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Macroparasite communities in European eels, *Anguilla anguilla*, from French Mediterranean lagoons, with special reference to the invasive species *Anguillicola crassus* and *Pseudodactylogyrus* spp.

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ABSTRACT

Key-words: *epidemiology, macroparasites, eels, Mediterranean lagoons, invasive species*

European eel parasites, in particular invasive species, are suspected to play a role in the decline in the populations of their host. The aims of this work were to describe the parasitic fauna of eels in French Mediterranean lagoons and to study the epidemiological trends of the invasive helminth species, the nematode *Anguillicola crassus* and the monogenean *Pseudodactylogyrus* spp., in regard to spatio-temporal dynamics, host biological characteristics and parasite community. A total of 418 eels was sampled in eight lagoons between March 2003 and June 2005. Our results revealed a total macroparasite richness of 23 species: 1 Monogenea, 13 Digenea, 2 Cestoda, 3 Nematoda, 2 Acantocephala and 2 Crustacea. We found no variation in *A. crassus* abundance in Salses-Leucate lagoon in the same month across years. However, the nematode abundance was higher in eels caught in summer than in those caught in winter. *Pseudodactylogyrus* sp. was not found in Salses-Leucate lagoon, except in July 2004. Comparisons between the lagoons on the same date showed that they could be separated into two groups for both species' abundance: Grau-du-Roi, Mauguio, Palavas and Vaccarès lagoons, where abundance was rather high, against Bages-Sigean, Pierre-Blanche, Salses-Leucate and Thau lagoons, where abundance was rather low or nil. We found significant negative relationships between *A. crassus* abundance and the length and age of eels. We also found a significant positive relationship between *A. crassus* and *Pseudodactylogyrus* sp. abundance. Finally, our results showed significant positive relationships between both *A. crassus* and *Pseudodactylogyrus* sp. abundance and the abundance of the digeneans *Prosorhynchus aculeatus* and *Lecithochirium gravidum*. We discuss the results in regard to the dynamics of invasions, the characteristics of the parasite life cycles and the ecology of eels.

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RÉSUMÉ

Communautés de macroparasites des anguilles européennes *Anguilla anguilla* dans les lagunes méditerranéennes françaises, avec une référence particulière aux espèces invasives *Anguillicola crassus* et *Pseudodactylogyrus* spp.

Mots-clés : *épidémiologie, macroparasites, anguilles, lagunes méditerranéennes, espèces invasives*

Les parasites de l'anguille européenne, en particulier les espèces invasives, sont suspectés de jouer un rôle dans le déclin des populations de leur hôte. Les objectifs de ce travail étaient de décrire la faune parasitaire des anguilles dans les lagunes méditerranéennes françaises et d'étudier les tendances épidémiologiques des espèces helminthes invasives, le nématode *Anguillicola crassus* et les monogènes *Pseudodactylogyrus* spp., en regard de la dynamique spatio-temporelle, des caractéristiques biologiques de l'hôte et de la communauté parasitaire. Un total de 418 anguilles a été échantillonné dans huit lagunes entre mars 2003 et juin 2005. Nos résultats ont révélé une richesse macroparasitaire totale de 23 espèces : 1 Monogenea, 13 Digenea, 2 Cestoda, 3 Nematoda, 2 Acantocephala et 2 Crustacea. Nous n'avons pas trouvé de variation dans l'abondance d'*A. crassus* d'année en année pour une même date d'échantillonnage dans la lagune de Salses-Leucate. En revanche, l'abondance du nématode était plus importante chez les anguilles capturées en été par rapport à celles capturées en hiver. *Pseudodactylogyrus* sp. n'a pas été rencontré dans la lagune de Salses-Leucate, sauf en juillet 2004. Les comparaisons effectuées entre les lagunes pour une même date ont montré que celles-ci pouvaient être séparées en deux groupes en regard de l'abondance des deux espèces : Grau-du-Roi, Mauguio, Palavas et Vaccarès, où les abondances étaient plutôt élevées, par rapport à Bages-Sigean, Pierre-Blanche, Salses-Leucate et Thau, où les abondances étaient plutôt basses ou nulles. Nous avons mis en évidence des relations négatives significatives entre l'abondance d'*A. crassus* et la taille ainsi que l'âge des anguilles. Nous avons aussi trouvé une relation positive significative entre les abondances d'*A. crassus* et de *Pseudodactylogyrus* sp. En dernier lieu, nos résultats ont révélé des relations positives significatives entre d'une part les abondances d'*A. crassus* et de *Pseudodactylogyrus* sp., et d'autre part les abondances des digènes *Prosorhynchus aculeatus* et *Lecithochirium gravidum*. Nous discutons les résultats en regard de la dynamique des invasions, des caractéristiques des cycles de vie parasitaires et de l'écologie des anguilles.

INTRODUCTION

The European eel, *Anguilla anguilla* (L.), has a complex life cycle that includes two oceanic migrations and a growth phase in continental waters. Adult eels spawn in the Sargasso Sea. Their transparent, leaf-like larvae (leptocephali) are transported from the spawning area toward the coastal waters of Europe and North Africa by the Gulf Stream and North-Atlantic Drift, where they metamorphose into glass eels, which migrate upstream to grow into the elver and yellow eel stages in freshwater. However, eels do not necessarily migrate into freshwater streams during the growth phase, and some individuals can remain in coastal lagoons (Tzeng *et al.*, 1997; Daverat *et al.*, 2004). At maturation, the yellow eels metamorphose into silver eels, which migrate downstream to the ocean to begin their spawning migration (reviewed by van Ginneken and Maes, 2005).

