The evolution of fish ectoparasite communities – the role of the ice ages

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ABSTRACT. The monogenean ectoparasite genera *Dactylogyrus* and *Gyrodactylus* are hyperdiverse, and yet monogenean communities infecting freshwater fish in the northern Holarctic are variable and often impoverished. This is a result of extinctions during periods of glaciation when the host fishes experienced range contraction. Fish species recolonised northern Europe by one of three routes; stenohaline fishes recolonised from the Black Sea basin via Danube-Rhine or Dnieper-Dniester-Vistula connections. These fish retain complex rich monogenean faunas with numerous species of *Dactylogyrus* and *Paradiplozoon*. Anadromous fishes, recolonising via marine migrations along the coast, and cold-water fishes surviving in refugia close to the ice sheets, have impoverished monogenean faunas, characterised by gyrodactylid and ancyrocephalid species. However, there may be great complexity, due to the evolution of new host-parasite interactions within specific watersheds before, during and after the Last Glacial Maximum (LGM). This is demonstrated using examples from the sticklebacks (*Gasterosteus aculeatus*) and the bullheads (*Cottus gobio*). Finally, the evolution of *Gyrodactylus salaris* from a clade of *G. thymalli* is described, and the role of glaciation in stimulating the evolution of numerous clades of the latter is discussed. This latter example represents a unique opportunity to study speciation by host shift in real time.

Key words: Holocene Phylogeography, Monogenea, post-glacial, *Gyrodactylus salaris*

Introduction

Over the past 50 years since Wisniewski's death, much effort has sought to demonstrate that vertebrates support communities of interacting parasite species, and to identifying the 'rules' which describe these interactions in a predictive way [1]. A rule which has survived scrutiny is that, in the Holarctic, birds have much more species-rich parasite communities than do either fish or some groups of mammals such as rodents [2]. This is despite the observation that some genera of monogenean (Platyhelminthes) fish ectoparasites are hyperdiverse, containing so many species that they make a measurable contribution to global biodiversity. These include *Dactylogyrus*, with 900 species described from the gills of 200 host species [3] and a probable total of around 10 000 species, and *Gyrodactylus*, a viviparous monogenean with over 400 species described from 200 hosts [4].

Gyrodactylus however infects a much wider phylogenetic range of hosts, under much more variable ecological circumstances, and so the total number of species is probably between 10 000 and 100 000 [4, 5]. Other monogenean genera also seem to be hyper-diverse, including ancyrocephalids from the Amazon Basin and the marine ancyrocephalid *Haliotrema*, which is widespread on coral reef fishes. Here then is a paradox. Within the Holarctic, the representation of monogeneans within fish ectoparasite communities is variable but generally species-poor. On the other hand, the total diversity within these genera of parasites is huge. These patterns show considerable, apparently inexplicable variation between fish species. For example, the pike, *Esox lucius*, and the burbot, *Lota lota*, are each infected by only two monogeneans throughout their Holarctic range. On the other hand, some cyprinids may be infected by up to 10 species of *Dactylogyrus* and 10 species of *Gyrodactylus*, with any one fish

being infected by several species. This paper sets out to interpret monogenean distribution patterns in terms of the impact of successive glaciations, and to discuss the variability of monogenean communities in relation to the post-glacial recolonisation history of their fish hosts.

The impact of the ice ages – the role of aquatic refugia

Over the past 2 million years, global climate has undergone profound, repeated perturbations leading to the cyclical cooling and warming of the planet. During cool phases, free water is locked in ice at the poles and in glaciers extending throughout the Northern Hemisphere, to be released during warm phases, when sea levels rise substantially. There is little agreement on the timing of the cold phases; they began and ended at different times in different parts of the world [6], but it is generally accepted that the Last Glacial Maximum (LGM) in Europe was as recent as 20 000 years ago, and that many poorly dispersing species are still in a post-glacial expansion phase, helped in many cases by human activity.

