

Richness and diversity of helminth species in eels from a hypersaline coastal lagoon, Mar Menor, south-east Spain

E. Mayo-Hernández^{1,2*}, J. Peñalver^{2,3}, A. García-Ayala^{2,6},
E. Serrano^{4,5}, P. Muñoz^{1,2} and R. Ruiz de Ybáñez^{1,2}

¹Departamento de Sanidad Animal, Universidad de Murcia, 30100, Murcia, Spain: ²Campus de Excelencia Internacional Regional 'Campus Mare Nostrum', Universidad de Murcia, Espinardo, 30100, Murcia, Spain: ³Servicio de Pesca y Acuicultura, D.G. de Ganadería y Pesca, Consejería de Agricultura y Agua de la Región de Murcia, JUAN XXIII, 30071, Murcia, Spain: ⁴Servei d'Ecopatologia de Fauna Salvatge, Departament de Medicina i Cirurgia Animal, Universitat Autònoma de Barcelona, 08193, Bellaterra, Barcelona, Spain: ⁵Estadística i Investigació Operativa, Departament de Matemàtica, Universitat de Lleida, Av. Jaume II, 69, Campus Cappont, E-25001, Lleida, Spain: ⁶Departamento de Biología Celular e Histología, Universidad de Murcia, 30100, Murcia, Spain

(Received 17 October 2013; Accepted 14 February 2014; First Published Online 31 March 2014)

Abstract

The composition and diversity of parasite communities and intestinal components, as well as infra-community structure, were assessed in eels *Anguilla anguilla*, from Mar Menor, a permanent Mediterranean hypersaline coastal lagoon. Data were used to determine whether this helminth community differs in composition and structure from that of eels in lagoons with lower salinity regimes and higher freshwater inputs. A total prevalence of 93% was detected. Specifically, parasites were identified as *Deropristis inflata*, *Bucephalus anguillae*, *Contracaecum* sp., *Anguillicoloides crassus* and two plerocercoid larvae belonging to the order Proteocephalidae, the marine species representing 91% of the isolated helminths. In the total community, digenetic trematodes were the dominant group of helminths, and *D. inflata*, an eel specialist, dominated both the component community and the infra-community. Richness and diversity were low but similar to those reported in other saline lagoons, and maximum species per eel did not exceed four. At the infra-community level, higher abundance than in other brackish or marine Mediterranean environments was detected. The findings provide further evidence of the similarity in composition and structure of helminth communities in eels from various Mediterranean coastal lagoons. Moreover, salinity-dependent specificities are well supported and reflect the life history of individual eels.

Introduction

The European eel, *Anguilla anguilla* (Linnaeus, 1758), is an economically important fish, with a geographical distribution that includes all European waters and the Mediterranean Basin. Over the past several decades, its

*E-mail: elviramayohdz@gmail.com

population has shown a sharp decline throughout Europe (ICES/EIFAC, 2003, 2004), which continued until 2012 (ICES/EIFAC, 2012). The same effect has been seen in the American eel (*Anguilla rostrata*) and the Japanese eel (*Anguilla japonica*) populations and thus should lead us to reflect on the causative factors of this decline, including possible impacts from fisheries, predation by birds and chemical pollution (Dekker, 2005). In order to protect the European eel stock, the European Commission requires that member states draw up national eel management plans at the river-basin level, collect data and take technical and legal measures to reduce mortalities related to anthropogenic factors (European Commission, 2007). In this context, the monitoring of eel population health (contaminants, pathogens and general condition indices) is mandatory in those European countries with a substantial eel population (ICES/EIFAC, 2011).

Pathogens can be considered as biological stressors. They do not always cause disease in fish, but they may be present in a subclinical or carrier state (Winton, 2001) as a potential causative factor in the decline of the eel population (Castonguay *et al.*, 1994; Dekker, 2004; Haenen *et al.*, 2009; Székely *et al.*, 2009). Thus, parasites have the same effect on their hosts as shown in *Anguillicoloides crassus*, the parasite studied most intensively since the 1980s (reviewed in Lefebvre *et al.*, 2012). However, broad studies on eel parasite fauna are less frequent, despite recommendations that researchers should incorporate native parasite richness as a risk factor in epidemiological models (Martínez-Carrasco *et al.*, 2011). In addition, parasites play a clear role in the impact of contaminants on fishes (Marcogliese & Pietrock, 2011), thus increasing the need for knowledge on parasite community composition to better evaluate the health status of eel populations.

