

The parasite community infecting flounders, *Platichthys flesus*, in the tidal Thames

H.E.M. El-Darsh and P.J. Whitfield*

Infection and Immunity Research Group, Division of Life Sciences,
King's College London, Campden Hill Road, London, W8 7AH, UK

Abstract

The composition of the parasite fauna of the flounder, *Platichthys flesus*, retrieved from two locations in the tidal Thames is described in detail for the first time. The combined parasite species list of the flounders from Lots Road in the upper tideway and West Thurrock in the middle tideway consisted of one protozoan (*Glugea stephani*), one monogenean (*Gyrodactylus* sp.), four larval digeneans (*Cryptocotyle concava*, *Timoniella imbutiforme*, *T. praeterita*, and *Labratrema minimus*), five adult digeneans (*Derogenes varicus*, *Lecithaster gibbosus*, *Podocotyle* sp., *Plagioporus varius*, and *Zoogonoides viviparus*), one larval cestode (unidentified tetraphyllidean), one or possibly more larval nematodes (unidentified) plus five adult nematodes (*Capillaria* sp., *Cucullanus heterochrous*, *C. minutus*, *Contraecum* sp. and *Goezia* sp.), two acanthocephalans (*Pomphorhynchus laevis* and *Acanthocephalus anguillae*), three copepods (*Lepeophtheirus pectoralis*, *Acanthochondria* sp. and *Lernaeocera branchialis*), and one mollusc (unidentified glochidia). The overall parasite community of flounders from Lots Road and West Thurrock were compared in terms of species richness and diversity. The parasite community in flounders from the former location in the upper tideway was found to be less diverse than that of its counterpart at West Thurrock in the middle estuary. The component community of Lots Road flounders was dominated by the acanthocephalan *Pomphorhynchus laevis*.

Introduction

There have been several parasitological studies on the flounder *Platichthys flesus* in the Thames Estuary in recent years (Munro *et al.*, 1989; Munro, 1992; Messoudi, 1993), from which several parasite species have been identified. Pilcher (1989) compiled a list of the known parasites of flounders of the Thames tideway for the National Rivers Authority (NRA), in which only four species were named. These were the nematode *Capillaria* sp. (erroneously identified as *Paracapillaria* sp. in the report), and the copepods *Lernaeocera branchialis*, *Lepeophtheirus pectoralis* and *Acanthochondria minuta*. Subsequently Munro (1992) described a further five parasite species, the digenean *Zoogonoides viviparus*, the nematode *Cucullanus heterochrous*,

other unidentified nematode larvae, and the acanthocephalans *Pomphorhynchus laevis* and *Acanthocephalus anguillae*. Messoudi (1993) added a further digenean metacercarial infection, *Cryptocotyle concava*, to this list bringing the cumulative total to ten species.

On the basis of the available information cited in these sources, it seems that the richness of the parasite community of flounders in the tidal Thames is rather impoverished compared to that of flounders in other regions of Britain and Europe. MacKenzie & Gibson (1970) identified as many as 27 macroparasite species in flounders in the Ythan Estuary, on the east coast of Scotland, and Möller (1974) found 14 parasite species utilizing flounders in the Kieler Forde in German waters. Sulgostowska *et al.* (1987), however, reported the presence of only seven helminths in a flounder sample of 663 fish retrieved from Gdansk Bay and the south-east Baltic. This apparently poor richness level is comparable to that of Thames flounders from which seven helminths have

* Author for correspondence.
Fax: 0171 333 4500
E-mail: phil.whitfield@kcl.ac.uk

also been reported, despite the fact that flounders are catadromous and vagile species (Kennedy *et al.*, 1986) that migrate annually between marine, brackish and fresh-water ecosystems. These attributes should, in themselves, positively influence the component parasite fauna of flounders in the Thames by increasing its richness and diversity (Esch *et al.*, 1988; Holmes, 1990; Kennedy, 1990). Evidently the previously described parasite fauna of flounders in the tidal Thames does not appear to be either rich or diverse. This could be the result of unknown biotic or abiotic factors, or simply because the fauna has been significantly underestimated and is in need of a more thorough and detailed appraisal to ascertain its actual composition.

The present investigation was therefore undertaken to determine the composition of the parasite fauna of flounders in the tidal Thames with greater comprehensiveness, and to understand some aspects of the epidemiology of the parasites discovered. Temporal and host-size related infection levels were monitored and discussed in relation to host movement within the estuary. In addition, a preliminary examination of the parasite community structure, richness and diversity of flounder hosts in the Thames Estuary was undertaken for the first time.

Materials and methods

Details of the sampling and examination of flounders for the epidemiological survey have been described in a previous paper (El-Darsh & Whitfield, 1999) which concentrated on an analysis of metacercarial infections. The examination of flounders for additional macro- and microparasites was undertaken in conjunction with the examination for metacercarial cysts. An external examination of the host's surface for ectoparasites preceded the examination for metacercarial cysts. After exposure and inspection of the visceral cavity for the presence of any parasites *in situ*, the alimentary tract was removed and placed in a petri dish containing teleost saline (7‰) before making a longitudinal incision along its length. Parasites were individually identified and their number and location in each organ recorded. In all, 390 flounders were examined.

The definitions provided by Bush *et al.* (1997) were used for the prevalences (denoted by % in tables) of each of the parasitic infections of the samples, and values of mean abundance (\bar{x}) and mean intensity (I). The flounders were also divided into three main samples as described in the previous paper (El-Darsh & Whitfield, 1999), i.e. 1992 Lots Road Power Station (NGR TQ 246 770) sample taken in January, February, March, April and October 1992; 1993 West Thurrock Power Station (NGR TQ 592 770) sample taken in June, July and August 1992; and 1993/94 Lots Road sample taken from November 1993 to October 1994.

For measurements of community structure, a generalized indirect comparison of the number of component species was undertaken for each of the main samples using the definition provided by Bush *et al.* (1990), i.e. component species are those that occur in at least 10% of the sampled fish. For a direct comparison, however, of the community structure of parasites of flounders at West

Thurrock and Lots Road a pair of more comparable samples was used, the constants being host size and season. Therefore the June, July and August West Thurrock sample was compared with the corresponding months in the 1993/94 Lots Road sample, which demonstrated a similar range of host lengths.

The measures used were the total number of parasite species, the number of component species, Simpson's Index (D) ($1/C$, where $C = \sum p_i^2$ and $p_i^2 = (N_i/N_T)^2$ where p_i is a proportion, n_i the number of individuals in the i th species and N_T the total number of individuals in the sample), and the Berger-Parker Dominance Index ($d = N_{\max}/N_T = p_{i\max}$ which expresses the proportion of the total sample (N_T) that is due to the dominant species, whose abundance = N_{\max}). The Percentage Similarity Index ($= \sum p_{i\min} [p_{ai}, p_{bi}] \times 100\%$, where $p_{i\min}$ represents the minimum proportion (p_i) demonstrated by each species common to both community a and community b) was used as a quantitative measure of similarity between West Thurrock and Lots Road, and Sorensen's or Czekanowski's Coefficient ($C_s = 2j/a + b$, where a = no. of species in community a, b = no. of species in community b, and j = no. of species common to both) was used as a qualitative measure of similarity (Southwood, 1978).