The impact of glaciation on mobile terrestrial animals is well established [7]. These were generally restricted to the warmer, wetter habitats of the Iberian Peninsula, Italy and the Balkan Peninsula, where woodland habitats persisted, possibly with refugia further north, as suggested for the Carpathians by Deffontaine et al. [8]. Many terrestrial species continue to show the signature of this refugial phase in their current population structures. The situation for aquatic organisms was much more complex. Glaciation brings about two competing pressures for aquatic organisms. In the first place, the environment becomes much colder, and their preferred thermal zone will occur at a lower latitude or altitude. But additionally, the locking of free water into ice results in the lowering of sea level, and the relative steepening of all rivers. In Northern America, these two factors worked together. The Mississippi-Missouri drainage runs from North to South, and so as fishes retreated south to maintain their thermal optimum, they also dropped downstream into preferred stream conditions. For this reason, the North American fish fauna has remained relatively diverse. In Northwest Europe, on the other hand, these two factors worked against each other. The rivers of the North European plain, the Seine, Rhine, Weser, Elbe, Oder, and Vistula all drain from South to North. To maintain their thermal optima, fish would have had to retreat south, upstream, into unfavourable flow conditions. A large part of the fish fauna of these rivers must have disappeared during the glacial maximum, because of this combination of sea level change and declining temperature. At the time of the LGM, only the rivers draining into the Black Sea, the Danube, Dniester, Dnieper, and Don, would have retained a substantial non-anadromous fish fauna. Fish could have recolonised the north European watersheds via two routes. In the first place, for most primary freshwater fishes (i.e., those unable to tolerate salt water) and their parasites, a return to North Europe occurred via connections between the upper reaches of the Danube into the Rhine system, and from the upper reaches of the Dniester/Dnieper system into the Vistula, via the Prikypat marshes of Belarus and Ukraine, during periods of high sea level. The importance of these routes is reflected in the prevailing pattern of species richness among freshwater fishes in Europe, with maximum diversity in the south east, declining towards the North and West [9]. The second route for recolonisation was by anadromous fishes (mostly salmonids, but also eels and sticklebacks), which were able to spread around the Eurasian coastline, colonising stepwise from river mouth to river mouth.

For some cold-tolerant fish, such as pike (*Esox lucius*), burbot (*Lota lota*), and the bullheads (*Cottus* spp.), a network of refugia also existed, in the form of a shifting pattern of large, ice-dammed lakes. Many can still be discerned today, including montane lakes such as Lake Constance (Switzerland) or Loch Ness (Scotland), and also Lakes Onega and Oneida, and the Baltic, the higher reaches of which remain brackish despite a connection to the ocean which began 11 000 years ago [10]. The Black Sea also was a freshwater lake until rising sea level in the Mediterranean breached it some 10 000 years ago [11]. Other large lakes lay within and around the current North Sea [12], and a series of very large ice-dammed lakes extended around the margin of the ice sheet in North Russia [13, 14]. The impact of these lakes regionally was such that the flow of northern-flowing rivers such as the Ob reversed, draining instead south to the Caspian Sea, and from there overtopping the Manych pass into the Black Sea [13].