European eel populations have suffered a steep decline throughout their distribution range since the early 1980s (Moriarty, 1987; Bruslé, 1990; Feunteun, 2002; Wirth and Bernatchez, 2003). Explanations for this decline include climate change, freshwater habitat destruction, physical obstructions to migrations, pollution, overfishing and diseases. Parasites are becoming a major concern in conservation biology because of their ability to evolve rapidly (Daszak *et al.*, 2000) and are now recognised to play an important role not only in aquaculture but also in natural systems (Altizer *et al.*, 2003). The epidemiology of parasites

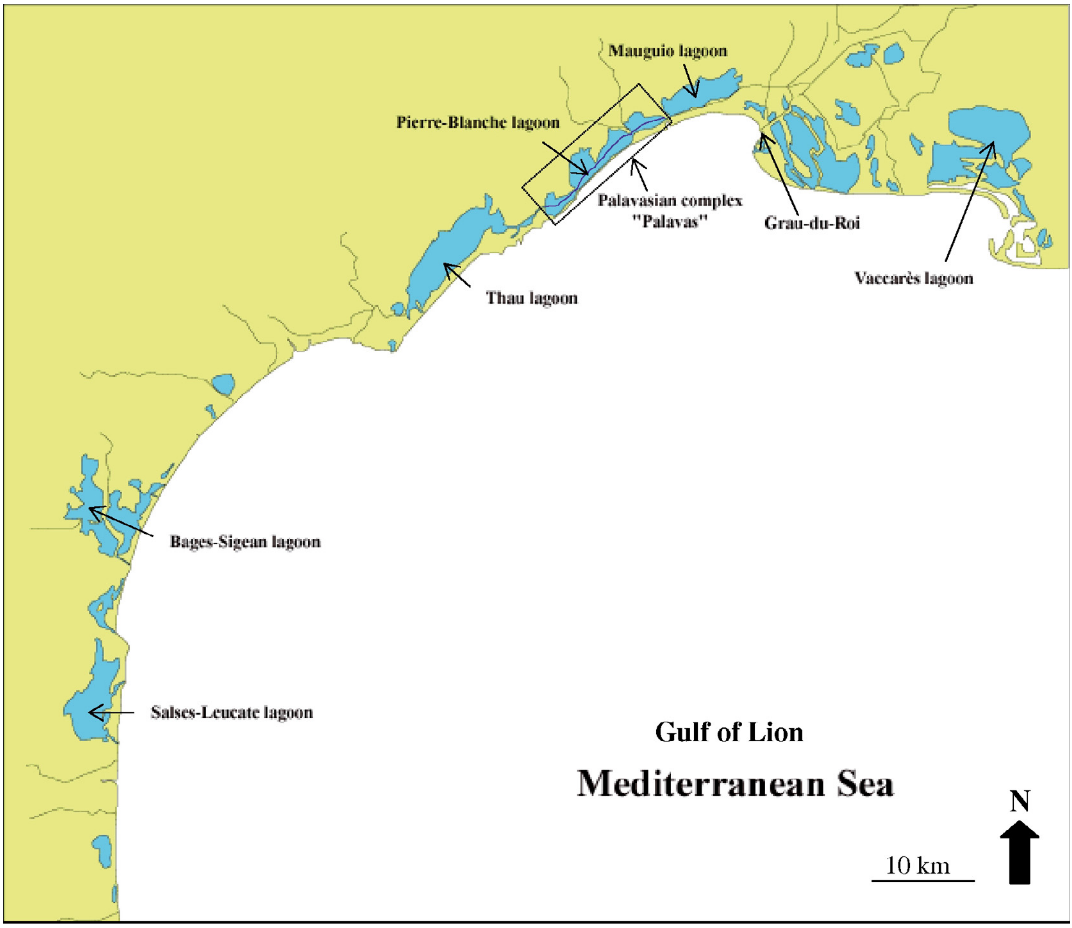

Figure 1
Geographic situation of sampled sites (2°55'E < longitude < 5°14'E; 42°47'N < latitude < 43°35'N).

Figure 1
Situation géographique des sites échantillonnés (2°55'E < longitude < 5°14'E ; 42°47'N < latitude < 43°35'N).

and the dynamics of their introduction in the case of invasive species thus need to be studied in order to protect endangered species.

The present study focused on eels caught in Mediterranean lagoons. First, we aimed to make an inventory of the parasitic fauna, on different dates, to evaluate the parasite pressure on the fish living in brackish water. Second, we intended to characterise the epidemiological trends of the invasive helminth species, the swimbladder nematode *Anguillicola crassus* and the monogenean *Pseudodactylogyrus* spp. (Kennedy, 2007), in regard to spatio-temporal dynamics, host biological characteristics and parasite community.

MATERIALS AND METHODS

> *SAMPLE COLLECTION, AND MORPHOLOGICAL AND EPIDEMIOLOGICAL ANALYSES*

Four hundred and eighteen European eels (*Anguilla anguilla*) were collected in eight Mediterranean lagoons or sites between March 2003 and June 2005 (Figure 1). The sampled

Table I
Morphological characteristics and ages of the eels sampled in eight Mediterranean lagoons between March 2003 and June 2005. Data are presented as mean ± standard deviation (minimal and maximal values). N, sample size; NA, not available.

Tableau I
Caractéristiques morphologiques et âges des anguilles échantillonnées dans huit lagunes méditerranéennes entre mars 2003 et juin 2005. Les données sont présentées sous forme de moyenne ± écart-type (valeurs minimale et maximale). *N*, taille de l'échantillon ; NA, donnée non disponible.