Results

During this investigation, several parasite species were discovered utilizing flounders as either definitive or intermediate hosts for the first time. Table 1 lists these newly recorded parasites along with parasites recorded in previous investigations of flounders in this region of the Thames.

From table 1 it is evident that significantly more parasite species infect flounders in the upper and middle Thames Estuary than were previously recognized (Pilcher, 1989; Munro, 1992; Messoudi, 1993). In those previous studies ten species had been identified from flounders in the tidal Thames, including seven helminths (one of which was a digenean metacercaria) and three ectoparasitic copepods. In the present study, 14 additional parasitic infections have been detected in flounders, including three new digenean (metacercarial) species.

The following sections are an overview of the infection characteristics of these parasites, including a detailed analysis of their infection parameters in relation to host size and monthly variations. Frequency distributions are described by reference to variance/mean ratios in the overall data tables. Parasite community richness, diversity and similarity comparisons are also considered between Lots Road and West Thurrock, Lots Road winter and Lots Road summer, and Lots Road 1992 and Lots Road 1994.

Epidemiological survey

Overall infection characteristics

The overall infection characteristics of the micro- and macroparasites of the three flounder samples are summarized in tables 2, 3, and 4. These tables show that only a few parasite species were frequently present in flounders retrieved from both the two sampling locations in the Thames tideway, including *Pomphorhynchus laevis*, the

Table 1. Updated list of parasite species infecting flounders, *Platichthys flesus*, in the tidal Thames.

Protozoa
<i>Glugea stephani</i>
Monogenea
<i>Gyrodactylus</i> sp.
Digenea (larval)
<i>Cryptocotyle concava</i> * ³
<i>Labratrema minimus</i>
<i>Timoniella imbutiforme</i>
<i>T. praeterita</i>
Digenea (adult)
<i>Deroogenes varicus</i>
<i>Lecithaster gibbosus</i>
<i>Podocotyle</i> sp.
<i>Plagioporus varius</i>
<i>Zoogonoides viviparus</i> * ²
Cestoda
Tetraphyllidean larvae
Nematoda
Unidentified nematode larvae* ²
<i>Contraecaecum</i> larvae and (pre-adults)
<i>Capillaria</i> sp.* ^{1,2}
<i>Cucullanus heterochrous</i> * ²
<i>C. minutus</i>
<i>Goezia</i> sp.
Acanthocephala
<i>Acanthocephalus anguillae</i> * ²
<i>Pomphorhynchus laevis</i> * ²
Crustacea
<i>Lepeophtheirus pectoralis</i> * ^{1,2}
<i>Acanthochondria</i> sp.* ^{1,2}
<i>Lernaecocera branchialis</i>
(In-copulo adults and larvae)* ^{1,2}
Mollusca
Glochidia (unidentified)

*Previously recorded parasites of flounders in the same location (sources ¹Pilcher, 1989; ²Munro, 1992; ³Messoudi, 1993).

predominant gut helminth at both sampling sites, the unidentified nematode larvae, and *Capillaria* sp. In addition, the West Thurrock sample harboured substantially more marine/estuarine parasite species than the Lots Road samples, whereas freshwater parasites such as *Acanthocephalus anguillae* and the glochidia were only detected in the Lots Road samples (tables 2–4).

Many parasite species were not sufficiently represented either in numbers or prevalence to be considered as component parasites, although they added to the overall richness of each sample. The epidemiological data has not been included for some parasite species since they were either not recognized as parasitic infections until later samples, i.e. the glochidia, or, because of the loose nature of their attachment, the individuals that were detected were not considered to be entirely representative of the true infrapopulations, i.e. the monogenean *Gyrodactylus* sp. These were therefore only included as a record of their presence.

The corresponding mean abundances, mean intensities, standard deviations, and variance to mean ratios

for the remaining parasites, in each flounder sample group are summarized in tables 2–4.

Temporal variations in infection levels

The 1993/94 Lots Road flounder sample was examined in an attempt to determine any temporal variations that were occurring in the parasite infection characteristics. The most prevalent parasites are presented in table 5 which summarizes the variations in their temporal infection levels in the three flounder samples, and also includes mean intensities and mean abundances. The infection characteristics of the remaining, less prevalent parasites are summarized in table 6. Details of the infection characteristics of the digenean metacercariae found in flounders are presented in El-Darsh & Whitfield (1999).

The monthly prevalences, mean abundances and mean intensities of *P. laevis* (table 5) were high throughout autumn and winter 1993/94, only fluctuating slightly during this period. They were reduced, however, in July 1994 after a gradual decline beginning in April.

No such discernible pattern related to season was seen in the infection parameters of the unidentified nematode larvae which fluctuated erratically throughout the year (table 5).

A slight reduction in the prevalences of the tetraphyllidean larvae was noticed over the sampling period with a complete absence in July and August 1994 (table 5). The larvae were also absent in the same corresponding months in the 1992 West Thurrock sample (table 5).

The nematode *Capillaria* sp. was generally present throughout the year with the exception of February 1994, although there was no prominent pattern. The prevalences remained relatively stable in the autumn of 1993 but fluctuated in the subsequent months (table 5). The summer monthly prevalences at West Thurrock, however, were much higher and consistent, in contrast to the corresponding months in the 1994 Lots Road sample (table 5). Any temporal pattern in the mean abundance and mean intensity of *Capillaria* sp. infection was similarly undetectable in the 1993/94 Lots Road sample.

The most evident temporal infection patterns were exhibited by the nematode *Goezia* sp. which only appeared during the late spring and early summer months of April and May at Lots Road, and June and July at West Thurrock (table 5).

Infection levels related to host size

The infections of the five most prevalent helminth parasites in the 1993/94 flounder sample, were examined further in relation to each host length category as a measurement of host size. The results are illustrated graphically in fig. 1 (a–e).

A very distinct pattern is apparent in the infection prevalences of *P. laevis* which increase steadily with flounder length, reaching a peak of 100% in flounders measuring 131–150 mm S.L. and over (fig. 1a). The mean abundance mirrors this pattern.

The unidentified nematode larvae did not exhibit any relationship correlated with flounder length, with length groups infected to varying degrees (fig. 1b). The mean abundance pattern of the infection, on the other hand, demonstrated an overall steady increase in this parameter related to host length (fig. 1b).

Table 2. The overall infection characteristics, arranged in descending order of prevalence, of the parasites of flounders, *Platichthys flesus*, retrieved from the upper Thames tideway at Lots Road in 1993/94 (n = 224).

