neusiedler See.

The *A. crassus* population in Neusiedler See seems to have stabilized with an average infection rate of 63%, similar to that in Lake Balaton (Molnar, 1992; Molnar *et al.*, 1994; Molnar & Szekely, 1995) and other European countries (Ashworth, 1994; Barus *et al.*, 1996; Palikova & Navratil, 2001; Lefebvre *et al.*, 2002a). The dynamics of *A. crassus* infection in Neusiedler See are similar to other European countries (Kennedy & Fitch, 1990; Molnar *et al.*, 1994; Barus *et al.*, 1996; Würtz *et al.*, 1998; Lefebvre *et al.*, 2002a; Audenaert *et al.*, 2003): the infection spread rapidly in the first few years following the introduction of the nematode and stabilized around a specific level of prevalence and mean intensity of infection.

Anguillicola crassus was first recorded in Neusiedler See in September 1988 (Konecny & Wais, 1993) where 2 of 10 eels were infected. Jagsch & Rydlo (1993) examined 95 eels at four sampling dates in 1991 with a prevalence range from 32 to 100% and intensities from 1 to 12 specimens. Konecny & Wais (1993) examined 90 eels during October 1991 to July 1992. The prevalence was 50% and the intensity ranged from 1 to 13 parasites per fish. Szekely *et al.* (1991) reported a prevalence of 100% *A. crassus* infection in eels caught in the Hungarian part of Neusielder See. Gönczy (1992) reported in Neusiedler See a similarly strong infected eel population (60%) as in Lake Balaton. A constant level of infection of *A. crassus* from 1994 to 2001 shown in this study supports the possibility of stabilization in infection levels occurring in Neusiedler See. Various mechanisms such as density dependent regulation of the parasite infrapopulation (Ashworth & Kennedy, 1999), host adaptation (Buchmann *et al.*, 1991, Höglund & Pilström, 1995; Kelly *et al.*, 2000) and mortality of heavily infected eels (Molnar *et al.*, 1994; Barus & Prokes, 1996; Lefebvre *et al.*, 2002b) have been suggested to explain this phenomenon.

The constant infection level of *A. crassus* is surprising considering the predicted decline and extinction of the eel in Neusiedler See. The parasite population appeared to show no reaction to the predicted changes in its definitive host population. So the question arose as to whether the eel population was in decline at all.

The eel is not an authochtonous fish species in Neusiedler See and was first stocked in 1958 (Herzig *et al.*, 1994). Stocking continued on a yearly basis and reached its maximum in the 1970s and stayed constant until the late 1980s with an average of about 4.5 million glass eels per year, leading to an estimated density of 150 eels per ha (Herzig *et al.*, 1994) compared to a density of just 67 eels per ha in Lake Balaton (Biro, 1992). Herzig *et al.* (1994) noted that only 20% of the lake area provided a suitable habitat for eels, leading to an estimated density of 750 eels per ha. This high density caused a decline in the growth rate (Paulovits & Biro, 1986) and condition factor (Jagsch & Rydlo, 1993) of eels in Neusiedler See. In 1991 and 1992 the stocking decreased drastically to only 40 kg (approx. 120,000 specimens) glass eel per year due to the rapid increase of the glass eel price. The total catches of eel in the 1970s and 1980s were between 40 to 120 tons per year and 51 tons in 1992 (Herzig *et al.*, 1994). Since the installation of the transboundary national park Neusiedler See–Seewinkel between Austria and Hungary in 1993, the stocking of eels has been prohibited and with the ongoing eel fishery, the eel population was expected to be extinct within 10 years (Herzig *et al.*, 1994).

More recent results from the fish ecological studies of the reed belt and following fish ecological monitoring, however, showed that despite a slight decrease in the eel population between 1994 and 1997, the eel stock in 2002 was at a similar level to that in the early 1990 s (Wolfram *et al.*, 2001; Wolfram & Mikschi, 2003). In contrast to the findings of this study, the results of the fish ecological investigations showed that the length frequency distribution, growth rate and condition factor of eels did not change from 1988 to 2002 and the average size of eels did not increase (Wolfram *et al.*, 2001; Wolfram & Mikschi, 2003). There appeared to be no decrease in the number of specimens in the smaller size classes and small eels (<15 cm) were caught regularly until 2002, indicating constant illegal stocking.

