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The Metazoan Parasites of Eels in Ireland: Zoogeographical, Ecological and Fishery Management Perspectives

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Abstract.—A new checklist of 36 metazoan parasites recorded in European eels *Anguilla anguilla* in Ireland is presented and reviewed. Some of these parasite taxa are eel specialists but most utilize a range of fish hosts. Many were accidentally brought to Ireland during fish introductions. Changing distributions of preferred intermediate hosts have affected some parasite species. Commercial transport of eels has been implicated in the introduction and spread of several potentially pathogenic parasites, including the Asian nematode *Anguillicola crassus*. The current status of this and two *Pseudodactylogyrus* species, similarly introduced to Ireland, is discussed. Analysis of parasite assemblages of Irish eel populations indicates that individual host characteristics, such as size and diet, are important at the infra-community level. Likewise, variation in biotic and abiotic features of ecosystems is reflected in composition and structure of eel parasite component communities. Environmental changes, such as eutrophication and species introductions, were found to affect eel parasite assemblages. Better regulation of fish introductions and translocations is needed to protect the ecological integrity of Ireland's freshwater systems and to avoid economic damage by nonindigenous parasites. Restrictions on live eel transport and on eel stocking programs may be necessary to protect recreational fisheries and the Irish aquaculture industry.

Introduction

The European eel *Anguilla anguilla*, whose overall distribution was recently reviewed by Dekker (2003), is one of the relatively small number of indigenous fish species that inhabit Ireland's inland waters (Moriarty and Fitzmaurice 2000). In addition to being widely distributed in Irish lakes and rivers, it also occurs in mixohaline and marine littoral habitats round the island (Healy 2003). The well-documented decline of the species in recent years (ICES 2002) has been less extreme in Ireland than in most other parts of its European range. This is generally attributed to the fact that, due to its geographical location, the island has relatively high natural juvenile eel recruitment and because the commercial exploitation of eel stocks, other than in the intensively managed Lough Neagh fishery, is generally low (Moriarty 1988; Callaghan and McCarthy 1992; McCarthy et al. 1999).

Parasites, apart from any economic considerations, are of considerable interest from biogeographical and ecological per-

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spectives. Their adaptive morphology and frequently complex life cycles, together with the increasingly recognized contribution that parasites make to biodiversity of aquatic ecosystems, has attracted the attention of many ecologists and fishery biologists (Dogiel et al. 1961; Price 1980; Esch et al. 1990). Likewise, knowledge of parasite distributions, and host-specificities, can be used to address evolutionary questions about their hosts (Marcogliese and Cone 1993). Parasites can provide indirect evidence on the migrations and trophic interactions of their hosts. Also, as is increasingly recognized, they can be used to provide information on anthropogenic impacts on the physical and chemical environments of their hosts (Lafferty 1997), as well as on the changes occurring in regional biotas due to introduction of nonindigenous species of hosts and pathogens (Kennedy 1994).

It is widely believed that parasites are disseminated and introduced into new localities by host movements, including natural and anthropochore dispersal (Kennedy 1993). Available data on fish parasites in Ireland and knowledge of their host-specificities suggests that fish introductions played an important role in the dispersal of many helminth and crustacean parasites (Holland and Kennedy 1997). Over half the freshwater fish species in Ireland are known to have been introduced by man and analyses of apparent discontinuities in parasite distributions of two acanthocephalans, *Pomphorhynchus laevis* and *Acanthocephalus anguillae*, were linked to the introduction of Cyprinidae by Kennedy et al. (1989).

In this paper we present a summary, and new species checklist, of the currently available information on metazoan parasites of eels in Ireland; we review the biogeographical and ecological factors that affect the composition of eel parasite communities in Irish aquatic habitats; and we discuss fishery management issues arising from the increased rate at which nonindigenous eel parasites are being introduced to Ireland.

Study Area

The northwestern European location of the island of Ireland and the influence of the North Atlantic Drift (Gulf Stream) contribute greatly to its mild, moist, temperate climate. Mean annual rainfall levels, which vary from about 750 mm in the eastern lowlands to 1,200 mm in western uplands, and the island's "saucer-shaped" topography are reflected in the variety of inland water-bodies that provide freshwater habitats for its fish. Mean annual air temperatures range from 9.5°C in the northeast to 10.5°C in the extreme south-east of the island, and summer lake water temperatures rarely exceed 20°C. Recent reviews of Irish freshwater habitats, with respect to water quality and fish ecology respectively, were given by Stapleton et al. (2000) and McCarthy and Cullen (2002). Information on environmental conditions in Irish estuaries and coastal zones was also given by Stapleton et al. (2000). A recent review of Irish wetlands by Otte (2003) includes details of coastal lagoons and other habitats of importance to eels. Details of sampling localities and places referred to in this paper are summarized cartographically in Figure 1.

Materials and Methods

Data on the distribution and infection parameters of metazoan parasites of eels from a series of Irish localities (Figure 1) were used to compile a national checklist of eel parasites; to describe geographical distributions of eel parasites in Ireland; and to analyze aspects of the ecology of eel parasite assemblages. Protocols adopted in earlier studies on Irish fish parasites (Conneely and McCarthy 1984) were employed subsequently