This work provides information on parasite communities in eels from Mar Menor, a Mediterranean coastal lagoon that maintains wider connections with the sea but has permanently higher salinity due to evaporative processes. Differences in salinity with the nearby marine environment are reflected in the organisms that inhabit these lagoons. Most parasitological studies have been focused on marine, brackish and freshwater habitats, while few have been conducted in non-permanent hypersaline environments (Kennedy *et al.*, 1997; Di Cave *et al.*, 2001), and none in a permanent hypersaline lagoon. It is broadly accepted that helminth communities in Mediterranean, and even non-Mediterranean, lagoons are quite similar in both composition and structure (Kristmundsson & Helgason, 2007). However, no work has tested whether parasite communities in eels inhabiting these permanently extremely hypersaline lagoons differ from those described in other populations. In this work, we will explore this question at both component community and infra-community levels.

Materials and methods

Area of study

Mar Menor lagoon lies in the SE region of the Iberian Peninsula (37°38'N, 0°42'W), Spain. This ecosystem is the largest saltwater lake in Europe, with an area of 180 km² and 73 km of coastline. The maximum depth is 7 m. It is

isolated from the sea by a 24-km-long sandbar known as La Manga. The water exchange and, therefore, passage of fish species between Mar Menor and the Mediterranean Sea occurs through natural openings or passages, and there are no artificial barriers that limit the passage of eels. The lagoon is choked and permanently hypersaline, with salinity levels (43–46.5 g/l) greater than that of the adjacent Mediterranean Sea, due to low precipitation, around 300 mm/year, and high evaporation rates, with a mean annual temperature of 18°C.

Collection and examination of eels

A total of 189 wild European eels with a mean length of 528.46 ± 72.05 mm and mean weight of 261.90 ± 115.48 g, were collected from Mar Menor lagoon by local fishermen throughout 2010 and were frozen until processing. Once thawed, the parasitological examination was conducted. For this purpose, eyes, skin, fins, gills, nostrils and the mouth cavity of each eel were examined for ectoparasites. Each eel was then dissected and the body cavity and mesenteries were inspected. Internal organs were cut and observed under a stereomicroscope. Gills and digestive tract were removed, washed over a sieve, and the recovered digestive content was also examined under a stereomicroscope. Swimbladders were dissected and macroscopically inspected for the presence of pre-adult and adult *A. crassus* in the lumen. Thereafter, swimbladders were frozen for subsequent examination of larval stages (L3 and L4) in the wall, following the method described by Martínez-Carrasco *et al.* (2011). Additionally, for detection of anisakid larvae, muscle tissue was artificially digested as described previously by Peñalver *et al.* (2010). Parasites were stored in 70% ethanol and identified following Schmidt (1986), Khalil *et al.* (1994), Moravec (1994), Gibson *et al.* (2002), Jones *et al.* (2005) and Gibbons (2010).

Data analysis

Analyses of the helminth community structure were carried out at two levels, component community and infra-community (see Holmes & Price, 1986). Prevalence, mean intensity and mean abundance of infection for each parasite species were defined according to Bush *et al.* (1997). Measures of component community structure were species richness, defined as the total number of parasitic species in the sample. The Shannon–Wiener Index was used to quantify the diversity, determining the proportion of individuals that represent each species present, and the Shannon–Wiener Evenness Index was chosen to account for evenness, producing a value of heterogeneity in the relative representation of species present. At both levels, the dominance among the different species was calculated with the Berger–Parker Dominance Index. Measurements of infra-community structure, carried out only on species collected in the digestive tract, were the maximum number of helminth species per eel, the proportion of eels with zero or one species of helminth, and the mean number of individuals and species per eel. The latter was obtained taking into account the total population of eels or only the infected

eels. In all cases, indices were calculated following Magurran (1988).