Parasite species	No. of parasites	No. of infected fish	%	\bar{x}	I	S.D.	S^2/\bar{x}
<i>Pomphorhynchus laevis</i>	5407	193	86	24	28	± 37	57.6
Unidentified nematode larvae	821	136	67	3.6	6	± 6.4	11.5
<i>Cryptocotyle concava</i> metacercariae	1125†	78	34.8	5.02	14.4	± 240	48
<i>Timoniella</i> spp. metacercariae	292†	42	18.8	1.3	6.95	± 17.7	13.7
<i>Capillaria</i> sp.	179	31	14	0.8	5.7	± 3.4	14.3
Tetraphyllidean larvae	317	26	12	1.4	12.2	± 6.8	33.2
<i>Labratrema minimus</i> metacercariae	158†	21	9.3	0.7	7.8	± 14.7	21
<i>Goezia</i> sp.	29	13	5.8	0.1	2.2	± 0.7	4.2
Glochidia	31	12	5.3	0.1	2.6	± 0.7	6
<i>Zoogonoides viviparus</i>	26	8	3.6	0.1	3.2	± 0.7	5
<i>Lecithaster gibbosus</i>	3	3	1.3	0.013	1	± 0.2	3
<i>Contracaecum</i> sp.	5	3	1.3	0.02	1.7	± 0.2	2.5
<i>Cucullanus heterochrous</i>	2	2	0.9	0.01	1	± 0.09	1
<i>Glugea stephani</i>	20‡	1	0.5	0.09	20	± 1.3	19.7
<i>Acanthocephalus anguillae</i>	12	1	0.5	0.05	12	± 0.8	12
<i>Plagioporus varius</i>	1	1	0.5	0.004	1	± 0.06	1
<i>Lepeophtheirus pectoralis</i>	1	1	0.5	0.004	1	± 0.06	1

†The metacercarial numbers utilized here (derived from El-Darsh & Whitfield, 1999) are not absolute but minimal numbers because of the difficulties associated with sampling the total body mass of fish.

‡*Glugea* parasite numbers relate to xenomas (spore containing capsules) rather than individual spores.

The tetraphyllidean larvae demonstrated a gradual increase in prevalence and mean abundance with increasing host length (fig. 1c).

Capillaria sp. is perhaps the parasite with the least discernible pattern of infection prevalences related to host size, and major fluctuations were observed between length categories (fig. 1d). The mean abundance, similarly, did not show any size-related pattern (fig. 1d).

Goezia sp. was restricted to flounders ranging between 111 mm to 150 mm long, a range corresponding to the late 1+, and early 2+ age classes (fig. 1e).

Frequency distribution of micro- and macroparasites of flounders

The variance to mean ratio (denoted by S^2/\bar{x} in the tables) was used to determine the level of over-dispersion in the frequency distribution patterns demonstrated by each parasite, and the results of these are included in tables 2–4. All the parasites that infected more than one flounder host individual were found to be over-dispersed, with values for the variance to mean ratio significantly greater than unity. The parasites with the greatest over-dispersion characteristics were *P. laevis*, the

Table 3. The overall infection characteristics, arranged in descending order of prevalence, of the parasites of flounders, *Platichthys flesus*, retrieved from the upper Thames tideway at Lots Road in 1992 (n = 121).

Parasite species	No. of parasites	No. of infected fish	%	\bar{x}	I	S.D.	S^2/\bar{x}
<i>Pomphorhynchus laevis</i>	4227	113	93	35	37	± 60.7	91
Unidentified nematode larvae	701	66	55	5.7	12.7	± 10.5	19.4
<i>Cryptocotyle concava</i> metacercariae	1709†	50/118*	42.4	14.5	34.2	± 345	46
<i>Timoniella</i> spp. metacercariae	122†	21/97*	21.6	1.25	5.8	± 10.2	8
<i>Labratrema minimus</i> metacercariae	109†	13/97*	13.4	1.1	8.4	± 16.6	15.1
<i>Capillaria</i> sp.	118	11	9	1	11	± 5.5	30.4
<i>Cucullanus heterochrous</i>	29	10	8	0.2	3	± 0.9	4
Tetraphyllidean larvae	32	4	3.3	0.3	8	± 2.5	20
<i>Zoogonoides viviparus</i>	34	3	2.5	0.3	11	± 2.6	22
<i>Goezia</i> sp.	3	3	2.5	0.02	1	± 0.2	1
<i>Glugea stephani</i>	68‡	2	1.7	0.6	34	± 6.1	66.3
<i>Cucullanus minutus</i>	1	1	0.8	0.01	1	± 0.09	1
Glochidia	–	–	–	–	–	–	–
<i>Gyrodactylus</i> sp.	–	–	–	–	–	–	–

*Sample size if different from n = 121.

†The metacercarial numbers utilized here (derived from El-Darsh & Whitfield, 1999) are not absolute but minimal numbers because of the difficulties associated with sampling the total body mass of fish.

‡*Glugea* parasite numbers relate to xenomas (spore containing capsules) rather than individual spores.

Table 4. The overall infection characteristics, arranged in descending order of prevalence, of the parasites of flounders, *Platichthys flesus*, retrieved from the middle Thames tideway at West Thurrock in 1992 (n = 45).

Parasite species	No. of parasites	No. of infected fish	%	\bar{x}	I	S.D.	S^2/\bar{x}
<i>Cryptocotyle concava</i> metacercariae	332†	23	51.1	7.4	14.4	± 2866	197.6
<i>Pomphorhynchus laevis</i>	335	21	46.6	7.4	16	± 12.9	22.6
<i>Cucullanus minutus</i>	27	16	35.5	0.6	1.7	± 1	1.6
<i>Capillaria</i> sp.	91	13	28.9	2	7	± 9	41
<i>Goezia</i> sp.	52	13	28.9	1.2	4	± 2.4	5
<i>Timoniella</i> spp. metacercariae	84†	9	20	1.9	9.3	± 81.8	43.9
Unidentified nematode larvae	39	9	20	0.9	4.3	± 2.6	8
<i>Lepeophtheirus pectoralis</i>	108	6	13.3	2.4	18	± 9.9	41.6
<i>Labratrema minimus</i> metacercariae	55†	6	13.3	1.2	9.2	± 13.5	11.3
<i>Cucullanus heterochrous</i>	7	5	11	0.2	1.4	± 0.5	1
<i>Lernaocera branchialis</i> larvae	70	4	8.9	1.6	17.5	± 6	62.5
<i>Lecithaster gibbosus</i>	18	3	6.7	0.4	6	± 1.7	7
<i>Podocotyle</i> sp.	12	3	6.7	0.3	4	± 1.5	1
<i>Zoogonoides viviparus</i>	5	3	6.7	0.1	1.6	± 0.4	2
<i>Plagioporus varius</i>	3	3	6.7	0.1	1	± 0.3	1
<i>Glugea stephani</i>	8‡	2	4.4	0.2	4	± 1.1	6.5
<i>Derogenes varicus</i>	4	1	2.2	0.1	4	± 0.6	4

†The metacercarial numbers utilized here (derived from El-Darsh & Whitfield, 1999) are not absolute but minimal numbers because of the difficulties associated with sampling the total body mass of fish.