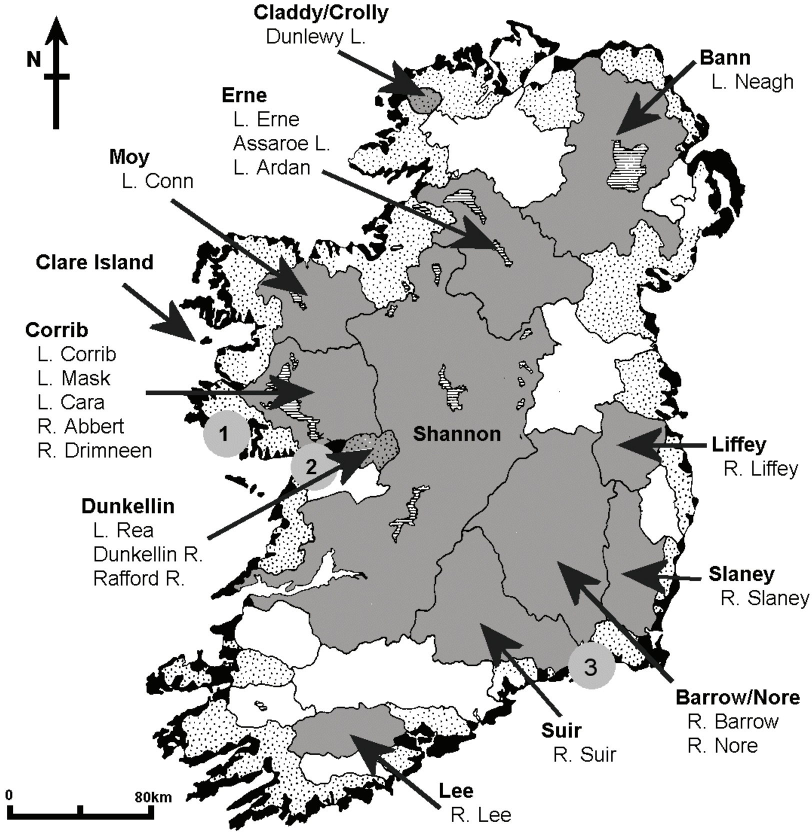

Figure 1. Map of Irish river catchment areas. Three estuarine/marine sites are also highlighted. 1) seashore at Carna, 2) Carnaroo Bay and 3) Cheekpoint on the Waterford Estuary. Catchment area is indicated by stippling. Solid black indicates direct drainage to the sea or small stream systems. Stippled areas indicate catchments of 100–500 km^2 and unstippled areas indicate catchments >500 km^2.

in a series of published (Conneely and McCarthy 1986; McCarthy and Rita 1991; Callaghan and McCarthy 1996; Copley and McCarthy 2001, 2005) and unpublished studies on parasites of eels in Ireland, from which the parasite community data for the present paper were obtained. A total of 1,067 individual eels were quantitatively examined for all metazoan parasites and much larger samples were examined specifically for nonindigenous taxa. Thus, data are available from widely distributed Irish localities (Figure 1) that include riverine, lacustrine, estuarine and marine littoral habitats. Parasitological terms recommended and defined by Margolis et al. (1982) and by Esch et al. (1990) have been adopted. TWINSPAN cluster analysis was undertaken on 28 eel parasite data sets from Irish localities, using the Community Analysis Programme (CAP) produced by Pisces Conservation Ltd., UK.

Results

A checklist of the metazoan parasites recorded in eels in Ireland recognizes 36 operational taxonomic units, mostly species (Table 1). The checklist is based on previously published observations as well as to the results (to mid 2003) of ongoing surveys of eel parasites

Table 1. Checklist of Irish eel parasites. A "?" indicates that the status is unknown or not clearly defined.

Group	Species	Authority	Introduced / Native	Eel habitat	Parasite infection location	Specialist eel parasites
Monogenea	*Pseudodactylogyrus anguillae*	Yin & Sproston 1948	Introduced	Freshwater	Gill	Specialist
	Pseudodactylogyrus bini	Kikuchi 1929	Introduced	Freshwater	Gill	Specialist
Digenea	*Helicometra fasciata*	Rudolphi 1819	Native	Marine	Intestine	
	Podocotyle atomon	Rudolphi 1802	Native	Marine	Intestine	
	Crepidostomum farionis	Muller 1784	Native	Freshwater	Intestine	
	Crepidostomum metoecus	Braun 1900	Native	Freshwater	Intestine	
	Sphaerostoma bramae	Muller 1776	Introduced ?	Freshwater	Intestine	
	Deropristis inflata	Molin 1859	Native	Marine	Intestine	Specialist ?
	Phyllodistomum sp.		Native	Freshwater	Urether	
	Lecithochirium rufoviride	Rudolphi 1819	Native	Marine	Intestine	
	Lecithochirium furcolabiatum	Jones 1933	Native	Marine	Intestine	
	Diplostomum chromatophorum	Brown 1931	Native	Freshwater	Eye	
	Diplostomum gasterostei	Williams 1966	Native	Freshwater	Eye	
	Diplostomum paraspathaceum	Shigin 1965	Native	Freshwater	Eye	
	Diplostomum pseudobaeri	Razmashkin & Andrynk 1978	Native	Freshwater	Eye	
	Diplostomum spathaceum	Rudolphi 1819	Native	Freshwater	Eye	
Cestoda	*Bothriocephalus claviceps*	Goeze 1782	Native	Freshwater	Intestine	Specialist
	Proteocephalus macrocephalus	Creplin 1825	Native	Freshwater	Intestine	Specialist
Nematoda	*Camallanus lacustris*	Zoega 1776	Introduced ?	Freshwater	Intestine	
	Capillaria sp.		?		Intestine	
	Cucullanus truttae	Fabricius 1794	Introduced ?	Freshwater	Intestine	
	Anguillicola crassus	Kuwahar, Nimi & Itagaki 1974	Introduced	Freshwater/Estuarine	Swimbladder	Specialist
	Paraquimperia tenerrima	Linstow 1878	Native	Freshwater	Intestine	
	Raphidascaris acus	Bloch 1779	Introduced ?	Freshwater	Intestine	
	Rhabdochona sp.		?	Freshwater	Intestine	
	Encysted larvae spp. Indet.		?	?	Body cavity	
Acanthocephala	*Acanthocephalus anguillae*	Muller 1780	Introduced	Freshwater	Intestine	
	Acanthocephalus clavula	Dujardin 1845	Native	Freshwater	Intestine	
	Acanthocephalus lucii	Muller 1780	Introduced	Freshwater	Intestine	
	Echinorhynchus gadi	Zoega 1776	Native	Marine	Intestine	
	Pomphorhynchus laevis	Muller 1776	Introduced	Freshwater	Intestine	
Hirudinea	*Piscicola geometra*	L.	Native	Freshwater	External	
	Hemiclepsis marginata	Muller 1844	Native	Freshwater	External	
Mollusca	*Anodonta cygnea*	L.	Native	Freshwater	Gill	
Crustacea	*Argulus foliaceus*	L.	Native ?	Freshwater	External	
	Ergasilus gibbus	von Nordmann 1832	Native	Freshwater	External	Specialist

