

Review

Extreme climatic events and host–pathogen interactions: The impact of the 1976 drought in the UK

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ABSTRACT

Intense, long droughts have increased in occurrence since the 1970s and have been linked with global climate change. Extreme climate alters the risk of pathogen infections and diseases in both animals and plants, although little is known about the impact of any single event on host–pathogen dynamics in a wide range of species. Evaluating past climatic events can provide valuable information on complex interactions that occur between hosts, pathogens, and the environment, thereby paving the way for predictive models and ultimately early and efficient response to disease threats. The present study reviews the substantial impact of the 1976 UK drought on climate-driven host–pathogen associations. This 16-month drought had a devastating effect on flora and fauna and is considered a benchmark for dry conditions in this country. Changes to the occurrence of infections in farmed and wild animals and plants are presented in terrestrial, freshwater, and marine ecosystems and the implications for pathogen transmission under extreme climate conditions are assessed.

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1. Introduction

Global climate change as a result of human activities is a widely accepted phenomenon. Average atmospheric and surface temperatures along with sea levels have risen significantly over the last 50 years. A warmer global climate system consequently accelerates the hydrological cycle, increasing the likelihood of extreme

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weather events such as droughts, heat waves, storms, and heavy rainfall with associated flooding (IOM, 2008). In particular, intense long droughts can have a devastating impact on regional agriculture, water resources and the environment (Sheffield et al., 2012).

Within the UK, at temperate latitudes, climate change is predicted to result in an increase in average temperatures of 2–4 °C by the 2080s with an increased frequency of heatwaves in summer and more intense recurrent rainfall events. However, annual precipitation may be little changed but summer rainfall could fall by up to 50%, offset by an increase in winter rainfall, with a greater risk of floods and drought (Hulme et al., 2002). These predicted changes will be more marked in the south of the country with a greater impact on natural than in agricultural systems (Chancellor and Kubiriba, 2006).

An increased occurrence of extreme weather events may, in turn, alter the risk of infectious disease incidence in a wide range of pathogens of animals and plants. Climate can directly influence both the replication rates and dissemination of pathogens and the movement, replication and abundance of hosts. Ecosystems and human behaviour will also be indirectly affected, thus leading to changes in the incidence, seasonal occurrence and geographical range of pathogens (IOM, 2008), although a number of additional differences in the degree of infectious disease risk separate farmed and wild organisms.

An important component of forecasting pathogen outbreaks in a changing climate can be derived from historical analysis which provides a valuable, wide-ranging, perspective on climate and infectious disease and contributes to our understanding of complex interactions between biological and physical environments. This paves the way for the development of predictive models and, thereby, for early and efficient responses to infectious disease threats (IOM, 2008).

The impact of extreme climatic events on a small number of, specific, host–pathogen relationships has previously been documented (Szidat, 1968; Kennedy, 1998; Overstreet, 2007) and drought, in particular, has long been known to have significant effects on the occurrence of parasitic diseases e.g. Szidat (1968).

Within the UK the potential effects of climate change have been assessed in a limited number of prominent infectious diseases of animals and plants (Baylis, 2006; Wilkinson, 2006; Chancellor and Kubiriba, 2006; Baylis and Githeko, 2006; Gale et al., 2009). These studies focus on pathogenic species that are of the greatest current importance to the UK (Baylis, 2006), including notifiable exotic diseases and non-notifiable endemic diseases resulting in the greatest economic losses. Although such prioritisation is concordant with an anthropocentric view of climate change it largely ignores the impact of pathogens on animals and plants that have no obvious medical, veterinary, or economic importance. Such an approach may be shortsighted as it leaves little room to consider the interconnected nature of organisms, their pathogens, and the way changes to species community structure that may be regarded as insignificant to social economics can cause a cascade of effects through ecosystems that can ultimately impact those animals and plants that are important to human welfare e.g. Marcogliese and Cone (1997).

A further weakness of studies focusing on only one or two species is the tendency to extrapolate results derived from this limited pool to other pathogens that share similar transmission strategies in order to create sentinels for making generalisations on the nature of the impact of particular biotic or abiotic factors (Kutz et al., 2005; Morand and Guegan, 2008). However, the response of a wide range of pathogens to any one factor or event has rarely been studied and therefore the validity of using a few ‘keystone’ species has not yet been proven. In the present study, by assessing the impact of one climatic event to the largest possible number of

species infecting animals and plants from terrestrial, freshwater and marine ecosystems, we hope to determine trends that will prove useful in the study of pathogens within both farmed and wild organisms in a changing climate.

Drought is a recurring feature of the UK climate and can be defined on the basis of meteorological, hydrological or agricultural factors and its range and scale of impact can be determined according to its duration and spatial extent (Marsh et al., 2007). Ten major droughts have been identified since 1800 and all but one persisted for at least a year, often longer, and were associated with one or more notably dry winters (Marsh et al., 2007). The 1976 drought is considered a benchmark for dry conditions, particularly across much of England and Wales (Marsh et al., 2007) but also throughout northwest Europe where similar harsh conditions occurred (Stubbs, 1977). During this period the lowest flows of British rivers were recorded and there was a severe impact on surface water and groundwater resources (Marsh et al., 2007). In addition, this drought may be particularly useful for studies on climate change as it followed a 5-year cycle of mild winters throughout western Europe from 1971 to 1976 (Wright, 1975; Meteorological Office, 1976; Perry, 1978). In temperate latitudes mild winter conditions are predicted to become more frequent in the future under climate change (Hulme et al., 2002) and therefore an example of an extreme climatic event associated with these conditions is particularly valuable.

The 1976 drought in the UK attracted a great deal of scientific and media attention (Hearn and Gilbert, 1977; Cox, 1978; Hill and Avery, 1978; Pereira et al., 1978; Doornkamp and Gregory, 1980) and consequently there is far more literature devoted to this extreme climatic event than any other severe drought in the 20th century. Furthermore, the 1970s represented a high point of animal and plant pathogen surveillance in the UK, encompassing a wide range of pathogens, and resulting in an extensive collection of data for this period, making the 1976 event particularly valuable for understanding complex large-scale host–pathogen interactions under the influence of extreme climate.

From a meteorological perspective the drought is defined as occurring over a 16-month period from May 1975 to the end of August 1976 and, with the exception of September 1975, each month had below average or average rainfall (Ratcliffe, 1978). The drought culminated in continuous very high temperatures throughout the summer of 1976, with extreme daily highs of over 30 °C occurring between 23rd June and 7th July, making it one of the warmest on record (Ratcliffe, 1976). At the end of August the weather broke and a period of heavy rainfall began which continued throughout the autumn (Ratcliffe, 1977a).

Based on the reported responses of a wide range of animals and plants, biologically the impact of the drought probably extended over a slightly different period likely beginning in the autumn of 1975 for some species, following that year’s dry summer, and continuing through 1976 and into 1977 for other species. However, different organisms responded in different ways with many species experiencing only short-term effects, with a rapid recovery after the drought broke (Hearn and Gilbert, 1977; Jeffers, 1977). Nevertheless, some species suffered more protracted symptoms. For example, during 1976 many tree species showed premature browning and withering of foliage, yet by the late summer of 1977 only beech had begun to die in large numbers due to the previous year’s drought stress (Jeffers, 1977; Doornkamp and Gregory, 1980). For the present review we consider a time scale from the summer (June–August) of 1976, when the drought reached its peak, to mid-1977 as the main period when the effects of host–pathogen interactions are most likely to occur.

The present study therefore assesses the impact of the 1976 drought on climate-driven host pathogen interactions in terrestrial, freshwater and marine systems, using as many examples as

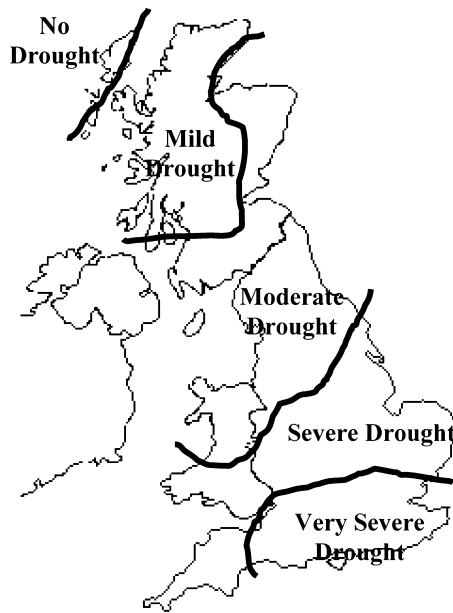


Fig. 1. UK regional drought intensity during 1976. Redrawn from Atkinson (1980).

could be found from both farmed and wild animal and plant host species. We have broadly defined pathogens to include those organisms that infect a host, animal or plant, that they require to complete their life cycles, those that are opportunistic generalists infecting a host that has reduced resistance due to drought stress, or those that may act as mechanical vectors for another, typically a bacteria or virus, transporting it from host to host, representing the main agent of transmission. Data are derived from published research articles, unpublished theses and other grey literature sources where available. It is also supplemented with unpublished data collected at the time as part of a long-term parasite monitoring programme of wildlife undertaken at Royal Holloway, University of London designated as 'Lewis et al. (unpublished observations)' All the source data for this review is contained in detailed online supplementary tables (Supplementary Tables 1–9).

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2013.12.001>.

The severity of the drought was not uniform over the entire British Isles. To aid understanding of changes to host–pathogen dynamics occurring in any particular geographical locality, the country can be characterised by the intensity of conditions experienced, relative to precipitation, potential evaporation, soil moisture deficit and runoff during the drought. Atkinson (1980) divided areas for this drought according to four categories namely mild drought (Mi) – covering most of western and northern Scotland; moderate drought (Mo) – in eastern and southern Scotland, northern England and northern Wales; severe drought (Se) – an area extending from Cornwall, Devon, and south Wales across the midlands of England to east Yorkshire in the north and Suffolk in the south; and very severe drought (Vs), a core area in southern and south-east England extending from Dorset, Somerset, and Gloucester in the west through to Essex and Kent in the east (Fig. 1). These categories were used in the present study to determine drought severity in each locality. The focus of this assessment is principally on effects occurring during the summer of 1976, which represents the culmination of the drought, with associated high temperatures, although both earlier and later effects are included where relevant.

This is a qualitative review of the available data, intended to provide an initial assessment of the impact of a major drought on

host–pathogen associations across a range of habitats and conditions. In order to better determine and broad changes in associations between pathogen occurrence and the drought a standardised effect, E , was calculated by granting studies showing either a positive effect, no or undetermined effect, or a negative effect on pathogens scores of 1, 0, and –1 respectively and then taking the mean. Statistical analyses were undertaken using a one-sample Wilcoxon Signed Rank test.

2. Terrestrial ecosystems

Within terrestrial ecosystems the lack of rainfall and high temperatures resulted in a serious decline of soil moisture during the summer of 1976. As the ground hardened there was an increase in erosion, which was exacerbated by the wet autumn that followed the ending of the drought (Hearn and Gilbert, 1977; Doornkamp and Gregory, 1980). As evapotranspiration rose the soil moisture deficit increased resulting in elevated levels of mortality of many plant species in grassland and lowland heaths leading to a large amount of bare ground (Hearn and Gilbert, 1977; Hopkins, 1978). As a consequence of these conditions wild fires became more frequent, causing extensive damage to many habitats (Hearn and Gilbert, 1977). Numerous invertebrate populations were affected by the low moisture and high temperatures. The longevity of many adult insects is reduced by low humidity and early mortalities were considered common during 1976 (Jeffers, 1977). Butterflies showed variable responses, with many species emerging earlier than usual (Hearn and Gilbert, 1977). Similarly, aphid species built up large numbers during the early part of the summer, due to high temperatures and whilst food sources were still unaffected by the drought. However, populations rapidly declined later on due to an increase in numbers of predators such as ladybirds (Hearn and Gilbert, 1977).