‡*Glugea* parasite numbers relate to xenomas (spore containing capsules) rather than individual spores.

digenean metacercariae, the unidentified nematode larvae, the tetraphyllidean larvae, and *Capillaria* sp.

Parasite-richness of the three flounder samples

As is evident in table 1, a cumulative total of 24 parasite species was detected in flounders collected from the

Thames tideway, belonging to most of the major parasitic taxa. Several of these parasites were found either at Lots Road or at West Thurrock or, more commonly, at both locations but exhibiting different prevalences.

The total number of parasite species detected in flounders in the 1992 West Thurrock sample was 17, these were detected in only 45 flounders retrieved from

Table 5. Infection characteristics of the most prevalent parasites (*Pomphorhynchus laevis*, nematode larvae, cestode larvae, *Capillaria* sp. and *Goezia* sp.

Months	<i>Pomphorhynchus laevis</i>			Unidentified nematode larvae			Tetraphyllidean larvae			<i>Capillaria</i> sp.			<i>Goezia</i> sp.		
	%	\bar{x}	I	%	\bar{x}	I	%	\bar{x}	I	%	\bar{x}	I	%	\bar{x}	I
Nov '93	100.0	37	37	78	6.5	8.3	29	5	17	21.4	0.6	3	0	0	0
Dec	100	44	44	67	3.2	4.8	29	3.8	13	16.6	2.6	15.8	0	0	0
Jan '94	88	20.6	23.6	63	4.1	6.6	0	0	0	25	2.7	11	0	0	0
Feb	100	44.7	44.7	75	2.1	4.2	16	1.4	8.5	0	0	0	0	0	0
Mar	100	–	–	–	–	–	–	–	–	–	–	–	0	0	0
Apr	82	27	34.5	45	2.6	5.8	15	2.2	14.4	3	0.1	3	0	0	0
May	77.7	11.8	15.2	25	0.6	2.2	11	1.7	14	11	0.8	6.5	25	0.7	2.6
Jun	83	21	25	91.6	6.1	6.6	4	0.2	4	42	1.5	3.7	12.5	0.2	1.7
Jul	56	3.5	6.2	64	2.4	3.7	0	0	0	4	0.1	3	0	0	0
Aug	96.4	14.7	15.2	85	8.3	9.7	0	0	0	10.7	0.2	2	0	0	0
Sep	100	10.6	10.6	62	2.1	3.4	12.5	0.4	3	12.5	0.3	2	0	0	0
Oct	100	30.6	30.6	40	3.1	7.8	10	0.3	3	20	0.8	4	0	0	0
Jan '92	94	38	40.4	88	6.9	7.8	0	0	0	19	0.3	1.3	0	0	0
Feb	90	20.3	22.5	70	6.2	8.9	0	0	0	0	0	0	0	0	0
Mar	96	27	28	66	7.4	11.2	8.3	0.1	2	4.1	0.2	4	0	0	0
Apr	92.3	27	29	38.5	2.5	6.6	0	0	0	3.8	0.2	5	11.5	0.1	1
Oct	100	29	29	–	–	–	–	–	–	–	–	–	–	–	–
Nov	94	55	58	36.3	6.7	18.4	3	0.8	27	18	3.2	17.5	0	0	0
Jun '92	33	13.6	41	0	0	0	0	0	0	33.3	1	3	66.7	5.3	8
Jul	47	6.5	14	19	1	5	0	0	0	27.7	2.3	8.3	30	1	3.2
Aug	50	7.2	14.3	33	0.7	2	0	0	0	33.3	0.8	2.5	0	0	0

Table 6. Monthly prevalences for the remaining parasites of flounders not presented in table 5.

Parasite species	1993		Lots Road 1994										Lots Road 1992					W. Thurrock 1992			
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Jan	Feb	Mar	Apr	Oct	Nov	Jun	Jul	Aug
<i>Cucullanus minutus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	42%	33%
																				0.61	0.83
<i>C. heterochrous</i>	-	4%	-	-	-	-	-	-	-	-	-	-	6%	5%	4%	4%	+	15%	33%	8%	16%
		0.04											0.06	0.1	0.04	0.08		0.6	0.7	0.11	0.16
<i>Contracaecum</i> larva	-	-	-	8%	-	-	3%	4%	-	-	-	-	-	-	-	-	-	-	-	-	-
				0.25			0.03	0.04													
<i>Contracaecum</i> pre-adult	-	-	-	-	4%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
					0.04																
<i>Zoogonoides viviparus</i>	-	4%	-	-	-	6%	8%	-	-	-	13%	10%	-	-	-	-	-	-	-	6%	17%
		0.04				0.2	0.4				0.4	0.2								0.1	0.3
<i>Plagioporus varius</i>	7%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	8%	-
	0.14																			0.08	
<i>Lecithaster gibbosus</i>	-	4%	-	-	-	-	-	8%	-	-	-	-	-	-	-	-	-	-	33%	6%	-
		0.04						0.08											1.3	0.39	
<i>Podocotyle</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6%	16%
																				0.3	0.16
<i>Derogenes varicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3%	-
																				0.1	
<i>Acanthocephalus anguillae</i>	7%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.07																				
<i>Lepeophtheirus pectoralis</i>	-	-	-	-	3%	-	-	-	-	-	-	-	-	-	-	-	-	-	33%	14%	-
					0.03														10.6	2	
<i>Lernaeocera branchialis</i> larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33%	8%	-
																			12	0.9	
Glochidia	-	-	-	75%	100%	3%	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
				2	3	0.03															
<i>Glugea stephani</i>	-	-	-	8%	-	-	-	-	-	-	-	-	-	-	-	4%	-	3%	-	3%	16%
				1.7											0.4		2		0.19	0.16	
<i>Gyrodactylus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	5%	-	-	-	-	-	-	-
														0.55							

Where possible, the mean abundance is also included below the percentage prevalence value. - Denotes absence in the monthly sample. + Denotes the presence of a parasite when the prevalence has not been determined.