Results

Composition of helminths

Summary data of the composition of the helminth community of eels from Mar Menor lagoon are presented in table 1. A total of 17,924 helminths were detected in the studied eels, belonging to six species: two digenetic trematodes, *Deropristis inflata* and *Bucephalus anguillae* (Špakulová *et al.*, 2002); two nematodes, *Contracaecum* sp. and *A. crassus*; and larvae belonging to the order Proteocephalidae. No ectoparasites were found in the skin or gills. Digenetic trematodes and cestode species, as well as *Contracaecum* sp., were observed in the lumen of the digestive tract. Additionally, *Contracaecum* sp. was localized in the muscle, both encapsulated and loosely attached to the mesenteries and the external wall of the intestine, rectum and stomach, or encysted in the wall. Finally, the nematode *A. crassus* was also detected in the swimbladder.

Prevalence of infection at a 95% confidence interval was 93% (87.8–95.8%, $n = 175$ infected eels), with a mean abundance of 95 ± 194.70 helminths per analysed eel and a mean intensity of 102 ± 200.87 helminths per infected eel. The higher records were for *D. inflata*, with a prevalence of 67%, a mean abundance of 68 ± 173.55 individuals per analysed eel and mean intensity of 101 ± 162.85 individuals per infected eel. Meanwhile, the lowest records were obtained for *Proteocephalidae* larvae, with a prevalence of 2%, a mean abundance of 1 ± 0.12 larvae per analysed eel and a mean intensity of 3 ± 0 larvae per infected eel.

Structure of helminth communities

Diversity characteristics of the helminth component community are summarized in table 2a. The digenetic trematodes were the dominant group of helminths; *D. inflata* dominated the helminth community in the lagoon and the Berger–Parker Dominance index was 0.72. The species richness was six and the maximum number of species per eel was four, found only in 1% of eels, while 67% of the sampled eels harboured only one or

two different helminth species, and 25% presented three different species. The Shannon–Wiener index was 0.72, while the Shannon–Wiener Evenness index was 0.40.

Characteristics of the intestinal infra-community of eels from Mar Menor lagoon are summarized in table 2b. A total of 17,877 helminths belonging to five species were recovered. At this level, prevalence of infection at a 95% confidence interval was 91% (85.9–94.6%, $n = 172$ infected eels). The mean abundance was 94 ± 194.66 helminths per analysed eel and the mean intensity 104 ± 201.71 helminths per infected eel. The abundance ranged from 0 to 1494 helminths per eel, with 1% of eels presenting four species, the maximum number of species per eel, while 61% harboured two or three different helminth species, and zero or one species were described in 38% of the analysed eels. As in the total helminth community, *D. inflata* dominated with a 0.72 Berger–Parker Dominance Index (table 2b).

Discussion

Composition of helminths

Relatively few studies have dealt with parasite communities of brackish or marine Mediterranean environments when compared to those of freshwater eels. This is the first survey of parasite communities from a permanently hypersaline Mediterranean lagoon, Mar Menor.

Parasite prevalence in our study was 93%, slightly higher than the 84% described in the Urbino pond in Corsica by Ternengo *et al.* (2005), where salinity rarely drops below 30‰, and similar to the prevalence of 90% described by Culurgioni *et al.* (2010) in St. Gilla lagoon (Sardinia), which is a temporary hypersaline environment ($\chi^2 = 0.12$, $df = 2$, $P = 0.94$). In Mar Menor the mean abundance was 95 ± 194.70 helminths per analysed eel, and the mean intensity was 102 ± 200.87 helminths per infected eel. Unfortunately, we cannot compare these values to other locations since other studies do not provide these total data.

All of the parasite species recovered in this study have been observed previously in European eels (Jakob *et al.*, 2009). As in other Mediterranean lagoons (Kennedy *et al.*, 1997; Di Cave *et al.*, 2001; Maillo *et al.*, 2005), eels from Mar

Table 1. The composition and levels of infection of the helminth community in 189 eels from the Mar Menor lagoon; mean values \pm standard deviation.

Helminth species	Site of infection	Prevalence (%)	Mean intensity (range)	Mean abundance
Digenetic trematodes				
<i>Deropristis inflata</i>	Digestive tract	67	101 ± 162.85 (0–1240)	68 ± 173.55
<i>Bucephalus anguillae</i>	Digestive tract	60	39 ± 47.30 (0–400)	23 ± 51.19
Nematodes				
<i>Contracaecum</i> sp.	Digestive tract	46	8 ± 9.98 (0–158)	4 ± 8.15
	Muscle	12	1 ± 0.39 (0–4)	1 ± 0.45
<i>Anguillicoloides crassus</i> *	Swimbladder	3	3 ± 0.44 (0–10)	1 ± 0.75
Cestodes				
<i>Proteocephalidae</i> larvae	Digestive tract	2	0.01 ± 0.10 (0–1)	1 ± 0.12

*Includes adult and larval stages.