Numbers of sawflies were reduced in south-east England due to the dryness of the soil inhibiting adult emergence, whilst ground beetles were also few in number until the heavy rainfall in September (Hearn and Gilbert, 1977). In northeast Scotland there was an increase in grasshopper populations because they were able to spread onto moorland habitats that would normally be too wet to support these species (Jeffers, 1977).

Many common garden bird species did not have successful breeding seasons in England due to the decline in invertebrate food supply, particularly earthworms, which also negatively affected badger and mole populations. The shortage of summer food and water may also have contributed to an increase in mortalities in the following winter for deer and wild ponies that had built-up inadequate fat reserves (Hearn and Gilbert, 1977).

In farmed conditions crop production was generally impeded, particularly grasslands. Although livestock remained generally fit, milk yields fell whilst lambs and grazing cattle took longer to fatten requiring supplementary feeding with hay and straw. Some cases of poisoning occurred from livestock foraging for food where pasture was bare. Poor quality water supplies also caused additional problems whilst the high temperatures resulted in some heat-related mortalities. In the longer term soil acting herbicides and residues had a reduced effectiveness and enhanced persistence due to the lower levels of moisture (Carter, 1978).

2.1. Animal hosts

2.1.1. Farmed conditions

A wide range of infectious diseases in farmed animals during the drought is recorded in the annual reports of the Chief Veterinary Officer in the Ministry of Agriculture, Fisheries and Food (MAFF). From the early 1970s onwards the government veterinary research laboratories undertook routine surveillance of incidents

affecting the health of farmed animals and the national occurrence of diseases were published as annual returns e.g. Brown (1977, 1978). However these figures represent only reported incidents that were successfully diagnosed as being caused by specific pathogens. Such data are therefore biased in representing disease-associated conditions that resulted in noticeable effects on animal welfare, but they do provide some important indications of annual changes in pathogen occurrence during this period in the form of a passive monitoring system (Thrusfield, 2005) and represents the most common form of pathogen monitoring due to the costs of providing accurate and representative sampling by active monitoring.

Annual occurrences of numerous infectious disease conditions were documented during the drought (Brown, 1977, 1978). However, many diseases are considered to have no direct relationship with climatic conditions and consequently remained relatively unaffected during 1976 (Brown, 1977, 1978). Pathogens considered in this section therefore have a well-documented relationship with environmental factors, particularly during the summer, or changes either directly or indirectly correlated with the prevalent climatic conditions in 1976.

Strongyloid and trichostrongyloid nematode parasites of cattle and sheep have direct life cycles with development and survival of free-living stages (egg and larvae) on pasture. Meteorological factors affecting the pasture will also alter nematode development and transmission (Thomas, 1974), with moisture being the key variable for survival (Stromberg, 1997). In the UK the principal nematode parasite of livestock is parasitic gastroenteritis caused by a range of trichostrongylid nematode species. The mode of infection differs between cattle and sheep due in part to different farming practices. Cattle that are generally free of infection are usually turned out in spring onto the pasture acquiring parasites that have overwintered on the herbage. Sheep, in contrast, generally remain outdoors throughout the year and therefore have a more complex mode of infection that is particularly influenced by the spring lambing season (State Veterinary Service, 1982).

Extensive field studies on these nematode species in cattle and sheep had taken place during the drought period e.g. Starr and Thomas (1980), Gibson et al. (1981) and Lancaster and Hong (1987). The drought had a substantial and consistent effect on these helminths, both delaying build up of larval worm numbers on the pasture until the autumn in regions suffering from drought intensities ranging from Mo to Vs, and generally causing a reduction in the number of annual diagnosed incidents throughout the UK.

In contrast, the pathogens cysticercosis and hydatidosis, caused by the cestodes *Cysticercus bovis* and *Echinococcus granulosus* respectively, appeared to remain unaffected by the drought (Brown, 1978; Blamire et al., 1980) despite egg survival on pasture also being influenced by moist conditions (Kassai, 1999).

A more complex picture is demonstrated by fascioliasis, a disease of sheep and cattle caused by the trematode *Fasciola hepatica*. This parasite utilises a semi-aquatic snail, *Galba truncatula*, as an intermediate host and pathogen outbreaks are strongly correlated with summer (May–October) rainfall (Ollerenshaw and Smith, 1969) which determines the availability of the snail host, the proportion that become infected, and the extent to which the infection matures in the snail and is passed out onto the herbage where the livestock host will passively ingest it (Ollerenshaw, 1983). Most disease occurs when the summer is persistently wet. Unlike earlier and later decades, the 1970s showed a succession of summers when below average rainfall occurred resulting in a gradual decline in disease incidence (Ollerenshaw, 1983). This trend is best illustrated by meat inspection records at abattoirs that show liver condemnation in

UK cattle falling between 1969 and 1978 (Blamire et al., 1980). The drought in 1976 may have exacerbated this deteriorating situation as it eradicated the majority of snail populations on pastures and prevented parasite eggs from hatching, effectively bringing the lifecycle to a standstill in many areas (State Veterinary Service, 1982). Consequently, national diagnosed incidents in the UK for cattle and sheep declined sharply in 1976 and continued to fall in subsequent years (Brown, 1978).

Coccidiosis is an important disease caused by the protozoan *Eimeria* spp. in livestock. It affects a wide range of farmed animals but is caused by different parasite species in each host group. Oocysts contaminate the pasture in host faeces and become transmitted to another host through grazing activity, with this parasite stage being highly susceptible to high temperatures and desiccation (MERCK, 2008). In sheep during 1976 there was a sharp decline in national diagnosed incidents rising again in 1977 but in cattle no decline was apparent until 1977 (Brown, 1978) suggesting that either the different *Eimeria* species in these two hosts were responding in dissimilar ways to the climatic conditions or different farming practices were responsible.

Ectoparasites, particularly ticks, lice, mites, fleas, and insects can be a major source of production losses in farmed animals (MERCK, 2008) and may be particularly susceptible to drought conditions (Jones and Kitron, 2000; Osacar-Jimenez et al., 2001; Bates, 2012). During the drought year the national diagnosed incidents of unspecified serious ectoparasitic infections did not appear to be substantially affected in any livestock (Brown, 1978).

Many forms of ectoparasites can act as vectors for other infectious diseases. Cattle ticks, in particular, may transmit babesiosis, tick-borne fever, and louping ill. During 1976 there was a decline in the number of diagnosed incidents of tick-borne fever but the occurrence of both babesiosis and louping ill remained relatively unchanged. In contrast, infections of sheep with tick-borne fever, tick pyaemia and louping ill during 1976 demonstrated only slight changes in the number of national diagnosed cases (Brown, 1978). These results suggest that the drought conditions elicited no substantial effects on the annual occurrence of these ectoparasites and the diseases they transmit.

In contrast, sheep scab, caused by the mite *Psoroptes ovis*, demonstrated more obvious responses. Infections may occur throughout the year although, typically, there is an increased incidence in the winter (Van den Broek and Huntley, 2003) due to the negative effects of summer temperature and humidity on mite oviposition rates and mortality, and seasonal management practices (French et al., 1999). During 1976, 101 outbreaks of scab were confirmed in the UK, but not a single incident occurred between June and September of that year, whilst during 1977, when more widespread compulsory dipping of sheep had been introduced, there were 54 confirmed outbreaks with 11 (20.4%) occurring in the June–September period (Brown, 1977, 1978). It seems likely that either directly or indirectly climatic conditions during the summer of 1976 negatively influenced pathogen occurrence over this period.

A range of insects are associated with livestock, may be important mechanical vectors of disease, and are particularly affected by climatic conditions (Sellers, 1980). The non-biting insect *Musca autumnalis*, the face fly, is a common vector for bovine keratoconjunctivitis, caused by the bacterium *Moraxella bovis*, and during the drought there was an unusual high incidence of disease (Brown, 1977; State Veterinary Service, 1982) probably associated with increased fly strike. However, the head fly, *Hydrotaea irritans*, also a non-biting insect, and a vector of summer mastitis, caused by the bacterium *Corynebacterium pyogenes*, should also have been favoured by the high temperatures but reported annual incidents of mastitis diagnosed due to *C. pyogenes*

showed no change from the previous year (Brown, 1977, 1978), although changes in seasonal occurrence cannot be ruled out.

Nevertheless, the warble fly (*Hypoderma bovis*, *H. lineatum*), a pest of cattle causing myiasis, did demonstrate changes. It is an obligate parasite with a larval stage that lives beneath the host skin for up to a year, although the adult fly survives for only a week. The drought was particularly favourable for insect occurrence, and consequently the national prevalence of warble fly in cattle rose to almost 40% in both 1976 and 1977, being especially virulent in southwest England (Se) (Brown, 1978; State Veterinary Service, 1982). It was considered that the drought may have altered the active season of the fly resulting in larvae prior to emergence continuing to migrate through the host body later than normally anticipated thereby avoiding the main period of insecticide application (Brown, 1978).

There was a sharp decline in the number of national diagnosed incidents of dermatophilosis (mycotic dermatitis) in cattle and sheep throughout the UK in 1976 (Brown, 1978). This skin infection is caused by the bacterium *Dermatophilus congolensis* and rainy periods facilitate its development, prevalence and seasonal occurrence because moisture helps the release of zoospores from pre-existing lesions as well as increasing the numbers of biting arthropods acting as mechanical vectors (MERCK, 2008). Its decline during the drought is therefore unsurprising.

Fungal infections are particularly susceptible to variations in climatic conditions (Ainsworth and Austwick, 1973). Dermato-phytosis (ringworm) is a skin infection caused by a range of fungal species. In livestock the disease is usually enzootic in herds with prevalence varying according to climate and the availability of natural reservoirs (Chermette et al., 2008). During 1976, there was a decline in national diagnosed incidents in cattle, sheep and pigs compared to other years (Brown, 1978), suggesting that the drought negatively affected fungal viability during this period.

Mycotic pneumonia is a fungal infection of the lungs usually caused by *Aspergillus* spp. or *Candida albicans* which are opportunistic infections arising from the inhalation of fungal spores from moist and mouldy straw or feed. High prevalences consequently occur in livestock maintained indoors in intensive housing units (Radostits et al., 2000). During 1976 there was a significant decline in the number of national diagnosed incidents in cattle and birds (Brown, 1978). It is likely that the low humidity conditions during the drought dried out much of the organic matter that acted as a source of fungal infection, inhibiting pathogen development.

Mycotic abortion in cattle is caused by a potentially wide range of fungal species. It is most prevalent in the UK during winter and spring with infections being directly correlated with the previous summers rainfall or through contact with mouldy hay and feedstuff (Ainsworth and Austwick, 1973). Existing records do not differentiate between fetopathy caused by individual fungal species, nevertheless there is a decline of incidents during both 1976 and 1977, reflecting climatic conditions in the previous summers (Brown, 1978; MAFF, 1979).

An additional consideration of extreme weather effects is that pathogens not normally considered to be climate related, may have altered occurrence due to amendments in farming practice resulting from the drought. For example the bacterium *Erysipelothrix rhusiopathiae* is ubiquitous and able to persist for a long period in the environment. It is a pathogen in a wide variety of farmed and wild animals and causes a range of disease conditions (Wang et al., 2010). In sheep *E. rhusiopathiae* is known to cause post-dipping lameness resulting from the contamination of dipping solutions used to treat livestock. (MERCK, 2008). In the UK throughout the 1970s a few incidents were usually reported during each year particularly in June and July, a time favoured by farmers for dipping, when cases normally dramatically increased.