A final feature of the refugial network for fish and their parasites in Northern Europe concerns the Channel River. This river, created when an ice lake
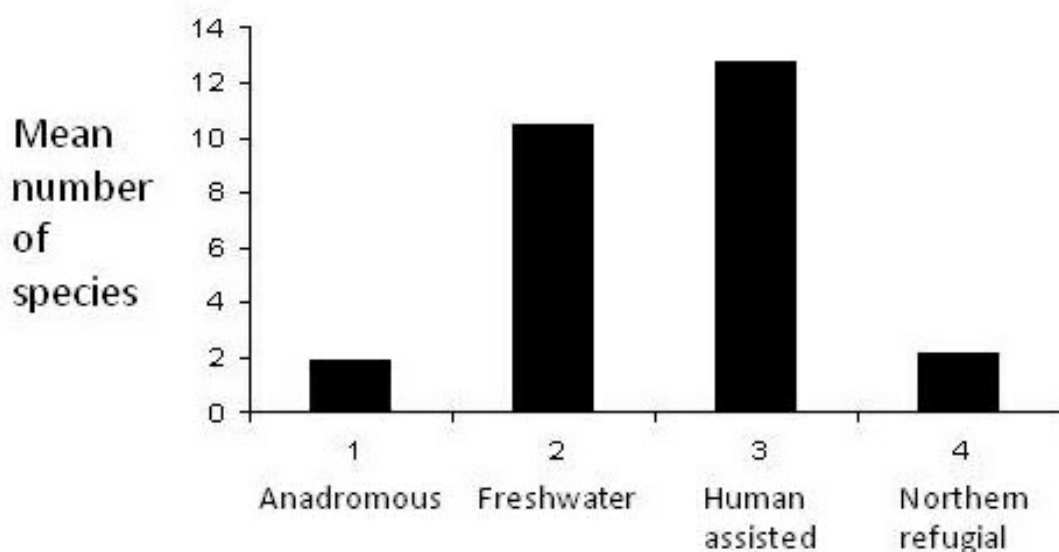
Fig. 1. Mean number of monogenean species infecting Northwest European fish which recolonised freshwater from different routes following the LGM. Anadromous; fish recolonising from salt water. Freshwater; fish recolonising from southern river basins via freshwater watershed connections. Human assisted; fish spread primarily by human assistance for aquaculture. Northern refugial; survived in lake and river refugia close to the ice sheet. Data on gyrodactylid monogeneans from GyroDb (www.GyroDb.net), for other monogeneans from Baylis host-parasite database (www.nhm.ac.uk/)

in the southern North Sea ruptured catastrophically, generating a megaflood, which carved and deepened the floor of the English Channel [15], drained through the current seabed between Britain and France, to an estuary some hundreds of kilometres west of the current shoreline of western Europe

Fig. 2. Proportion of different types of monogenean infecting Northwest European fish which recolonised freshwater from different routes following the LGM. Data sources as in Fig. 1

[16]. In addition to carrying the drainages of the Thames, Weser, and Rhine, this massive river system captured major rivers in southern Britain, including the Solent River, and a probable river system draining low-lying areas between Britain and Ireland, draining a huge area currently submerged as the Continental Shelf of Western Europe. The role of this area as a refugium for aquatic organisms is entirely unstudied, although the extent of the habitat within the continental shelf suggests that it played a major role during the LGM.
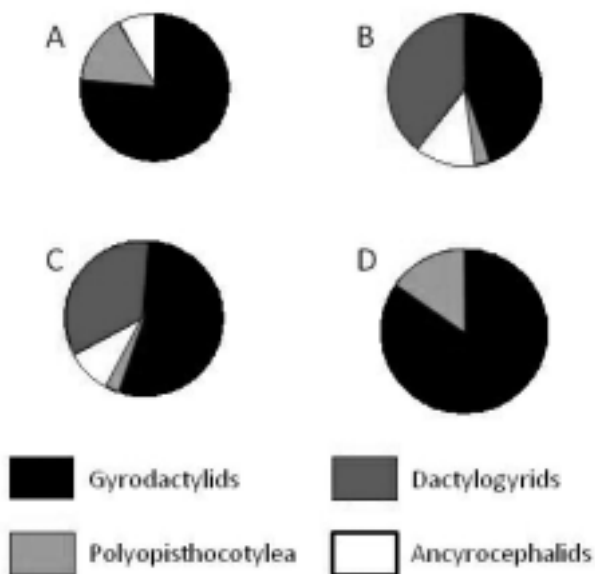
The impact of the ice ages – factors in the extinction of monogeneans