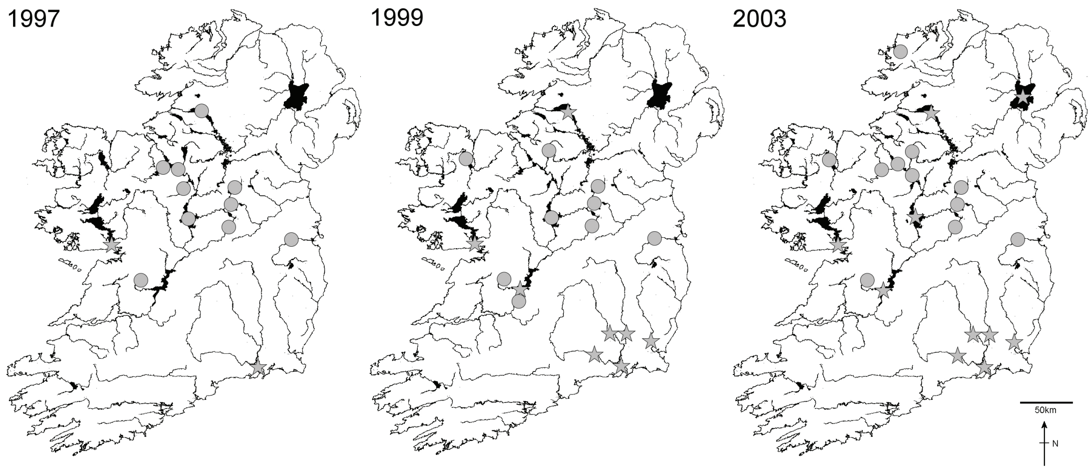

Figure 2. Maps showing the results of surveys of eels carried out to assess the spread of *Anguillicola crassus* in 1997, 1999 and 2003. *A. crassus* was present at sites marked with a star, and absent at sites marked with a circle.

throughout Ireland. In addition to the taxonomic checklist, Table 1 also provides information on the presumed biogeographic status of species in Ireland; the types of aquatic habitat in which they occur; the locations, on or in eels, they parasitize; and the identity of taxa regarded as specialist parasites of eels. Most (78%) of the taxa listed were recorded in eels captured in freshwater habitats, as opposed to estuarine/marine areas of which, so far, only a smaller number (17%) are characteristic. Some eels sampled in estuarine/marine localities had substantial numbers of freshwater parasites, but these are presumed to have been acquired prior to migration by the host eel into the marine capture locality. Most (81%) of the parasites recorded on or in Irish eels can be regarded as generalists, or in some cases accidental parasites, though six or seven are generally recognized as specialist parasites of eel (Table 1).

The first record of the nonindigenous swim bladder nematode *Anguillicola crassus* in Ireland, (McCarthy et al. 1999), was from eels captured in 1997 in the Waterford estuary in southeast Ireland. This discovery prompted a parasitological survey of the northeastern River Erne system (Evans and Mathews 1999; Evans et al. 2001a) and led to a series of investigations on eel parasites throughout the island in an attempt to track the dispersal patterns of *A. crassus* and other introduced eel parasites. The rapid spread of the nematode to the principal exploited eel fisheries in Ireland is shown in Figure 2. The parasite is now known to occur in the major southeastern Irish rivers (Barrow, Nore, Suir and Slaney Rivers), as well as in the central River Shannon system, the western Lough Corrib system, the northwestern River Erne catchment and in the major Lough Neagh fishery in Northern Ireland.

Some results of a recent survey of gill parasites of Irish eels (authors' unpublished data), captured at a variety of localities throughout the island, are summarized in Figure 3. The known distributions of two nonindigenous monogenetic flukes, *Pseudodactylogyrus anguillae* and *P. bini*, both eel specialists, are illustrated in Figure 3a. Both species are now widely distributed in Ireland. The copepod *Ergasilus gibbus,* an eel specialist, which has generally only been recorded from brackish water habitats in Britain and