However, during 1976 there was a drastic reduction in the number of diagnosed incidents of post-dipping lameness with no peak during the summer. This change was likely to be associated with the acute shortage in piped water supplies prevalent at this time reducing and delaying the frequency of sheep dipping in the country (Brown, 1977).

2.1.2. Wild conditions

A range of infectious diseases are known from wild animals in the UK but only a limited number were being studied over this period. As in the case of farmed animals it seems likely that those diseases requiring an invertebrate vector or host for transmission would be most affected. For example, the levels of infections of protozoan (Haematozoa) blood parasites of 20 species of non-migratory birds from Tregaron, Mid Wales (Mo), undertaken in August 1976 were lower than normal for these hosts in the UK, and this was likely to be due to a decline in the number of suitable blood feeding arthropod vectors, usually adults of blackflies or mosquitoes, that normally bred in a nearby bog that had dried out (Peirce and Mead, 1978).

However, a more complex picture emerges when the vector is also an ectoparasite on the host. For example, the viral disease myxomatosis has a devastating effect on wild rabbit populations. Patterns of disease occurrence through the year are influenced by the seasonal mass movement of the rabbit flea, the main vector of myxomatosis in Britain (Ross et al., 1989). Population dynamics of the flea are strongly influenced by climatic conditions, particularly those found within rabbit burrows where variations in depth, soil type and texture can determine thermal insulation and humidity levels (Osacar-Jimenez et al., 2001). The disease was studied in wild rabbits from three farmland sites between 1971 and 1978 in the UK (Ross et al., 1989). Two sites were on lowland farms in West Sussex (Vs) and Hampshire (Vs) whilst the third was on an upland farm site in south Wales (Se). Myxomatosis outbreaks in Hampshire were recorded throughout the study period, with no substantial changes over the drought period compared to other years, whilst in Wales only occasional cases were observed. In contrast, on the farmland in west Sussex the rabbit population remained moderately high throughout the study period. Summer disease outbreaks were recorded up to 1976, but no incidents were detected in either the following summer or 1978. This may potentially be due to the flea vector being unable to survive drought-associated changes in the microclimate of rabbit burrows that occurred at this specific location where potential soil moisture deficits were over 400 mm by August 1976 compared to the long-term average (1956–1975) of 100–150 mm (Taylor et al., 1980).

In contrast, studies using capture-release methods of wild rodents infected with blood parasites that also utilise insect ectoparasitic vectors demonstrate variable consequences of drought exposure. Two geographical populations were studied in Powys (Se), Wales, and Berkshire (Vs), England between 1976 and 1978 (Healing, 1981). During 1976 there were unusual mid summer peaks in new infections of *Babesia* sp. and *Hepatozoan* sp., protozoans transmitted by ticks, not replicated in subsequent years. New infections of *Trypanosoma* sp. and *Bartonella* sp., transmitted by flea vectors, also demonstrated an atypical late summer/autumn peak in Berkshire. In Wales, however, *Bartonella* sp. peaked in the early summer of 1976 (Healing, 1981).

Differences in the epidemiology of insect-borne diseases depend on specific biological features of pathogens, vectors and hosts (Randolph, 2004). As ectoparasite vectors such as fleas and ticks are particularly susceptible to temperature and humidity which influence development and emergence (Randolph, 2004; Medvedev and Krasnov, 2008), changes in the seasonality of blood parasites that utilise them as vectors are not unexpected and these

differences may reflect individual responses of each vector species to extreme climate.

As shown by [Healing \(1981\)](#), small mammals, such as voles and mice, are particularly useful in studying wildlife diseases. Similar studies on parasitic infections within a population of field mice, *Apodemus sylvaticus*, in a woodland site near Egham (Vs), Surrey, were undertaken with monthly monitoring using faecal samples and blood smears of trapped, and then released individuals. Parasitic species richness was found to be highest in 1976 compared to other years, largely due to a sudden occurrence in previously unrecorded infections of protozoans and bacteria (*Bartonella* sp., *Babesia microti*, *Trypanosoma microti*) in the blood smears (Lewis et al., unpublished observations).

This increase in species richness may be due to a habitat which remained relatively favourable for small mammal hosts during the drought. The woodland which occupies a lower slope and valley floor of a hillside and is crossed by streams previously had a history of sustaining a bacterial infection in the rodent population during hot and dry weather ([Lewis and Twigg, 1972](#)). This woodland site may therefore have acted as a refuge for rodent immigrants against the harsh climatic conditions during the summer of 1976 whilst adjoining areas declined in their ability to support wildlife.

An analysis of faecal samples demonstrated a wide range of helminth species in the mouse population. The 1976 drought had only a limited effect on the occurrence of these parasites in this sheltered locality mainly associated with changes in seasonality of juvenile host infections. In particular, infections of juvenile mice with the nematode *Heligmosomoides polygyrus* over the summer period were significantly lower in 1976 than in other years suggesting that survival and viability of free-living larvae in the drought-affected soil was probably reduced ([Lettini and Sukhdeo, 2006](#)), although prevalences in adult mice remained unchanged, presumably because they harboured infections acquired during the previous autumn and winter ([Lewis and Hargreaves, 1978](#); Lewis et al., unpublished observations). In addition, infections of both adult and juvenile mice with the trematode *Corrigia vitta* were influenced by the drought. There was a surge of infections acquired by both juveniles, which had remained free of infection during the summer, and by adult mice in the autumn of 1976 during the prolonged heavy rainfall that accompanied the breaking of the drought. This resulted in significantly higher prevalences for this period compared with other years (Lewis et al., unpublished observations). This increase is also likely to be associated with a rise in the activity and availability of infected molluscan and arthropod intermediate hosts following improved climatic conditions ([Sternberg, 2000](#); [Simpson et al., 2012](#)).

The relative stability of parasite populations in older small mammals in this locality compares well with long-term annual studies of adult *A. sylvaticus* and *Sorex araneus* from a grassland site in Rogate (Vs), West Sussex. Seven species of helminths were recorded from *A. sylvaticus* and ten species from *S. araneus* with little change in species richness between years (Lewis et al., unpublished observations; [Morley and Lewis, 2008](#)). Levels of helminth infections demonstrated variable changes during the drought. In general most species appeared to be largely unaffected by the climatic conditions and demonstrated little change in the prevalence of infections between years in the adult host population. However, in *A. sylvaticus* the occurrence of the nematode *Syphacia stroma* during 1976 significantly declined compared to other years. Transmission of this nematode species occurs by contact between hosts. Therefore, host density is more likely to influence infection levels than climatic conditions suggesting the decline in *S. stroma* infections was only indirectly attributable to the drought. In contrast, in the shrew host, *S. araneus*, the hymenolepid cestode *N. singularis* which uses a range of beetle species as intermediate hosts ([Prokopic, 1968](#)), had a

significantly higher prevalence in the drought year (Lewis et al., unpublished observations). However, no other hymenolepid species from the shrew demonstrated any comparable change during 1976, suggesting that climate alone was not responsible.

On the other hand, infections of both shrews and mice with trematodes during the drought year in Rogate were absent or substantially declined ([Morley and Lewis, 2008](#)). Neither an examination of juvenile hosts nor their seasonal occurrence was studied at this locality and therefore comparable drought-induced changes with the occurrence of parasites apparent in Egham remain unknown.

However, further details on the viability of small mammal parasite life cycles during the drought at Rogate were obtained from long-term investigations on terrestrial molluscs, intermediate hosts for many species of helminths. The land snail *Discus rotundatus* was the principal host at this site. From sampling of this snail undertaken each September positive correlations of trematode (cercariae) prevalence and summer rainfall and maximum winter temperature were apparent with a significant decline of infections in 1976 ([Morley and Lewis, 2008](#)), although infections of trematode metacercariae remained largely unaffected by the drought. Similarly, rhabditoid nematode infections in this host were also not significantly affected. On the other hand, infections of the cestode *Molluscotaenia crassicolex* were positively correlated with high spring and summer rainfall and the absence of any molluscan infections during 1976 was therefore not surprising ([Morley and Lewis, 2008](#)). When these findings are compared with those found concurrently in small mammals it appears that where infections are seriously affected by drought in one host it is compensated by some degree of stability in the other host within the life cycle, thereby allowing a rapid recovery once conditions become more favourable ([Morley and Lewis, 2008](#)).

Insects are also hosts to a range of pathogens. Fungal infections of aphids by the genus *Entomophthora* are highly pathogenic with outbreaks at least being partly responsible for reducing insect populations ([Carter et al., 1980](#)). Climatic conditions are very important in the development of fungi as a high humid atmosphere is necessary for sporulation and consequently during periods of low rainfall infections cannot be sustained ([Carter et al., 1980](#)). Thus, on a farmland site near Rothamstead (Vs), Hertfordshire, less than 1% of cereal aphids were infected in July 1976 compared with peaks of 79% during the same period in 1974 ([Jones, 1979](#)). Poor climatic conditions in the drought year for fungal infections were also confirmed in nearby field experiments undertaken on the field bean aphid, *Aphis fabae*. Here, artificial introductions of *Erynio neoaphidis* and *Neozygites fresenii* into the insect population briefly became established but failed to spread ([Wilding, 1981](#)). Nevertheless it appears that *N. fresenii* was more tolerant of the dry, hot weather conditions suggesting that where the drought was less severe, there was a risk of at least some fungal species establishing in aphid populations. A more widespread survey of pathogen incidence in the turnip moth (*Agrotis segetum*) in England Wales also supports this hypothesis with infections of *Entomophthora* sp. being significantly reduced in both 1976 and 1975 compared to 1977 despite atypically large host populations occurring during the drought year ([Sherlock, 1983](#)).

Insect parasitoids are cosmopolitan pathogens with larval stages commonly occurring in arthropod larvae. During 1976 considerable variations in the occurrence of hymenopteran free-living adult parasitoids were presumably related to the response of the host organism to the drought ([Hearn and Gilbert, 1977](#)). For example, species of Braconidae, parasitic on leaf-mining dipterans, were very uncommon at sites where they were usually abundant in Bedfordshire (Se) during 1976, possibly due to the poor growth of hosts as a result of the wilting of their food supply ([Hearn and Gilbert, 1977](#)). In contrast, parasitism of leaf mining moth larvae by

parasitoid insects of *Achrysocharoides* sp. in Cheshire (Mo) demonstrated little change in prevalence due to the drought compared with other years over the period 1974–1977 (Bryan, 1983).

Cereal aphids are commonly infected with insect parasitoids and were extensively studied in England during the 1970s. In Hertfordshire (Vs) studies on the *Aphidius* spp. parasitoids showed that *Metopolophium dirhodum* was most commonly attacked host aphid between 1975 and 1979 except in 1976 when *S. avenae* was preferred (Dean et al., 1981) possibly because this species was especially numerous during this year (Jones, 1979). The prevalence of infections of aphids in both Norfolk (Se) and Hertfordshire (Vs) peaked earlier in the summer, with a higher number of mummified hosts during 1976 than in other years (Jones, 1979; Carter et al., 1980). This is supported by a study in west Sussex (Vs), which also found an earlier peak of abundance of free-living *Aphidius* adults in this year (Vickerman, 1982). Nevertheless parasitism failed to negatively affect the aphid population in 1976 because the climate was favourable for aphid migration and multiplication (Jones, 1979).

Hyperparasitism of parasitoids by other insect obligatory parasites is also common and is frequently a major factor in reducing the number of primary parasitoids emerging from aphid hosts (Carter et al., 1980). In Norfolk (Se) during 1976 there was a greater species richness of hyperparasites (8 species) than in either 1977 (3 species) or 1978 (5 species) although in all years *Dendrocerus carpenteri* was the most dominant species (Carter et al., 1980). In Hertfordshire (Vs) the prevalence of hyperparasitism in 1976 was lower than in other sampled years throughout the 1970s with a greater number occurring in parasitoids of *S. avenae* rather than *M. dirhodum* (Dean et al., 1981) possibly due to the increased number of this host species during the drought (Jones, 1979).

