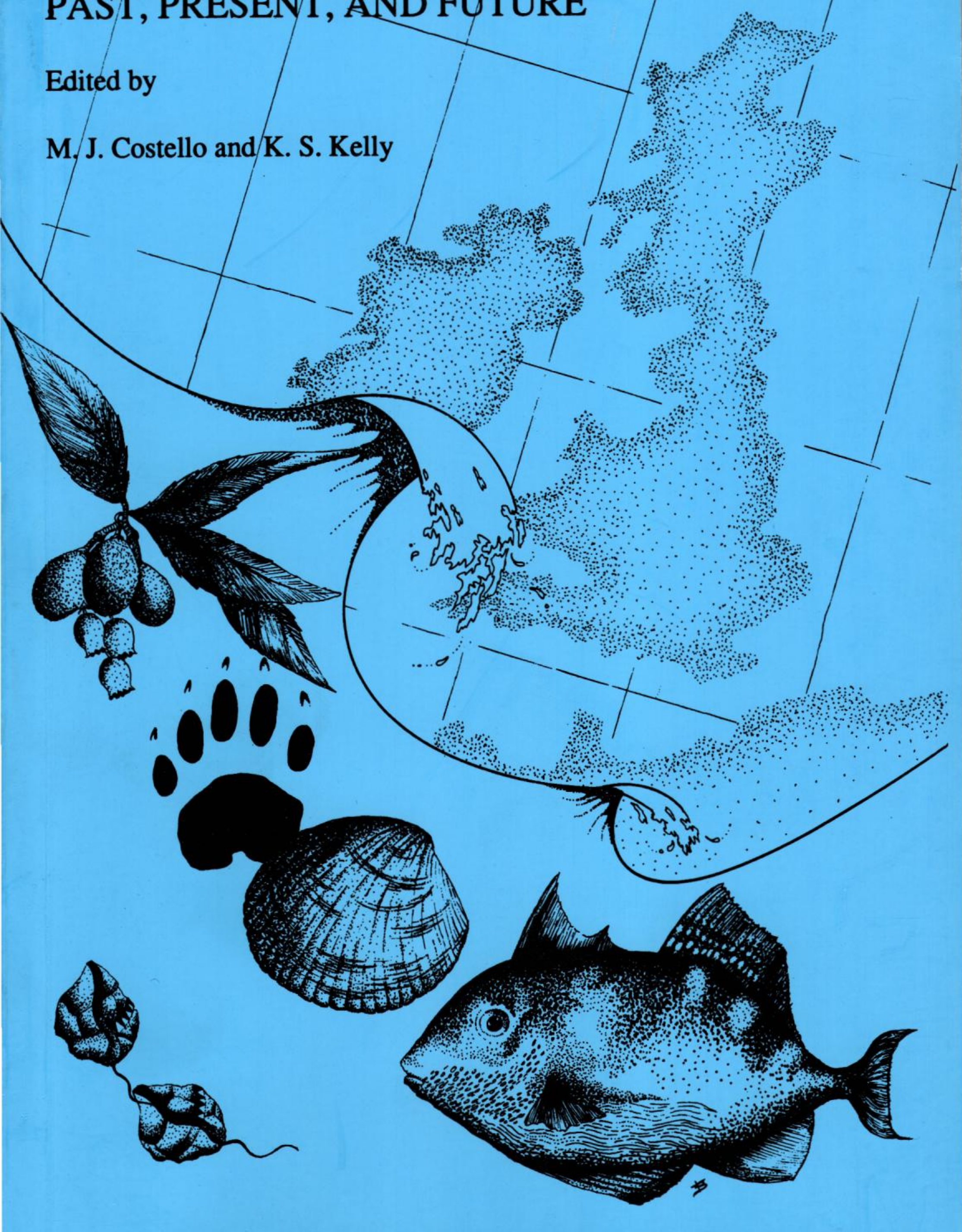
BIOGEOGRAPHY OF IRELAND
PAST, PRESENT, AND FUTURE

Edited by

M. J. Costello and K. S. Kelly



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Biogeography of Ireland: past, present, and future.

Editors

Mark J. Costello and Katherine S. Kelly

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Occasional Publication of the Irish biogeographical Society
Number 2, 1993.

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Introduction

The insular nature of Ireland has resulted in its fauna and flora being a unique subset of species present elsewhere in Europe. Knowledge of both the presence and absence of species, and their sometimes differing ecology in Ireland and elsewhere in Europe assists the understanding of the roles of climate, man's activities, and the environmental limitations and colonizing abilities of species in making the world what it is today. Perhaps of greater importance is that this knowledge aids prediction of the impacts of environmental change (be it induced by man or not) on ecosystems, and the biological resources and processes within them on which our lives depend.

Since the last conference on Irish biogeography in 1983 (Sleeman *et al.*, 1986), it has become widely accepted that human activities are influencing climatic change on a global level. It is predicted that mean global temperature will rise by 0.5 to 1.0ºC by the end of this century, and by 3.0 to 6.0ºC by 2100 (Houghton *et al.*, 1990). Sea level may rise by 10 cm by 2020, and between 30 to 110 cm by 2100 (Houghton *et al.*, 1990). The last biogeography conference focused on the effects of the last Glaciation, about 10,000 years ago, on Ireland's fauna and flora. Hence, in planning the present conference presenters of papers were asked to consider the last 10,000 years, the present, and the implications of future environmental change on Ireland's fauna and flora. In view of the imminent changes in sea-level, and the interests of two of the sponsoring organizations, papers on marine biogeography were also requested.

The first paper (Coxon) provides a review of the geological and fossil pollen evidence of Ireland's past climate and vegetation cover. Following this, hypotheses on the origin of mammals (particularly badger, otter, stoat, and mink) in Ireland are developed from population morphometrics (Lynch and Hayden), and the role of past and present environmental factors in determining the distribution of the strawberry tree in Ireland are described (Mitchell). Examples of how the present distributions of species may be affected by microclimate, habitat suitability and sea conditions are provided for saxifrages (Waldren and Scally), a terrestial amphipod (O'Hanlon and Bolger), and phytoplankton (Raine, McMahon and Roden), respectively.

Subtle changes in sea temperature can have marked effects on marine fauna. Ireland's seas were polar about 10,000 years ago, but about 5,000 years ago they were warmer than today and sea-level was higher (Praeger, 1950). The marine nature reserve, Lough Hyne, became marine about 4,000 years ago (Buzer, 1980, 1981) and has an amphipod crustacean fauna more similar to that of the Mediterranean than the south coast of the British Isles or Atlantic coasts of Europe. This warm-water relict fauna is believed to survive due to the higher summer temperatures in the lough than the adjacent coast (Costello and Myers, 1991). Such relict faunas, and fossil records may assist our prediction of the future effects of warmer temperatures and sea-level change on biological systems. In this volume, the possible influence of sea temperature change on Ireland's marine fauna and fisheries is discussed (Minchin), while the occurrence of trigger fish in Irish waters is reviewed from a biogeographical perspective (Quigley, Flannery and O'Shea). Furthermore, the impact of sea-level change on the distribution of cockles is predicted (Wilson).