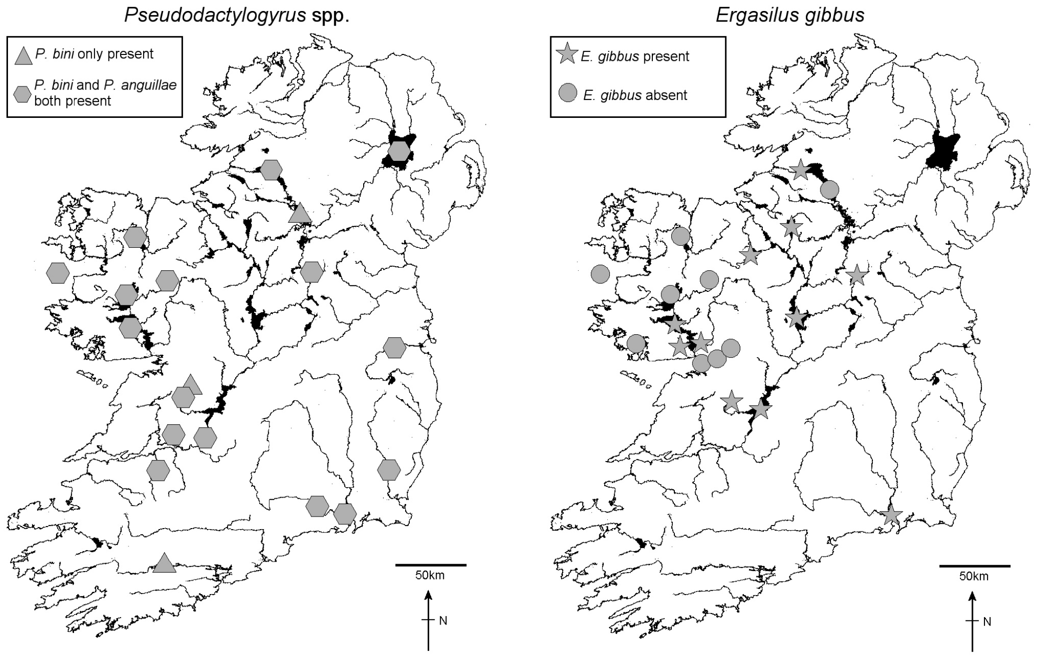

Figure 3. Maps of Irish river systems showing the results of surveys for (a) *Pseudodactylogyrus* species and for (b) the presence or absence of *Ergasilus gibbus.*

mainland Europe, has been found to occur regularly well inland in Ireland. For example, it has been found (Figure 3b) in lakes in the Shannon, Corrib and Erne River basins, as well as in estuarine eels from the southeastern Waterford area (Figure 3b).

Purcell and McCarthy (unpublished data) interpreted variation in eel parasite community composition as a function of population structure and diet of their host community, as inferred from two eel samples from Lough Derg, the largest River Shannon lake (Table 2). The samples were obtained respectively from the littoral and sublittoral zones of the lake, and they differed in respect of eel sizes and diets. The composition of their parasite assemblages reflected these differences (Table 2).

Larger eels from deeper habitats had greater parasite burdens and greater diversity in their parasite communities. Likewise, reflecting increased piscivory, the larger eels were more likely to have parasites such as *Camallanus lacustris* that they had acquired through ingestion of perch fry. Abundances of certain parasites (e.g., *Ergasilus gibbus*) were similarly linked to body size. In the case of the encysted metacercarial flukes, *Diplostomum spathaceum*, higher abundance in the deep water eel sample may also be due to progressive accumulation of these long-lived parasites by the older eels.

A dendrogram (Figure 4) based on TWINSPAN cluster analysis of parasite assemblage composition in 28 samples of Irish eels grouped localities in a manner that reflected the types of habitats from which the eels were obtained. Riverine sites and marine sites are both represented by discrete sample clusters. Among lake samples, dendrogram results corresponded to lake trophic status, as inferred from water quality data that included chlorophyll-a and total phosphorus concentrations and Secchi disk measures of water clarity (data from Stapleton et al. 2000 and various unpublished sources).

Table 2. Mean abundances of parasites of eels in two Lough Derg samples with differing trophic ecology.

Site	Littoral	Deep
No. eels	71	147
Mean eel length (cm)	27	49
Important prey species	*Asellus aquaticus*	*Asellus aquaticus* *Perca fluviatilis*
Diplostomum spathaceum	1.65	9.40
Ergasilus gibbus	0.05	3.00
Acanthocephalus clavula	–	6.8
A. lucii	7.3	3.87
A. anguillae	0.05	0.90
Bothriocephalus claviceps	–	0.65
Paraquimperia tenerrima	5.15	0.27
Raphidascaris acus	–	0.10
Sphaerostoma bramae	0.01	3.30
Proteocephalus macrocephalus	0.02	0.09
Camallanus lacustris	0.75	19.50
Crepidostomum metoecus	0.13	1.49
Capillaria sp.	–	0.05

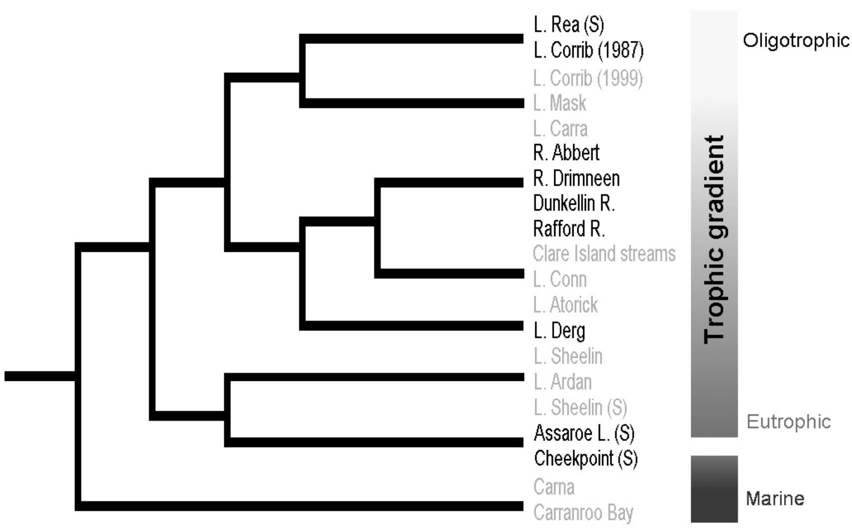

Figure 4. Results of a TWINSPAN analysis on the abundances of eel parasites recorded from 20 different surveys. (S) at three locations indicates that the eels surveyed were silver; all other samples were of yellow eels. Alternation of dark and light fonts indicates the groups of locations which correspond to each TWINSPAN limb.