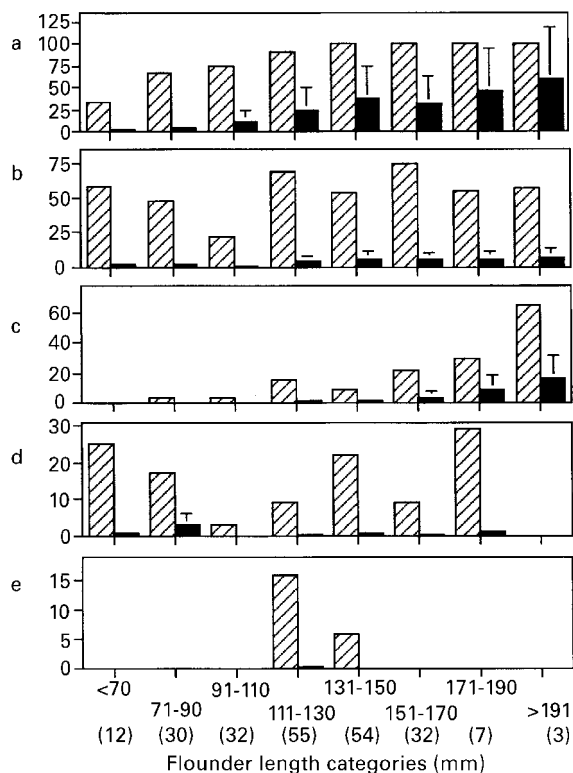


Fig. 1. The percentage prevalence (▨) and mean abundance (■) of some helminth parasites in ascending flounder length categories (sample size included in parenthesis). a, *Pomphorhynchus laevis*; b, unidentified nematode larvae; c, tetraphyllidean larvae; d, *Capillaria* sp.; e, *Goezia* sp.

that location (*Timoniella imbutiforme* and *T. praeterita* are referred to by their generic names *Timoniella* spp. in this investigation as they could not be conveniently differentiated during the course of the epidemiological examination). During the same sampling year, a total of 13 parasite species were removed from 121 flounders retrieved from Lots Road. In 1993/94, however, the Lots Road flounder sample yielded significantly more parasite species, numbering 17 in total. The difference in the number of parasite species detected in the two Lots Road samples was attributed mainly to the difference in the sample size. To test this assumption, a species richness-sample effort curve (Martínez, 1995) was used to determine if the sample size was sufficient to produce a good estimate of the pool of parasites utilizing flounders in each location. The results of this test are presented in fig. 2(a-c). These curves reach a continuing maximum level when the sample size has discovered a high percentage of the total parasite species available in the host population, thus indicating the effectiveness of the sample size.

It is evident from these sample effort graphs that the size of the 1993/94 Lots Road sample (fig. 2a) was sufficient to produce a good estimate of the true parasite-richness of the corresponding fish communities at the time of sampling. However, the 1992 West Thurrock

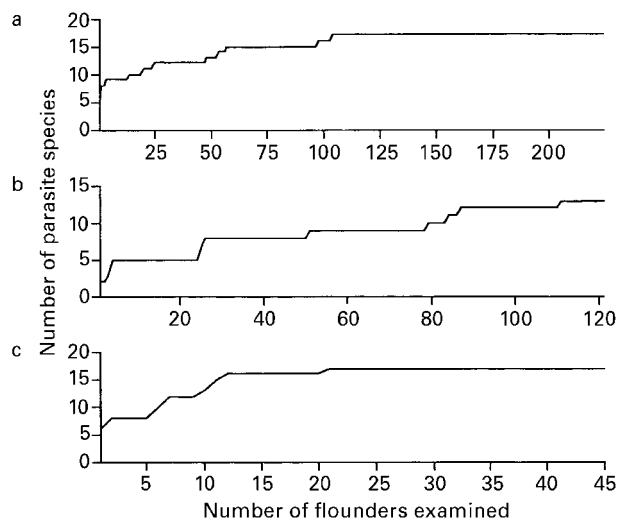


Fig. 2. Species richness-sample effort curve for each of the three flounder samples retrieved between January 1992 and September 1994. a, Lots Road flounder sample 1993/94; b, Lots Road flounder sample 1992; c, West Thurrock flounder sample 1992.

sample effort curve, although superficially similar to the 1993/94 Lots Road sample, in fact resembled more closely that of the 1992 Lots Road sample effort curve, or perhaps an enlarged portion of the left side of the 1993/94 sample effort curve. Therefore, both the 1992 flounder samples from Lots Road and West Thurrock were not sufficiently large to disclose the overall parasite community of flounders collected from both these two sites in the tideway, but were nevertheless large enough to demonstrate the presence of the more common parasite species that represent the component community of each location.

Table 7 summarizes the main characteristics of each sample, and identifies at least six component parasite species in the 1993 Lots Road sample, but ten in the West Thurrock sample, despite the differences in the sample sizes.

The suggestion from the table, therefore, is that the parasite community of flounders at West Thurrock is much richer than that at Lots Road sampled over two different periods, and possibly more diverse. However, a direct comparison of the component community of the three samples was not possible since they were retrieved in different seasons. A comparison was possible, however, between the June, July and August months of the 1993/94 Lots Road samples with the West Thurrock samples which were retrieved in the same corresponding months in 1992. This comparison is presented below.

Component community

Lots Road vs. West Thurrock

The total number of parasites detected in the summer (June, July and August) samples of both Lots Road (1994), and West Thurrock (1992) flounders were compared for richness, dominance and diversity. The results are

Table 7. Characteristics of the parasite fauna of the three main flounder samples.

Characteristics	Lots Road 1993/94	Lots Road 1992	West Thurrock '92
Number of fish examined	224	97*	45
No. of fish infected (%)	91.5	96.6	91.1
No. of parasite species†	16	13	16
Total no. of parasites	8409	6088	1239
No. of allogenic species	1	1	1
No. of autogenic species	15	12	15
No. of component parasites‡	6	5	10
No. of specialists	None	None	None
p_i of dominant species	0.643	0.562	0.270
Identity of dominant species	<i>P. laevis</i>	<i>P. laevis</i>	<i>P. laevis</i>
Character of dominant species	Generalist, autogenic	Generalist, autogenic	Generalist, autogenic

*The number of flounders examined for all parasites including the metacercarial cysts in the 1992 Lots Road sample.

†Includes all the parasite species identified except for the microsporidian, *Glugea stephani*.

‡As defined by Bush *et al.* (1990).

presented in table 8. From the table it can be concluded that the component parasite community of West Thurrock flounders comprised ten parasite species in the summer, whereas Lots Road flounders harboured only five during the same season, despite a total of 15 parasites being detected in the former, and ten in the latter. Richness in itself, however, is not a valid measure of diversity, and distribution of dominance must also be taken into account when examining this aspect of the component community.

The parasite community of Lots Road flounders has a large Berger-Parker Dominance Index provided by the acanthocephalan *Pomphorhynchus laevis*. Consequently

the distribution of dominance was minimal, and the diversity was considerably lower (Kennedy & Pojmanska, 1996) than that of West Thurrock.

In contrast, although *Pomphorhynchus laevis* appears the overall dominant species, in terms of p_i values, in West Thurrock flounders, it is nevertheless closely rivalled by *Cryptocotyle concava*, which demonstrates an almost identical p_i value to the former (table 8). Consequently there is a more even distribution of dominance, shared between these two species and to a lesser extent between the remaining components of the parasite community, and hence the comparatively higher diversity observed.

Table 8. The relative abundance (presented as a proportion p_i of the total number of parasites) of each species detected in the June, July and August samples retrieved from West Thurrock (1992) and Lots Road (1994), and a comparison of the dominance, diversity and similarity of the parasite communities at the two locations.