Table 2. Diversity characteristics of the helminth community and infra-community of eels from Mar Menor lagoon; mean values \pm standard deviation.

(a) Component community structure	
Number of eels	189
Species richness	6
Maximum number of helminth species/eel	4
Shannon–Wiener Index	0.72
Shannon–Wiener Evenness Index	0.40
Berger–Parker Dominance Index	0.72
Dominant Species	<i>Deropristis inflata</i>
(b) Infra-community structure	
Percentage of infected eels	91%
Mean number of helminth species	1.81 \pm 0.92
Mean number of helminth species in infected eels	1.99 \pm 0.80
Maximum number of helminth species/eel	4
Proportion of eels with 0 or 1 species of helminth	38%
Berger–Parker Index	0.72
Dominant species	<i>Deropristis inflata</i>

Menor also harbour freshwater, marine and euryhaline parasitic species. However, there are differences in prevalence and abundance of these parasitic species between lagoons, probably since their salinity range influences the abundance of the intermediate hosts.

In Mar Menor, the prevalence of generally common parasites in freshwater eels was 0.1%, much lower than the prevalence registered in other parasitological surveys in saline lagoons. According to Kennedy *et al.* (1997), 50% of eels from lagoons with salinities ranging from 10 to 48‰ harboured parasitic species generally found in freshwater eels, and the prevalence of these parasites was 35.7% in eels from Adriatic lagoons with a salinity range from 15 to 42‰ (Di Cave *et al.*, 2001). In this sense, the low salinity in other Spanish lagoons (e.g. Delta del Ebro, 3–36‰ salinity range) would contribute to a higher rate of parasitic species common in freshwater eels (66.7%, Maïllo *et al.*, 2005).

Eel specialist parasites are usually the most prevalent and abundant in lagoons (Kennedy *et al.*, 1997). Accordingly, three of the species detected in Mar Menor in the present study (*D. inflata*, *B. anguillae* and *A. crassus*) are eel specialists. Furthermore, the two digenetic trematodes, a group generally scarce in freshwater eels in Europe but, according to previous studies, common in brackish and marine European eels (Di Cave *et al.*, 2001; Kennedy, 2006), dominated the parasite community.

Deropristis inflata has mainly been observed in eels from brackish and saline environments (Jakob *et al.*, 2009). In Mar Menor, this digenetic trematode presented a high prevalence of 67%, similar to the 70% prevalence described in Urbino pond by Ternengo *et al.* (2005), and exceeding values reported in Mediterranean lagoons with lower salinities (Benajiba, 1991; Kennedy *et al.*, 1997; Di Cave *et al.*, 2001; Maïllo *et al.*, 2005; Culurgioni *et al.*, 2010). In all of these studies, *D. inflata* prevalence was higher as salinity increased, with the exception of Acquatina lagoon (Italy), possibly reflecting its smaller size and its isolation from other lagoons (Poulin & Morand, 1999). On the

contrary, the prevalence of *D. inflata* in Mar Menor was lower than the 73.8% and 93.9% prevalences described by Di Cave *et al.* (2001) in two North Adriatic lagoons with lower salinity. However, their mean abundances of 29.7 \pm 67 and 38.6 \pm 60.9 individuals per analysed eel, respectively, were lower compared to the 101 \pm 162.85 individuals per analysed eel detected in Mar Menor. This fact could be related to the existence of extensive eel farming in both lagoons, as increased eel population densities facilitate the spread of parasites (Arneberg *et al.*, 1998; Morand & Poulin, 1998; Arneberg, 2001, 2002). Much lower *D. inflata* mean abundances were also reported in eels from other Mediterranean lagoons, from 9.45 \pm 1.96 (Ternengo *et al.*, 2005) to 0.3 \pm 0.9 individuals per analysed eel (Di Cave *et al.*, 2001).