Lagoon	Sampling date	*N*	Weight (g)	Length (mm)	Age (years)
Salses-Leucate	March 2003	38	46.4 ± 18.6 (21.3–98.5)	311 ± 36 (250–400)	4.3 ± 0.7 (3.0–6.0)
	March 2004	28	58.8 ± 44.5 (16.1–258.9)	337 ± 61 (239–555)	3.5 ± 1.0 (2.0–5.0)
	July 2004	30	14.2 ± 18.6 (1.7–97.0)	211 ± 60 (102–404)	3.0 ± 0.8 (2.0–4.5)
	June 2005	18	48.9 ± 14.2 (29.6–76.3)	322 ± 30 (266–377)	NA
Bages-Sigean	February 2004	29	53.8 ± 15.9 (23.8–87.0)	327 ± 31 (263–386)	2.7 ± 0.8 (1.0–4.0)
	July 2004	22	43.8 ± 29.0 (7.2–98.2)	298 ± 59 (191–399)	3.0 ± 1.0 (1.5–4.5)
	June 2005	27	42.9 ± 43.5 (13.4–224.5)	303 ± 63 (229–510)	NA
Thau	July 2004	17	63.0 ± 28.7 (23.3–116.9)	336 ± 47 (256–409)	2.6 ± 0.4 (2.0–3.5)
"Palavas"	July 2004	22	16.0 ± 5.6 (5.7–28.8)	229 ± 28 (170–283)	2.3 ± 0.6 (1.5–3.5)
Pierre-Blanche	July 2004	12	70.2 ± 32.4 (27.4–154.9)	364 ± 46 (283–460)	3.1 ± 1.1 (1.5–4.5)
	June 2005	119	81.3 ± 76.4 (9.4–306.6)	352 ± 89 (196–567)	NA
Mauguio	July 2004	18	28.2 ± 9.9 (12.3–50.7)	261 ± 32 (200–312)	2.7 ± 0.8 (1.5–4.5)
Grau-du-Roi	July 2004	16	45.0 ± 50.8 (5.8–214.5)	289 ± 77 (185–505)	2.4 ± 0.9 (1.5–4.5)
Vaccarès	July 2004	22	40.7 ± 26.3 (10.2–111.5)	307 ± 52 (204–408)	2.8 ± 0.9 (1.5–4.5)

lagoons, corresponding sampling dates and sample sizes are given in Table I. Eels were caught by professional fishermen at Salses-Leucate, Bages-Sigean and Pierre-Blanche lagoons. They were provided by a fish trade company for Thau, the Palavasian complex ("Palavas"), Mauguio and Vaccarès lagoons and for the Grau-du-Roi. Note that (i) Grau-du-Roi is a fairway that is hydrologically connected with several lagoons of the Camargue gardoise, and (ii) Pierre-Blanche lagoon belongs to the Palavasian complex. Eels caught at Salses-Leucate in July 2004 came from freshwater small streams located inside a sea bass (*Dicentrarchus labrax*) farm that is physically connected with the lagoon. Eels were brought back to the laboratory alive and maintained on ice until dissection, which was carried out the same day. Prior to dissection, eels were anaesthetised in 0.1 mL·L^{-1} Eugenol (Merck Schuchardt OHG, Hohenbrunn, Germany) and then weighed (total mass, to the nearest 0.1 g) and measured (total length, in mm). The morphological characteristics of the eels are reported in Table I. The eels were then beheaded. We focused our investigation on macroparasites. Swimbladder lumens were immediately examined macroscopically for the recovery of fourth-stage larvae and adults of *Anguillicola crassus* (third-stage larvae were not counted). The gills and the digestive tract were immediately and quickly frozen to avoid excessive damage to parasites, and were later examined under a binocular microscope. All the adult parasites were recovered and some of them were mounted under a cover slide for further identification. Species identification was done when possible and classical epidemiological parameters (abundance, prevalence and mean intensity) were calculated according to Bush *et al.* (1997) for each sampling date and site. Moreover, the abundance of each species was calculated for all of the sampled eels.

> *OTOLITH ANALYSIS*

Sagital otoliths were isolated, embedded in resin and ground (X 600 and X 1000 grit). After using an EDTA solution, otoliths were stained with toluidine blue to visualise annual rings. The age estimation was made by counting the winter rings (Moriarty, 1983; Lecomte-Finiger, 1985). Ages are reported in Table I.

> *STATISTICAL ANALYSES*

We decided to focus analyses on invasive species: the nematode *A. crassus* and the monogenean *Pseudodactylogyrus* sp.

Kruskal-Wallis non-parametric tests were performed to test for differences in *A. crassus* and *Pseudodactylogyrus* sp. abundance among the different dates that were sampled at Salses-Leucate lagoon: March 2003, March 2004, July 2004 and June 2005. Moreover, Kruskal-Wallis tests were performed to test for differences in *A. crassus* and *Pseudodactylogyrus* sp. abundance among the different sites that were sampled in July 2004: Salses-Leucate, Bages-Sigean, Thau, “Palavas”, Pierre-Blanche, Mauguio, Grau-du-Roi and Vaccarès. If $P < 0.05$, Dunn’s test (multiple comparison post-test) was later performed to identify significant pair-wise differences.

Correlations between *A. crassus* abundance and eel length, eel age (host biological characteristics) and the abundance of *Pseudodactylogyrus* sp., *Deropristis inflata*, *Prosorhynchus aculeatus* and *Lecithochirium gravidum* (the most abundant parasite species for all of the sampled eels) were performed with the use of the Spearman correlation coefficient. In the same way, we performed correlations between *Pseudodactylogyrus* sp. abundance and eel length, eel age and the abundance of *A. crassus*, *D. inflata*, *P. aculeatus* and *L. gravidum*.