The last conference noted that when considering dispersal and colonization mechanisms undue weight should not be given to a few well-known species. Hence new reviews and case studies on particular groups of species were also welcome. These have been provided for both mayflies (Connolly and McCarthy), and millipedes (Doogue, Fairhurst, Harding and Jones).

Man's activities alter both the immigration and extinction rates, largely through species introductions and the alteration of habitats. However, native and alien species are not necessarily synonymous with desirable and undesirable, and natural extinction and immigration continues to occur. The equilibrium theory of island biogeography not only predicts that the number of species on an island is proportional to its area and distance from the mainland, but that at equilibrium the turnover of species is constant, and that the immigration and extinction rates of species are equal (MacArthur and Wilson, 1967). While the species-area relationship may be approximated for some groups of species (McCarthy, 1986), whether Ireland's fauna and flora has reached equilibrium is less clear. Has the addition of new, so called alien species, resulted in, or been balanced by, the extinction of resident or native species? Ireland's stonefly fauna has not decreased this century, in contrast to extinctions in mainland Europe (Costello, 1988). Native freshwater amphipod species have been replaced by introduced immigrant species locally (Costello, in press), but whether extinction at a national level will occur is not known. However, changes in the relative abundance of species may have important implications for the conservation of our natural heritage (e.g. endemic species and sub-species, biodiversity) and development of biological resources (e.g. aquaculture, fisheries, agriculture).

Biogeography is a multi-disiplinary science, involving taxonomists, geographers, modellers, oceanographers, environmental scientists, and other specialists drawn from both amateur and professional backgrounds. In this volume, most of these disciplines have been brought together and the effects of future environmental change predicted. Future studies should build on this work and pay particular attention to comparing the distribution and abundance of animals and plants to environmental conditions (especially temperature), at local, regional, and global scales.

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Irish Quaternary biogeography, climate and the interglacial record

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Summary

The record of Pre-Holocene Quaternary biogeography in Ireland is fragmentary because successive glaciations and long cold periods have removed evidence of temperate stage deposition. However, like most of north western Europe, interglacials with temperate floras can be identified. The progressive impoverishment of the flora with repeated cycles of climatic deterioration can be identified from the sub-tropical floras of the Early Tertiary, to the warm temperate ones of the Late Tertiary/Early Quaternary to the cool temperate floras of the later parts of the Quaternary. This paper summarizes the floristic evidence we have from the Quaternary Period in Ireland.

Introduction

The overriding influence on Quaternary ecosystems has been the massive and regular shifts in climate which are controlled by the Earth's astronomical position relative to the Sun and by the secondary responses of global climate systems to these major forcing factors (Imbrie and Imbrie, 1979; Hays *et al.*, 1976; Berger, 1992). In north western Europe climatic changes have been manifested as oscillations between cold, cool and warm episodes with the colder periods being considerably longer than the warm ones (Lowe and Walker, 1984; Sibrava *et al.*, 1986). Such changes in environmental conditions have had a profound effect on plant (and animal) distributions in Europe by forcing repeated migration events some of which have led to regional extinctions (Nilsson, 1982).

Although it is known from the detailed oceanic oxygen isotope records that there have been many climatic oscillations during the Quaternary (with at least seven substantial cold periods in the last 700,000 years alone), the Irish terrestrial record is very limited with only one or two interglacials represented. However the few palaeobotanical records that are available to us give important glimpses of Ireland's former vegetation during this critical period, and allow us to assess the vegetation's response to environmental controls including climate. This paper will briefly review our current knowledge of the vegetation of Ireland during the latter part of the Tertiary Period and the temperate stages (interglacials) of the Quaternary (which covers *ca*. the last 1.7 million years, Table 1) and will highlight some of the more important biogeographical implications of the Irish Quaternary record.

Table 1. Geological terms used in this paper. Ages given are approximations, e.g. the onset of the Quaternary (*) varies according to different authorities (and the nature of the evidence they use) between 1.6 and 2.4 million years.

Era	Period	Epoch	Duration of unit	Age of beginning of unit
			Millions of years before present	
Cenozoic	Quaternary	Holocene	0.01 (i.e. 10,000 years)	0.01
		Pleistocene	1.69	1.7*
	Tertiary	Pliocene	5	7
		Miocene	19	26
		Oligocene	12	38
		Eocene	16	54
		Palaeocene	11	65

The Pre-Quaternary (Tertiary) vegetation

In many areas of Ireland the landscape appears to have been merely modified by events during the Quaternary. The evidence of the existence of elements of a Tertiary landscape are reviewed by Mitchell (1980, 1985) and his examples include basins, pediments, large scale tectonic effects, erosion surfaces, limestone solution features and deeply weathered rock. Sites of particular importance that also contain biogenic materials (allowing biostratigraphic dating) give us an insight into the pre-glacial vegetation of Ireland (Table 2, Figure 1).

Table 2. A summary of sites (Figure 1) with important Pre-Pleistocene deposits in Ireland.

The Interbasaltic Formation (e.g. at The Giant's Causeway).

Nature of deposit: Numerous interbasaltic weathering horizons with soils formed on upper surfaces.
Age of deposit: Palaeogene.
Main floral components identified: *Pinus, Tsuga, Cupressus, Araucaria, Alnus* and a number of angiosperms and ferns (Watts, 1970; Mitchell, 1981).

Lough Neagh Clays.

Nature of deposit: 350 metres of predominantly lacustrine and swamp sediments that were deposited in a subsiding basin.
Age of deposit: Oligocene (Chattian or Rupelian).
Main floral components identified: *Sequoia, Alnus, Nyssa, Quercus* (?), *Tilia* (?) and an important component of Taxodiaceae and associated taxa suggesting that the vegetation was predominantly that of a lowland swamp. (Watts, 1970; Boulter, 1980; Wilkinson *et al.*, 1980).

Ballymacadam, Co. Tipperary

Nature of deposit: A solution pipe in the Carboniferous Limestone with an infill that includes clay sediments rich in biogenic material.
Age of deposit: Oligocene affinities probably similar in age to the Lough Neagh Clays (Watts, 1970; Boulter and Wilkinson 1977; Boulter, 1980).
Main floral components identified: Gymnosperms, "*Quercus*-type", *Engelhardtia, Symplocos,* Ericaceae and occasional Palmae

Hollymount, Co. Laois

Nature of deposit: 20 m of organic sediments in an enclosed limestone depression.
Age of deposit: Miocene.
Main floral components identified: Hayes (1978) identified a pollen assemblage listed by Watts (1985) as being predominantly composed of *Pinus, Quercus, Corylus, Myrica* and Ericales. Also present at Hollymount were the pollen of *Taxodium*-type, *Symplocos, Tsuga, Sciadopitys, Liquidambar* and Palmae-type.