The factors leading to the extinction of monogenean species relate to the low temperatures experienced during glacial maxima, and the small and fragmented nature of the host populations they were forced to survive in. Obviously, if the host became extinct, then the parasites must necessarily follow. No monogenean has an extended survival period in the environment, and so local host extinction, even for a brief period, leads to parasite extinction. This is the principle upon which control of *Gyrodactylus salaris* using rotenone treatment is based [5]. At low temperature, egg production declines, and the time to hatching increases [17], extending the parasite

life cycle beyond the point at which it can be completed within one summer, especially when the onset of glacial conditions leads to a shortening of the summer period. Under these circumstances, it is the larger polyopisthocotylean and some dactylogyrid parasites, which are most likely to be unable to complete their longer life cycles and therefore go extinct. The smaller gyrodactylids, which exhibit a degree of progenesis [5], can complete their life cycles within a shortened summer period. Gyrodactylids are also tolerant of very low temperatures; several are known from Antarctic ice fishes [4], and *G. salaris* on salmon can tolerate 0.5˚C during winter, although reproduction ceases [18, 19]. This factor may allow for the apparently greater preponderance of gyrodactylids amongst fishes, which survived in northern refugia (Fig. 2).

On the other hand, the microparasitic [20] gyrodactylids induce unstable population interactions with their hosts [21], and require large, interconnected host populations with a ready supply of naďve fishes for persistence. These conditions may be difficult to satisfy within relatively small glacial refugia close to the ice sheet, and this may represent another reason for the extinction of gyrodactylids during glacial maxima.

Recolonisation patterns for freshwater fish and their parasites

The routes of recolonisation of freshwater fishes have had fundamental effects on their parasite communities, whether via freshwater connections from drainage basins in the South and East, via the sea, or if the fish survived in refugia, close to the ice.

1. Freshwater recolonisers

The first, and largest, group are those fish which were entirely unable to cope with either the cold or the altered flow conditions, and which became extinct in rivers flowing into the Baltic or North Atlantic. These included the majority of cyprinids, including *Leuciscus* species; the bream, *Abramis brama*; the tench, *Tinca tinca*; the rudd, *Scardinius erythrophtalmus*; and the loaches, *Barbatula barbatula* and *Misgurnus misgurnus*. The diversity of these fish still shows a marked impoverishment moving north and west through Europe, and *Abramis brama* and *Rutilus rutilus* did not reach Ireland until taken there by Man during the 16th and 17th centuries. The spread of many of these species has been via human intervention, either directly for food (e.g., *Cyprinus carpio* in the post-Roman peri-

od) or indirectly, through the burgeoning canal network of the 17th and 18th centuries [22].

These fish have monogenean faunas (Fig. 1), which are far richer than either those of anadromous fishes or of species which survived in northern refugia. In particular, they are infected by numerous species of Diplozoidae, which are almost completely absent from anadromous and refugial fishes. This pattern is also visible when diplozooid diversity is mapped geographically (Fig. 3). Countries within the Danube (Bulgaria, Czech Republic, Serbia, Hungary etc.) or Black Sea drainage basins (Ukraine, Belarus, Central Russia, Eastern Russia) have the greatest diversity of diplozooids. Poland has a particularly rich diplozooid fauna, partly because this has been investigated thoroughly, but also because it has received species both from the south and from the east. The dactylogyrid monogeneans are also particularly well represented in this group of fishes.
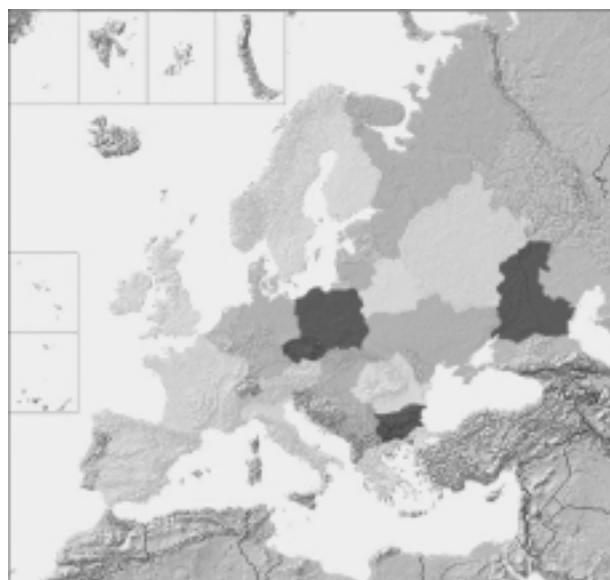