Discussion

The European eel is an important indigenous component of the species-poor insular freshwater fish fauna of Ireland. It has a history of exploitation dating from over five thousand years ago to the present. Eels are currently commercially fished only during the yellow and silver eel life history stages, though elvers were once used as a food item in some southern localities. The euryhaline eel is widely distributed in Irish lakes and rivers and, as observed by Callaghan and McCarthy (1992) in the Dunkellin River, it can occur in very high densities in coastal rivers and lower reaches of larger rivers. Healy (2003) recorded eels in 32 of the 38 coastal lagoons she studied and the species has also been found at many estuarine and marine littoral sites. However, though the biology of the eel has been well researched in Irish inland waters, relatively little is known about its ecology or parasitology in marine and mixohaline waters.

The list of metazoan parasites presented in Table 1 includes a total of 36 taxa, indicating that the parasitofauna of eels is in not an impoverished, insular, one. Earlier studies in western Ireland, such as those of Conneely and McCarthy (1986) who recorded 13 species of parasites in eels from the Corrib catchment and Callaghan and McCarthy (1996), who recorded 15 species from the small Dunkellin River system, dealt exclusively with eels sampled in freshwater. These and some other records of Irish eel parasites (Kane 1966; Kennedy 1966; Kennedy 1974; Kennedy 1992; Kennedy and Moriarty 1987; Purcell and McCarthy 1995; McCloughlin and Irwin 1991) were included in the recent checklists of Irish freshwater fish parasites compiled by Holland and Kennedy (1997). They listed 20 helminth and crustacean eel parasites for Ireland and noted that the same number was recorded in British eels. These, together with other published observations (Evans et al. 2001b; Evans and Matthews 2000) and the results presented above, suggest that eel parasite assemblages in Ireland are comparable to those in Britain. They may also be comparable to those of nearby continental European countries. In Denmark, for example, Koie (1988a, 1988b) recorded 41 metazoan parasites in eels. The present checklist may include some species that improved taxonomy would show were invalid and this is especially likely among the strigeid eye-flukes. The relatively high number included (Table 1) in the Irish checklist reflects the publication by McCloughlin and Irwin (1991) of records, based on use of a Russian key provided originally by Shigin (1986). These records should be validated by use of modern molecular taxonomic methods and investigations on adult flukes. It is also likely that additional studies will add further helminths to the list, and it is expected that these will mostly be species of nematodes and Digenea with marine life cycles, as comparatively few marine or estuarine Irish eels have yet been examined for parasites. However, the absence of some eel parasites, such as the specialist nematode *Spinitectus inermis* or the generalist cestode *Trianophorus nodulosus,* may reflect biogeographical barriers and incomplete postglacial recolonization of the island. Such effects can be seen in many free-living components of the Irish biota (McCarthy 1986). However, it seems that *S. inermis,* though listed as a freshwater specialist by Kennedy (1992), is more prevalent in estuarine eel populations. If this is the case, then its discovery in Ireland can be anticipated. In the case of another specialist parasite of European eels *Daniconema anguillae*, found in Danish eels (Koie 1988a, 1988b), the situation is less clear-cut and suggests that further research on nematode parasites of Irish eels is needed. The widespread occurrence (Figure 3) of the copepod *Ergasilus gibbus* in Irish inland waters is of interest, as studies on this species elsewhere in Europe suggest it occurs more typically on eels in coastal, brackish water, habitats (Conneely and McCarthy 1986).

Information on parasites of eels elsewhere in Europe suggests that faunal species richness in Ireland may be underecorded at present and that records of up to eight more metazoan species can probably be anticipated. This is particularly true for estuarine and marine eels in Ireland which have only been studied to a minor degree so far. Thus, the total number of such parasites infecting Irish eels may be up to 44, over half the total number listed for European eel throughout its entire range (Reimer 1999). Irish eels are likely to be infected with a greater number of other types of pathogens than is suggested by present records and these would also serve to highlight the diversity of parasites affecting this host. Only limited studies have been undertaken on the Protozoa and microbial pathogens of eels in Ireland, though at least three species of the former have been recorded. The leech-transmitted blood parasite *Trypanosoma granulosum,* observed in western Irish eels, was investigated by Zintl et al. (1997); *Myxidium* sp. have been regularly noted on gills of Irish eels; and external *Ichthyopthirius multifiliis* infections have been noted periodically in eels retained by fishermen and in ascending elvers obstructed by low-flow or artificial obstacles. Likewise, occasional observations have been made on fungal, *Saprolegnia* sp., infections (authors' unpublished data) in eels retained by fishermen and occasional viral/bacterial infections have been noted in Irish eels (J. McArdle, Marine Institute, personal communication).

The species richness of the eel parasite fauna in Ireland (Table 1) is comparable to those recorded in Denmark by Koie (1988a,b), and in Britain by Kennedy (1990) and others. Eel parasite species richness is high in comparison with most other well studied fish hosts in Ireland. In this regard it is interesting to note that the eel is a well-established indigenous species in Ireland. Conneely and McCarthy (1986) pointed out that the native brown trout *Salmo trutta* had a higher number of metazoan parasites than other species investigated in western Ireland. Likewise, indigenous arctic char *Salvelinus alpinus* populations harbor relatively diverse parasite assemblages (Conneely and McCarthy 1984; Doherty and McCarthy 2000) and this historical biogeographical dimension seems to be a general feature of Irish fish parasite assemblages (Holland and Kennedy 1997). However, other ecological factors are also important determinants of the diversity of parasites infecting Irish eels. The well-known migratory and euryhaline aspects of European eel biology are obviously important in this regard. As a consequence of the range of aquatic habitats used by eels in Ireland, eels have a greater probability of being infected by localized or habitat-specific parasites. Likewise, they are exposed to potential exchanges of parasites from virtually all the other fish species occurring in inshore or freshwater habitats in Ireland and such interactions are known to contribute significantly to the composition of fish parasite communities (Leong and Holmes 1981). The ontogenetic trophic niche shifts in the life history of eels, which are linked to body-size and prey availability, involve a progressive change from planktivory to piscivory, and are recognized as contributing to the relative species richness of eel parasite communities (Conneely and McCarthy 1988; Kennedy 1990).