2.2. Plant hosts

2.2.1. Farmed conditions

The economic importance of farmed plants has ensured that their diseases are particularly well studied. Annual surveys of commercial crops have been undertaken in England and Wales since 1970 for wheat fungal diseases and since 1967 for diseases of spring barley (King, 1977; Polley and Thomas, 1991; Polley et al., 1993). In general during 1976 fungal pathogens either showed a decline in annual incidence or remained unaffected by the drought, although some pathogens such as *Stagonospora nodorum*, which demonstrated inconsistent changes in incidence between host species or the leaf and ear of wheat, whilst the incidence in England and Wales of mildew in barley and oat crops remained the same at around 100%, the severity of this disease was greatly increased (Polley et al., 1993; Rowe, 1979). In Ayr (Mi), west Scotland, barley mildew was also severe, developing earlier in the season and achieving high severity levels by July (Channon, 1981). Nevertheless, levels of air-borne spores above the crops were relatively low and these concentrations declined rapidly by late June–early July as the barley foliage died off during the high temperatures and ceased to support the fungus (Channon, 1981).

Only a few diseases demonstrated regional differences in severity during 1976. For example, wheat infections of *S. tritici* in both the east (Se) and south-east (Vs) of England had a reduced severity but increased in Yorkshire/Lancashire (Mo) compared with the long-term average. For brown rust there was an increase in severity in northern England (Mo) and Wales (Mo–Se) but a decline in Yorkshire/Lancashire (Mo). The severity of sharp eyespot in wheat declined slightly in the southeast (Vs) but increased in the east midlands (Se) whilst nodal fusarium declined in severity in the east and west midlands (Se) and southwest England (Se) but

increased in the north (Mo) and Yorkshire/Lancashire (Mo) (Polley and Thomas, 1991).

Similarly in barley brown rust and *R. secalis* demonstrated regional severity differences in England and Wales. Brown rust severity declined in the east (Se), southwest (Se) and Yorkshire/Lancashire (Mo) whilst increasing in severity in the west midlands (Se) and Wales (Mo–Se). In contrast *R. secalis* severity declined in the southwest (Se) and southeast (Vs) and increased in severity in the east and west midlands (Se), Yorkshire/Lancashire (Mo) and the north (Mo) (Polley et al., 1993).

These changes in incidence and severity of fungi during the drought are probably caused mainly by differences in the tolerance of spores or resting structures between pathogen species to low moisture and high temperature conditions. Survival is a significant factor when adverse conditions exist between the time of sporulation and infection, but is relatively less important for those pathogens with particularly resistant spores. For many species a film of free moisture, either from rainfall or dew, on the surface of leaves is essential for infection, although requirements in the duration and intervals between wetting periods differ between pathogens (Rotem, 1978). In contrast, fungal soil-borne plant pathogens are less affected by atmospheric conditions than airborne species (Rotem, 1978). Consequently responses of individual pathogens to climatic conditions will have structured the progress of disease in the plant host community. Nevertheless, host susceptibility to fungal diseases is also influenced by temperature and osmotic stress. These may indirectly affect disease development by either weakening the plant, increasing the chances of successful fungal establishment or priming the host antifungal defences prior to pathogen attack (Rosenzweig et al., 2001; Conrath et al., 2002; Doohan et al., 2003).

More specific surveys on a range of pathogens were also being undertaken at this time. Dark leaf spot (*Alternaria brassicicola*) is a fungal disease of brassicas. Wind disseminated spores are the main agents of disease spread. Climatic conditions therefore influence the epidemiology of *A. brassicicola* with spore release being more closely related with changes in relative humidity rather than temperature, although crop harvesting can also result in a massive release of spores (Humpherson-Jones and Maude, 1982).

Surveys of farms in Essex and Suffolk (Se–Vs) found that in 1976 both fewer sites and individual plants were infected with *A. brassicicola* resulting in a low level of disease severity compared with other sampled years (Humpherson-Jones, 1983). More detailed measurements of air-borne spores and seed pod infections in a north Essex farm (Se) also demonstrated they both had significantly lower occurrence throughout the summer of 1976 except when crops were cut and threshed (Humpherson-Jones and Maude, 1982).

These results compare well with long-term measurements of air-borne *Alternaria* spp. spore numbers in Cardiff (Se) and Derby (Mo). During 1976 the majority of spores in Derby, a city close to many arable production areas, were found earlier in June, rather than the normal August peak, with no spores being recorded by October. Nevertheless, the overall seasonal (June–October) occurrence of spores in this year showed little difference from other years, although there were an increased number of days with 100 or more spores/m³ of air. In contrast, in Cardiff, which is close to the sea and far removed from any major arable farmland areas, the numbers of airborne spores was much lower, with counts being most positively correlated with winds overland from the north. During the drought seasonal spore totals showed little difference from the long-term average but yearly peak values were much lower and there was a small decline in the number of days with 100 or more spores/m³ of air. Monthly spore variation throughout 1976 generally showed lower numbers compared with other years

between June and August with peaks in September rather than October (Corden et al., 2003).

Measurements of other fungal diseases also showed reduced spore releases during the summer of 1976. For example, in Kent (Vs) no ascospores of apple canker (*Nectria galligena*) were released between June and mid-October in that year. Indeed, for this species throughout the entire drought, from June 1975 to October 1976, there were no large releases of ascospores (Crosse, 1977; Talboys, 1978).

These results suggest that the geographical seasonal spread of airborne fungal spores was particularly influenced by the drought. This may have altered disease development in host plants as spore concentrations may have been too low during periods of growth when the plants are particularly vulnerable to infection. Nevertheless, it is clear that regional differences play a large part in airborne spore dynamics and disease outbreaks.

In contrast, soil-borne fungi appear to have been less affected by drought conditions with little change in disease severity, although some regional differences were apparent (Dixon, 1980; Harrison, 1981). These results are not unexpected as fungal soil-borne plant pathogens are less affected by changes in atmospheric conditions than airborne species (Rotem, 1978).

Unlike fungal infections, only a limited amount was known of bacterial infections at this time. Climatic conditions play a key role in disease outbreaks of fireblight in fruit trees caused by *Erwinia amylovora* spreading rapidly in hot, wet weather (Billing, 1980). In Kent (Vs) there was a low level of new infections in 1976 but existing infections progressed markedly during the wet autumn after the drought broke, whilst in irrigated orchards severe infections occurred during the following winter and spring (Billing, 1980). Long-term studies of fireblight in an orchard near Bristol (Vs), Avon, found that the first cases were not recorded until the wet autumn of 1976. However, subsequent outbreaks were associated with biennial years of profuse blossom. Byrde et al. (1986) concluded that the climatic conditions during 1976 had conditioned many young trees to biennial fruit bearing and consequently a related pattern of disease occurrence followed.

Many viral diseases are transmitted between plant hosts by insect vectors and a number of virus-vector associations were studied during the 1970s. Barley yellow dwarf virus (BYDV) is an insect-borne pathogen of cereals. Outbreaks are determined by the number of infective aphid vectors migrating into the emerging crop, resulting in primary infection foci of infected plants and insects, followed by a secondary spread within the crop. Climate plays a key role for viral transmission, particularly influencing aphid biology (A'brook, 1981). In west Wales (Se) during 1976 the numbers of the major aphid vectors, *Rhopalosiphum padi* and *R. insertum*, was drastically reduced and consequently few individuals were found to be virus-carriers. However, other aphid species, which are normally of minor importance for viral transmission, increased in abundance and consequently became the main vectors during this drought period, although the total number of infected insects was modest compared with other years (A'brook and Dewar, 1980).

In contrast, the occurrence of yellowing viruses of sugar beet, transmitted by *Myzus persicae*, during 1976 demonstrated little evidence to suggest that the drought had any major effect on virus epidemiology (Thresh, 1980, 1983).

However, monitoring of hop varieties in the west midlands (Se) and Kent (Vs) showed that from late July to early August 1976, after the period of extremely high temperatures, a conspicuous line pattern appeared in the leaves of many plants which was attributed to the Prunus necrotic ringspot virus (PNRSV). At the same time an apparent resurgence of the virus was detected in plants known to contain latent infections of PNRSV, suggesting that

stress due to drought was a contributing factor to the unusual PNRSV outbreaks in these English hop varieties (Crosse, 1977).

Nematode worms that are parasitic on plants are widely distributed and can often infect a range of plant species. Their survival off the host is influenced by environmental conditions particularly soil moisture and temperature (Trudgill, 1995; Neher, 2010). The majority of plant-parasitic nematodes can be found in the soil and comprise ectoparasites, that remain in the ground and feed on plant roots, and endoparasites, which enter through roots and feed on a variety of plant tissues (Poinar, 1983). Long-term studies on crop damage attributed to cyst nematodes in eastern England (Se) showed that the number of new cases of damage to cereals by *Heterodera avenae* had significantly declined in 1976 (7 cases) compared to other years (Savage, 1979).

However, detailed field trials of *H. avenae* in crop roots in Bedfordshire (Se) found that in 1976, although crop growth was poor due to the drought, the density of female worms on roots was greater than in other years, despite fecundity being low, with the overall *H. avenae* populations becoming slightly increased (Kerry et al., 1982a). Fungal parasitism is the major factor limiting the multiplication of *H. avenae*, killing females, reducing their fecundity and parasitising nematode eggs. Few female nematodes were infected with the fungus *Nematophthora gynophila* in 1976 but infections with the more drought tolerant *Verticillium chlamydosporium* were still relatively common (Kerry et al., 1982b). Nevertheless, females on average produced fewer eggs in 1976 than in other years because the period in which they could feed was considerably shortened due to the premature death of crops. A similar observation on the feeding and fecundity of *H. avenae* during this year in mid Wales (Mo) was made by Cook (1977). Consequently reduced fungal parasitism was offset by a lower nematode fecundity resulting in only a limited change to the population dynamics of these parasites.

Nevertheless, other nematode species may have been more substantially affected. *Ditylenchus dipsaci* is widely dispersed in vegetable seeds but onion seed samples examined for export between 1953 and 1978 showed that in samples exported in the winter of 1976/1977 the incidence of *D. dipsaci* had declined to zero (Green and Sime, 1979). The degree of infection of this species is mainly dependent on the level of nematode density and their activity in the soil at the time of planting (Seinhorst, 1956). The drought could therefore have negatively affected either one or both of these factors resulting in such a low incidence.

However, long-term studies on the nematodes *Globodera pallida* and *G. rostochiensis* in potatoes show a more complex picture. Sampling of irrigated microplots in south Wales (Se) found that early crop harvesting led to a decline in *G. pallida* in every year between 1971 and 1978 except during 1976. Exceptional high temperatures during this summer encouraged a more rapid development followed by an increase in numbers. However, the population dynamics of *G. rostochiensis* remained largely unaffected during the same period probably due to differing temperature requirements for optimal development (Webley and Jones, 1981).

Harsh climatic conditions during the summer of 1976 had a number of effects on pesticide treatments against pathogens. The drought lessened the effectiveness of many kinds of pesticides, particularly the granular formulas due to the low levels of moisture in the soil preventing optimal penetration of the substrate (Carter, 1978). In field trials using the pesticides aldicarb and oxamyl against the nematodes *Heterodera schachtii* and *H. goettingiana* Whitehead et al. (1979) and Batterby et al. (1980) found that treatment proved to be ineffective over the summer of 1976 due to the inadequate distribution of chemicals in dry soil. The uptake of fungicides into cereals was impaired resulting in the levels of barley mildew being as high in treated as untreated crops (Carter, 1978). It is unknown how much the inability to control pathogens

chemically during this period contributed to their prevalence in farmed plants, but it seems likely that this factor may have only exacerbated the climatically dominated changes in disease occurrence during 1976.