Fig. 3. Distribution of Diplozooidae within Europe. Number of species of *Diplozoon*, *Paradiplozoon* or *Eudiplozoon* within political units, as derived from Fauna Europaea (www.fauneur.eu). The tints represent countries within which 0, 1, 2–5, 6–10 or 11+species have been recorded, the darkest tint representing the most species-rich countries. There is a concentration of species in countries within the Danube drainage basin, or within the drainage basins of the major eastern rivers, the Dniester, Dnieper, and Don

2. Anadromous recolonisers

The second group of species are those anadromomous fishes able to disperse and colonise the Eurasian coastline from the sea. They include the lampreys (which are not infected by monogeneans),

the majority of salmonids including *Salmo salar* and *S. trutta*, but also the sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*, and the shads (*Alosa* spp.).
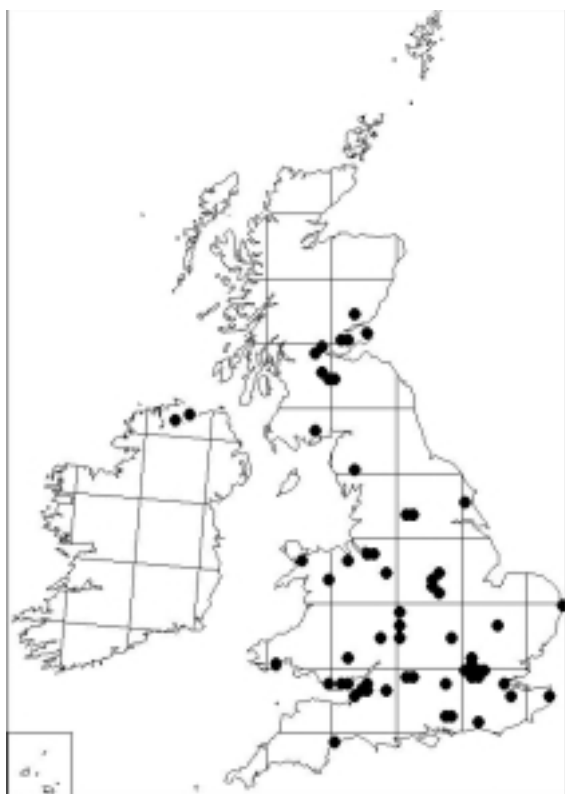

Fig. 4. Distribution of *Gyrodactylus* spp. on three-spined stickleback, *Gasterosteus aculeatus*, in Britain. A. *Gyrodactylus arcuatus*, a euryhaline species, colonising Scottish Islands via the sea. B. *G. gasterostei*, a stenohaline Channel River species. C. *G. alexanderi*, a North American species surving in refugia during the LGM. Mapping with DMAP (www.dmap.co.uk)

In general the anadromous recolonisers are infected by relatively few freshwater monogeneans, because these do not tolerate transport between river mouths through salt water when the host disperses. Anadromous salmonids and sticklebacks can also reproduce in streams bordering large lakes, a strategy lending itself to the development of refugial populations of fish and parasites, although this pattern may be obscured by later dispersal via the sea. This is well illustrated by the stickleback *Gasterosteus aculeatus*, which can breed in small streams close to the edge of glaciers. The distribution of mitochondrial haplotypes in northern Eurasia suggests that a massive post-glacial replacement of sticklebacks from the sea took place [23, 24]. The parasites, however, suggest a different story. *G. aculeatus* in Eurasia is infected by four different gyrodactylid species. The most widely distributed is *G. arcuatus*, a euryhaline species ranging from Turkey [25] to Iceland [26], and as *G. avaloniae* (either a sibling species or a synonym) extending down the American Atlantic Seaboard [27]. Within the United Kingdom, this species is found throughout the mainland, and also on isolated islands around the coast of Scotland (Fig. 4A), consistent with dispersal via marine sticklebacks colonising streams from the