Bucephalus anguillae (formerly *B. polymorphus* according to Špakulová *et al.*, 2002), a digenetic trematode found only in brackish and marine waters, has a prevalence of 60% in eels from Mar Menor, higher than values recorded for other Mediterranean lagoons, where prevalence ranged from 2.4 to 55% (Di Cave *et al.*, 2001; Culurgioni *et al.*, 2010). The mean abundance of this parasite in Mar Menor was also higher, with 23 \pm 51.19 individuals per eel analysed, compared to these other lagoons, where values ranged between 0.1 \pm 0 and 9.6 \pm 37 individuals per eel analysed (Di Cave *et al.*, 2001). As described for *D. inflata*, the exception was the mean abundance of *B. anguillae*, with 22.2 \pm 69.3 individuals per analysed eel in Valle Figheri (Italy), a similar value to that described in Mar Menor eels despite its lower salinity. On the other hand, the absence of *B. anguillae* in the Ebro Delta lakes is notable, and probably due to their high freshwater inputs.

Anguillicoloides crassus is an invader species introduced into Europe with Japanese eels from the Far East (Køie, 1988). This parasite can survive in a wide range of salinities, as observed both under experimental and wild conditions (Kirk *et al.*, 2000 and Jakob *et al.*, 2009, respectively). Infection levels are thought to be lower in marine environments than in freshwater ones. Nevertheless, a high prevalence of 46.4% has been reported in eels from a marine environment in Sweden (Wielgoss *et al.*, 2008), and in eels from a hypersaline estuary with a salinity of 46.77‰, *A. crassus* prevalence reached 71.87% (Loukili & Belghyti, 2007). In Mediterranean lagoons, the prevalence of *A. crassus* ranged from 9.1% (Di Cave *et al.*, 2001) to 43.5% (Rahhou *et al.*, 2001), but the absence of this parasite in four Italian lagoons (Acquatina, Fogliano, Monaci and Caprolace) with salinities between 17 and 48‰ (Kennedy *et al.*, 1997; Di Cave *et al.*, 2001) is notable. In the present study, the prevalence of *A. crassus* was only 3%, similar to the value previously described by Martínez-Carrasco *et al.* (2011), and showed very low mean abundance with 3 \pm 0.44 individuals per analysed eel and low mean intensity with 1 \pm 0.75 individuals per infected eel. The prevalence of this parasite depends on the presence of the intermediate host, mainly copepods, and none of the most abundant copepods in Mar Menor have been described as possible intermediate hosts of *A. crassus* (Martínez-Carrasco *et al.*, 2011). Therefore, it may be that eels entering the lagoon are already infected.

In Mar Menor, *Contracaecum* sp., an allogenic species, showed a prevalence of 49% with a mean abundance of 3.67 \pm 8.30 individuals per analysed eel. This record is

higher than values cited in most other Mediterranean lagoons, where the parasite is less prevalent, ranging from 4.5 to 25% (Di Cave *et al.*, 2001, Culurgioni *et al.*, 2010) or even absent (Kennedy *et al.*, 1997; Maíllo *et al.*, 2005; Ternengo *et al.*, 2005), probably due to the fact that Mar Menor lagoon and associated wetlands are important sites for wintering and breeding waterfowl (Fernández *et al.*, 2005). Similarly, high *Contracaecum* sp. prevalences of 61.9% and 69.7% were reported in eels from Acquatina and Valle Figheri lagoons, respectively. The high prevalence in these lagoons must relate to the use of the lagoons by the bird definitive hosts (Di Cave *et al.*, 2001). The presence of the anisakid *Contracaecum* sp. has a negative implication, not only for the health of the eel stocks, but also in relation to its role as a potential zoonotic agent (Culurgioni *et al.*, 2010).

Twenty different species of cestodes have been described in European eels, but only five have been cited in brackish or marine waters, while none has been recorded in permanent hypersaline waters. Just two of them (*Bothriocephalus claviceps* (Goeze, 1782) and *Proteocephalus macrocephalus* (Crepling, 1825)) were found in Mediterranean brackish lagoons. *Bothriocephalus claviceps* showed a prevalence of 0.62% in Delta del Ebro and *P. macrocephalus* ranged from 2.1% in Encanyissada (Delta del Ebro) to 9.1% in Valle Figheri (Maíllo *et al.*, 2005 and Di Cave *et al.*, 2001, respectively). In the present work, a low prevalence of Proteocephalidae larvae (2%) was detected in the permanent hypersaline lagoon.