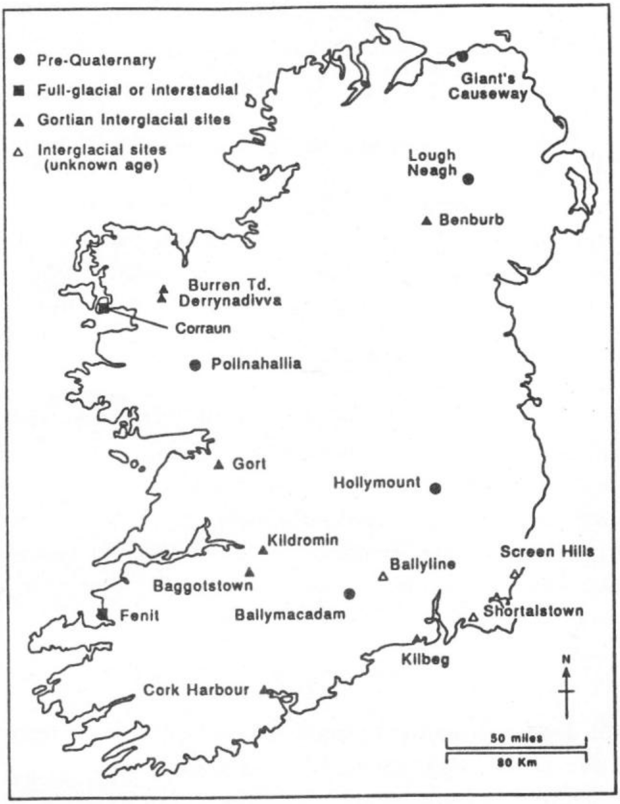


Figure 1. Location of key sites referred to in the text.

Pollnahallia: the end of the Tertiary and the onset of the Quaternary.

Geological investigations at this site (Coxon and Flegg, 1987) revealed a complex network of gorges and caves in the limestone now covered by superficial material including glacigenic deposits. Palynological work suggested that the lignite infilling the base of the limestone gorge was Pliocene. Since the original study a further continuous core through the lignite has been taken, and a further lignite bed has been discovered lying on the surface of the limestone (Figure 2). Within the lignite the alternating deposition of organic rich sediment, clays and silts with sand horizons suggests that this unit represents deposition in predominantly slow moving water; the sand horizons indicating faster flow and the finer sediments standing water.

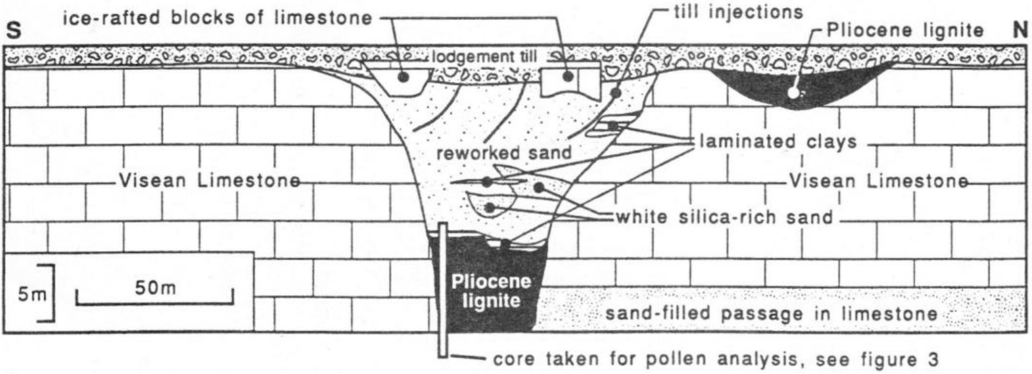
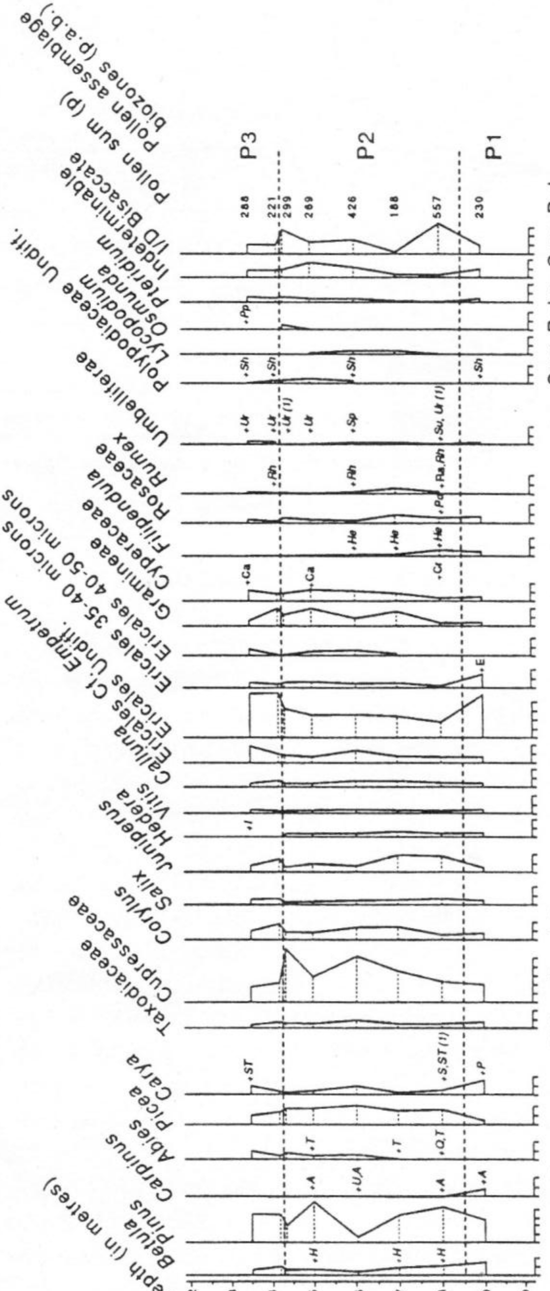


Figure 2. Schematic cross section of the deposit at Pollnahallia.

The pollen diagram (Figure 3) appears to represent a vegetation cover dominated by ericaceous, cupressaceous and coniferous trees and assorted shrubs. Little can be said regarding the exact nature of the more important elements of the vegetation, beyond that the landscape certainly had a cover of heath associated with *Pinus* and *Picea*. *Abies* appeared in the vegetation by the mid-point of P2. The tree(s) and/or shrub(s) species contributing to the rain of Cupressaceae are an unknown.

Trees not mentioned above that were growing close enough to the gorge at Pollnahallia to contribute pollen include *Betula, Ulmus, Quercus, Tsuga, Alnus, Carpinus* and *Pterocarya* (the latter two taxa only during P1), *Carya*, Taxodiaceae, *Sequoia*, and *Sciadopitys*. This represents a wide range of taxa, possible species and habitats. Many of the latter list are only present at background levels, perhaps indicating a regional rather than local presence. Some change in forest composition is indicated by the early disappearance of *Carpinus* and *Pterocarya* and the appearance of *Abies* later in P2.

The partially exotic flora of Pollnahallia was preserved below a wind-blown silica sand, probably a Tertiary weathering residue, which was mobilized as the vegetation cover was destroyed by climatic deterioration at the onset of the Pleistocene.