sea. *Gyrodactylus gasterostei*, on the other hand, is a stenohaline species unable to disperse via the sea. This species has a distribution primarily within the catchment of the Channel River, in rivers bordering the North Sea, and does not occur north of the Baltic. Within the UK, it has a predominantly southern and eastern distribution, suggesting that it spread from the original Channel River catchment, aided by the development of canals in the 18th century [22]. *G. gasterostei* also occurs within Eastern Ireland (Fig. 4B), suggesting a role for tributaries of the Channel River in allowing its survival through the LGM.

The most enigmatic gyrodactylid infecting *G. aculeatus* in Eurasia is *G. alexanderi*. This American gyrodactylid has a predominantly Pacific distribution [27], but seven populations have been found in Scotland and northern England (Fig. 4C). It presumably invaded the Atlantic Basin 100–200 000 years ago, with its host [28]. This species must have survived the LGM in Scotland, and all of the sites are close to known glacial refugia. This shows that sticklebacks survived the LGM in refugia close to the ice sheet, although subsequently the genetic signal of their survival was swamped by the influx of marine fishes.

3. Northern refugial species

The third group of fish include those able to tolerate cold water, and therefore to survive close to the ice sheet. The most distinctive refugial survivors are fish of large lakes, such as the predators *Lota lota* and *Esox lucius*. Both currently extend to high latitudes in Eurasia and North America, and it is therefore reasonable to assume they could survive in large lakes around the edges of the ice sheet during glacial maxima. This is also the case for Arctic charr, *Salvelinus alpinus*, and whitefish, *Coregonus* spp., which retain a refugial population structure at lower latitudes although within the Arctic Circle populations are anadromous. These refugial species have a distinctive genetic structure, and are often severely bottlenecked. *Esox lucius*, for example, has a highly restricted genetic diversity in Northern Eurasia, suggesting a single origin for these fishes in Northwestern Europe at least [29, 30]. Fish from North America and southern Europe are more distinct, suggesting a pattern of local differentiation in particular refuges but also significant bottlenecking either during or after the LGM. *E. lucius* in Northern Europe has only two monogenean parasites, *Gyrodactylus lucii* and *Tetraonchus monenteron*. The most likely explanation of this paucity is that,

like the host, the parasite fauna of *Esox* has been extensively bottlenecked during and after the LGM, leading to an impoverishment of its monogenean fauna. The burbot, *Lota lota*, shows a similar pattern. Mitochondrial diversity [31] suggests glacial survival in a relatively small number of refugia in both Eurasia and North America. Eurasian burbot is infected by two gyrodactylids, *G. lotae* and *G. alexgusevi*, which are almost identical morphologically although quite divergent at a molecular level, suggesting a relatively ancient divergence [32]. One or both of these species is also present in North America [33], although further work is needed to identify exactly which species (or both) colonised North American fishes.

Fishes which survived glaciation in running water present a special case. For reasons already discussed, few river fish survived close to the ice sheet in rivers, and only three species appear to have done so in Northern Eurasia. The bullheads, *Cottus gobio* and *C. poecilopus*, are characteristic of cold fast flowing streams, and probably had a more widespread distribution at the LGM than today [34]. These fish show a complex pattern of gyrodactylid infection, based probably on their refugial history. *Cottus gobio* is infected in the south of its range by *Gyrodactylus cotti*, a species which has not been recorded outside of the Danube basin. Further north, this bullhead is infected with *G. hrabei*, a marine-derived species which probably originated via host shifts from *C. poecilopus* (see [35]). In Britain, *C. gobio* is also infected by a further gyrodactylid, the Channel River endemic *G. rogatensis*, which probably originated via a host shift from a salmonid.