Differences in species composition and parasite abundances in two samples of eels (Table 2), obtained from littoral and sub-littoral areas of Lough Derg in the River Shannon, illustrate the effects of variation in feeding habits of eels of differing sites and habitats. The data on three acanthocephalan species (*Acanthocephalus clavula, A. lucii* and *A. anguillae*) reflect the importance of the aquatic isopod *Asellus* in eel diets in the Shannon lakes. A high level of multiple acanthocephalan species infections in Irish eels has been noted previously (Kennedy and Moriarty 1987; Kennedy 1992; Callaghan and McCarthy 1996). This phenomenon is partly attributable to the fact that though *Asellus aquaticus*, intermediate host to *A. lucii* and *A. anguillae*, is progressively competitively displacing *Asellus meridianus*, intermediate host of *A. clavula*, both isopod species still co-exist in the larger Irish lakes (McCarthy 1986). Another frequently noted feature of Irish eel parasite assemblages is the higher abundance of certain parasites in larger eels (Conneely and McCarthy 1986; Callaghan and McCarthy 1996). In the case of the data presented in Table 2, this effect can be illustrated by the very high abundance of *Camallanus lacustris* in sub-littorally sampled Lough Derg eels. This nematode, which is very prevalent in the Eurasian perch *Perca fluviatilis* population, occurs regularly as a secondary infection in larger eels that feed extensively on perch fry. The infection (Table 2) of larger Lough Derg eels by the tapeworm *Bothriocephalus claviceps* also probably involved ingestion of juvenile fish that had recently ingested copepods infected with *B. claviceps* larvae. Conneely and McCarthy (1986) commented previously on this phenomenon. Subsequently, Kennedy et al. (1992) argued that heavy infections of eels with cestodes provided indirect evidence of planktivory. However, the almost total absence of direct observations of plankton in diets of larger eels in Irish and other European studies on eel feeding habits is difficult to ignore. This is especially so when, as in the present investigations, fry of Cyprinidae and perch, with their stomachs full of recently ingested zooplankton, are regularly observed in stomach contents of larger sized eels.

Variation in eel parasite assemblages can potentially yield information on the feeding habits and local movements of eels. Conneely and McCarthy (1986) noted riverine parasites in lake dwelling eels and lacustrine parasites in river eels, and concluded that these were indicative of movements by individual eels between lake and river habitats in the western Irish Corrib catchment area. Similarly, ongoing studies of marine and mixohaline eel populations in western Ireland (authors' unpublished data) show that eels captured in such habitats are infected by freshwater parasites. It is hoped that further analyses of the parasite assemblages of such eel populations, combined with microprobe analyses of their otolith Sr/Ca ratios (Tsukamoto and Arai 2001) and tracking of tagged individuals, will provide a better understanding of the local migratory activities of European eels.

Parasite assemblages of fishes and other aquatic hosts appear to generally reflect the community structure and ecosystem processes of their habitats. Thus, as initially revealed by the pioneering studies of Wisniewski (1958) in Polish lakes, eutrophic lakes are characterized by parasite faunas in which allogenic species (which use piscivorous birds as definitive hosts) predominate (Esch et al. 1990). The results presented in Figure 4 suggest that variation in eel parasite communities from a series of Irish aquatic habitats reflects the prevailing environmental conditions, particularly trophic status. Various studies (Reimer 1995; Lafferty 1997) indicate the potential effects of environmental change on parasite assemblages. Thus, in addition to its potential use as a "sentinel species" in biomonitoring of pollution, eels may provide indirect parasitological evidence of a variety of anthropogenic impacts on their habitats.

The extent to which species introductions and host translocations have impacted the aquatic parasite fauna of Ireland is evident in the composition of the parasite assemblages of Irish eels. The steady colonization (Figures 2 and 3) of Irish eel populations by nonindigenous parasites, including the Asian swim bladder nematode *A. crassus* and two gill-inhabiting *Pseudodactylogyrus* species in the past decades is of concern to fishery managers. The importance of commercial transport of eels in dispersal of *A. crassus* has been recognized previously in Britain and elsewhere in Europe (Kennedy and Fitch 1990). The initial record (McCarthy et al. 1999) of *A. crassus,* in was from a site close to the Rosslare ferry port used by continental eel dealers, which suggests that the introduction of this nematode involved anthropochore dispersal via eel transport vehicles. The pattern in which it has spread subsequently to Ireland's major commercially exploited eel stocks (Figure 2) in the rivers Shannon, Erne, Corrib, and to Ireland's premier eel fishery on Lough Neagh, mirrors the routes taken by eel dealers transporting live eels. The dispersal of *A. crassus* within different river systems has been variable. It appears to have spread more rapidly through the River Erne catchment (Evans and Mathews 1999; Evan et al. 2001a) than in the Shannon system (Figure 2), where eel fishing is more regulated and fishermen are assigned individual fishing zones. The biogeographical status of the two *Pseudodactylogyrus* species now present in Ireland has been discussed by Kennedy (1993, 1994) who, unlike most European fish parasitologists, does not consider them likely to be introduced species. However, in Ireland the sequential recording of *P. anguillae, P. bini* and *A. crassus* in well researched eel populations such as those in the western Irish River Corrib catchment (Conneely and McCarthy 1984, 1986; McCarthy and Rita 1991; and new records in Figures 2 and 3) strongly suggest that at least in Ireland all three of these helminths are nonindigenous. Furthermore, the transport of live eels for commercial purposes seems also to have been important in the widespread dispersal of the *Pseudodactlyogyrus* species. However, perhaps because of their direct life cycles, these gill-flukes appear to have dispersed more rapidly to unexploited Irish eel populations and more remote locations. The spread of *A. crassus* and the *Pseudodactylogyrus* species to Ireland from continental Europe where they are all now widespread illustrates the ease with which aquatic pathogens can be distributed by human agency. The potential risks to Ireland's economically important recreational fisheries and developing aquaculture industry that could arise if live transport of eels continues to take place in a relatively unregulated manner is now more widely recognized and this may lead to stricter control measures. Furthermore, as stocking with infected eels has been shown to be important in the spread of *A. crassus* in other European countries such as Belgium (Belpaire et al. 1989; Audenaert et al. 2003), proposals to enhance productivity of Irish eel fisheries by means of inter-river system elver stocking will also have to be critically reviewed.