One scale increment = 5% pollen (p)

U = *Ulmus*
A = *Alnus*
Q = *Quercus*
St = *Sciadopitys*
H = *Pinus*
T = *Tsuga*

S = *Sequoia*
P = *Pterocarya*
I = *Ilex*
E = Ericales >50 microns

Ca = Caryophyllaceae
Cr = Cruciferae
He = *Helianthemum*
Rh = *Rhamnus*
Ra = Ranunculaceae
Po = *Potentilla*

Ur = *Urtica*
Su = *Succisa*
Sp = *Sparganium* (sum P + Aquatics)
Sh = *Sphagnum*
Is = *Isoetes*
Pp = *Polypodium*

Figure 3. Percentage pollen diagram from the deposit at Pollnahallia.

Although specific identifications are rare from the Irish Middle and Late Tertiary, the flora represented at Irish sites can be seen to have contained a small element of the exotic taxa that became regionally extinct from Europe after the Late Tertiary/Early Pleistocene. The regional impoverishment of the European flora at the onset of the Pleistocene is covered by Watts (1988) in a stimulating review in which he notes "...the first glaciation was a biological catastrophe of far greater consequence than any subsequent Pleistocene glaciation". He points out that some taxa became extinct, some survived in refugia (with much more limited ranges) and others were lost to Europe but survived in distant areas, e.g. the Far East and North America.

The Quaternary

The Global Cenozoic sequence from long marine, lacustrine and terrestrial sequences exhibits a characteristic record with a decline in temperature throughout the Miocene culminating in numerous step-like changes in climatic conditions over the last 2.5 million years. The overriding control on such vast variation in climate are three predominant characteristics of the Earth's astronomical position relative to the Sun, which vary cyclically over time on different wavelengths (Imbrie and Imbrie, 1979; Lowe and Walker, 1984). The effect of these climatic changes is spatially very variable and their periodicity has altered during the Quaternary (a point emphasised by Watts, 1988). However in northwestern Europe the last 750,000 years have been characterised by long periods (*ca*. 50-100,000 years) of cold climates interspersed with shorter periods (*ca*. 10-15,000 years) of warmer (temperate) conditions (called interglacials). Quaternary climatic change has produced a geological record dominated by sediments deposited under glacial, periglacial and temperate environmental conditions. The record is often fragmentary especially when deposited terrestrially. Extensive glaciation has left Ireland with only a partial record of glaciations prior to the last one (Midlandian), and likewise a very poor record of the many temperate episodes that Ireland must have experienced. The lack of continuous sedimentary records, in particular the absence of biostratigraphically usable organic sequences, has meant that the elucidation of an agreed Quaternary succession has not been possible.

The Quaternary geology of Ireland has been studied since the mid-nineteenth century when Agassiz visited the country and geologists began to look for evidence that ice had altered the landscape. The development of the analysis of Irish Quaternary deposits is reviewed by Edwards and Warren (1985).

The interglacial record: Quaternary biostratigraphy

In the 19th Century an interglacial deposit of peat and mud lying below glacial deposits in the banks of the Boleyneendorrish River, near Gort, Co. Galway (Figure 1) was discovered and described by Kinahan (1865, 1878). Subsequently the site was rediscovered, and a comprehensive account of the deposit was published (Jessen *et al.*, 1959): the site has been used as the type site of the Gortian Interglacial. Since then the details of eight other interglacial sites have been collected (not all published). Although the level of information available from these interglacial sites is variable and the age of all of the sites is not clear most of the sequences are similar to the record from the interglacial site at Gort.

Pre-Gortian interglacials

The deposit at Pollnahallia (above) represents part of the Pliocene and possibly the onset of the Pleistocene, but after this point there is no documented record of the Early Pleistocene recorded in Ireland apart from a glacially reworked fauna of marine shells that originated in the Irish sea basin (Mitchell, 1981). However, a deposit of laminated, lacustrine, clay over 25 metres thick was discovered filling a solution feature (similar to those containing Tertiary sediments, Table 2) in Carboniferous limestone below glacial sediments near Ballyline, Co. Kilkenny (Coxon and Flegg, 1985) (Figure 1). Unfortunately there were few samples available from the site for palynological work or for characterising the overlying glacial sediments and the deposit requires reinvestigation before any firm conclusions can be drawn. From the evidence available a preliminary pollen diagram was drawn (Figure 4). The pollen assemblages were typical of Middle Pleistocene sequences in Europe.

The pollen record of the sediments suggest that the deposit represents a period when climatic conditions ameliorated to allow development of a forest cover including *Abies, Picea, Ulmus, Alnus, Quercus, Carpinus, Pterocarya* and *Taxus*. The forest was an open one with areas covered by Gramineae, Ericales and numerous herbs. The deposits covering this forest / heath / grassland stage were 10 m thick. Subsequently the forest taxa decline, perhaps indicating soil or climatic deterioration, and *Pinus, Picea,* Gramineae and herbaceous taxa become more dominant.

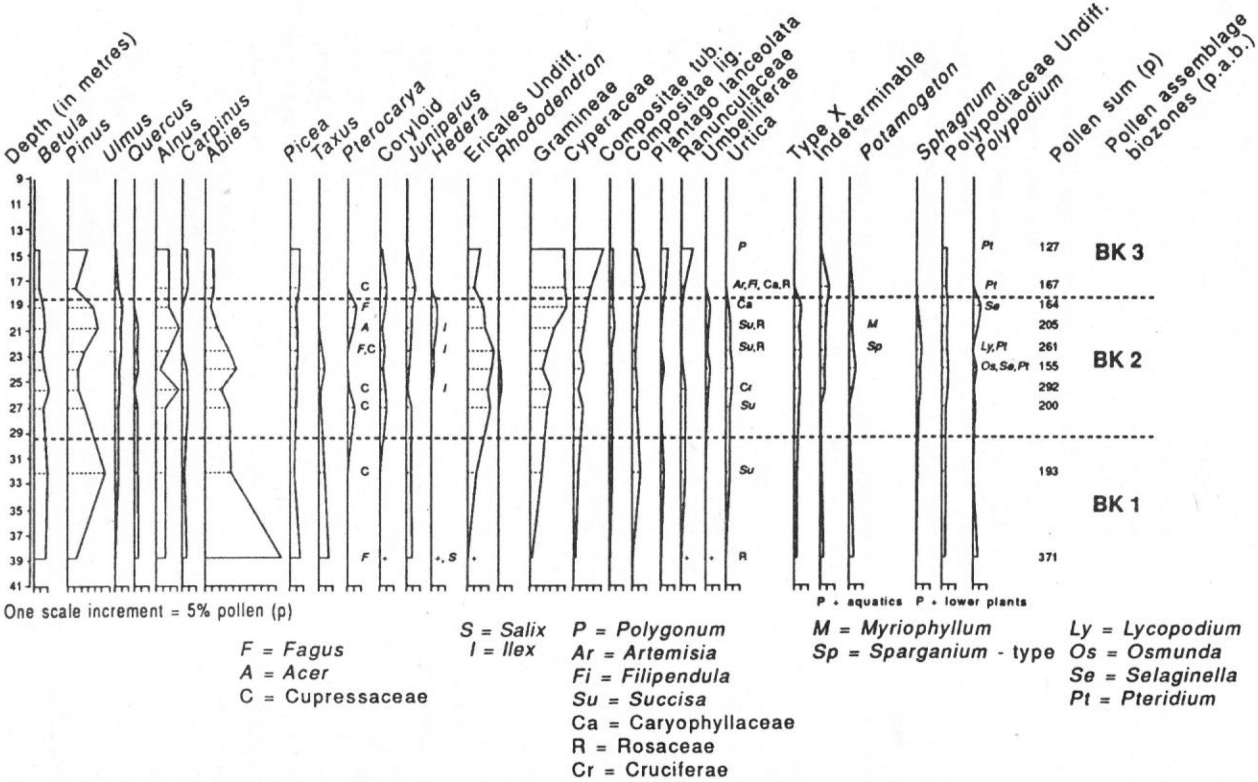


Figure 4. Percentage pollen diagram from the deposit at Ballyline.