	Lots Road			West Thurrock			
	%*	n_i	p_i	%*	n_i	p_i	p_i min
<i>Pomphorhynchus laevis</i>	58.4	987	0.611	46.6	335	0.270	0.270
Unident. nematode larvae	80.5	438	0.271	20	39	0.031	0.031
<i>Capillaria</i> sp.	18.2	45	0.028	28.9	91	0.073	0.027
Tetraphyllidean larvae	1.3	4	0.002	–	–	–	–
<i>Goezia</i> sp.	3.9	5	0.003	28.9	52	0.042	0.003
<i>Cucullianus minutus</i>	–	–	–	35.5	27	0.022	–
<i>C. heterochrous</i>	–	–	–	11	7	0.006	–
<i>Contraecaeum</i> sp.	1.3	1	0.001	–	–	–	–
<i>Cryptocotyle concava</i>	14.3	97	0.060	51.1	332	0.268	0.060
<i>Timoniella</i> spp.	10.4	21	0.013	20	84	0.068	0.013
<i>Labratrema minimus</i>	2.6	16	0.010	13.3	55	0.044	0.010
<i>Zoogonoides viviparus</i>	–	–	–	6.7	5	0.004	–
<i>Lecithaster gibbosus</i>	2.6	2	0.001	6.7	18	0.015	0.001
<i>Podocotyle</i> sp.	–	–	–	6.7	12	0.009	–
<i>Derogenes varicus</i>	–	–	–	2.2	4	0.003	–
<i>Lepeophtheirus pectoralis</i>	–	–	–	13.3	108	0.087	–
<i>Lernaecocera branchialis</i>	–	–	–	8.9	70	0.056	–
Σ		1616	1		1239	0.998	0.415
Simpson's Diversity Index		2.22			5.88		
Berger-Parker Dominance Index		0.611			0.270		
Czekanowski's Coefficient				0.64			
% Similarity Lots Road vs. W. Thurrock				41.5			

*Percentage prevalence of each species in the June, July and August samples only.

Table 9. A comparison of the dominance, diversity and similarity of the parasite communities of Lots Road flounders during two different seasons, winter and summer.

Characteristics	Lots Road winter*	Lots Road summert
Number of fish examined	44	77
No. of parasite species	12	10
No. of component parasites	8	5
Total no. of parasites	2936	1616
Berger-Parker Index of dominant species	0.601	0.611
Identity of dominant species	<i>P. laevis</i>	<i>P. laevis</i>
Sum p_i^2	0.411	0.451
Simpson's Diversity Index	2.43	2.22
Czekanowski's Coefficient		0.81
% Similarity winter vs. summer		75.8%

*Representing December, January and February 1993/94 Lots Road samples.

†Representing June, July and August 1993/94 Lots Road sample.

The differences in the exhibited dominance and diversity in the two different communities, as well as the difference in richness, have also contributed to the poor Percentage Similarity between the two localities despite both being from the same estuary. Sorensen's (or Czekanowski's Coefficient), a qualitative measure of similarity, is slightly higher than the Percentage Similarity and thus suggests that there is some measure of overlap between the two communities, at least in the type of parasite species present.

Finally, it is important to note that although some parasites demonstrate significantly high prevalences, enough to assign component species status to them, they are not present in sufficient numbers to contribute or make an impact on community diversity, i.e. *Cucullanus minutus* exhibited a prevalence of 35.5% in the West Thurrock sample, allowing it recognition as a member of the component community, but its p_i^2 value was less than 0.001 and therefore it made no significant contribution to the diversity.

Lots Road summer vs. Lots Road winter

The temporal infection characteristics of several of the parasite species in the 1993/94 Lots Road sample, represented by their prevalences, indicated a poor presence in the summer months (June, July and August) in contrast to the winter (December, January and February) (tables 5 and 6). This was assumed to reflect on the richness and diversity of the community, and therefore a direct comparison of the two seasons was considered to test the validity of this assumption. Table 9 shows that Lots Road flounder samples harboured a component community comprising as many as eight species in winter, whereas summer samples harboured only five. Diversity, however, remained relatively similar (winter = 2.43, summer = 2.22). Quantitative and qualitative similarity indices were exceptionally high suggesting that the component parasite community was generally unaltered, both in species and proportion, across the two seasons.

Lots Road 1992 vs. Lots Road 1994

Long-term stability of the parasite community of flounders in the Lots Road region over the epidemiological

survey period was tested between April 1992 and April 1994, the results of which are included in table 10. The number of species in the component community of flounders remained relatively unchanged in April 1992 and April 1994, and the high qualitative and quantitative similarity indices imply that the same species are effectively present in similar proportions.

Pomphorhynchus laevis dominated in both these samples exhibiting almost identical p_i values, which probably conferred most of the quantitative Similarity Index between the two, and lowered the Diversity Index value in each sample. The most important fact, however, that can be deduced from the results is that the infection with *P. laevis* remained almost unchanged over the duration of the sample period (1992/1994) implying an underlying stability in the population biology of this species and consequently of the parasite community at Lots Road.

Discussion

This study has provided evidence of the presence of a much richer parasite fauna occupying flounders in the Thames tideway than was previously recognized. Prior to this investigation, the parasite fauna of flounders in the upper Thames tideway was believed to consist of only seven helminths and three parasitic copepods (Munro, 1992; Pilcher, 1989; Messoudi, 1993). An additional 11 helminths, one protozoan and one parasitic molluscan species are described here for the first time infecting flounders in the Thames tideway (table 1). Not all of these, however, were present in both Lots Road and West Thurrock flounders, possibly due to the influence of the upstream freshwater river on the former location, and the marine lower estuary on the latter (Pilcher, 1989; Chen, 1994). For example, freshwater parasites such as glochidia and *Acanthocephalus anguillae* were more prominent in Lots Road flounders, whereas marine parasites such as *Lernaecera branchialis*, *Lepeophtheirus pectoralis*, *Podocotyle* sp., and *Plagioporus varius* occurred mainly in West Thurrock flounders. Nevertheless, the overriding fact remained that flounders at both locations were dominated, or co-dominated, by estuarine parasites.

Table 10. The overall results comparing the structure of the component parasite community of flounders retrieved from Lots Road in April 1992 and April 1994.