Structure of helminth communities

Similar to changes in composition of the component community, richness and diversity usually decrease with higher salinity (Kennedy *et al.*, 1997). Richness in Mar Menor (six species) agreed with the expected values for saline lagoons, which ranges between 3 and 18 species (revised in Kristmundsson & Helgason, 2007). Moreover, richness in Mar Menor eels matches even more closely the values described for hypersaline lagoons, ranging from 3 to 8 species (Kennedy *et al.*, 1997; Di Cave *et al.*, 2001). Shannon–Wiener diversity indices for most of the Mediterranean lagoons were similar and relatively high. In Tyrrenian lagoons, the index ranged from 0.86 to 1.34 (Kennedy *et al.*, 1997), in Adriatic lagoons values were between 0.71 and 1.45 (Di Cave *et al.*, 2001), and in Delta del Ebro lagoons it ranged from 0.98 to 1.41 (Maíllo *et al.*, 2005). As expected, the lowest Shannon–Wiener diversity indices corresponded to 0.72 in Mar Menor and in saline Italian lagoons, with 0.71 in Acquatina lagoon, 0.85 in Comaccio and 0.86 in Caproccale (Kennedy *et al.*, 1997; Di Cave *et al.*, 2001).

Our results confirm that lagoons are the preferred habitat for the digeneans *D. inflata* and *B. anguillae* (Di Cave *et al.*, 2001), and that eels in coastal lagoons host a broadly similar helminth community, regardless of the location of the lagoon (Di Cave *et al.*, 2001). However, in Languedoc Region (France), *A. crassus* was the dominant species (Benajiba, 1991). This is probably due to the introduction of this parasite into this ecosystem shortly before the study, as the infection rate of this nematode meant that it spread rapidly in the first few years following its appearance (Kennedy & Fitch 1990; Audenaert *et al.*, 2003). Another

exception is the dominance of the monogenean *P. anguillae* in Ebro Delta lagoons, attributable to the greater influence of fresh water.

Infra-community structure

Five different species were described in the digestive tract of European eels from Mar Menor (intestinal infra-community richness). The maximum number of species per eel was four, in agreement with the maximum value found in all other European studies. This result confirms the theory of Kennedy *et al.* (1997) regarding the similarity in the structure, though not the composition, of infra-communities of eels from fresh and brackish waters. Nevertheless, an abundance of 94 ± 194.66 helminths per analysed eel was detected in this study, being higher than in other Mediterranean coastal lagoons.

The infra-community was dominated by digenetic trematodes. The dominant species in the digestive tract was *D. inflata*. This coincident dominance is responsible for the high levels of similarity between and within lagoons (Maíllo *et al.*, 2005). Further studies should analyse the interactions between all of these parasites, which may be in competition.

Our results provide support for the hypothesis that helminth community composition and structure in eels from a permanent and choked lagoon do not differ significantly from those in eels from other Mediterranean environments, even in a permanently hypersaline lagoon. Despite overall similarities in parasite species composition, salinity-dependent specificities are well supported and reflect the life history of individual eels.

Acknowledgements

The authors are thankful to Dr Saraivia and Dr M. Hermida for their assistance in the identification of anisakids.

Financial support

This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflict of interest

None.

References

- Arneberg, P. (2001) An ecological law and its macro-ecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* **24**, 352–358.
- Arneberg, P. (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.
- Arneberg, P., Skorping, A., Grenfell, B.T. & Read, A.F. (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London, Series B* **265**, 1283–1289.