Due to ongoing illegal stocking measures, probably by local fishermen, the host population did not decline after 1993. Thus the stabilized *A. crassus* infection level over the last decade in Neusiedler See seems to reflect the stability of the eel population.

As mentioned above, the rate of *A. crassus* infection in Neusiedler See was similar to Lake Balaton, but unlike in this Hungarian lake, no mass mortalities of eel have occurred in Neusiedler See since the introduction of the parasite. This is surprising as these two lakes have similar biotic and abiotic characteristics. The reported parasite-induced host mortalities were all associated with the impact of adverse environmental stressors. Mass mortalities in Lake Balaton in 1991 and 1992 (Molnar *et al.*, 1991, 1994, 1995; Molnar, 1992) and in the Vranov Reservoir in the Czech Republic in 1994 and other reservoirs in South Moravia in 1995 (Barus, 1994, 1995; Barus *et al.*, 1999) occurred in combination with high-density eel stocks, high temperatures and low dissolved oxygen levels (Barus *et al.*, 1999; Kirk, 2003). Under high population densities of definitive hosts and broad spectra of intermediate and paratenic hosts, within a relatively short time after introduction the parasite population densities are known to increase. There then follows a period of high infection prevalence due to frequent reinvasions of the definitive host (Barus *et al.*, 1999). High water temperatures significantly accelerate the parasite's life cycle and, at the same time, increase the oxygen consumption of the fish host (Barus *et al.*, 1999). Furthermore, Molnar (1993) observed an increased oxygen demand of eels infected with *A. crassus*. These stressors exist in Neusiedler See to the same extent as in Lake Balaton. Moreover, the eel density is much higher in Neusiedler See and the water temperature in this shallow lake exceeds 30°C in some areas during the summer.

Comparing infection levels of *A. crassus* between Neusiedler See and Lake Balaton, the prevalence of *A. crassus* is somewhat similar, but the mean intensity was lower in Neusiedler See than in the western and central regions of Lake Balaton where mass mortalities occurred in 1991 and 1992 (Molnar *et al.*, 1994). Molnar (1993) and Molnar *et al.* (1993), however, stated that the severity of the damage is determined by the thickening of the swimbladder wall rather than by the number of worms present in the swimbladder. Fish free from parasites showed signs of a previous infection and exhibited the most severe pathological signs (Molnar *et al.*, 1994). In Neusiedler See thickened, fibrotic swim bladder walls were found very rarely during this investigation and no enhanced eel mortality or moribund eels were recorded in the lake. Abnormal eel behaviour due to anguillicolosis as described by Barus & Prokes (1996) and Barus *et al.* (1999) or enhanced mortality of infected fish due to electrofishing or handling stress (Molnar *et al.*, 1991) were not observed during the present study.

Molnar *et al.* (1994), Barus (1994) and Barus & Prokes (1996) found evidence for size-related mortality in Lake Balaton and in the Vranov reservoir. In Lake Balaton larger fish (>65 cm) harboured substantially higher numbers of adults and larvae of *A. crassus* than did smaller ones and in eels longer than 50 cm, the number of eels with a severely or moderately thickened swimbladder wall was much higher than that of eels with thin swimbladder walls. Eels in Neusiedler See rarely exceed a body length of 50 cm, due to a high population density and intensive fishing (Herzig *et al.* 1994; Wofram *et al.*, 2001; Wolfram & Mikschi, 2003). Thus the smaller body size of eels and the consequential lower parasite burden and minor alterations of the swimbladder might explain the absence of eel mass mortalities in Neusiedler See.