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References

Audenaert, V., T. Huyse, G. Guemans, C. Belpaire, and F. A. M. Volkaert. 2003. Spatio-temporal dynamics of the parasitic nematode *Anguillicola crassus* in Flanders, Belgium. Diseases of Aquatic Organisms 56:223–233.

Belpaire, C., D. De Charleroy, K. Thomas, P. Van Damme, and F. Ollevier. 1989. Effects of eel restocking on the distribution of the swimbladder nematode *Anguillicola crassus* in Flanders, Belgium. Journal of Applied Ichthyology 5:151–153.

Callaghan, R. M., and T. K. Mc Carthy. 1992. Variations in population structure and growth rate of eels in the Dunkellin river system, western Ireland. Irish Fisheries Investigations Series A 36:61–69.

Callaghan, R. M., and T. K. Mc Carthy. 1996. Metazoan parasite assemblages of eels in the Dunkellin catchment, western Ireland. Archives of Polish Fisheries 4:147–174.

Conneely, J. J., and T. K. Mc Carthy. 1984. The metazoan parasites of freshwater fishes in the Corrib catchment area, Ireland. Journal of Fish Biology 24:363–375.

Conneely, J. J., and T. K. Mc Carthy. 1986. Ecological factors influencing the composition of the parasite fauna of the European eel, *Anguilla anguilla* (L), in Ireland Journal of Fish Biology 28:207–219.

Conneely, J. J., and T. K. Mc Carthy. 1988. The metazoan parasites of trout (*Salmo trutta*) in western Ireland. Polish Archives of Hydrobiology 35:443–460.

Copley, L., and T. K. Mc Carthy. 2001. The first record of the monogenean gill fluke *Pseudodactylogyrus bini* (Kikuchi 1929) in Ireland, with observations on other ectoparasites of River Erne eels. Irish Naturalists' Journal 26:405–413.

Copley, L., and T. K. Mc Carthy. 2005. Some observations on endoparasites of eels, *Anguilla anguilla* (L), from two lakes in the River Erne catchment. Irish Naturalists' Journal 28:31–34.

Dekker, W. 2003. On the distribution of the European eel (*Anguilla anguilla*) and its fisheries. Canadian Journal of Fisheries and Aquatic Sciences 60:787–799.

Dogiel, V. A., G. K. Petrushevski, and Y. I. Polyanski. 1961. Parasitology of fishes. Oliver and Boyd, Edinburgh.

Doherty, D., and T. K. Mc Carthy. 2000. The metazoan parasites, diets and general biology of arctic char *Salvelinus alpinus* in two Irish lakes. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 27:1056–1061.

Esch, G. W., A. W. Shostak, D. J. Marcogliese, and T. M. Goater. 1990. Patterns and processes in helminth parasite communities: an overview. Pages 1–19 *in* G.W. Esch, A. Bush, and J. Aho, editors. Parasite communities: patterns and processes. Chapman and Hall, London.

Evans, D. W., and M. A. Matthews. 1999. *Anguillicola crassus* (Nematoda, Dracunculoidea); first documented record of this swim bladder parasite in eels in Ireland. Journal of Fish Biology 55:665–668.

Evans, D. W., and M. A. Matthews. 2000. First record of *Argulus foliaceus* on the European eel in the British Isles. Journal of Fish Biology 57:529–530.

Evans, D. W., M. A. Matthews, and C. A. Mc Clintock. 2001a. The spread of the eel swimbladder nematode *Anguillicola crassus* through the Erne system, Ireland. Journal of Fish Biology 59:166–168.

Evans, D. W., M. A. Matthews, and C. A. Mc Clintock. 2001b. First record of *Pomphorhynchus laevis* (Acanthocephala) in fishes from Northern Ireland. Journal of Fish Biology 59:166–168.

Healy, B. 2003. Coastal lagoons. Pages 51–78 *in* M. Otte, editor. Wetlands of Ireland: distribution, ecology, uses and economic value. University College Dublin Press, Dublin.

Holland, C. V., and C. R. Kennedy. 1997. A checklist of parasitic helminth and crustacean species recorded in freshwater fish from Ireland. Biology and Environment: Proceedings of the Royal Irish Academy 97B:225–243.

International Council for the Exploration of the Seas (ICES). 2002. Report of the ICES/ EIFAC Working Group on Eels. ICES CM2002/ACFM:03.

Kane, M. B. 1966. Parasites of Irish freshwater fishes. Scientific Proceedings of the Royal Dublin Society 18B:205–220.

Kennedy, C. R. 1966. The helminth parasites of some Irish freshwater fish. Irish Naturalists' Journal 15:196–199.