All statistical analyses were conducted with Statistica 6.0 software (StatSoft, Inc.).

RESULTS

> *PARASITIC FAUNA IN EELS FROM MEDITERRANEAN LAGOONS*

Table II shows the epidemiological results for the identified parasite species, on a total of 418 eels sampled in eight Mediterranean lagoons between March 2003 and June 2005. The total macroparasite richness constituted 23 species, of which 8 were identified: 1 Monogenea: *Pseudodactylogyrus* sp., 13 Digenea: *Bucephalus* sp., *Deropristis inflata*, *Helicometra* sp., *Lecithochirium gravidum*, *Prosorhynchus aculeatus* and Digenean sp. 1 to 8, 2 Cestoda: Cestode sp. 1 and 2, 3 Nematoda: *Anguillicola crassus* and Nematode sp. 1 and 2, 2 Acantocephala: *Acanthocephalus anguillae* and Acanthocephalan sp. 1, and

Table II

*Epidemiological parameters of the identified parasite species of the eels sampled in eight Mediterranean lagoons between March 2003 and June 2005. Ab., abundance, for which data are presented as mean ± standard deviation; Prev., prevalence in %; Int., intensity, for which data are presented as mean ± standard deviation (minimal and maximal values); Cl., class; Ni., niche; N, Nematoda; M, Monogenea; D, Digenea; A, Acantocephala; S, swimbladder; G, gills; GU, gut; * indicates that only swimbladders were examined for parasite recovery; —, not found.*

Tableau II

Paramètres épidémiologiques relatifs aux espèces parasites identifiées chez les anguilles échantillonnées dans huit lagunes méditerranéennes entre mars 2003 et juin 2005. Ab, abondance, pour laquelle les données sont présentées sous forme de moyenne ± écart-type ; Prev., prévalence en % ; Int., intensité, pour laquelle les données sont présentées sous forme de moyenne ± écart-type (valeurs minimale et maximale) ; Cl., classe ; Ni., niche ; N, Nematoda ; M, Monogenea ; D, Digenea ; A, Acantocephala ; S, vessie natatoire ; G, branchies ; GU, tube digestif ; * indique que seuls les parasites de la vessie natatoire ont été recherchés ; —, non présent.

			Salses-Leucate				Bages-Sigean			Thau	"Palavas"	Pierre-Blanche		Mauguio	Grau-du-Roi	Vaccarès
			March 03	March 04	July 04	June 05	Feb. 04	July 04	June 05*	July 04	July 04	July 04	June 05*	July 04	July 04	July 04
Cl.	Ni.	Species (family)														
N	**S**	*Anguillicola crassus* (Dracunculoidea)														
		Ab.	0.16 ± 0.59	0.07 ± 0.26	1.53 ± 1.68	1.39 ± 4.55	—	—	1.00 ± 4.61	1.29 ± 4.34	6.82 ± 5.64	—	0.08 ± 0.35	16.00 ± 9.39	9.50 ± 10.24	5.45 ± 6.08
		Prev.	7.89	7.14	66.67	16.67	—	—	14.81	23.53	86.36	—	5.04	94.12	75.00	77.27
		Int.	2.0 ± 1.0 (1–3)	1.0 ± 0.0 (1–1)	2.3 ± 1.6 (1–6)	8.3 ± 9.5 (1–19)	—	—	6.8 ± 11.5 (1–24)	5.5 ± 8.3 (1–18)	7.9 ± 5.3 (1–19)	—	1.5 ± 0.5 (1–2)	15.3 ± 10.1 (1–33)	10.4 ± 8.6 (1–26)	6.5 ± 6.2 (1–26)
M	**G**	*Pseudodactylogyrus* sp. (Ancyrocephalidae)														
		Ab.	—	—	1.03 ± 1.16	—	—	0.05 ± 0.21		0.24 ± 0.44	2.68 ± 5.18	—		3.35 ± 3.76	5.94 ± 13.30	55.41 ± 119.87
		Prev.	—	—	53.33	—	—	4.55		23.53	59.09	—		52.94	81.25	90.91
		Int.	—	—	1.9 ± 0.9 (1–3)	—	—	1.0 (1)		1.0 ± 0.0 (1–1)	4.5 ± 6.1 (1–21)	—		6.3 ± 2.6 (2–11)	7.3 ± 14.5 (1–55)	61.0 ± 124.6 (1–484)
D	**GU**	*Bucephalus* sp. (Bucephalidae)														
		Ab.	0.24 ± 0.91	2.14 ± 6.01	—	0.72 ± 2.37	3.21 ± 13.30	—		—	—	—		—	—	—
		Prev.	7.89	17.86	—	16.67	10.34	—		—	—	—		—	—	—
		Int.	3.0 ± 1.7 (1–4)	12.0 ± 9.8 (5–27)	—	1.3 ± 0.6 (1–2)	31.0 ± 34.4 (2–69)	—		—	—	—		—	—	—
		Deropristis inflata (Acanthocolpidae)														
		Ab.	2.55 ± 8.41	0.04 ± 0.19	0.23 ± 1.10	0.89 ± 1.28	2.45 ± 5.78	6.91 ± 9.05		54.12 ± 49.48	58.36 ± 85.85	14.00 ± 20.14		43.00 ± 39.78	58.19 ± 84.51	10.50 ± 21.18
		Prev.	23.68	3.37	6.67	44.44	51.72	81.82		94.12	86.36	83.33		100	100	45.45
		Int.	9.8 ± 15.4 (1–47)	1.0 (1)	3.5 ± 3.5 (1–6)	2.0 ± 1.2 (1–4)	4.1 ± 7.3 (1–29)	8.4 ± 9.4 (1–29)		53.0 ± 51.0 (1–152)	67.6 ± 89.1 (1–328)	15.0 ± 22.0 (1–75)		42.5 ± 40.3 (1–125)	39.6 ± 48.1 (1–145)	22.2 ± 27.5 (1–78)

Table II
Continued.