- Audenaert, V., Huysse, 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.
- Benajiba, M.H.** (1991) Les parasites de l'anguille européenne *Anguilla anguilla* L., 1758: (poisson teleosteen) dans la region du Languedoc. PhD thesis, Université Clermont-Ferrand II, France.
- 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.
- Castonguay, M., Hodson, P.V., Couillard, C.M., Eckersley, M.J., Dutil, J.D. & Verreault, G.** (1994) Why is recruitment of the American eel, *Anguilla rostrata*, declining in the St. Lawrence River and Gulf? *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 479–488.
- Culurgioni, J., De Murtas, R. & Figus, V.** (2010) Helminth parasites of European eel *Anguilla anguilla* L. from St. Gilla lagoon (Sardinia, South western Mediterranean). *Ittiopatologia* **7**, 97–106.
- Dekker, W.** (2004) Slipping through our hands. Population dynamics of the European eel. PhD thesis, Universiteit van Amsterdam, Netherlands.
- Dekker, W.** (2005) *Report of the Workshop National Data Collection European eel*. Fiskeriverket, Swedish Board of Fisheries, Sweden, September.
- Di Cave, D., Berrilli, F., De Liberato, C., Orecchia, P. & Kennedy, C.R.** (2001) Helminth communities in eels *Anguilla anguilla* from Adriatic coastal lagoons in Italy. *Journal of Helminthology* **75**, 7–13.
- European Commission** (2007) Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union* **248**, 17–23.
- Fernández, J.M., Selma, M.A.E., Aymerich, F.R., Sáez, M.T.P. & Fructuoso, M.F.C.** (2005) Aquatic birds as bioindicators of trophic changes and ecosystem deterioration in the Mar Menor lagoon (SE Spain). *Hydrobiologia* **550**, 221–235.
- Gibbons, L.** (2010) *Keys to the nematode parasites of vertebrates*. Supplementary Volume. 416 pp. Wallingford, CABI International.
- Gibson, D.I., Jones, A. & Bray, R.A.** (2002) *Keys to the Trematoda*. Volume 1. 544 pp. Wallingford, CABI International.
- Haenen, O.L.M., Van Ginneken, V.J., Engelsma, M.Y. & Van den Thillart, G.E.E.J.M.** (2009) Impact of eel viruses on recruitment of European eel. pp. 387–400 in Van den Thillart, G., Dufour, S. & Rankin, J. (Eds) *Spawning migration of the European eel. Reproduction Index, a useful tool for conservation management*. Fish and Fisheries Series. Berlin, Springer-Verlag.
- Holmes, J.C. & Price, P.W.** (1986) Communities of parasites. pp. 187–213 in Anderson, D.J. & Kikkawa, J. (Eds) *Community ecology: pattern and process*. Oxford, Blackwell Scientific Publications.
- ICES/EIFAC.** (2003) *Report of the ICES/EIFAC Working Group on Eels (WGEEL)*. ICES CM 2003/ACFM, 06, France, September, 2002.
- ICES/EIFAC.** (2004) *Report of the ICES/EIFAC Working Group on Eels (WGEEL)*. ICES CM 2004/ACFM, 09, Spain, October, 2003.
- ICES/EIFAC.** (2011) *Report of the 2011 Session of the Joint EIFAC/ICES Working Group on Eels (WGEEL)*. ICES CM 2011/ACOM, 18, Portugal, September, 2011.
- ICES/EIFAC.** (2012) *Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL)*. ICES CM 2012/ACOM, 18, Denmark, September 2012.
- Jakob, E., Walter, T.R. & Hanel, J.A.** (2009) Checklist of the protozoan and metazoan parasites of European eel (*Anguilla anguilla*): checklist of *Anguilla anguilla* parasites. *Journal of Applied Ichthyology* **1**–49.
- Jones, A., Bray, R.A. & Gibson, D.I.** (2005) *Keys to the Trematoda*. Volume 2. 768 pp. Wallingford, CAB International and The Natural History Museum.
- Kennedy, C.R.** (2006) *Ecology of the Acanthocephala*. 248 pp. New York, Cambridge University Press.
- 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* **43**, 287–301.
- Kennedy, C.R., Di Cave, D., Berrilli, F. & Orecchia, P.** (1997) Composition and structure of helminth communities in eels *Anguilla anguilla* from Italian coastal lagoons. *Journal of Helminthology* **71**, 35–40.
- Khalil, L.F., Jones, A. & Bray, R.A.** (1994) *Keys to the cestode parasites of vertebrates*. 751 pp. Wallingford, CAB International.
- Kirk, R.S., Kennedy, C.R. & Lewis, J.W.** (2000) Effect of salinity on hatching, survival and infectivity of *Anguillicola crassus* (Nematoda: Dracunculoidea). *Diseases of Aquatic Organisms* **40**, 211–218.
- Køie, M.** (1988) Parasites in European eel *Anguilla anguilla* (L.) from Danish freshwater, brackish and marine localities. *Ophelia* **29**, 93–118.
- Kristmundsson, A. & Helgason, S.** (2007) Parasite communities of eels *Anguilla anguilla* in freshwater and marine habitats in Iceland in comparison with other parasite communities of eels in Europe. *Folia Parasitologica* **54**, 141–153.
- Lefebvre, F., Wielgoss, S., Nagasawa, K. & Moravec, F.** (2012) On the origin of *Anguillicoloides crassus*, the invasive nematode of anguillid eels. *Aquatic Invasions* **7**, 443–453.
- Loukili, A. & Belglyti, D.** (2007) The dynamics of the nematode *Anguillicola crassus*, Kuvahara 1974 in eel *Anguilla anguilla* (L. 1758) in the Sebou estuary (Morocco). *Journal of Parasitology Research* **100**, 683–686.
- Magurran, A.E.** (1988) *Ecological diversity and its measurement*. New Jersey, Princeton University Press.
- Maíllo, P.A., Vich, M.A., Salvadó, H., Marqués, A. & Gracia, M.P.** (2005) Parasites of *Anguilla anguilla* (L.) from three coastal lagoons of the River Ebro delta (Western Mediterranean). *Acta Parasitologica* **50**, 156–160.
- Marcogliese, D.J. & Pietrock, M.** (2011) Combined effects of parasites and contaminants on animal health: parasites do matter. *Trends in Parasitology* **27**, 123–130.
- Martínez-Carrasco, C., Ruiz de Ybañez, R., Peñalver, J., Mayo-Hernández, E., García-Ayala, A. & Muñoz, P.** (2011) Prevalence of *Anguillicoloides crassus* (Nematoda, Dracunculoidea) in wild European eels