2.2.2. Wild conditions

Interactions between drought and pathogens are particularly important in perennial plants, such as forest trees. Compared to agrosystems, forests are relatively unmanaged and are more likely to be affected by naturally occurring stressors such as drought (Desprez-Loustau et al., 2006). It is probable that drought stress, in association with increased insect feeding activity, renders trees more susceptible to fungal infections that are normally only weakly parasitic or saprophytic and may be 'latent' infections already present in the tree population (Bevercombe and Rayner, 1980; Ford, 1982; Gibbs, 1997). The 1976 drought provides a range of examples to support this hypothesis. For example, in sycamore trees there was an increased occurrence of diamond bark disease, sooty bark disease, and bark necrosis (Abbott et al., 1977; Bevercombe and Rayner, 1980; Gregory, 1982). Beech trees also suffered an increase in bark necrosis as well as strip cankers (Lonsdale, 1980, 1983; Hendry et al., 1998), however, 'sooting', a covering of aphid honeydew containing *Cladosporium herbarum*, on sycamore, oak and lime was less frequent in Norfolk (Se) than usual (Hearn and Gilbert, 1977).

A more complex picture of tree–fungal interactions emerges from studies on Dutch elm disease during the drought. This disease has a devastating effect on elm tree populations and is mainly transported from tree to tree by the beetle vector *Scolytus* spp., with only limited direct transmission by root contact between trees. The drought in southern England (Vs) created favourable conditions for beetle activity but their feeding resulted in much less disease than normal with a lower number of new diseased individuals in forests already harbouring the infection. It would appear that the frequency in which the fungus established itself in the xylem was particularly low, and in those trees where it did establish and develop sufficiently for visible symptoms to appear there was only a slow disease progression through the tree. This resulted in less beetle-initiated infections than normal (Gibbs and Greig, 1977).

However, due to stress induced by drought, beetles were able to breed in undiseased as well as moribund trees, and this may have offset reduced transmission efficiency of the disease during this period (Gibbs and Greig, 1977). Consequently in southern England there was a smaller increase in disease during 1976 than in previous years (Hearn and Gilbert, 1977). Nevertheless, in northern England (Mo) and north Wales (Mo–Se) before 1976 the disease was less prevalent due to decreased susceptibility of the most common elm species, *Ulmus glabra*, and cooler summers, resulting in a slower annual build-up of beetle populations. However, in 1976 the beetle population increased rapidly and because of drought stress there was an elevated tree susceptibility resulting in an increased disease severity in these regions. Additional outbreaks were also reported in southern Scotland (Mo) for the first time in a large number of new and widespread locations (Hearn and Gilbert, 1977).

Nevertheless, fungal infections were not restricted to trees. During the autumn of 1976 evergreen shrubs were also found to show varying degrees of canker, die-back and premature leaf fall in Bangor, Wales (Mo), and Hampshire (Vs) associated with a range of pathogenic and opportunistic fungal species recovered from the necrotic tissue (Shattock and Askew, 1980). It is likely that infections of this kind may also have been widespread in wild plant species at this time.

Nematode parasites are often associated with woodland trees and forests in the UK (Boag, 1974). Studies on nematodes infecting

a Sitka spruce nursery plantation in Perthshire (Mi), Scotland, found that under the mild drought conditions experienced in this area in 1976 the population dynamics of three species in the forest were largely unaffected (Boag, 1981, 1982) suggesting some degree of tolerance to modest levels of desiccation and high temperatures. However, in 1976 the occurrence of adult *Trichodorus primitivus* in these sampled soil demonstrated only a single protracted spring peak, instead of normal double spring and autumn increases, before numbers declined to low levels which did not recover until spring 1977 (Boag, 1981). Plant parasitic nematodes are known to have different optimum temperature ranges for feeding, hatching, reproduction and survival (Neilson and Boag, 1996) and it is likely that the seasonal shift in *T. primitivus* occurrence may reflect an increased sensitivity to the climatic conditions during 1976 compared with other species.

3. Freshwater ecosystems

The drought had its biggest impact on freshwater ecosystems causing widespread effects on water resources and animal communities. Record low flows were recorded in many UK rivers (Hamlin and Wright, 1978), although the severity fluctuated on a regional basis dependent on the yield capacity and retention of individual river catchments (Clarke and Newson, 1978). By August 1976 the capacity of reservoirs had also reached very low levels, despite the implementation of strict water management procedures (Hamlin and Wright, 1978). Water levels fell considerably in many lakes with some smaller ponds drying out. The falling water velocities/levels were accompanied by increasing temperatures, reduced dissolved oxygen levels and eutrophication (Hearn and Gilbert, 1977).

Pollution of waterways was a common problem, often associated with an increased proportion of sewage effluent in rivers compared with the diminishing supply from groundwater sources (Davies, 1978). There was consequently a large increase in nutrients such as phosphorous and nitrates in river water leading to eutrophication and by the end of the summer there were also large increases in chlorides and sulphides. As flows continued to diminish severe saline incursions occurred in the lower reaches of many rivers. When the drought broke in September 1976 the rapid increase in water flows due to heavy rainfall resulted in a serious deterioration of water quality from urban runoff and the discharge of storm sewage dramatically deoxygenating river water. Nitrate concentrations continued to rise during this post-drought period and did not fall until March 1977 (Davies, 1978).

These physical and chemical changes had a number of major impacts on freshwater organisms. Rising water temperatures, nutrient enrichment, and a decrease in dissolved oxygen resulted in many large scale mortalities of salmonid and cyprinid fish (Brooker et al., 1977; Hearn and Gilbert, 1977; Tucker, 1978). Nevertheless, where water quality conditions did not significantly deteriorate, higher temperatures favoured improved spawning of coarse fish with populations increasing at many sites (Hearn and Gilbert, 1977).

Macro-invertebrate communities demonstrated variable responses to the drought conditions. In upland streams and rivers reduced water flows resulted in a decrease in river depth and width and hence an overall decline in colonisable habitats for invertebrates. Consequently there was a reduction of up to 60% of some populations (Cowx et al., 1984), with similar reductions also occurring in many still water habitats that suffered from lowered water levels (Hearn and Gilbert, 1977). Nevertheless, in mid and lowland flowing water habitats, although species richness often declined, the density of macro-invertebrate communities increased despite lowered water levels (Brooker and Morris, 1980;

Extence, 1981; Wright et al., 2003) probably due to nutrient enrichment.

Increased eutrophication, in connection with elevated temperatures may have been responsible for large numbers of algal blooms reported during this period (Hearn and Gilbert, 1977; Tucker, 1978) particularly in water reservoirs (Davies, 1978). However, in some reservoirs, which endured an extreme lowering of water levels with a reduced retention time to maintain piped water supplies to consumers, algal numbers were depressed (Bryan, 1982). Macrophytic plants also benefited from these conditions, growing and flowering abundantly (Hearn and Gilbert, 1977).

Populations of waterbirds showed variable responses to the drought, dependent on the level of deterioration of their resident aquatic habitats. In sites with lowered waterlevels, bird populations generally declined, although waders benefited from increased areas available for feeding and nesting. Where water levels remained reasonably high, bird populations increased dramatically (Hearn and Gilbert, 1977).

The low water flows in lowland rivers caused elevated salinity levels as salt water penetration increased and this resulted in the replacement of freshwater fish and invertebrates with estuarine or marine species along large stretches of rivers immediately upstream of estuaries (Andrews, 1977; Hearn and Gilbert, 1977).

3.1. Animal hosts

3.1.1. Farmed conditions

Although monitoring of fish diseases of veterinary importance by Government research laboratories was being undertaken at this time it remained at a rudimentary level. Annual diagnosed incidents were being published (Brown, 1977, 1978) but there was no attempt to differentiate between fish in wild, semi-wild i.e. lightly managed for angling purposes, ornamental, or farmed conditions. Fish in these various habitats experience differing degrees of stress and risk of acquiring pathogen infections, and hence annual returns of diagnosed incidents must be treated with some caution as outbreaks may reflect deteriorating conditions in only one kind of fishery. Nevertheless the conditions under which fish farming is undertaken has long been recognised to be significantly more stressful and prone to disease outbreaks than other kinds of habitats (Woo et al., 2002). Diseases at these localities are also more likely to be reported than those occurring in other fisheries and therefore it is reasonable to assume that those incidents reported in Brown (1977, 1978) are more likely to reflect disease outbreaks under farmed conditions.

For most fish farms high water temperatures posed problems during the summer of 1976. Trout farms with good water supplies were largely unaffected by the drought, but those with inadequate supplies suffered severe effects. Such farms resorted to recirculating some water, which in turn aggravated the problem of maintaining temperatures below 20 °C (State Veterinary Service, 1982). Consequently mortalities were widespread and in one Lincolnshire farm 10 tonnes of adult trout, 1.25 tonnes of brood fish, and 300,000 fry were lost to excessive high temperatures (Davies, 1978). Under such conditions outbreaks of fish diseases were inevitable, with diagnosed incidents of unspecified gill disease, costiasis (caused by the ectoparasitic protozoan *Ichtyobodo necator*), furunculosis (caused by the bacterium *Aeromonas salmonicida*), and Saprolegniosis (caused by *Saprolegnia parasitica*) drastically increasing during 1976 (Brown, 1977, 1978), likely reflecting a drought-induced deterioration in water quality. Saprolegniosis was also associated with wild fish mortalities during this period.

The drought was also implicated in reactivating the viral disease infectious pancreatic necrosis (IPN) in stressed farmed

stock that harboured infections (State Veterinary Service, 1982). Nevertheless, the limited number of serious diagnosed incidents was the same as in 1975 but greater than that found in the following year when no cases were reported (Brown, 1978).

The emergence of a new disease of farmed fish was also recorded at this time, namely bacterial kidney disease (BKD) which is a serious debilitating condition of mainly freshwater salmonids caused by the bacterium *Renibacterium salmoninarum*. Prior to 1976 BKD had previously been recorded in Scottish wild salmon principally in the Dee river system. However, during the drought the disease was recorded for the first time in farmed rainbow trout from two hatcheries in Scotland (Mi-Mo) (Bruno, 1986).

3.1.2. Wild conditions

Drought effects on the occurrence of pathogens in aquatic animals at this time can be broadly divided into those occurring in flowing and still water habitats. In flowing water conditions a number of changes in host–pathogen dynamics were apparent. Water mites are characteristic components of aquatic invertebrate fauna, which achieve dispersal through larval parasitism of aquatic or semi-aquatic insects (Di Sabatino et al., 2000). Studies on *Sperchon setiger* parasitising blackflies, *Simulium* spp., from a chalk stream in Dorset (Vs) showed a number of changes to the infection dynamics during 1976. In the stream, water flow was low and temperatures were high which resulted in a reduced number of adult insect hosts emerging. In comparison with other years, the prevalence, intensity, and abundance of mites on the simuliids in 1976 were much higher, probably associated with the low number of available hosts (Gledhill et al., 1982).

In the River Rother, West Sussex, at Haben Bridge (Vs) annual sampling for the occurrence of parasites in aquatic hosts in each September during the 1970s highlighted a range of drought effects in 1976. Sampling of the crustacean *Gammarus pulex* revealed no infections of the acanthocephalan *Polymorphus minutus* prior to 1976. However, during the drought an annual peak in prevalence occurred, declining in subsequent years (Lewis et al., unpublished observations). This peak is likely to be associated with both low water levels and flow rates over the summer, which favour both parasite transmission in aquatic hosts and the nesting of waterbirds (Marcogliese, 2001), the definitive hosts of *P. minutus*.