The possible involvement of other factors such as secondary bacterial infections in infected eels with swimbladder lesions (Csaba *et al.*, 1993) in the aetiology of eel mortality in Lake Balaton is suggested by Bekesi *et al.* (1997). Balint *et al.* (1997) reported that deltamethrin, the active ingredient of the insecticide K-Othrin 1 ULV used against mosquitoes in Lake Balaton played a major role in the eel mass mortalities in 1991 and especially in 1995. In Lake Balaton insecticides might have been an additional stressor for eels infected with *A. crassus* and as insecticides were never applied for large scale mosquito defence in Neusiedler See, this could be another reason for the lack of eel mass mortalities in Neusiedler See.

Acknowledgements

The staff of the Biological Station Illmitz and the Institute of Ecology and Conservation Biology, University of Vienna are thanked for advice and technical support during the study.

References

Ashworth, S.T. (1994) Possible regulation in the *Anguillicola crassus* host-parasite system. pp. 141–150 *in* Pike, A.W. & Lewis, J.W. (*Eds*) *Parasitic diseases*. Samara Publishing Ltd, Tresaith.

Ashworth, S.T. (1995) The dynamics and regulation of *Anguillicola crassus* (Nematoda) populations on the European eel. PhD thesis, University of Exeter.

Ashworth, S.T. & Kennedy, C.R. (1999) Density-dependent effects on *Anguillicola crassus* (Nematoda) within its European eel definitive host. *Parasitology* **118**, 289–296.

Audenaert, V., Huyse, T., Goemans, G., Belpaire, C. & Volckaert, F.A.M. (2003) Spatio-temporal dynamics of the parasitic nematode *Anguillicola crassus* in Flanders, Belgium. *Diseases of Aquatic Organisms* **56**, 223–233.

Bagenal, T.B. & Tesch, F.W. (1978) Age and growth. pp. 101–136 *in* Bagenal, T.B. (*Ed.*) *Methods for assessment of fish production in fresh waters*. IBP Handbook No. 3, 3rd edn. Oxford, Blackwell Scientific Publications.

Balint, T., Ferenczy, J., Katai, F., Kiss, I., Kraczer, L., Kufcsak, O., Lang, G., Polyhos, C., Szabo, I., Szegletes, T. & Nemcsok, J. (1997) Similarities and differences between the massive eel (*Anguilla anguilla* L.) devastations that occurred in Lake Balaton in 1991 and 1995. *Ecotoxicology and Environmental Safety* **37**, 17–23.

Barus, V. (1994) Uhorum hrozi smrt. *Rybarstvi* **11**, 328–329.

Barus, V. (1995) First record of *Anguillicola crassus* (Nematoda) in the Morava River drainage basin. *Helminthologia* **32**, 89.

Barus, V. & Prokes, M. (1996) Length–weight relations of uninfected and infected eels (*Anguilla anguilla*) by *Anguillicola crassus* (Nematoda). *Folia Zoologica* **45**, 183–189.

Barus, V., Halacka, K. & Prokes, M. (1996) Presence and distribution of the nematode *Anguillicola crassus* in the European eel in the Morava River drainage basin, Czech Republic. *Živočišná Výroba* **41**, 219–224.

Barus, V., Moravec, F. & Prokes, M. (1999) Anguillicolosis of the European eel (*Anguilla anguilla*) in the Czech Republic. *Czech Journal of Animal Science* **44**, 423–431.

Bekesi, L., Hornok, S. & Szekely, C. (1997) Attempts to analyse *Anguillicola crassus* infection and the humoral host response in eels (*Anguilla anguilla*) of Lake Balaton, Hungary. *Acta Veterinaria Hungarica* **45**, 439–445.

Benajiba, M.H., Silan, P., Marques, A. & Bouix, G. (1994) Protozoaires et metazoaires parasites de l'anguille *Anguilla anguilla* L., 1758: structures temporelles de leurs populations dans une lagune mediterraneenne. *Annales de Sciences Naturelles, Zoologie* **15**, 141–149.