Characteristics	Lots Road 1992	Lots Road 1994
Number of fish examined	26	33
No. of parasite species	8	10
No. of component parasites	4	5
Total no. of parasites	904	1292
p_i of dominant species	0.772	0.771
Identity of dominant species	<i>P. laevis</i>	<i>P. laevis</i>
Sum p_i^2	0.618	0.605
Simpson's Diversity Index	1.62	1.65
Czekanowski's Coefficient		0.78
% Similarity 1992 vs. 1994		60.1%

Epidemiology

The most prevalent helminth parasite of the gut was *Pomphorhynchus laevis* in both West Thurrock and Lots Road flounders, although the prevalences were markedly different at both locations. Munro (1992) showed that this was mainly due to the difference in the spatial distribution of the intermediate host of this species, *Gammarus zaddachi*, in the estuary which is at the seaward limit of its ecological range at West Thurrock. In addition, the different feeding habits employed by flounders in the upper and middle estuary affect this parameter to a certain extent. Koie (1983) also found that the geographical distribution of the intermediate hosts of digenean parasites of the common dab, *Limanda limanda*, was one of the important factors influencing the presenting prevalences of these parasites in varying locations, especially if they were acquired through feeding. Flounders are opportunistic feeders, feeding on whatever organisms are available (Chen, 1994) and, in the upper estuary, where *G. zaddachi* is present in large numbers, there appears to be little variety in the parasite fauna of the gut (table 8). In the middle estuary, however, where there are more food organisms available and *G. zaddachi* is less prominent, the gut helminths are more varied and more prevalent, including species such as *Capillaria* sp., *Cucullanus minutus*, *C. heterochrous*, *Goezia* sp., *Lecithaster gibbosus*, *Zoogonoides viviparus*, and *Plagioporus varius*.

Seasonal changes in parasite prevalence were not apparent in Lots Road flounders, possibly because species such as *P. laevis* were being continually recruited throughout the year, despite a drop in the level of cystacanth prevalences in the intermediate host in the winter (Munro, 1992). Similarly, the unidentified nematode larvae, which are believed to be potentially invasive all year round (Chubb, 1980), were generally unaffected. The only parasite that demonstrated any seasonal tendencies was *Goezia* sp., which appeared in April and May in Lots Road flounders and continued through to July in West Thurrock flounders. Little is known of this species in the tidal Thames. It is not known if an intermediate host is involved in its transmission. It is however, apparent that factors related to temperature may be a consideration, either as a direct influence, or through the differences in feeding behaviour associated with spring and summer which could have triggered this occurrence (Dogiel, 1961; Chubb, 1980).

Only three parasites, *P. laevis*, the unidentified nematode larvae, and the tetraphyllidean larvae, demonstrated any direct relationship between infection levels and host length. Both *P. laevis* and the tetraphyllidean larvae are recruited through continual feeding on their intermediate hosts, *G. zaddachi* and copepods respectively (Chubb *et al.*, 1987; Munro, 1992). The unidentified nematode larvae, on the other hand, although not demonstrating any increase in prevalence with host length, did nevertheless increase in mean abundance, therefore suggesting that these parasites accumulate over time. This is not an unusual finding for nematode larvae which can remain in an infected host for prolonged periods (especially in cold climates) before escaping from their capsules or being transferred to the final host (Chubb, 1980). An interesting observation was made on the nematode *Goezia* sp. which appeared to predominate in 1+ age class flounders. Almost thirty infected individuals were examined, all of which were found to be in this size group (fig. 1). The cause of this pattern, however, is not clear at the present time but could be related to the feeding behaviour of this size group.

Parasite community richness and diversity

The main observations made on the component parasite community of West Thurrock flounders and Lots Road flounders are summarized below. This analysis refers only to parasite species occurring at prevalences of 10% or above.

1. The component parasite community of flounders retrieved from West Thurrock during the summer (1992) consisted of as many as ten parasite species, whereas those collected from Lots Road during the same season, but in a different year (1994), harboured a component community of only five species.
2. The overall parasite community of West Thurrock flounders was found to be substantially more diverse than that of Lots Road flounders (West Thurrock parasite community $D=5.88$, Lots Road parasite community $D=2.22$), and consisted mainly of marine or lower estuarine parasites. Lots Road flounders harboured estuarine parasites only as constituents of their component parasite fauna, although marine parasites were intermittently encountered in the overall number of species.

3. The component parasite community of Lots Road flounders was dominated by an upper estuarine parasite, *Pomphorhynchus laevis*, to the almost complete exclusion of any other parasite species. West Thurrock flounders, on the other hand, harboured a parasite community co-dominated by two species, *P. laevis* and the lower estuarine parasite *Cryptocotyle concava*.

There are numerous factors that influence the diversity and richness of the parasite communities of fish, but it is generally understood that marine fish harbour a larger and more diverse parasitic fauna than their freshwater counterparts (Holmes, 1990). This is partly due to the relatively wider geographical range of marine fish, and partly to the richer invertebrate and vertebrate communities that characterize these localities (Kennedy, 1975; Price & Clancy, 1983; Kennedy *et al.*, 1986). Vagile fish, such as flounders, are even more prone to such influences as they enter different ecosystems during their migrations (Dogiel, 1964; Kennedy *et al.*, 1986; Holmes, 1990; Kennedy, 1990).

The fact, however, that young flounders spend most of their developmental life in upper estuarine locations, feeding almost exclusively on *G. zaddachi* (Munro *et al.*, 1989; Munro, 1992; Chen, 1994), has evidently had some effect on their parasite fauna, particularly in the Thames Estuary. The dominance of *P. laevis* in the component parasite community of these flounders is, therefore, a direct consequence of this feeding behaviour. The remaining components of the parasite community of these fish, the unidentified nematode larvae, *Capillaria* sp., *Cryptocotyle concava* and *Timoniella* spp., are likely to be acquired in the lower or middle estuary (see El-Darsh & Whitfield, 1999) during their annual migration in winter. They subsequently remain within the flounders as they travel back upstream.

At West Thurrock, the picture is slightly different as *G. zaddachi* becomes less abundant, less important as a food source, and consequently flounders become more opportunistic in their feeding habits (Hardisty & Badsha, 1986; Chen, 1994). Other invertebrates are consumed or encountered in the process and, if they harbour parasitic infections, the parasite community consequently becomes more diverse. Flounders, for instance, are known to feed on molluscs such as *Hydrobia ulvae* in the lower estuary (Van Den Broek, 1979), which are believed to harbour sporocysts of *Cryptocotyle concava* and *Timoniella* spp., and both these infections are components of parasite communities of West Thurrock and Lots Road flounders. Close spatial association between flounders and the molluscs upon which they are feeding will increase the probability of fish infection by cercariae released from those molluscs.

Despite the large difference in the diversity of the parasite community at West Thurrock and Lots Road (during the summer), the qualitative Similarity Index (Sorensen's = 0.60) has registered a substantial degree of similarity in the type of parasitic infections at the two sites in the Thames. This, however, is to be expected as both autogenic and allogenic parasites (but particularly the latter since they can cross land barriers) are known to confer a certain degree of similarity in the parasite communities of the same host, within and between different localities (Esch *et al.*, 1988). If an autogenic parasite has

the ability to tolerate variations in salinity that may be encountered by the host during short stays in a different habitat, i.e. a marine environment, the potential of that parasite to confer similarity between locations becomes more substantial (Esch *et al.*, 1988). In this respect, it is probably the presence of *P. laevis*, the dominant parasite at Lots Road and the co-dominant parasite at West Thurrock, that contributes to the high degree of qualitative similarity between Lots Road and West Thurrock, and even more so in the similarity at Lots Road between summer and winter, where it is the dominant parasite species during both seasons. The presence of *C. concava* as part of the component parasite community of Lots Road flounders is probably also partially responsible for some of the observed similarity between the two locations.