Protozoan parasites of the common frog, *Rana temporaria*, at this locality had a higher species richness during the drought year compared with previous years (Lewis et al., unpublished observations). Nevertheless the prevalence of common individual species did not significantly change except for one exception. Both *Nyctotherus cordiformis* and *Opalina ranarum* are very common protozoan parasites with similar life cycles that regularly co-occur in the rectum of *R. temporaria* (Smyth and Smyth, 1980; Wilbert and Schmeier, 1982). During the dry period of 1975 and the drought of 1976 the prevalence of *N. cordiformis* significantly declined whilst that of *O. ranarum* remained relatively unaffected (Lewis et al., unpublished observations). The life cycle of both species is controlled by the endocrine activity of infected adult frogs during host breeding in the spring. Parasites produce cysts that enter the water and are eventually eaten by developing tadpoles (Smyth and Smyth, 1980; Smyth, 1994). However, tadpoles acquire *Opalina* spp. earlier in their development than *N. cordiformis*, which also reproduce more slowly (Schorr et al., 1990), and these factors associated with differing responses each species shows to environmental conditions (Schorr et al., 1990) may have induced the decline of *N. cordiformis*.

Sampling of blood protozoan parasites from the bullhead, *Cottus gobio*, in this upland river site at Haben Bridge, demonstrated that only one species, the haemoflagellate *Cryptobia* sp., regularly occurred in this fish. This parasite is transmitted by leeches and during 1976 there was a significant decline in the prevalence of

this species in the bullhead compared to other sampled years (Lewis et al., unpublished observations). This may be associated with a reduction in the leech population in the river as monitoring of leeches in other upland English rivers during the drought demonstrated that populations were significantly negatively affected due to severe reductions in mean water depth and flow (Elliot, 2004).

However, the impact of the drought on waterways and consequently host–parasite interactions is not consistent throughout the entire length of a river. Studies on lowland rivers that run through urban London before discharging into the Thames reveal a contrasting situation to upland rivers such as the River Rother. These flowing water stretches neither suffered desiccation nor reduced flows during 1976 because of the substantial input of treated sewage. During summers of the 1970s up to 75% of urban London river water may have been sewage effluent (Hinge, 1980) leading to significant nutrient enrichment and subsequent changes to invertebrate fauna. In 1976 this resulted in an increase in many invertebrate species in London rivers (Extence, 1981). In the London stretch of the River Lee (Vs) the highest levels of infections of the haemoflagellate *Trypanosoma cobitis* in gudgeon (*Gobio gobio*) occurred during the summer of 1976 compared with other years (Letch and Ball, 1979). This is probably associated with a significant increase in the populations of the leech intermediate host in this location (Extence, 1981), as an increase in leech density and feeding would facilitate parasite transmission to a larger number of hosts. These two examples of leech-transmitted fish protozoans therefore show that localised differences in drought-induced changes to invertebrate vectors can cause widely disparate impacts on pathogen occurrence.

The effects of the drought on minor waterways were also devastating leading to localised major disruptions to host–parasite interactions. For example, annual September sampling of invertebrates from a stream draining Harting Pond, in Sussex (Vs) between 1973 and 1975 revealed a range of helminth species in the community. However, in 1976 Harting Pond was severely affected by the drought and the drainage stream temporarily dried out, resulting in the local extinction of the invertebrate population, thereby interrupting parasite transmission (Lewis et al., unpublished observations). This situation is likely to be reflected in many streams in the UK during this period where water flow was severely disrupted.

Parasite infections in still water habitats were also often affected by the drought. In lakes and ornamental ponds high temperatures resulted in the rapid multiplication of fish ectoparasites particularly the crustacean *Argulus* spp. (State Veterinary Service, 1982), due to their sensitive to thermal changes (Ozer and Erdem, 1999), with some associated host mortalities being reported (State Veterinary Service, 1982).

Extensive long-term studies on the helminth parasites of numerous coarse fish species (Kennedy, 1998, 2001; Kennedy et al., 2001) have been undertaken at Slapton Ley, Devon (Se) since the early 1970s. This shallow eutrophic lake occurs on the coast of southwest England and supports a dynamic and unstable fishery (Kennedy, 1996). The drought is known to have caused a drastic reduction in water levels with the lake splitting into two separate basins before heavy rainfall in the autumn of 1976 saw a dramatic return to normality (Van Vlymen, 1979). The splitting of the lake during this period led to the lower basin, where the majority of the fishery resided, to be isolated from 70% of the inflowing water, increasing its hydraulic residence time, allowing nutrient levels to rise, with a significant increase in nitrate concentrations (O'Sullivan, 1994). In turn, this nutrient enrichment triggered numerous algal blooms of *Gleotrichia* spp. and other blue-green algae (Hearn and Gilbert, 1977), although the climatic conditions did not lead to a particularly large increase in the water temperature of the ley

(Burrough and Kennedy, 1979). Even though the lake suffered extensively during the drought it remained a viable open water habitat and consequently attracted increased numbers of water birds. During 1976 populations in particular of mute swan, Common teal, and mallard rose substantially (Elphick, 1996). These changes imposed on the lake by the drought had a notable effect on the fish helminth fauna.

The prevalence of trematode eyeflukes in roach remained relatively constant in the range of 80–100% over a number of years but by August 1976 the intensity of infection was substantially higher than at any other time of study with larger numbers of fish harbouring more than 100 metacercariae in the eyes (Burrough, 1978).

Similarly, recruitment rates (mean increase in intensity per month) of *Tylodelphys clavata* in perch during 1976 rose sharply in first year (0+) fish compared with other sampled years (Kennedy, 1981a).

It is likely that increases in intensities of eyeflukes during the drought are associated with the fluctuating water levels and eutrophic conditions in the lake induced by the extreme climatic conditions, which will favour both the development of large snail populations, the intermediate hosts of trematodes, and improve the transmission success of free-living parasite stages to both fish and molluscs in a gradually shrinking water body. Nutrient enrichment has been shown to cause changes of this kind in trematode infections in a number of aquatic habitats (Johnson et al., 2010).

An additional eyefluke species, *T. podicipina*, also occurs in perch at Slapton Ley. This species was not considered to have been present in fish during the summer drought but was probably introduced to the lake during the latter part of 1976 by birds (Kennedy, 1981b, 2001), which were attracted to the lake in increased numbers during the drought (Elphick, 1996).

The cestode *Ligula intestinalis* has been present in Slapton Ley since the early 1970s (Kennedy and Burrough, 1981). This tapeworm infects in turn a copepod, a fish, principally roach, and finally a piscivorous bird. The rise in prevalence in fish during the spring and summer of each year is due to the acquisition of new infections in the previous autumn, as fish carrying mature infections do not appear to survive through each winter (Kennedy and Burrough, 1981). The conditions experienced in the lake during 1976 therefore only manifested themselves in the following year when the prevalence of infection in roach showed a much larger peak, earlier in the year during April, with the intensity of infection also increasing (Kennedy and Burrough, 1981). These effects are likely to be due to multiple changes that occurred in the lake during 1976, principally eutrophication which favours the transmission of fish helminths that utilise zooplankton as intermediate hosts (Morley and Lewis, 2010) due to increased host population levels. This factor, associated with an elevated in the bird population and fluctuating water levels (Van Vlymen, 1979; Hanzelova, 1992; Elphick, 1996), led to an increase in the density of host populations and thereby greater parasite transmission.

For the remaining helminth species parasitising fish only limited data exists which demonstrates that parasite composition remained relatively stable up to the mid 1980s (Kennedy, 1998). The main exception is the acanthocephalan *Acanthocephalus lucii* in eels. Prior to 1976 this parasite was often prevalent in the fish population (Kennedy, 1975) but was absent from 1977 onwards (Kennedy, 1998). The intermediate host for this parasite is the crustacean *Asellus aquaticus*, which is not found in the lake itself but occurs in its feeder streams, suggesting that eels acquire infections by occasionally migrating into these habitats (Kennedy, 1975). During 1976 the stream flows were severely reduced and the marsh and reedswamp that they drain into before entering the

open water of the ley were virtually dehydrated (Van Vlymen, 1979). These conditions could have either interfered with the ability of eels to move into the feeder stream or caused a decline in the *A. aquaticus* population thereby interrupting transmission of *A. lucii*. The subsequent extinction of this parasite from the lake's eel population, which itself remained stable, suggests that biotic or abiotic conditions never returned to a state which favoured the recovery of *A. lucii* to its former level.

Periodic epizootic events of the coarse fish perch, *Perca fluviatilis*, occurred throughout the 1960s and 1970s within the UK (Bucke et al., 1979). These large-scale fish mortalities were characterised by severe epidermal lesions associated with a wide variety of fungal and bacterial infections. These may either be the primary pathogenic agents or opportunistic secondary infections, although it seems unlikely that any one individual pathogen species was responsible for all epizootics.

During the drought year in England there was a sharp increase in incidents of ulcerated perch, and occasionally roach, although unlike previous years few events led to the mass mortality of fish (Bucke et al., 1979). One major exception occurred in Lake Windermere within the English Lake District (Mo) with mortalities beginning in January 1976 and continuing throughout the year, such that by mid-July the number of caught perch had been severely reduced with as much as 90–100% of netted fish being diseased. During 1976, perch mortalities exceeded 98% with an estimated 1 million adult fish having died (Bucke et al., 1979). Although no single aetiological agent could be definitively linked with these mortalities, fungal infections, particularly *Saprolegnia* sp., found in the epidermal lesions were suspected as being one of the most likely causes in this locality. These oomycete pathogens are responsible for devastating infections of fish, and hence have been implicated in the decline of many wild populations (Van West, 2006). The vegetative growth of *Saprolegnia parasitica*, an endemic species in freshwater habitats, can be either enhanced or reduced by changes in the chemical constituents of dissolved organic matter (Meinel et al., 2007). Climate has a profound effect on the concentrations of these substances in lake water (Curtis, 1998) and it is therefore possible that changes in the water quality of Lake Windermere during the drought facilitated the development of *Saprolegnia* sp., which in turn resulted in the large-scale mortality of perch.

Botulism in waterfowl within the UK has been reported on numerous occasions since 1969 (Ortiz and Smith, 1994). It is usually caused by *Clostridium botulinum* type C, an anaerobic bacterium, acquired by ingesting rotting organic matter and is responsible for considerable global annual mortalities, sometimes on a large scale, of birds on lakes, mudflats and marshes (Ortiz and Smith, 1994). Type C organisms, which do not grow or produce toxins at temperatures of 10 °C or less are considered warm weather pathogens and the incidence of the disease was closely related to the number of days in summer when the maximum air temperature reached 21 °C or more and there was an excess of water evaporation over rainfall (Smith, 1979). Outbreaks of botulism in wildfowl in the Norfolk Broads (Se), which is an extensive area of numerous lakes and waterways, were recorded in both 1975 and 1976 (Borland et al., 1977; Smith, 1979; State Veterinary Service, 1982). These outbreaks were particularly severe in 1976 because the drought reduced the water level and its flow resulting in the considerable drying out of bankside areas and hence creating ideal conditions for the multiplication of *C. botulinum* (State Veterinary Service, 1982). The widespread outbreak in this area may have contributed to the first incidence of botulism in terrestrial birds, pheasants, which occurred close by in July 1976 (Borland, 1976).

On the other hand reports of botulism in birds across the entire country suggest a more complex picture. During 1976 numerous

outbreaks of botulism were recorded, although few appeared to be as severe as those in 1975 (Lloyd et al., 1976; Hearn and Gilbert, 1977; State Veterinary Service, 1982). It is likely that either by this stage the disease was well recognised and attracted less public attention, and hence fewer notifications being recorded, or that due to the severity of the drought, pools normally frequented by gulls had dried up by the time the birds left their breeding sites (State Veterinary Service, 1982). The general conclusion of the Royal Society for the Protection of Birds was that nationally in 1975 outbreaks were more numerous and severe than those experienced in 1976 (Hearn and Gilbert, 1977).