Biro, P. (1992) Die Geschichte des Aals (*Anguilla anguilla* L.) im Plattensee (Balaton). *Österreichs Fischerei* **45**, 197–207.

Buchmann, K., Pedersen, L.O. & Glamann, J. (1991) Humoral immune response of European eel *Anguilla anguilla* to a major antigen in *Anguillicola crassus* (Nematoda). *Diseases of Aquatic Organisms* **12**, 55–57.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms:

Margolis *et al*. revisited. *Journal of Parasitology* **83**, 575–583.

Csaba, G., Lang, M. & Szekely, C. (1991) Uj fonalfereg, az *Anguillicola crassus* megjelenese Magyaroszagon. *Halaszat* **84**, 66–67.

Csaba, G., Lang, M., Salyi, G., Ramotsa, J., Glavits, R. & Ratz, F. (1993) The nematode *Anguillicola crassus* (Nematoda, Anguillicolidae) and its role in the death of eels in Lake Balaton during 1991. *Magyar Allatorvosok Lapja* **48**, 11–21.

Gönczy, J. (1992) Adatok es feltetelezesek az angolna-pusztulas körülmenyeinek tisztazasahoz. *Halaszat* **1992/1**, 21–23.

Haenen, O.L.M., van Benning, P. & Dekker, W. (1994) Infection of eel *Anguilla anguilla* (L.) and smelt *Osmerus eperlanus* (L.) with *Anguillicola crassus* (Nematoda, Dracunculoidea) in the Netherlands from 1986 to 1992. *Aquaculture* **126**, 219–229.

Hartmann, F. (1994) Untersuchungen zur Biologie, Epidemiologie und Schadwirkung von *Anguillicola crassus* Kuwahara, Niimi & Itagaki 1974, einem blutsaugenden Parasiten in der Schwimmblase des Europäischen Aals (*Anguilla anguilla*). 1st edn. Aachen, Shaker Verlag, 1–139.

Herzig, A., Mikschi, E., Auer, B., Hain, A., Wais, A. & Wolfram, G. (1994) Fischbiologische Untersuchung des Neusiedler Sees. *Biologisches Forschungsinstitut für Burgenland, Bericht*, **81**, 1–125.

Herzig, A., Kubecka, J. & Wolfram, G. (2002) Fish distribution in the open water and littoral of Neusiedler See (Austria): a matter of habitat structure and abiotic factors, International Conference on Limnology of Shallow Lakes. Balatonfüred, Hungary 25–30 May 2002, p. 79.

Höglund, J. & Pilström, L. (1995) Mechanical isolation and characterization of antigens from adult *Anguillicola crassus*. *Fish and Shellfish Immunology* **5**, 51–60.

Jagsch, A. & Rydlo, M. (1993) Der Aal – ein Problem für den Neusiedler See? *Biologisches Forschungsinstitut für Burgenland, Bericht*, **79**, 47–50.

Kelly, C.E., Kennedy, C.R. & Brown, J.A. (2000) Physiological status of wild European eels (*Anguilla anguilla*) infected with the parasite nematode. *Anguillicola crassus. Parasitology* **120**, 195–202.

Kennedy, C.R. & Fitch, D.J. (1990) Colonization, larval survival and epidemiology of the nematode *Anguillicola crassus* parasitic in the eel, *Anguilla anguilla*, in Britain. *Journal of Fish Biology* **36**, 117–131.

Kennedy, C.R., Nie, P., Kaspers, J. & Paulisse, J. (1992) Are eels (*Anguilla anguilla* L.) planktonic feeders? Evidence from parasite communities. *Journal of Fish Biology* **41**, 567–580.

Kirk, R.S. (2003) The impact of *Anguillicola crassus* on European eels. *Fisheries Management and Ecology* **10**, 385–394.

Knopf, K., Würtz, J., Sures, B. & Taraschewski, H. (1998) Impact of low water temperature on the development of *Anguillicola crassus*, parasitic in the final host *Anguilla anguilla*. *Diseases of Aquatic Organisms* **33**, 143–149.