Early and Middle Pleistocene (Pre-Cromerian) interglacials in Britain contain a number of 'relic' taxa (West, 1980) not recorded at Ballyline. These taxa include *Tsuga* and *Eucommia*, the latter only as isolated pollen grains. The Cromerian and Hoxnian Interglacials (for stratigraphic information see West, 1980) both contain most of the taxa recorded at Ballyline whilst the later, Upper Pleistocene, Ipswichian Interglacial contains no *Pterocarya* or *Fagus*. It is possible that the Ballyline site represents part of a Middle Pleistocene temperate stage complex (possibly pre- or post-dating the Gortian) that has been hitherto unrecorded or that the material was reworked or derived. The fact that the pollen record contains a second *Carpinus* peak supports the idea that the record may be a complex one, and it is also worth recording that it is not known how much of an interglacial sequence is recorded at Ballyline.

The pollen diagram resembles those of Gortian age in many important respects, but equally important differences led the authors to avoid direct correlation to either the Gortian or to particular temperate stages in the British or Continental Pleistocene records. Although worth recording there are insufficient data from this site to warrant a new stratotype.

The Gortian (penultimate) Interglacial

Eight sites around Ireland (Figure 1) record an important interglacial succession that can be assigned with some confidence to the Gortian Interglacial whose sequence has been described biostratigraphically using the characteristic floral assemblages that can be recognised at the more complete sites. The evidence from the Gortian suggests a very diverse and rich flora (Watts, 1985). Abbreviated pollen diagrams from six of the more complete sites (Figure 5) can be seen to follow a general pattern (Watts, 1985). However the interglacial does not seem to complete a full cycle (*sensu* Iversen, 1958; Turner and West, 1968) but comes to an abrupt end (discussed below). Selected taxa from a Gortian pollen diagram (Figure 6) show the typical vegetational succession of the middle and latter parts of the interglacial. The vegetational sequence of the Gortian can be generalized as follows:

Zone 1. A late-glacial vegetation that developed during climatic amelioration and included pioneering plants such as *Salix*, *Juniperus* and *Hippophae* as well as a diverse herb flora and *Betula* scrub.

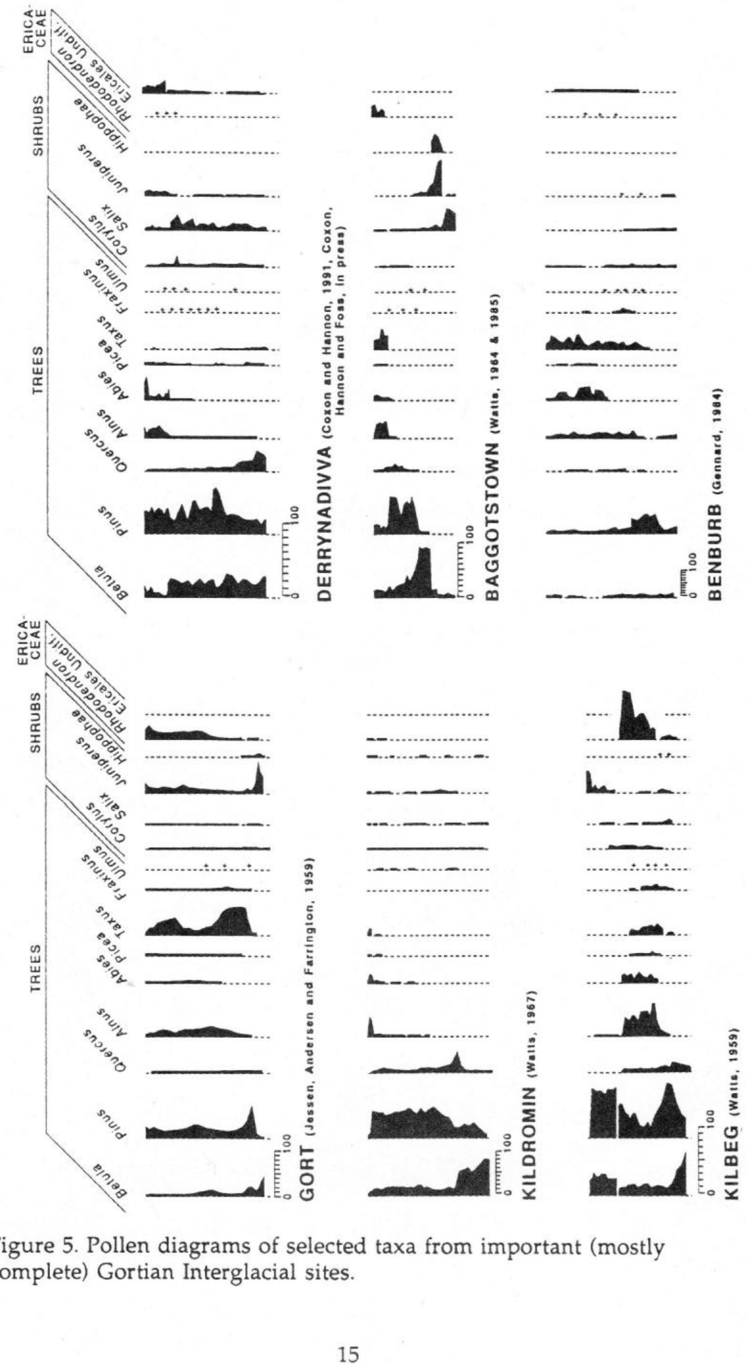
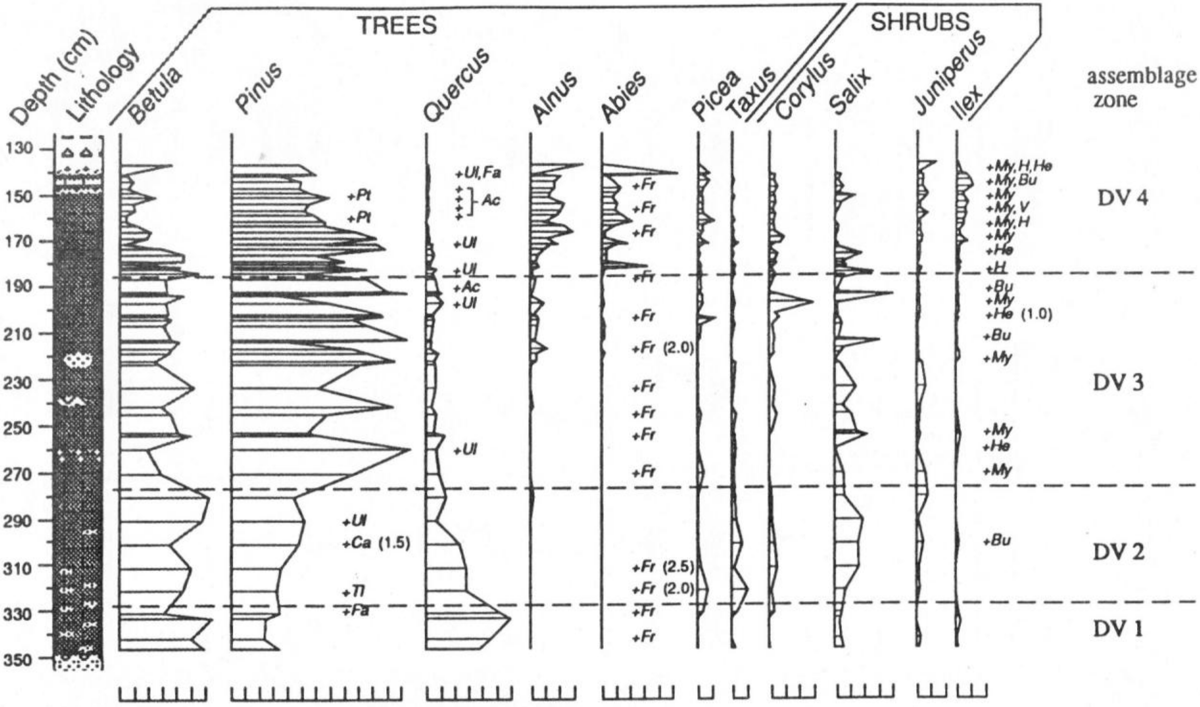