Studies on trematode cercarial infections of the freshwater snail *Radix peregra*, that all utilise waterfowl as definitive hosts, in a shallow lake in Humberside (Se) demonstrated substantially higher prevalences during July–September 1976 compared with other years (Radlett, 1978). This lake was spring-fed and consequently the water level remained constant throughout the drought, thereby attracting large populations of birds. Such an increase in the density of birds and their associated parasites in this locality is likely to have been a dominant factor in the increased prevalence of these trematodes in the intermediate snail host.

3.2. Plant hosts

In contrast to studies on animals in freshwater habitats, very little is known about the pathogens of aquatic plants for this period. 'Sooting', a covering of aphid honeydew invested with the fungus *Cladosporium herbarum*, was much more common in reeds than usual in Norfolk (Se), corresponding with its decline in terrestrial plants in this locality during the drought (Hearn and Gilbert, 1977).

A range of organisms are parasitic on freshwater phytoplankton. The prevalence of parasites is strongly influenced by host abundance, with epidemics more likely to occur once an upper threshold of host density is exceeded (Park et al., 2004; Kagami et al., 2007). Although conditions during 1976 favoured the development of algal blooms in a number of aquatic habitats throughout the country (Hearn and Gilbert, 1977), in the English Lake District (Mo) long-term studies on algal parasites found no evidence of either excessive phytoplankton blooms or fungal epidemics on *Ceratium* spp. (Harris et al., 1979; Canter and Heaney, 1984). Unfortunately the parasites of phytoplankton do not appear to have been studied at other locations for this period and it is therefore unknown if in those habitats where algal blooms were reported whether there were corresponding changes in the occurrence of their pathogens.

4. Marine ecosystems

The general effects of the drought on marine ecosystems were less well documented in comparison with terrestrial and freshwater habitats. By early September 1976 surface sea temperatures in the open ocean were on average as high as 2 °C above normal (Ratcliffe, 1977b) with peaks of 19.1 °C being recorded in the western English channel during the preceding month (Marine Biological Association, 1977). In the North Sea summer climatic conditions were particularly favourable for phytoplankton blooms with an unusual long period of corresponding dinoflagellate toxin levels being recorded in mussels over this period (Ayres and Cullum, 1978). The abundance of three of the most common macrofauna species, namely the polychaetes *Heteromastus*, *Levinsonia* and *Prinospio* also increased between 1976 and 1977 in this area (Frid et al., 2009).

On the coast there was extensive drying out of marshes in some estuaries, with increased salinity levels, resulting in large-scale mortalities of crustacean species (Hearn and Gilbert, 1977). In

addition a decrease in freshwater output and elevated nutrient levels from many rivers triggered large-scale algal blooms (Marine Biological Association, 1977; Crawford et al., 1979).

On upper rocky shores some species of algae, such as *Fucus serratus*, disappeared or their abundance and distribution was severely reduced (Schonbeck and Norton, 1978; Little and Smith, 1980; Dicks and Hartley, 1982). Furoid algae provide an important role as food and shelter from heat and desiccation for grazing animals in the intertidal zone. Dead algae also sustain the biota in nearby sediment beaches where low in situ production is substantially boosted by the energy derived from their decomposition (Kendall et al., 2004). Consequently a decline in furoid cover will reduce biodiversity and after the 1976 drought the abundance of grazers such as the mollusc *Littorina littoralis* (Little and Smith, 1980) and species of barnacles and limpets (Dicks and Hartley, 1982) in the upper shore zone were reduced in some areas.

4.1. Farmed conditions

Fish farming of marine salmonids was only initiated on the west coast of Scotland in 1970 (Rae, 2002) and by 1976 the industry in the UK was still at a relatively embryonic stage. Thus only limited monitoring of diseases took place, with the most prominent pathogens being sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*), which are pathogenic ectoparasites of salmonid fish. A range of biotic and abiotic factors can influence the occurrence and development of the parasites on fish, particularly temperature, salinity, and water velocity (Costello, 2006). In Scotland, sea lice have been present on farmed salmon (*Salmo salar*) since the industry was first established (Rae, 2002). However, the first serious epizootics in Scottish (Mi–Mo) cage-reared salmon were only reported in the autumn of 1976 (Wootton et al., 1982). It is possible that during the summer drought, both elevated sea temperatures and a decrease in freshwater river discharge (Ratcliffe, 1977b; Hearn and Gilbert, 1977), resulted in increased salinities in estuaries and associated coastal areas, which in turn favoured louse development on the farmed fish during this period.

These outbreaks of sea louse infections may also have contributed to the emergence of a new disease in farmed Atlantic salmon at this time, namely pancreas disease (PD). This is an infectious viral disease causing extensive pathology to farmed marine salmonids that was first recognised in 1976 from fish farms in Scotland (Mi–Mo) (McVicar, 1987). High burdens of sea lice, along with various management practices, are the main elements associated with PD epizootics (Rodger and Mitchell, 2007).

4.2. Wild conditions

In coastal areas a number of changes to pathogen dynamics may be attributed to the drought. Studies on trematode infections in the intertidal mollusc *Littorina littorea* on an exposed shore in north Wales (Mo) found that prevalences were significantly reduced during the summer of 1976 (Hughes and Answer, 1982) probably due to a lowered host resistance to temperature and desiccation of infected littorinids (McDaniel, 1969) which can result in summer mortalities of host populations in excess of 90% (Lauckner, 1987).

Drought-induced effects were also apparent in estuarine trematode communities, for example, *Meiogymnophallus minutus* is commonly found in coastal marine animals in the UK, occurring in turn within the bivalves *Scobicularia plana*, *Cerastoderma edule*, and a definitive bird host, *Haematopus ostralegus occidentalis*, and has been studied in the Burry inlet, an estuary in south Wales (Se) since 1963 (James et al., 1977; Sannia, 1977). During 1976 the prevalence of summer cercarial infections in *S. plana* were substantially higher than other years. In contrast, mean numbers of metacercarial infections in *C. edule* during 1976 were found to

have drastically declined (Sannia, 1977). Such differences may be associated with the drought-imposed changes in host population densities occurring in the estuary.

On the eastern coast of Scotland from July 1976 onwards samples of the lesser octopus, *Eledone cirrhosa*, both from the Firth of Forth (Mo) and also maintained in tanks supplied with non-recirculated sea water pumped from St. Andrews bay (Mo) began to develop a progressive ulceration of the skin which was followed by oedema of the body tissues and eventually death (Polglase, 1980). The causal pathogen was identified as the thraustochytrid *Ulkenia amoeboides* (Polglase et al., 1986), a marine protist and a common component of microbial consortia in the sea. Thraustochytrids are habitual saprobes of dead plant material and are likely only to be opportunistic pathogens of animals (Raghukumar, 2002). They appear to be inhibited by antimicrobial secretions and thus their numbers will only normally increase once decomposition has begun. Consequently phytoplankton detritus may support high densities of thraustochytrids and in the North Sea their populations have been shown to increase towards the end of the algal period in June (Raghukumar, 2002). Elevated concentrations of these protists, associated with increased plant detritus during 1976 from large-scale phytoplankton blooms (Marine Biological Association, 1977; Ayres and Cullum, 1978) and seaweed mortalities (Little and Smith, 1980) could have combined with high levels of temperature stress during the summer to produce optimum conditions for this disease outbreak in octopuses.

In the open seas only a limited amount of information on pathogens at this time is available. *Dissodinium pseudolunula* is a dinoflagellate parasitic on the eggs of marine planktonic copepods in northern temperate seas. In order to survive through the winter when the host is absent and other living conditions are unfavourable, the development of *D. pseudolunula* terminates in free-living resting spores (Drebes, 1978, 1981). Long-term monthly studies of phytoplankton and zooplankton in the North Sea and the northeast Atlantic recorded the occurrence of *D. pseudolunula* resting spores. In each annual plankton sample most cysts, containing spores, were recorded in waters surrounding the British Isles. However, no cysts were recorded in 1977, the only year this occurred (John and Reid, 1983). Drebes (1981) considered that the absence of spores is likely to be due to the scarcity of *D. pseudolunula* during the preceding year. Both parasitic dinoflagellates and their zooplanktonic host show strong seasonal cycles (Colebrook, 1982; Coats, 1999) and it is possible that changes in the temperature, nutrient cycles, salinity, or other physical factors in the oceans during the extreme climatic conditions experienced in western Europe during 1976 may have resulted in variations in the distribution and abundance of either host or parasite, which in turn caused a significant decline in the *D. pseudolunula* spore population in the following year.

Monitoring of fish diseases in the open seas around the British Isles was being periodically undertaken throughout the 1970s, with studies on *Ichthyophonus hoferi*, a fungal disease in a range of marine fish, regularly occurring during this period. An endemic area of disease in haddock and plaice occurred in the Orkney–Shetland channel, but there was little evidence to suggest that any major changes in the prevalence levels of either fish species had taken place over the drought period (McVicar, 1982), suggesting that at least some fish diseases in the open ocean may not have been influenced by these climatic conditions.

5. Concluding remarks

The 1976 drought provides an excellent example of the diverse and complex effects on climate-driven animal and plant host–pathogen interactions under extreme conditions. Although data for a wide range of species were collected during 1976, these can only

Table 1

The effects of the 1976 UK drought on climate-driven plant and animal pathogens in terrestrial and aquatic ecosystems.

	Number of studies			<i>E</i>	<i>P</i>
	Effect				
	Positive	Unaffected/undetermined	Negative		
Ecosystem					
Animal (combined)					
Terrestrial	10	33	44	−0.39	<0.001
Farmed conditions	2	11	22	−0.57	<0.001
Wild conditions	8	22	22	−0.27	0.011
Aquatic	26	2	10	0.42	0.008
Farmed conditions	8	0	0	1.00	0.005
Wild conditions	18	2	10	0.27	0.131
Total farmed conditions	10	11	22	−0.28	0.034
Total wild conditions	28	24	32	−0.07	0.431
Total	36	35	54	−0.13	0.058
Plant (combined)					
Terrestrial	25	17	27	−0.03	0.782
Farmed conditions	10	14	22	−0.26	0.034
Wild conditions	15	3	5	0.43	0.025
Total farmed conditions	10	14	22	−0.26	0.034
Total wild conditions	16	4	5	0.44	0.016
Total	26	18	27	−0.01	0.891
Individual pathogens					
Animal					
Fungi	2	2	10	−0.57	0.021
Nematodes	0	8	13	−0.62	<0.001
Trematodes	7	3	12	−0.23	0.251
Arthropods	5	8	7	−0.10	0.564
Bacteria	6	0	3	0.33	0.317
Virus	2	1	2	0.20	0.564
Protozoan	9	2	6	0.18	0.439
Plant					
Fungi	20	11	19	0.02	0.873
Nematodes	3	4	5	−0.17	0.480
Terrestrial ecosystems					
Fungi	19	11	29	−0.17	0.149
Nematodes	3	12	18	−0.45	0.001
Trematodes	1	3	6	−0.50	0.059
Protozoans	4	1	3	0.12	0.705
Aquatic ecosystems					
Fungi	3	1	0	0.75	0.082
Trematodes	6	0	6	0.00	1.000
Protozoans	5	2	3	0.20	0.480
Total					
Fungi	22	12	29	−0.11	0.327
Nematodes	3	12	18	−0.45	0.001
Trematodes	7	3	12	−0.23	0.251
Cestodes	2	10	1	0.08	0.564
Arthropods	5	8	7	−0.10	0.564
Bacteria	7	1	4	0.25	0.366
Virus	4	4	3	0.09	0.705
Protozoan	9	2	6	0.18	0.439
Absolute total	60	52	78	−0.09	0.125

represent a small fraction of the total pathogen biodiversity within the UK. Nevertheless such data can form the basis of a much broader assessment of drought effects on temperate host–pathogen associations.