Tableau II
Suite.

			Salses-Leucate				Bages-Sigean			Thau	"Palavas"	Pierre-Blanche		Mauguio	Grau-du-Roi	Vaccarès
			March 03	March 04	July 04	June 05	Feb. 04	July 04	June 05*	July 04	July 04	July 04	June 05*	July 04	July 04	July 04
Cl.	**Ni.**	Species (family)														
		Helicometra sp. (Opecoelidae)														
		Ab.	0.53 ± 1.39	0.57 ± 1.23	–	0.11 ± 0.32	1.10 ± 2.91	1.00 ± 4.69		–	–	0.25 ± 0.62		–	0.13 ± 0.50	–
		Prev.	23.68	21.43	–	11.11	31.03	4.55		–	–	16.67		–	6.25	–
		Int.	2.2 ± 2.2 (1–6)	2.7 ± 1.2 (1–4)	–	1.0 ± 0.0 (1–1)	3.6 ± 4.4 (1–15)	22.0 (22)		–	–	1.5 ± 0.7 (1–2)		–	2.0 (2)	–
		Lecithochirium gravidum (Hemiuridae)														
		Ab.	2.84 ± 3.77	2.46 ± 5.66	0.80 ± 1.83	3.67 ± 4.07	6.03 ± 12.18	1.68 ± 6.16		–	–	7.67 ± 10.69		–	0.06 ± 0.25	–
		Prev.	60.53	39.29	23.33	83.33	68.97	22.73		–	–	83.33		–	6.25	–
		Int.	4.7 ± 3.9 (1–15)	6.3 ± 7.8 (1–26)	3.4 ± 2.4 (1–8)	4.4 ± 4.1 (1–15)	8.8 ± 13.9 (1–61)	7.4 ± 12.1 (1–29)		–	–	9.2 ± 11.1 (1–32)		–	1.0 (1)	–
		Prosorhynchus aculeatus (Bucephalidae)														
		Ab.	2.00 ± 7.98	24.39 ± 54.61	–	–	–	0.05 ± 0.21		–	0.23 ± 1.07	–		–	–	–
		Prev.	15.79	39.29	–	–	–	4.55		–	4.55	–		–	–	–
		Int.	12.7 ± 17.6 (1–47)	62.1 ± 74.0 (1–174)	–	–	–	1.0 (1)		–	5.0 (5)	–		–	–	–
A	**GU**	*Acanthocephalus anguillae* (Echinorhynchidae)														
		Ab.	0.18 ± 0.98	0.04 ± 0.19	–	–	–	–		–	–	–		–	–	–
		Prev.	5.26	3.57	–	–	–	–		–	–	–		–	–	–
		Int.	3.5 ± 3.5 (1–6)	1.0 (1)	–	–	–	–		–	–	–		–	–	–

Table III
Differences in Anguillicola crassus *(top right) and* Pseudodactylogyrus *sp. (bottom left) abundance for each pair of dates sampled in Salses-Leucate lagoon (Dunn's tests). ns, P > 0.05; ***, P < 0.001.*

Tableau III
Différences dans les abondances d'*Anguillicola crassus* (en haut à droite) et de *Pseudodactylogyrus* sp. (en bas à gauche) pour chaque paire de dates échantillonnées dans la lagune de Salses-Leucate (tests de Dunn). ns, *P* > 0,05 ; ***, *P* < 0,001.

Anguillicola crassus **/ *Pseudodactylogyrus* sp.**	March 2003	March 2004	July 2004	June 2005
March 2003		ns	***	***
March 2004	ns		***	***
July 2004	***	***		ns
June 2005	ns	ns	***	

2 Crustacea: Copepod sp. 1 and 2. The five most abundant species for the whole sample were *D. inflata* (17.01 parasites), *Pseudodactylogyrus* sp. (5.41 parasites), *P. aculeatus* (2.82 parasites), *L. gravidum* (2.11 parasites) and *A. crassus* (1.99 parasites). The macroparasite richness per lagoon ranged between 4 (Bages-Sigean, February 2004) and 12 species (Bages-Sigean, July 2004). Mean abundance ranged between 0.03 (Nematode sp. 2) and 58.36 (*D. inflata*) parasites. Prevalence ranged between 3.33 (Nematode sp. 2) and 100% (*D. inflata*). Mean intensity ranged between 1 (Copepod sp. 1, *Pseudodactylogyrus* sp. and *Helicometra* sp.) and 82.5 (Digenean sp. 1) parasites.

> *EPIDEMIOLOGICAL TRENDS OF THE INVASIVE SPECIES*

Anguillicola crassus and *Pseudodactylogyrus* sp. abundance was different among dates at Salses-Leucate lagoon (Kruskal-Wallis test: $H = 53.95$, $P < 0.0001$ and $H = 51.31$, $P < 0.001$, respectively). *Anguillicola crassus* abundance was not significantly different between March 2003 and March 2004 and between July 2004 and June 2005, but was significantly lower in March 2003–March 2004 compared with July 2004–June 2005 (Table III). *Pseudodactylogyrus* sp. abundance in July 2004 was significantly higher compared with all the others (Table III).