Figure 5. Pollen diagrams of selected taxa from important (mostly complete) Gortian Interglacial sites.



One scale increment = 5% pollen (P)

Key to abbreviated taxa:
Trees: Ac - *Acer*, Ca - *Carpinus*, Fa - *Fagus*, Fr - *Fraxinus*, Pt - *Pterocarya*, Tl - *Tilia*, Ul - *Ulmus*. Shrubs: Bu - *Buxus*, H - *Hippophae*, He - *Hedera*, My - *Myrica*, V - *Viscum*.

Figure 6. Percentage pollen diagram (trees and shrubs only) from the Gortian temperate stage deposit at Derrynadivva. From Coxon and Hannon, 1991.

Zone 2. As soils stabilized and the climate improved the late-glacial pioneering vegetation was shaded out by *Betula* and *Pinus* woodland, and many other thermophilous trees and shrubs (e.g. *Quercus, Ulmus, Ilex* and *Corylus*) were expanding from their glacial refugia and migrating into Ireland. This forest was frequently disturbed by fire (Coxon, *et al.*, in press) and did not develop into a mature mixed oak forest (unlike interglacial sites in neighbouring Britain).

Zone 3. The latter part of the Gortian Interglacial is typified by the appearance and/or dominance of *Picea, Abies, Alnus, Taxus* and a very diverse flora of Ericaceae which, along with sedimentological evidence, indicates that wet conditions and bog development were predominant. These taxa either migrated late into the landscape or were favoured by the wetter conditions and decreasing soil fertility.

Termination of Zone 3. At all of the sites that contain a long record (Figures 5 and detail on Figure 6) the sequence is abruptly terminated, and although many of the Gortian deposits are ice-rafted lenses and not *in situ* there is sufficient evidence of a conformable transition from the wooded, ericaceous heath of Zone 3 to an open landscape vegetation to conclude that sudden climatic deterioration truncated the interglacial cycle. This sudden end to the interglacial may have been due to the proximity of Ireland to the important Polar Front of the North Atlantic during the onset of the subsequent glaciation, a situation not unlike that proposed by Watts (1985) to explain marked environmental change during the Nahanagan Stadial.

The Gortian floral assemblages provide detailed biostratigraphic information, but in Ireland the lack of interglacial deposits of other ages, the lack of absolute dates, the unique nature of the Irish vegetation, and the distance between the Gortian sites and the type sites of British and European interglacials has meant that a firm biostratigraphic correlation cannot be made. The most likely age for the Gortian Interglacial is equivalent to the Hoxnian of Britain and the Holsteinian of Europe, i.e. the penultimate interglacial that occurred some 240,000-220,000 years ago (Mitchell, 1976, 1981; Watts, 1985) although some evidence suggests it may be older. Attempts have been made to date the Gortian using uranium-thorium disequilibrium methods at Burren Townland (Heijnis, 1992) where two uncorrected dates give ages of 180ka and 191ka suggesting a correlation with Oxygen-Isotope Stage 7 or 9. Heijnis (1992) also quotes preliminary work at the Gortian type site at Boleyneendorrish, Co. Galway where an age in excess of 350 ka was obtained making a correlation with Oxygen-Isotope Stage 7 less likely.

This correlation is based on the occurrence of taxa (and assemblages) found in the Gortian including the following:

A. The importance of *Hippophae* in the early part of the interglacial and *Abies* in the latter part - this is similar to Hoxnian records.

B. The presence of Type X (cf. Oleaceae - the olive family, see Turner, 1970; Phillips, 1976; West, 1980), a palynomorph restricted in British and European interglacials to the penultimate interglacial.

C. The presence of *Azolla filiculoides*, an aquatic found only in pre-last interglacial deposits in Europe.

A number of taxa have interesting fossil records. *Rhododendron ponticum*, is found as a fossil in Gortian sediments but now has a relic distribution (Cross, 1975; Godwin, 1975 and see Figure 7) in Turkey, Portugal, Spain and Syria. So the Gortian vegetational sequence is, like the Irish Holocene one, unique and thus difficult to correlate. *Rhododendron* is absent from the penultimate interglacial in Europe only being found in Early Middle Pleistocene sites in central and south eastern Europe (Figure 7) where it may have had a widespread European distribution.

Fascinatingly, other taxa with unique Holocene distributions are found in Gortian sequences including *Erica mackaiana*, *Erica* cf. *ciliaris* (both now occurring near Roundstone in Co. Galway) and *Daboecia cantabrica* (also found in the Connemara area). These taxa have their main distributions in southwestern France, Portugal and Spain, and their occurrence in this interglacial is interesting as it suggests they have some antiquity in the Irish flora. Much attention has been placed on the organic sequences at Fenit, Co. Kerry which have been assigned to the end of the Gortian (Mitchell, 1970, 1976). However, the palynological evidence suggests that these latter sediments were deposited in cool temperate conditions. Uranium-thorium dating of the biogenics gives an age of between 115,000 and 120,000 years. This age implies that the deposit belongs within Oxygen Isotope Stage 5 of the marine record (Lowe and Walker, 1984), possibly towards the end of 5e (dated to 132-122,000 years - Bowen *et al.*, 1986) or more likely during 5d or the beginning of 5c. The latter is suggested by the pollen which indicates a slight amelioration in climate towards the top of the deposit (Heijnis *et al.*, 1993).