- (*Anguilla anguilla* L.) from Mar Menor lagoon (western Mediterranean, Spain). *Revue de Médecine Vétérinaire* **162**, 154–158.
- Morand, S. & Poulin, R.** (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.
- Moravec, F.** (1994) *Parasitic nematodes of freshwater fishes of Europe*. 473 pp. Prague, Academia.
- Peñalver, J., Dolores, E.M. & Muñoz, P.** (2010) Absence of anisakid larvae in farmed European sea bass (*Dicentrarchus labrax* L.) and gilthead sea bream (*Sparus aurata* L.) in southeast Spain. *Journal of Food Protection* **73**, 1332–1334.
- Poulin, R. & Morand, S.** (1999) Geographical distances and the similarity among parasite communities of nonspecific host populations. *Parasitology* **119**, 369–374.
- Rahhou, I., Melhaoui, M., Lecomte-Finiger, R., Morand, S. & Chergui, H.** (2001) Abundance and distribution of *Anguillicola crassus* (Nematoda) in eels *Anguilla anguilla* from Moulouya Estuary (Morocco). *Helminthologia* **38**, 93–97.
- Schmidt, G.D.** (1986) *CRC handbook of tapeworm identification*. 675 pp. Boca Raton, CRC Press.
- Špakulová, M., Macko, J.K., Berrilli, F. & Dezfuli, B.S.** (2002) Description of *Bucephalus anguillae* (Trematoda: Bucephalidae), a parasite of the eel *Anguilla anguilla* (Anguillidae) from a brackish water lagoon of the Adriatic Sea. *Journal of Parasitology* **88**, 382–387.
- Székely, C., Palstra, A., Molnár, K. & Van den Thillart, G.** (2009) Impact of the swim-bladder parasite on the health and performance of European eels. pp. 201–226 in Van den Thillart, G., Dufour, S. & Rankin, J. (Eds) *Spawning migration of the European eel. Reproduction Index, a useful tool for conservation management*. Fish and Fisheries Series. Berlin, Springer-Verlag.
- Ternengo, S., Levron, C., Desideri, F. & Marchand, B.** (2005) Parasite communities in European eels *Anguilla anguilla* (Pisces, Teleostei) from a Corsican coastal pond. *Vie et Milieu* **55**, 1–6.
- Wielgoss, S., Taraschewsk, I.H., Meyer, A. & Wirth, T.** (2008) Population structure of the parasitic nematode *Anguillicola crassus*, an invader of declining North Atlantic eel stocks. *Molecular Ecology* **17**, 3478–3495.
- Winton, J.R.** (2001) Fish health management. pp. 559–639 in Wedemeyer, G.A. (Ed.) *Fish hatchery management*. 2nd edn. Bethesda, American Fisheries Society.