Køie, M. (1991) Swimbladder nematodes (*Anguillicola* spp.) and gill monogeneans (*Pseudodactylogyrus* spp.) parasitic on the European eel (*Anguilla anguilla*). *Journal du Conseil Internationale Exploration de Mer* **47**, 391–398.

Konecny, R. & Wais, A. (1993) Occurrence of *Anguillicola crassus* in eels of Lake Neusiedl, Austria. *Folia Parasitologica* **40**, 327.

Lefebvre, F., Contournet, P., Priour, F., Soulas, O. & Crivelli, A.J. (2002a) Spatial and temporal variation in *Anguillicola crassus* counts: results of a 4 year survey of eels in Mediterranean lagoons. *Diseases of Aquatic Organisms* **50**, 181–188.

Lefebvre, F., Contournet, P. & Crivelli, A.J. (2002b) The health state of eel swimbladder as a measure of parasite pressure by *Anguillicola crassus*. *Parasitology* **124**, 457–463.

Möller, H., Holst, S., Lüchtenberg, H. & Petersen, F. (1991) Infection of eel *Anguilla anguilla* from the River Elbe estuary with two nematodes, *Anguillicola crassus* and *Pseudoterranova decipiens*. *Diseases of Aquatic Organisms* **11**, 193–199.

Molnar, K. (1992) Csendes-ocean tersegeböl szarmazo fonalfergek okoztak a balatoni angolnaelhullast. *Halaszat* **1992/1**, 17–18.

Molnar, K. (1993) Effect of decreased oxygen content on eels (*Anguilla anguilla*) infected by *Anguillicola crassus* (Nematoda, Dracunculoidea). *Acta Veterinaria Hungarica* **41**, 349–360.

Molnar, K. & Szekely, C. (1995) Parasitological survey of some important fish species of Lake Balaton. *Parasitologia Hungarica* **28**, 63–82.

Molnar, K., Szekely, C. & Baska, F. (1991) Mass mortality of eel in Lake Balaton due to *Anguillicola crassus* infection. *Bulletin of the European Association of Fish Pathologists* **11**, 211–212.

Molnar, K., Baska, F., Csaba, G., Glavits, R. & Szekely, C. (1993) Pathological and histopathological studies of the swimbladder of eels *Anguilla anguilla* infected by *Anguillicola crassus* (Nematoda, Dracunculoidea). *Diseases of Aquatic Organisms* **15**, 41–50.

Molnar, K., Szekely, C. & Perenyi, M. (1994) Dynamics of *Anguillicola crassus* (Nematoda, Dracunculoidea) infection in eels of Lake Balaton. *Folia Parasitologica* **41**, 193–202.

Molnar, K., Szakolczai, J. & Vetesi, F. (1995) Histological changes in the swimbladder wall of eels due to abnormal location of adults and second stage larvae of *Anguillicola crassus*. *Acta Veterinaria Hungarica* **43**, 125–127.

Moravec, F. (1992) Spreading of the nematode *Anguillicola crassus* (Dracunculoidea) among eel populations in Europe. *Folia Parasitologica* **39**, 247–248.

Moravec, F. (1996) Aquatic invertebrates (snails) as new paratenic hosts of *Anguillicola crassus* (Nematoda: Dracunculoidea) and the role of paratenic hosts in the life cycle of this parasite. *Diseases of Aquatic Organisms* **27**, 237–239.

Moravec, F. & Skorikova, B. (1998) Amphibians and larvae of aquatic insects as new paratenic hosts of *Anguillicola crassus* (Nematoda: Dracunculoidea), a swimbladder parasite of eels. *Diseases of Aquatic Organisms* **34**, 217–222.

Moravec, F. & Taraschewski, H. (1988) Revision of the genus *Anguillicola* Yamaguti, 1935 (Nematoda: Anguillicolidae) of the swimbladder of eels, including descriptions of two new species *A. novaezelandiae* sp.n. and *A. papernai* sp.n. *Folia Parasitologica* **35**, 125–146.