The high degree of similarity found between the 1993/94 winter and summer samples (table 9), and the April 1992 and April 1994 samples (table 10) implied short-term and long-term stability, respectively, of the parasite community of Lots Road flounders. This is probably conferred by the dominance of *P. laevis* in each of the samples, acting as a stable determinant in the upper estuarine ecosystem (Kennedy, 1993).

In conclusion, we find that the differences in the aquatic ecosystems of Lots Road and West Thurrock, coupled with the vagility and the feeding habits of the flounder host, have influenced the richness and diversity of the parasite communities harboured within the fish in the two different locations. The greater marine influence at West Thurrock and the opportunistic feeding of flounders in this region of the Thames have resulted in a richer, more diverse and more evenly spread parasite community than that of Lots Road flounders which, although harbouring abundant parasite numbers, nevertheless remains comparatively poorer in terms of richness and diversity.

Acknowledgements

We would like to thank Professor C.R. Kennedy for the invaluable suggestions he made in the context of the quantitative analyses of the parasite community, Mr Reg Reed for assistance with fish sampling and the staff at Lots Road and West Thurrock Power Stations for making the fish sampling possible.

References

- Bush, A.O., Aho, J.M. & Kennedy, C.R. (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* **4**, 1–20.
- 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.
- Chen, C.Y. (1994) Aspects of the ecology of flounder (*Platichthys flesus* L.) in the upper and middle Thames Tideway. PhD thesis, University of London.
- Chubb, J.C. (1980) Seasonal occurrence of helminths in freshwater fishes. Part III Larval Cestoda and Nematoda. *Advances in Parasitology* **18**, 1–120.
- Chubb, J.C., Pool, D.W. & Veltkamp, C.J. (1987) A key to the species of cestodes (tapeworms) parasitic in British and Irish freshwater fishes. *Journal of Fish Biology* **31**, 517–543.

- Dogiel, V.A.** (1961) Ecology of parasites of freshwater fishes. pp. 1–48 in Dogiel, V.A., Petrushevski, G.K. & Polyanski, Y.I. (Eds) *Parasitology of fishes*. Edinburgh, Oliver and Boyd.
- Dogiel, V.A.** (1964) *General parasitology*. Edinburgh, Oliver and Boyd.
- El-Darsh, H.E.M. & Whitfield, P.J.** (1999) Digenean metacercariae (*Timoniella* spp., *Labratrema minimus* and *Cryptocotyle concava*) from the flounder, *Platichthys flesus*, in the tidal Thames. *Journal of Helminthology* **73**, 103–113.
- Esch, G.W., Kennedy, C.R., Bush, A.O. & Aho, J.M.** (1988) Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonisation. *Parasitology* **96**, 519–532.
- Hardisty, M.W. & Badsha, K.S.** (1986) Seasonal abundance, growth, feeding, and age composition of flounder (*Platichthys flesus* (L.)) populations of the Severn Estuary and the Bristol Channel. *International Journal of Environmental Studies* **27**, 89–114.
- Holmes, J.C.** (1990) Helminth communities in marine fishes. pp. 101–130 in Esch, G.W., Bush, A.O. & Aho, J.M. (Eds) *Parasite communities: patterns and processes*. London, Chapman and Hall.
- Kennedy, C.R.** (1975) *Ecological animal parasitology*. Oxford, Blackwell Scientific Publications.
- Kennedy, C.R.** (1990) Helminth communities in freshwater fish: structured communities or stochastic assemblages? pp. 130–156 in Esch, G.W., Bush, A.O. & Aho, J.M. (Eds) *Parasite communities: patterns and processes*. London, Chapman and Hall.
- Kennedy, C.R.** (1993) The dynamics of intestinal helminth communities in eels *Anguilla anguilla* in a stream: long-term changes in richness and structure. *Parasitology* **107**, 71–78.
- Kennedy, C.R. & Pojmanska, T.** (1996) Richness and diversity of helminth parasite communities in the common carp and in three more recently introduced carp species. *Journal of Fish Biology* **48**, 89–100.
- Kennedy, C.R., Bush, A.O. & Aho, J.M.** (1986) Patterns in helminth communities: why are birds and fish different? *Parasitology* **93**, 205–215.
- Koie, M.** (1983) Digenetic trematodes from *Limanda limanda* (L.) (Osteichthyes, Pleuronectidae) from Danish and adjacent waters, with special reference to their life-histories. *Ophelia* **22**, 201–228.
- MacKenzie, K. & Gibson, D.I.** (1970) Ecological studies of some parasites of plaice *Pleuronectes platessa* L. and flounder *Platichthys flesus* (L.). pp. 1–41 in Taylor, A.E.R. & Muller, R. (Eds) *Aspects of fish parasitology. Symposia of the British Society for Parasitology*. Oxford, Blackwell Scientific Publications.
- Martínez, V.M.V.** (1995) Processes structuring the helminth communities of native cichlid fishes from southern Mexico. PhD thesis, University of Exeter.
- Messoudi, A.** (1993) Studies on the heterophyid digenean *Cryptocotyle concava* in a second intermediate host, the flounder *Platichthys flesus*. MPhil thesis, University of London.
- Möller, H.** (1974) Untersuchungen über die parasiten der flunder (*Platichthys flesus*, L.) in der Kieler Forde. *Berichte Deutscher Wissenschaftliche Kommission für Meeresforschung* **23**, 136–149.
- Munro, M.A.** (1992) Studies on the estuarine strain of *Pomphorhynchus laevis* (Acanthocephala) in the Thames Estuary. PhD thesis, University of London.
- Munro, M.A., Whitfield, P.J. & Diffley, R.** (1989) *Pomphorhynchus laevis* (Müller) in flounder, *Platichthys flesus* L., in the tidal River Thames: population structure, microhabitat utilisation and reproductive status in the field and under conditions of controlled salinity. *Journal of Fish Biology* **35**, 719–735.
- Pilcher, M.** (1989) *Tidal Thames fisheries survey, Thames East*. London, National Rivers Authority Report No. TE 710.
- Price, P.W. & Clancy, K.M.** (1983) Patterns in number of helminth parasite species in freshwater fishes. *Journal of Parasitology* **69**, 449–454.
- Southwood, T.R.E.** (1978) *Ecological methods*. London, Chapman and Hall.
- Sulgostowska, T., Banaczyk, G. & Grabda-Kazubska, B.** (1987) Helminth fauna of flatfish (Pleuronectiformes) from Gdansk Bay and adjacent areas (south-east Baltic). *Acta Parasitologica Polonica* **31**, 231–240.
- Van Den Broek, W.L.F.** (1979) Infection of estuarine fish populations by *Cryptocotyle lingua* (Creplin). *Journal of Fish Biology* **14**, 395–402.

(Accepted 6 December 1998)

© CAB International, 1999