Anguillicola crassus and *Pseudodactylogyrus* sp. abundance was different among sites in July 2004 (Kruskal-Wallis test: $H = 84.52$, $P < 0.0001$ and $H = 62.34$, $P < 0.001$, respectively). Dunn's tests showed that lagoons could be roughly separated into two groups in regard to both species' abundance: Grau-du-Roi, Mauguio, "Palavas" and Vaccarès, where abundance was rather high, against Bages-Sigean, Pierre-Blanche, Salses-Leucate and Thau, where abundance was rather low or nil (Table IV).

We found significant negative relationships between *A. crassus* abundance and the length ($P < 0.05$) and age ($P < 0.001$) of eels. We found significant positive relationships between *A. crassus* abundance, and *Pseudodactylogyrus* sp. ($P < 0.0001$), *P. aculeatus* ($P < 0.0001$) and *L. gravidum* ($P < 0.0001$) abundance (Table V). We found significant positive relationships between *Pseudodactylogyrus* sp. abundance and *P. aculeatus* ($P < 0.0001$) and *L. gravidum* ($P < 0.0001$) abundance (Table V).

DISCUSSION

We found a total macroparasite richness of 23 species. This represents almost half of the total number of helminths (55 species) that have been described in European eels

Table IV
Differences in Anguillicola crassus *(top right) and* Pseudodactylogyrus *sp. (bottom left) abundance for each pair of lagoons sampled in July 2004 (Dunn's tests). ns, P > 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001.*

Tableau IV
Différences dans les abondances d'*Anguillicola crassus* (en haut à droite) et de *Pseudodactylogyrus* sp. (en bas à gauche) pour chaque paire de lagunes échantillonnées en juillet 2004 (tests de Dunn). ns, *P* > 0,05 ; *, *P* < 0,05 ; **, *P* < 0,01 ; ***, *P* < 0,001.

Anguillicola crassus / ***Pseudodactylogyrus* sp.**	Salses-Leucate	Bages-Sigean	Thau	"Palavas"	Pierre-Blanche	Mauguio	Grau-du-Roi	Vaccarès
Salses-Leucate		ns	ns	ns	ns	***	ns	ns
Bages-Sigean	ns		ns	***	ns	***	***	***
Thau	ns	ns		**	ns	***	*	*
"Palavas"	ns	*	ns		***	ns	ns	ns
Pierre-Blanche	ns	ns	ns	ns		***	**	**
Mauguio	ns	*	ns	ns	ns		ns	ns
Grau-du-Roi	ns	***	*	ns	**	ns		ns
Vaccarès	**	***	***	ns	***	ns	ns	

Table V
Correlations between Anguillicola crassus/Pseudodactylogyrus *sp. abundance and eel biological characteristics/most abundant parasite species for all of the sampled eels. r, Spearman correlation coefficient.*

Tableau V
Corrélations entre d'une part les abondances d'*Anguillicola crassus/Pseudodactylogyrus* sp., et d'autre part les caractéristiques biologiques des anguilles/les espèces parasites les plus abondantes pour l'ensemble des anguilles échantillonnées. *r*, coefficient de corrélation de Spearman.

	Anguillicola crassus	*Pseudodactylogyrus* sp.
Eel length	$r = -0.170$ $P < 0.05$	$r = -0.092$ $P > 0.05$
Eel age	$r = -0.246$ $P < 0.001$	$r = -0.014$ $P > 0.05$
Pseudodactylogyrus* sp. or *A. crassus	$r = 0.695$ $P < 0.0001$	$r = 0.695$ $P < 0.0001$
Deropristis inflata	$r = 0.039$ $P > 0.05$	$r = 0.128$ $P > 0.05$
Prosorhynchus aculeatus	$r = 0.475$ $P < 0.0001$	$r = 0.491$ $P < 0.0001$
Lecithochirium gravidum	$r = 0.459$ $P < 0.0001$	$r = 0.383$ $P < 0.0001$

(Kennedy, 2007), which suggests that parasite diversity in eels in Mediterranean lagoons is high. The wide range of values in parasite abundance, prevalence and intensity highlights the predominance of some species in the parasite community: *Deropristis inflata*, *Pseudodactylogyrus* sp., *Prosorhynchus aculeatus*, *Lecithochirium gravidum* and *Anguillicola crassus*.

We found no variation in the nematode abundance in Salses-Leucate lagoon in the same month across years. However, *A. crassus* abundance was higher in eels caught in early summer than in those caught in late winter. This result suggests that stabilisation of the infection dynamics may have occurred in this site. Moreover, *A. crassus* infection would be dependent on abiotic and/or biotic factors associated with season. Both these results are consistent with infection patterns previously described in Vaccarès and Malagroy lagoons (Camargue) between 1997 and 2000 by Lefebvre *et al.* (2002b) and in Mauguio lagoon between 1988 and 1989 by Benajiba *et al.* (1994). Comparison between our results and those of Lefebvre *et al.* (2002b) also suggests the existence of a stabilised infection in Vaccarès lagoon from 1997 to 2004. Indeed, Lefebvre and collaborators found an abundance of 4 parasites, a prevalence of 70% and a mean intensity of 4–6 parasites, which is close to our results. However, comparison between our results and those of Benajiba *et al.* (1994) suggests an increase in *A. crassus* infection in Mauguio lagoon between 1988/1989 and 2004. Indeed, Benajiba and collaborators found a prevalence of 30–40% and a mean intensity of 3 parasites, which is lower than what we found (prevalence: 94% and mean intensity: 15 parasites). Taken together, these studies show that nematode infection dynamics differ among lagoons. Thus, continuous monitoring may be necessary. The seasonal pattern of *A. crassus* infection, which may to a certain extent be explained by variation in temperature (Höglund *et al.*, 1992) and in feeding habits of eels, suggests that the detrimental effect of the nematode on the eel demography in Mediterranean lagoons would be maximal during the summer (Lefebvre *et al.*, 2002a), when oxygen availability is usually low and bacterial infections frequent. The monogenean *Pseudodactylogyrus* sp. was not found in Salses-Leucate lagoon, except in July 2004. A previous study showed that records of *P. anguillae* in Salses-Leucate lagoon were anecdotal (Fazio *et al.*, 2005). This result suggests unfavourable environmental conditions for the parasite in this site.