Kennedy, C. R. 1974. A checklist of British and Irish freshwater fish parasites with notes on their distribution. Journal of Fish Biology 6:613–644.

Kennedy, C.R. 1990. Helminth communities in freshwater fish: structured communities or stochastic assemblages. Pages 131–156 *in* G. W. Esch, A. Bush and J. Aho, editors. Parasite communities: patterns and processes. Chapman and Hall, London.

Kennedy, C. R. 1992. Field evidence of interactions between acanthocephalans *Acanthocephalus anguillae* and *Acanthocephalus lucii* in eels. Ecological Parasitology 1:122–134.

Kennedy, C. R. 1993. Introductions, spread and colonization of new localities by fish helminth and crustacean parasites in the British Isles: a perspective and appraisal. Journal of Fish Biology 43:287–301.

Kennedy, C. R. 1994. The ecology of introductions. Pages 189–208 *in* A.W. Pike and J.W. Lewis, editors. Parasitic diseases of fish. Samara Publishing, Cardigan, UK.

Kennedy, C. R., R. M. Bates, and A. F. Brown. 1989. Discontinuous distributions of the fish acanthocephalan *Pomhorhynchus laevis* and *Avanthocephalus anguillae* in Britain and Ireland. Journal of Fish Biology 34:607–619.

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

Kennedy, C. R., and C. Moriarty. 1987. Co-existence of congeneric species of Acathocephala: *Acanthocephalus lucii* and *A. anguillae* in eels *Anguilla anguilla* in Ireland. Parasitology 95:301–310.

Kennedy, C. R., P. Nie, J. Kaspers, and J. Paulise. 1992. Are eels planktonic feeders? evidence from parasite communities. Journal of Fish Biology 41:567–580.

Koie, M. 1988a. Parasites in European eel *Anguilla anguilla* (L.) from Danish freshwater, brackish and marine localities. Ophelia 29:93–118.

Koie, M. 1988b. Parasites in eels *Angulla anguilla* (L.) from eutrophic Lake Esrum, Denmark. Acta Parastitologica Polonica 33:89–100.

Lafferty, K. D. 1997. Environmental parasitology: what can parasites tell us about human impacts on the environment. Parasitology Today 13:251–255.

Leong, T. S., and J. C. Holmes. 1981. Communities of metazoan parasites in open water fishes of Cold Lake, Alberta. Journal of Fish Biology 18:693–713.

Marcogliese, D., and D. K. Cone. 1993. What metazoan parasites of eels tell us about evolution of American and European eels. Evolution 47:1632–1635.

Margolis, L., G. W. Esch, J.C. Holmes, A.M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology (Report of an *ad hoc* committee of the American Society of Parasitologists). Journal of Parasitology 68:131–133.

McCarthy, T. K. 1986. Biogeographical aspects of Ireland's invertebrate fauna. Occasional Publication of the Irish Biogeographical Society 1:67–81.

McCarthy, T. K., and P. Cullen. 2002. Ireland's changing freshwater habitats: anthropogenic impacts, fishery management problems and ecohydrological perspectives. Ecohydrology and Hydrobiology 2:143–148.

McCarthy, T. K., P. Cullen, and W. O'Connor. 1999. The biology and management of River Shannon eel populations. Fisheries Bulletin (Dublin) 17:9–20.

McCarthy, T. K., and S. D. Rita. 1991. The occurrence of the monogenean *Pseudodactylogyrus anguillae* (Yin and Sproston) on migrating silver eels in western Ireland. Irish Naturalists' Journal 23:473–477.

McCloughlin, T. J. J., and S. W. B. Irwin. 1991. The occurrence of eyeflukes in fish from the Erne catchment area. Irish Naturalists' Journal 23:409–414.

Moriarty, C. 1988. The eel in Ireland. Went Memorial Lecture, 1987. Royal Dublin Society Occasional Papers in Science and Technology No. 4.

Moriarty, C., and P. Fitzmaurice. 2000. Origin and diversity of freshwater fishes in Ireland. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 27:128–130.

Otte, M. 2003. Wetlands of Ireland: distribution, ecology, uses and economic value. University College Dublin Press, Dublin.

Price, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey.

Purcell, P., and T. K. McCarthy. 1995. Metazoan parasite assemblages of yellow eels (*Anguilla anguilla* L.) in Lough Derg. Abstracts of the Fifth Environmental Researcher's Colloquium, University College Cork, 13–15 January.

Reimer, L. W. 1995. Parasites, especially of piscine hosts, as indicators of eutrophication. Applied Parasitology 36:124–135.

Reimer, L. W. 1999. Krankheiten, parasiten und schadinungen. Pages 301–322 *in* F. W. Tesch, editor. Der Aal Paraey Buchverlag and Blackwell Scientific Publications Wissenschafts-verlag, Berlin.

Shigin, A. A. 1986. Trematode fauna of the USSR. *Diplostomum metacercariae.* Izdatel'stvo "Nauka". Moscow. (Original in Russian; English translation provided by J. Chubb, Liverpool University)

Stapleton, L., M. Lehane, and P. Toner. 2000. Ireland's environment: a millennium report. Environmental Protection Agency, Dublin.

Tsukamoto, K., and T. Arai. 2001. Faculative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. Marine Ecology Progress Series 220:265–276.

Wisniewski, W. L. 1958. Characterization of the parasitofauna of an eutrophic lake. Acta Parastitologica Polonica 6:1–64.

Zintl, A., R. R. Poole, H. P. Voorheis, and C. Holland. 1997. Naturally occurring *Trypanosoma granulosum* infections in the European eel, *Anguilla anguilla* from the west coast of Ireland. Journal of Fish Diseases 20:333–341.