Neumann, W. (1985) Schwimmblasenparasit *Anguillicola* bei Aalen. *Fischer und Teichwirt* **11**, 322.

Paggi, L., Orrechia, P., Minervini, R. & Mattiuci, S. (1982) Sulla comparsa di *Anguillicola australiensis* Johnston et Mawson 1940 in *Anguilla anguilla* del Lago di Bracciano. *Parassitologia* **24**, 140–144.

Palikova, M. & Navratil, S. (2001) Occurrence of *Anguillicola crassus* in the water reservoir Korycany (Czech Republic) and its influence on the health condition and haematological indices of eels. *Acta Veterinaria Brno* **70**, 443–449.

Paulovits, G. & Biro, P. (1986) Age determination and growth of eel, *Anguilla anguilla*, in lake Fertö, Hungary. *Fisheries Research* **4**, 101–110.

Pazooki, J. & Szekely, C. (1994) Survey of the paratenic hosts of *Anguillicola crassus* in Lake Velence, Hungary. *Acta Veterinaria Hungarica* **42**, 87–97.

Peters, G. & Hartmann, F. (1986) *Anguillicola*, a parasitic nematode of the swim bladder spreading amonst the eel population in Europe. *Diseases of Aquatic Organisms* **1**, 229–230.

Rolbiecky, L. (2002) On the role of paratenic hosts in the life cycle of the nematode *Anguillicola crassus* in the Vistula Lagoon, Poland. *Acta Ichthyologica et Piscatoria* **32**, 109–116.

Schabuss, M., Konecny, R., Belpaire, C. & Schiemer, F. (1997) Endoparasitic helminths of the European eel, *Anguilla anguilla*, from four disconnected meanders from the rivers Leie and Scheldt in western Flanders, Belgium. *Folia Parasitologica* **44**, 12–18.

Szekely, C. (1994) Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary. *Diseases of Aquatic Organisms* **18**, 11–20.

Szekely, C. (1995) Dynamics of *Anguillicola crassus* (Nematoda: Dracunculoidea) larval infection in paratenic hosts fishes of Lake Balaton, Hungary. *Acta Veterinaria Hungarica* **43**, 401–422.

Szekely, C. (1996) Experimental studies on the infectivity of *Anguillicola crassus* third stage larvae (Nematoda) from paratenic hosts. *Folia Parasitologica* **43**, 305–311.

Szekely, C., Lang, M. & Csaba, G. (1991) First occurrence of *Anguillicola crassus* in Hungary. *Bulletin of the European Association of Fish Pathologists* **11**, 162–163.

Tesch, F.W. (1977) *The eel. Biology and management of anguillid eels*. 434 pp. London, Chapman & Hall.

Thomas, K. & Ollevier, F. (1992) Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. *Diseases of Aquatic Organisms* **13**, 165–174.

Thomas, K. & Ollevier, F. (1993) Hatching, survival, activity and penetration efficiency of second-stage larvae of *Anguillicola crassus* (Nematoda). *Parasitology* **107**, 211–217.

Wolfram, G. & Mikschi, E. (2003) *Fischökologisches Monitoring Neusiedler See 1998–2002*. 46 pp. Biologische Station Neusiedler See Biologisches Forschungsinstitut für Burgenland, Bericht.

Wolfram, G., Mikschi, E., Wolfram-Wais, A. & Hain, A. (2001) *Fischökologische Untersuchung des Schilfgürtels des Neusiedler Sees*. 141 pp. Biologische Station Neusiedler See Biologisches Forschungsinstitut für Burgenland, Bericht.

Würtz, J., Knopf, K. & Taraschewski, H. (1998) Distribution and prevalence of *Anguillicola crassus* (Nematoda) in eels *Anguilla anguilla* of the rivers Rhine and Naab, Germany. *Diseases of Aquatic Organisms* **32**, 137–143.

(Accepted 10 December 2004)