Analysis of associations between the occurrence of pathogens and the drought has shown that with the standardised effect, *E*, there is a variable response to this extreme climatic event (Table 1). In general, terrestrial animal pathogens, both overall and individually under wild and farmed conditions, were significantly negatively affected but in aquatic ecosystems there was a positive response. In contrast, plant pathogens in terrestrial systems demonstrated highly inconsistent changes under the drought

with farmed conditions causing largely negative changes and wild conditions predominantly positive resulting in an overall result demonstrating little change in pathogen occurrence.

Similar levels of variation are apparent for individual pathogen groups. Overall, nematodes were the one group which was consistently and significantly negatively affected by the drought in both wild and farmed conditions and host type. For ‘total animal’ results across conditions and ecosystems they were also joined by fungal pathogens. Fungi were also consistently negatively affected in animal and plant terrestrial farmed conditions but were inconsistently affected in terrestrial wild conditions. Plant fungi, in particular, were generally negatively affected under farmed

conditions but positively affected in the wild, although these specific changes may be associated with the sampled hosts, predominantly grassland crops in farmed conditions and trees and shrubs in the wild.

Although it may be considered that meta-analysis of this dataset could provide a more rigorous approach to understanding and quantifying the available evidence it is neither suitable nor feasible for applying to the present diverse data set due to wide variations in the duration and way data was collected and assessed between each individual study. Nevertheless, our general analysis of this data remains preliminary and the results although broadly applicable, regardless of the design and analysis in each original study, must be treated cautiously due to the inherent limitations of categorising and assessing data in this manner (Heck et al., 2003). It is certainly clear that although the data on a large scale may show the broad manner in which the drought affected pathogens, on smaller scales individual studies on particular host–pathogen associations or habitats may not conform to these general conclusions indicating the complex way pathogens can react to extreme changes in environmental conditions at the local level.

Unsurprisingly, given their economic importance, the highest numbers of records at this time were recorded for farmed animals and plants. Nevertheless, additional factors, related to the management of farmed animals and plants, can reduce or eliminate the impact of climate on pathogen occurrence. For example, in plant diseases the severity in any one location may be associated with cultivar resistance, previous cropping, pesticide usage and sowing date (Polley et al., 1993). Pathogen severity in farmed animals is influenced by farming practices, land use, the movement of livestock, wildlife reservoir hosts and the use of antibiotics and other veterinary pharmaceuticals (Lebarbenchon et al., 2008; Gale et al., 2009). In addition, the stability of farmed vertebrate populations compared with their wildlife counterparts may be an important factor. Wildlife is affected by a range of dominant abiotic and biotic factors that can regulate population structure such as social dominance, patterns of home range, territoriality, and predation that can influence pathogen susceptibility (Malan et al., 1997; Morley and Lewis, 2008). In contrast pathogens in farmed conditions rarely achieve any form of stability in the host community largely due to human management practices, particularly the use of pharmaceuticals to control the impact of disease. The aim here is to maximise animal and plant production, and this results in parasite communities which are less diverse than those found in the wild (Malan et al., 1997; Stancampiano, 2004). Despite these factors the drought appeared to have an overriding impact on pathogen occurrence in farmed and wild organisms particularly for helminth parasites, such as nematodes, as well as fungal infections.

The severity of the drought had a profound effect on the seasonality of many pathogens, particularly fungi and nematodes. There were extensive changes to the initiation, persistence, spread and intensity of infectious diseases, especially in animal hosts. A striking characteristic of the 1976 event is the altered occurrence of fungal infections in both plants and animals. A common result of the drought, particularly in both wild and farmed animals, was a reduction in fungal pathogens due to high temperatures/low humidity's negatively affecting spore survival and distribution. However, in plants a more complex picture emerges as a result of the drought and is dependent on degrees of host stress caused by the climatic conditions and the extent of insect feeding damage, which can facilitate fungal infectivity. Many pathogens, such as nematodes in both animal and plant hosts, were absent from hosts over the summer of 1976, only reappearing with heavy rainfall associated with the breaking of the drought. The seasonality of infectious disease is influenced by a range of parameters including

variation in host birth/death rates, behaviour, and immunity as well as the biology of pathogen free-living stages (Altizer et al., 2006). Nematodes in particular are able to undergo anhydrobiosis, the ability to temporarily stop all metabolic processes in response to extreme desiccation, and this may have aided their rapid return in some terrestrial habitats once the drought broke. Nevertheless, successful anhydrobiosis is dependent on a slow rate of initial desiccation and the duration and relative humidity of the period that they are maintained in this state (Crowe and Madin, 1975; Lettini and Sukhdeo, 2006). Survival of nematodes is impaired if anhydrobiosis conditions are too harsh and this factor may have played a role in the viability of some nematode populations at the local scale.

Interactions between pathogens during the drought may also be affected. For example fungi will often infect free-living nematode larvae and eggs in the terrestrial environment and may be an important regulating factor in the soil (Levine, 1980). During the drought there was some evidence to suggest that fungal infections of nematodes were reduced e.g. Kerry et al. (1982b), although ultimately this benefit was offset by the direct effects of climatic conditions on the helminth.

Moisture is critically important for the development, survival and movement of helminth larvae, such as nematodes, and it is apparent that the drought severely affected host–pathogen encounter rates. Changes in invertebrate hosts/vectors population dynamics also impacted pathogen occurrence, either with early seasonal initiation, where hosts/vectors underwent precocious summer population development, such as in many insect–pathogen associations, or prolonged summer aestivation, leading to delayed parasite initiation, as in the case of terrestrial mollusc–trematode associations. Ultimately, with substantial heavy rainfall following the drought there was a rapid return to normality and few long-term changes were apparent. Without such prolonged precipitation, whilst temperatures were still above the threshold for the development of free-living pathogens and the activity of invertebrate hosts/vectors, it seems likely that a return to more balanced host–pathogen dynamics would have been far more protracted.

Pathogen occurrence changes spatially relative to climate, latitude, elevation and geology (Ostfeld et al., 2005; Reisen, 2010) and consequently geographical variations in pathogen occurrence throughout the UK are well known e.g. Polley et al. (1993) and Van Dijk et al. (2008). Where sufficient data exists regional differences in drought severity do result in changes to pathogen occurrence, especially apparent for studies on the pathogens of farmed plants where variations in pathogen severity broadly changed with increasing latitude (Polley et al., 1993). In rivers there is an apparent difference between upland and lowland stretches in pathogen response to drought, dependent on geographical variations in the impact of low rainfall on flowing water habitats. However, in general there is not enough data to draw strong overall conclusions.

Nevertheless, it can be seen that in south-east England, which experienced the most severe drought conditions and also coincidentally was the area with the greatest number of pathogen records, extensive changes to host–pathogen dynamics are apparent in both animals and plants and in all ecosystems. However, physical and geological aspects on a local scale make a major contribution to the viability of individual habitats under drought stress. For example, herbaceous plants and trees in freely draining soils were particularly affected by drought stress and were more influenced by pathogens than plants growing on soils with greater moisture retention e.g. Bevercombe and Rayner (1980). Ultimately the impact of drought on pathogens, which may change on a local spatial scale is largely independent of the intensity of the drought at a regional level.

Changes in the geographical distribution of pathogens have been suggested to be a major consequence of climate change (IOM, 2008). During the 1976 drought there is only limited evidence to suggest that the geographical range of certain species had changed. The best examples include the northward spread of Dutch Elm disease facilitated by the increased activity of the beetle vector during this period. On the other hand, the wind-borne spread of plant fungal spores was largely impeded by the drought due to the restricted release of spores from infected hosts, suggesting that the geographical spread of these pathogens to new locations was limited. Nevertheless, when aquatic habitats were unable to support wildlife the extensive movement of water birds will have been an important factor in the spread of pathogens, although only the introduction of the trematode *T. podicipina* to Slapton Ley in Devon can clearly be associated with conditions at this time.

Host switching has been suggested to occur more frequently under the pressure of a changing climate (Brooks and Hoberg, 2007; Morley, 2010), although only limited evidence for this can be found during the drought. This is not unsurprising given that most field studies usually focus either on a single host species or a host–parasite association, thereby overlooking a pathogen switch to another host, particularly if the latter is not one traditionally monitored by epidemiological investigations. However, two good examples from 1976 were recorded, both involving insects, either as vectors for the plant virus BYDV (A'brook and Dewar, 1980) or as hosts for parasitoids (Dean et al., 1981). In both cases the insects were aphids and this group may therefore prove a useful invertebrate model for further investigations of host-switching under climatic change.

In terms of identifying any 'keystone' pathogen species or host–pathogen associations for climatic studies the present review has shown that for terrestrial systems, the response of the free-living larval stage of parasitic animal and plant nematodes in the soil under both farmed and wild conditions demonstrate a degree of uniformity in their altered seasonality and may be worthy of further study. There was a tendency for infections over the summer period to be arrested, although the reasons for this may not be the same across all host–nematode associations. It is likely that the response of free-living larvae in the soil to climatic conditions is potentially a key factor. But there is no single model nematode species that can be used as a 'keystone' because both species and stages of nematodes exhibit a variety of adaptations. Different combinations of these adaptations are associated with survival characteristics in the environment (Perry, 1999), and individual nematode species are likely to demonstrate subtle differences in responses to extreme climatic conditions.

Nevertheless, it has been suggested that parasitic helminths in general may be highly sensitive indicators of climate change (Van Dijk et al., 2010). However, in the present review both trematodes and fungi appear to show the most dramatic changes in occurrence but as groups remain difficult to use as indicator species because of their extreme variability in responses within plant and animal host communities as well as between terrestrial and aquatic habitats. In contrast, the way in which cereal aphids and their pathogens respond to extreme climate, and the ease in which they can be collected and examined, would appear to make them a promising host–pathogen association for studies in terrestrial habitats.

Freshwater systems experienced the most extreme conditions during the drought and a wide range of pathogens and host–pathogen associations were affected during this period. But no single group appears to be an obvious candidate for use as a 'keystone' mainly because none were studied in all the different kinds of habitats available. However, a range of other studies suggest that larval trematode infections in molluscs may be sensitive bioindicators of animal host diversity, abundance and trophic interactions e.g. Morley and Lewis (2006) and Hechinger

et al. (2008). They may also be a suitable model host–pathogen association for studying climatic effects in pathogen dynamics. In the present study molluscan–trematode interactions were substantially influenced in terrestrial and marine systems and were probably similarly affected in freshwater habitats. Further studies on their suitability for monitoring the effects of climate on host–parasite systems would be worthwhile.

In conclusion, the 1976 drought had extreme effects on the dynamics of some climate-driven host–pathogen associations, although in general, these appear to be relatively short-lived, largely due to the heavy rainfall arriving to break of the drought. Effects on host–pathogen associations were also discernible in northern Europe and Scandinavia. Although these studies are few in number and scattered over a wide geographical area they appear to broadly conform to effects in the UK where drought conditions were at their most severe e.g. Olsson and Holtenius (1980), Becker and Levy (1982) and Nansen et al. (1989). Nevertheless, it is self-evident that extreme climatic events of this kind may have more profound impacts over a longer rather than shorter terms. In the UK the longest known period of drought lasted for 20 years, albeit with brief wet periods, from 1890 to 1910 (Marsh et al., 2007). The results from 1976 suggest that if an event of such duration were repeated then such a change in climate would undoubtedly induce permanent changes to many host–pathogen associations in this country.

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