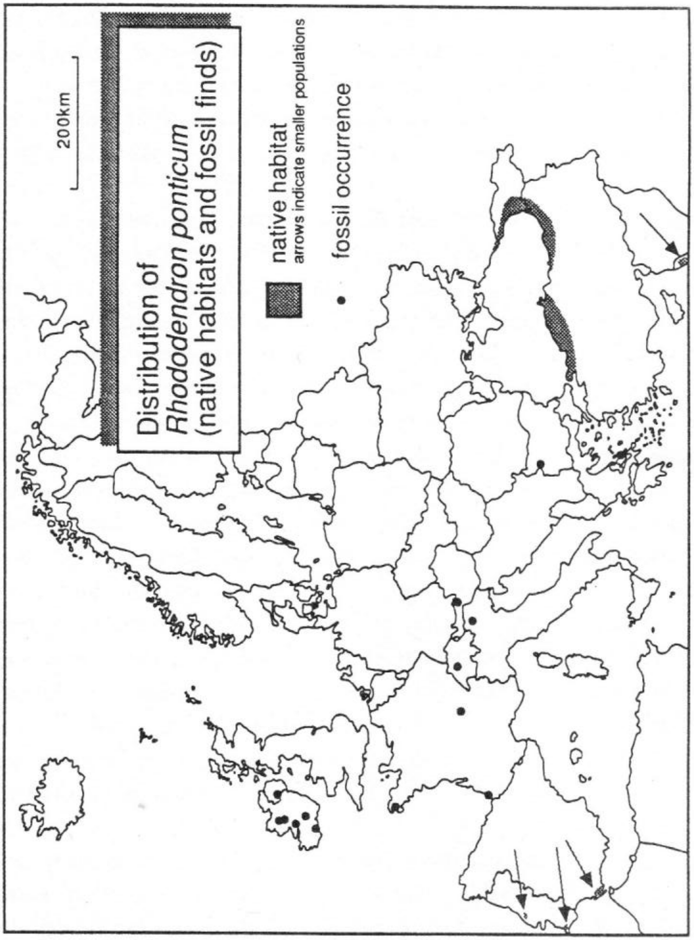


Figure 7. Distribution of *Rhododendron ponticum* (native habitat and fossil occurrence).

The Last Interglacial

Although well-documented from Britain (as the Ipswichian Interglacial - e.g. West, 1980), from Europe (as the Eemian Interglacial - e.g. Watts, 1988) and from ocean cores as oxygen isotope stage 5e (Shackleton, 1969) the last interglacial has not been identified in Irish terrestrial sediments. Warren (1979, 1985) has suggested that the Gortian represents the last interglacial on a number of grounds. The most important of these were the stratigraphic relationship of the organic sequence at Fenit to the Courtmacsherry Raised Beach, and the fact that Warren identified deposits of only the last glaciation age (Midlandian) overlying Gortian Interglacial sediments (see Watts, 1985 for a discussion of the biostratigraphic objections).

There remains the problem of the missing last interglacial and Mitchell (1976, 1981) has tentatively suggested that the upper part of the sequence at Baggotstown (Watts, 1964) and the estuarine sand at Shortalstown, Co. Wexford (Colhoun and Mitchell, 1971) might represent this temperate stage. The problem is that both sites require reinvestigation. The important part of the Baggotstown stratigraphy is far from clear as the log had to be reconstructed from the spoil of a dug well, the sediments at Shortalstown appear to have been glacitectonically disturbed, and the biological information is not detailed enough to be absolutely characteristic of an Ipswichian age. Indeed the pollen diagram from Shortalstown could represent a Middle (or even Early-) Pleistocene sequence reworked from the Irish Sea basin, a scenario made more possible by the recording of a seed of *Decodon* sp. (a taxon recorded from the Pliocene and Early Pleistocene of Europe (Mitchell, 1981)) from the deposit. The lack of other "relic" taxa precludes further speculation, although it is worth noting that Colhoun and Mitchell recorded a pollen grain of *Tsuga*. It can be concluded that like the upper part of the Baggotstown sequence the estuarine sediments from Shortalstown warrant further analysis.

Recently (December 1990) a reworked ball of organic detritus was recovered from a sand and gravel unit in the Screen Hills end moraine by A. M. McCabe (McCabe and Coxon, in press). This sediment contained the following (main) pollen types (as a % of the total pollen sum excluding lower plants and aquatics = 517): *Betula* (8%), *Pinus* (15%), *Carpinus* (14%), *Picea* (9%), *Corylus* (14%), *Ilex* (3.5%), Ericaceae undiff. (4%), Rosaceae (6%) and Umbelliferae 9%. This assemblage is unlike any other recorded in

Ireland but is very similar to Ipswichian and Eemian assemblages particularly in the importance of *Carpinus*. It is a pity that more of this material is not available as it probably represents the Last Interglacial in Ireland.

As mentioned above the organic sediments at Fenit post-date the Eemian and represent an onset of cooler conditions prior to the Last Glaciation (Heijnis *et al.*, 1993).

Conclusions

As can be seen from the above discussion the record of Quaternary temperate interludes in Ireland is a very incomplete one. However, enough evidence is available to allowing the piecing together the history of the Irish flora prior to the Holocene and to recognize that it is similar to those from the Quaternary of other parts of Europe. Further advances in this research field will be relying heavily on the discovery of additional temperate stage deposits and the application of modern dating techniques.

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Multivariate morphometrics and the biogeography of Irish mustelids

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Summary

There exists some confusion as to the means by which mammals recolonized Ireland after the last glacial period. In this paper, multivararaiate morphometric techniques are used to examine cranial variation between Irish, English and Scottish mustelid populations, and to test various hypotheses concerning the origin of the Irish populations. Little evidence was found for colonization *via* a landbridge between northeast Ireland and Scotland. The possibility of human aided introduction is discussed.

Introduction

Six species of carnivorous terrestrial mammal occur in Ireland. Five of these are members of the family Mustelidae: the stoat *Mustela erminea* L., the American mink *M. vison* Schreber, the pine marten *Martes martes* L., the otter *Lutra lutra* L. and the badger *Meles meles* L. The other carnivore present is the red fox (*Vulpes vulpes* L., a canid). Whilst the American mink is a known introduction (dating from the 1950's; Smal, 1988), it has been assumed that the other species naturally colonized Ireland *via* a landbridge during the postglacial period (Mitchell, 1986). However, man's past usage of, and traffic in, mammals raises the possibility that some of the mammalian species present on this island were introduced, either deliberately or accidentally, by man.