4. *Gyrodactylus salaris* and *G. thymalli* – an example of a host shift in a refugial species

The third fish tolerant of cold running water, which survived close to the ice sheet, was the grayling, *Thymallus thymallus*. The grayling in Northern Europe consists of a number of distinct lineages which recolonised the Baltic basin as the ice sheet receded [36, 37]. This fish is implicated in the origin of the *Gyrodactylus salaris* epidemic on salmon in Norway, and so the status of its monogenean community deserves closer attention.

Salmo salar is primarily a marine fish, returning to freshwater to reproduce. The current distribution is greatly fragmented, mainly as a result of human interference, making reconstruction of its parasite fauna very difficult, because the species is missing from so much of its former range. However, *S. salar* appears to lack specific monogenean parasites in

freshwater, although it is infected by *Gyrodacty-loides bychowskyi* during the marine phase. Recently however, perhaps as recently as the past 200 years, salmon have become infected with another gyrodactylid as a result of a host shift (host capture) of a species normally infecting *Thymallus thymallus*. This parasite was first described from salmon in Sweden [38] and was named *G. salaris*. A second species, *G. thymalli* was described from grayling, *Thymallus thymallus* by Zitnan [39]. In molecular terms, *G. salaris* and *G. thymalli* are more or less identical, and should strictly be regarded as a single species [40–44], in which case the name *G. thymalli* would be a junior synonym of *G. salaris*. However, because of ambiguities in the specific status of these two forms, they are usually still regarded as separate species in the literature (see [5]). When first discovered in a Swedish fish farm [38], *G. salaris* was probably moderately pathogenic [45]. In the 1970s this highly pathogenic gyrodactylid was introduced into Norway, and has since been spread widely with salmon restocking programmes. The human-assisted introduction of *G. salaris* into Norway has been an environmental disaster. Direct costs, in terms of loss of revenue from salmon fishing, increased costs of surveillance and the costs of eradication extend into billions of Euros over the past 30 years. Indirect costs of Europe-wide surveillance and angler education to prevent the further spread of the pathogen are incalculable. The environmental costs of eradication, either by the use of rotenone to poison all infected fish in a river, or the more recent use of Aluminium ions to selectively poison gyrodactylids, have been largely ignored [5]. And yet, although the spread of *G. salaris* has been facilitated by Man, the initial host shift and subsequent spread on salmon was probably always likely to happen, and part of the post-glacial expansion of this gyrodactylid. Host shifts represent the normal mode of speciation in gyrodactylids. Examination of gyrodactylid phylogenies (e.g., [46]) shows that the most closely related species are always found on different host species. This is strong evidence that speciation events accompany host shifts. At a molecular level, *G. thymalli* is a highly diverse taxon. Every river which has been studied has a distinct molecular haplotype suggesting that *G. thymalli*, like its host, is a glacial relict species, which has been diversifying in different watersheds for a considerable period of time. One lineage (clade I) spread west, probably from ice lake refugia to the east of the Baltic ice

Fig. 5. Comparison of phylogeography of grayling (*Thymallus thymallus*) and associated *Gyrodactylus thymalli*. Areas occupied by *T. thymallus* clades I-IV (shaded) based on Koskinen et al. [36] and Gum et al. [37]. Distinct *G. thymalli* clades indicated by different symbols, based on Hansen et al. [42, 43] and Meinilaa et al. [44]

sheet, another (clade II) spread North into Norway from rivers to the south of the Baltic. At least one or two other lineages are implicated in founding grayling populations further west in Europe [36, 37] (Fig. 5), and more will be found with further research. These populations spread to their current distribution following the LGM, although their origin as genetically distinct stocks is much older. *G. thymalli*, shows a much deeper genetic structure [42, 43]. Populations of the parasite from grayling within the eastern clade I of the host, from Finland and from Lake Onega, are as different from each other as they are from populations infecting the southern grayling clades II and III, from Norway, Britain and Slovakia (Fig. 5). Either the parasite has diverged very rapidly (since the LGM) within individual streams in Europe, or there is a trace of an older structure in the parasite population which has survived the subsequent re-expansion of grayling, in the same way as that discussed earlier for *G. alexanderi* on sticklebacks. Most excitingly, the boundaries of the parasite clades do not precisely map to those of the host clades, indicating that some spread of the parasite onto novel host genotypes has occurred (Fig. 5). The precise watershed within which the host shift to salmon occurred has not yet been identified, but two distinct haplotype clusters of *G. salaris* on salmon have been described, sug-