Comparisons among sites on the same date revealed that lagoons could be separated into two groups in regard to both species' abundance: Grau-du-Roi, Mauguio, "Palavas" and Vaccarès, where abundance was rather high, against Bages-Sigean, Pierre-Blanche, Salses-Leucate and Thau, where abundance was rather low or nil. This result suggests that abiotic and biotic environmental similarities within each of these groups of lagoons may favour (in the former group) or disfavour (in the latter group) both parasite infections. Thus, *A. crassus* and *Pseudodactylogyrus* sp. would be sensitive to the same environmental conditions.

We showed an increase in *A. crassus* abundance as the length of eels decreased. This correlation may result from differential transmission between small and large eels due to change in feeding behaviour. Small eels generally feed on small prey such as crustaceans, and progressively become piscivorous as their size increases (Tesch, 2003). *Anguillicola crassus* has a complex life cycle that includes one obligatory intermediate host, usually copepods (De Charleroy *et al.*, 1990), and one non-obligatory paratenic host, usually small fishes (Thomas and Ollevier 1992a; Székely, 1994). Therefore, our result suggests that transmission rates of *A. crassus* by paratenic hosts may be lower than by intermediate hosts in Mediterranean lagoons. This finding may not be a general trend in nematode transmission because other studies showed a positive (Thomas and Ollevier, 1992b; Lefebvre *et al.*, 2002b; Audenaert *et al.*, 2003) or no relationship (Würtz *et al.*, 1998) between parasite abundance and the size of eels. Our results are consistent with those of Schabuss *et al.* (1997) and Gargouri Ben Abdallah and Maamouri (2006), who showed a negative relationship between the two parameters. We showed an increase in *A. crassus* abundance as the age of eels decreased. This result is quite surprising as we expected a positive relationship between these two parameters. Indeed, in the absence of an effective immune response as in the present case (Knopf, 2006; Nielsen and Esteve-Gassent, 2006), longer exposure time should favour accumulation of parasites in hosts. It may also be true for eels. Thus, our result could arise from higher mortality in the oldest infected eels (and their resulting absence in the samples). We found significant positive relationships between *A. crassus* abundance, and *Pseudodactylogyrus* sp., *Prosorhynchus aculeatus* and *Lecithochirium gravidum* abundance. These results may reflect interspecific facilitation and/or similarities in transmission routes between species. *Prosorhynchus aculeatus* and *L. gravidum* may facilitate the passage of the L3 larvae of *A. crassus* through the intestinal wall and/or may have the same intermediate hosts. The interaction between the nematode and the monogenean is more difficult to understand as these species occupy different niches within the eels, and because *Pseudodactylogyrus* sp. has a simple life cycle. The most plausible explanation is that *A. crassus* would disturb the swimming and preying behaviours of infected eels, which would enhance the encounter with the infective stages (oncomiracidia) of *Pseudodactylogyrus* sp.

We found significant positive relationships between *Pseudodactylogyrus* sp. abundance, and *P. aculeatus* and *L. gravidum* abundance. As these digeneans and *Pseudodactylogyrus* sp. occupy different niches within eels and have different life cycles, this result may be explained by similarities in habitats between the intermediate hosts of the digeneans and the oncomiracidia of the monogenean. Finally, there was no relationship between *Pseudodactylogyrus* sp. abundance and the length of eels. This result is quite surprising, because the general trend of *Pseudodactylogyrus* infections is an enhanced parasite establishment by larger host area (Buchmann, 1989; Nie and Kennedy, 1991; Matejusova *et al.*, 2003).

CONCLUSION

The nematode *A. crassus* and the monogenean *Pseudodactylogyrus* sp. have differences and similarities in their epidemiological status in Mediterranean lagoons. Differences could be related to temporal variation in both infections. In Salses-Leucate lagoon, *Pseudodactylogyrus* sp. infection seems to be constant through time, while *A. crassus* infection follows a seasonal pattern, with the highest infection in summer. Moreover, we add that *A. crassus* infection seems to spread in some lagoons such as Mauguio. Our few results on Bages-Sigean and Pierre-Blanche lagoons (where the nematode was not found in 2004 and was in low abundance in 2005) may also confirm this trend. Similarities between the two infections exist when considering their spatial aspects. Both monogenean and nematode infections seem to be positively linked in space. Moreover, there is a spatial trend amongst lagoons. The parasite pressure appears to be higher in the eastern lagoons than in the western ones.

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REFERENCES

Altizer S., Harvell D. and Friedle E., 2003. Rapid evolutionary dynamics and disease threats to biodiversity. *Trends Ecol. Evol.*, *18*, 589–596.

Audenaert V., Huyse T., Goemans G., Belpaire C. and Volckaert F.A.M., 2003. Spatio-temporal dynamics of the parasitic nematode *Anguillicola crassus* in Flanders, Belgium. *Dis. Aquat. Org.*, *56*, 223–233.