gesting that it occurred either once or twice. One cluster comprises all the very pathogenic *G. salaris* haplotypes on Norwegian salmon [42], while the other comprises less pathogenic haplotypes collected from rainbow trout in fish farms, from Arctic charr [47] and from salmon in Denmark [48].

Much remains to be discovered about the *G. salaris*/*G. thymalli* host shift. The factors responsible are not known, although it may be related to the introduction of rainbow trout to Europe in the 1890s [5], providing a host on which strain hybridisation and introgression could take place. Alternatively this could have been a shift occurring entirely without human assistance. Identification of the precise river stock of *G. thymalli*, which underwent the host shift, will be an important step in resolving this point.

Predicting future change

What of the future? Clearly post-glacial adjustment of monogenean faunas is not complete in Europe, even without the rise in temperature and sea levels due to human mediated carbon dioxide release. In fact, human mediated transfaunation is likely to be far more important in extending monogenean distributions in the future than is climate change. We have already experienced at least two waves of such human-mediated fish movement, the first in the medieval period when fish species (*Cyprinus carpio* for example) were disseminated widely for food; a second phase took place in the 17th–19th centuries as canal networks connected previously disparate river systems. Now, the human-mediated spread of fish species is proceeding at an increasing rate. Garcia-Berthou et al. [49] record 264 introductions of 123 aquatic species, most of them fishes, introduced into 6 European countries. Generally the parasitological consequences of such introductions are slight, but are entirely unpredictable. Kennedy [50], for example, listed 6 monogenean species successfully introduced into Britain, one from America. None of these have caused problems to date, but their future performance cannot be predicted. A general problem is the overall lack of historical data on monogenean distributions and taxonomy in western Europe; despite the existence of resources such as Fauna Europaea (www.faunaeur.org), it remains difficult to obtain baseline data on monogenean distributions against which recent introductions or range expansions can be measured.

Summary

It is clear that those fish species which recolonised Northern Europe as anadromous migrators, or which persisted in refugia close to the ice sheet, have significantly impoverished monogenean communities. On the other hand, fish which recolonised via freshwater, or were assisted by human intervention, have richly diverse monogenean faunas. The factors leading to the extinction of monogeneans during the ice ages are quite clear, and relate to a combination of low temperature, host extinction, and survival of hosts in small fragmented refugia. What is not clear, however, are the factors leading to the expansion of monogenean faunas during interglacials. The frequency of host shifts in molecular phylogenies of gyrodactylids [46, 51] attests to the occurrence of such expansions. Furthermore, the discovery of *Gyrodactylus salaris*, undergoing a host shift from its original host the grayling *Thymallus thymallus*, represents perhaps the best example of speciation in real time since the discovery of *Rhagoletis pomonella* feeding on apples [52]. The factors responsible for host shifts and subsequent speciation events remain unclear. Did *G. salaris* transfer to salmon because salmon had no native gyrodactylids with which to compete? Or was the host shift facilitated by the import of non-native salmonids into Europe for aquaculture during the 20th century? Kennedy [50] notes that host species with species-poor parasite communities should be more prone to invasion by host-shifting species than those (e.g., cyprinids) with species-rich communities. However, do successful host shifts onto fish with poor monogenean communities lead to disease outbreaks (as with *G. salaris*) because stabilising competitive interactions with other monogeneans do not take place, or does extinction of a monogenean lead to potential disease outbreaks because of destabilisation of the competitive network amongst the monogenean species present? Answers to these questions are urgent during this period of rapid environmental change and human mediated – transfaunation across natural boundaries.

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