Benajiba M.H., Silan P., Marques A. and Bouix G., 1994. Protozoaires et métazoaires parasites de l'anguille *Anguilla anguilla* L., 1758 : structures temporelles de leurs populations dans une lagune méditerranéenne. *Ann. Sci. Nat. Zool. Biol. Anim.*, *15*, 141–149.

Bruslé J., 1990. L'anguille européenne (*Anguilla anguilla*), une espèce jugée commune jusqu'à la dernière décennie, mérite-t-elle d'acquérir aujourd'hui le statut d'espèce menacée ? *Bull. Soc. Zool. Fr.*, *114*, 61–73.

Buchmann K., 1989. Relationship between host size of *Anguilla anguilla* and the infection level of the monogeneans *Pseudodactylogyrus* spp. *J. Fish Biol.*, *35*, 599–601.

Bush A.O., Lafferty K.D., Lotz J.M. and Shostak A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.*, *8*, 575–583.

Daszak P., Cunningham A.A. and Hyatt A.D., 2000. Wildlife ecology – Emerging infectious diseases of wildlife – Threats to biodiversity and human health. *Science*, *287*, 443–449.

Daverat F., Elie P. and Lahaye M., 2004. Microchemistry contribution to a first approach to the diversity of life histories of eels from the lower part of the Gironde-Garonne-Dordogne watershed. *Cybium*, *28*, 83–90.

De Charleroy D., Grisez L., Thomas K., Belpaire C. and Ollevier F., 1990. The life cycle of *Anguillicola crassus*. *Dis. Aquat. Org.*, *8*, 77–84.

Fazio G., Lecomte-Finiger R., Bartrina J., Moné H. and Sasal P., 2005. Macroparasite community and asymmetry of the yellow eel *Anguilla anguilla* in Salses-Leucate lagoon, Southern France. *Bull. Fr. Pêche Piscic.*, 378–379, 99–113.

Feunteun E., 2002. Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. *Ecol. Eng.*, *18*, 575–591.

Gargouri Ben Abdallah L. and Maamouri F., 2006. Spatio-temporal dynamics of the nematode *Anguillicola crassus* in Northeast Tunisian lagoons. *C. R. Biol.*, *329*, 785–789.

Höglund J., Andersson J., Wickström H. and Reizenstein M., 1992. The distribution of *Anguillicola* in Sweden and its association with thermal discharge areas. *Ir. Fish. Invest., A Freshw.*, *36*, 143–149.

Kennedy C.R., 2007. The pathogenic helminth parasites of eels. *J. Fish Dis.*, *30*, 319–334.

Knopf K., 2006. The swimbladder nematode *Anguillicola crassus* in the European eel *Anguilla anguilla* and the Japanese eel *Anguilla japonica*: differences in susceptibility and immunity between a recently colonized host and the original host. *J. Helminthol.*, *80*, 129–136.

Lecomte-Finiger R., 1985. L'âge de l'anguille européenne (*Anguilla anguilla*). *J. Appl. Ichthyol.*, *4*, 178–192.

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

Lefebvre F., Contournet P., Priour F., Soulas O. and Crivelli A.J., 2002b. Spatial and temporal variation in *Anguillicola crassus* counts: results of a 4 year survey of eels in Mediterranean lagoons. *Dis. Aquat. Org.*, *50*, 181–188.

Matejusova I., Simkova A., Sasal P. and Gelnar M., 2003. Microhabitat distribution of *Pseudodactylogyrus anguillae* and *Pseudodactylogyrus bini* among and within gill arches of the European eel (*Anguilla anguilla* L.). *Parasitol. Res.*, *89*, 290–296.

Moriarty C., 1983. Age determination and growth rate of eels, *Anguilla anguilla*. *J. Fish Biol.*, *23*, 257–264.

Moriarty C., 1987. Factors influencing recruitment of the Atlantic species of anguillid eels. *Am. Fish. Soc. Symp.*, *1*, 483–491.

Nie P. and Kennedy C.R., 1991. Occurrence and seasonal dynamics of *Pseudodactylogyrus anguillae* (Yin & Sproston) (Monogenea) in eel, *Anguilla anguilla* (L.), in England. *J. Fish Biol.*, *39*, 897–900.

Nielsen M.E. and Esteve-Gassent M.D., 2006. The eel immune system: present knowledge and the need for research. *J. Fish Dis.*, *29*, 65–78.

Schabuss M., Konecny R., Belpaire C. and 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 Parasitol.*, *44*, 12–18.

Székely C., 1994. Paranetic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary. *Dis. Aquat. Org.*, *18*, 11–20.

Tesch F.W., 2003. The Eel, Fifth Edition, Thorpe JE, Oxford, UK, 408 p.

Thomas K. and Ollevier F., 1992a. Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. *Dis. Aquat. Org.*, *13*, 165–174.

Thomas K. and Ollevier F., 1992b. Population biology of *Anguillicola crassus* in the final host *Anguilla anguilla*. *Dis. Aquat. Org.*, *14*, 163–170.

Tzeng W.N., Severin K.P. and Wickström H., 1997. Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. *Mar. Ecol. Prog. Ser.*, *149*, 73–81.

van Ginneken V.J.T. and Maes G.E., 2005. The european eel (*Anguilla anguilla*, Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Rev. Fish Biol. Fish.*, *15*, 367–398.

Wirth T. and Bernatchez L., 2003. Decline of North Atlantic eels: a fatal synergy? *P. Roy. Soc. Lond. B Bio.*, *270*, 681–688.

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