There is currently some controversy as to the location (and indeed existence) of post-glacial landbridge(s) between Britain and Ireland (Yalden, 1981; Devoy, 1985; Mitchell, 1986; Preece *et al.*, 1986; Sleeman *et al.*, 1986). Devoy (1985) conducted an exaustive review of the evidence for five proposed connections, and found the greatest amount of evidence for a 'low soggy, possibly shifting and partially discontinuous' linkage between northeast Ireland and Scotland dated between 10,200 and 11,400 years B.P. He found little evidence for a connection between Wales and Ireland (as proposed by Mitchell, 1986) or for a landbridge dated prior to 12,000 years B.P. (as proposed by Yalden, 1981). It is generally accepted that, if such a landbridge existed, it was relatively short-lived, discontinuous, and unlikely to have provided a suitable habitat for many of the current mammalian fauna (Corbet, 1962; Yalden, 1981; Devoy, 1985; Stuart *et al.*, 1985). There appears to be little evidence for 'organized oakwoods advancing ... carrying those forest animals, the red deer and the wild boar, along with them' advocated by Mitchell (1986).

In this paper a hypothesis is developed about the method by which carnivores colonized Ireland. A preliminary examination of the variation between British and Irish populations of the badger, stoat, otter and mink using a multivariate statistical examination of cranial measurements, is reported, and it is shown how such data could help test the hypothesis. In addition, other methods by which this question can be addressed are suggested.

A scenario to explain the occurrence of carnivore species

The existence of a species on the Irish mainland can be explained by four possible (non-exclusive) hypotheses; (i) The species survived the glacial period in ice-free refugia, (ii) the species recolonized the country *via* a filter land-bridge, (iii) the species was accidentally introduced by man, and (iv) the species was deliberately introduced by man. Given these four possible options, the following scenario is proposed to explain the occurence of the Carnivora in Ireland.

The fauna of the Castlepook Interstadial (35,500 years B.P.) is fairly well documented and includes a number of species which occur either at present or in the recent past, namely wolf (*Canis lupus* L.), mountain hare (*Lepus timidus* L.) and stoat (Stuart *et al.*, 1985). With the subsequent climatic deterioration (during which time two-thirds of the islands landmass was covered with glaciers), a number of the species present would have faced adverse conditions and would have become extinct. Species adapted to tundra conditions (wolf, hare, arctic fox (*Alopex lagopus* L.), lemming (*Dicrostonyx torquatus* Pallas and *L. lemmus* L.), reindeer (*Rangifer tarandus* L.), giant Irish deer (*Megaceros giganteus* Blumenbach) and stoat) would have survived to recolonize the island during the

Woodgrange Interstadial, as previously suggested by Fairley (1984). This range contraction, and subsequent expansion, may explain the sub-specific status of the Irish hare and stoat, perhaps due to long-term isolation from the British stock from which it must have originated. During the interstadial, a landbridge between Britain and Ireland would have allowed some natural recolonization, but colonists would have faced a genetic bottleneck as well as the further deterioration of climate that was to characterise the Nahanagan Stadial. This rapid climatic change would have resulted in only the subarctic faunal element surviving into the start of the Littletonian, and the extinction of the giant Irish deer and reindeer. Subsequent climatic amelioration may have resulted in the further loss of species such as the two lemmings (Stuart *et al.*, 1985; Yalden, 1992). The colonization of the island by man (approx 9,000 years B.P.) would have allowed accidental or deliberate introduction of species. Thus, the stoat and wolf may have survived the Devensian Cold Stage in refugia, whilst the fox, pine marten, badger, and perhaps the extinct wildcat (*Felis silvestris* Schreber), were post-glacial immigrants (either natural or aided by man). The aquatic otter could have naturally colonized Ireland at any stage, as the Irish sea (especially at northeast Ireland) may not have proved a barrier to colonization. Therefore, the stoat may represent the only surviving native carnivore to occur in Ireland.

If this scenario explains the origin of the Irish carnivore fauna, it allows a number of hypotheses to be formulated, and falsified;

1. It might be expected that, if the main migration route of a species was *via* Scotland, then one might expect recent Irish populations of that species to resemble, not its climatic and latitudinal equivalents in Wales and central England, but Scottish populations (Savage, 1966).

2. 'Relict' species, such as the stoat, should be morphologically (and genetically) more distinct from British populations than are populations of post-glacial immigrants.

3. Recent introductions should be less differentiated from their parent populations than older introductions.

Given the above, one might expect the separation between British and Irish stoat populations (relict species) to be greater than that between the mink populations (recent introduction), with the badger and otter population (past introduction/natural colonization) separations being intermediary.

Testing the hypotheses

Multivariate techniques have proved useful in the examination of variation between vertebrate populations (Thorpe, 1976). If one is willing to assume, or can prove, that patterns of morphological variation are concordant with patterns of genetic variation, one can use morphology as a tool to aid the tracing of a species' past-history throughout its range. Cranial traits have, in general, a high heritability (e.g. Atchley *et al.*, 1981) and multivariate techniques have in the past identified differences between electrophoretically distinct mammalian populations (e.g. Patton and Smith, 1990; Lynch *et al.*, 1993). In the past, morphometry has been successfully utilized to study postglacial colonization in Canadian stoat populations (Eger, 1990) and island colonization in foxes (Collins, 1991). Thus, similar studies may prove enlightening in the study of the recent history of Irish mammals.

Methods

Material was available from museum and private sources (see Acknowledgements). Eleven cranial measurements were taken from intact skulls of adult badger, otter, mink and stoat (see Lynch *et al.*, 1993 for details of age estimation and measurements taken). Measurement error in these eleven traits is relatively small (Lynch and O' Sullivan, 1993). Table 1 outlines the samples used. Badger sexes were mixed as the degree of sexual dimorphism exhibited in the species is small, particularily when compared to other mustelids (Lynch *et al.*, 1993; Lynch and O' Sullivan, 1993). Data were log transformed prior to subjection to a multiple group principal component analysis (MGPCA; Thorpe, 1988). The MGPCA derives within-group size and shape vectors. These derived variables were entered into a canonical variate analysis (CVA) which assesses variation between samples. A CVA on all the component scores from a MGPCA gives identical results to a CVA on the original data (Thorpe, 1988). If the MGPCA shows the existence of a "size" component, then a CVA on the remaining "shape" components alone gives a "size-out" CVA that can be compared to the ordinary, or "size-in" CVA. All analyses were carried out using the SAS$^{(tm)}$ statistical package (Version 6.06). SAS/IML code for the analyses is given in Lynch (1993) and copies of the raw data are lodged in the archives of the National Museum of Ireland (Natural History Division), Dublin.

Table 1. Samples used in the current study.

Species	Sex	Ireland	England	Scotland
Badger	Mixed	104	102	32
Otter	Male	25	5	23
Stoat	Male	12	12	16
Mink	Male	10	14	24

Results

There were significant differences between Irish, Scottish and English populations of all four species examined (Table 2; Figure 1). Irish badgers and otters were more like English specimens than Scottish. Irish stoats were more like those from England when one considers the 'size in' analysis, but equidistant from Scottish and English populations when only shape variation is considered (Table 2). Irish mink were most similar to those from Scotland. Furthermore, for the otter, badger and stoat, five out of the six comparisons (Table 2) show Irish populations to be most similar to English rather than Scottish populations. The sixth comparison, the "size-out" analysis of the stoat sample, indicated equal separation between the populations, perhaps reflecting the relative long period since a common ancestor. Thus there is no evidence for colonization *via* a Scotland-Ireland landbridge (Hypothesis 1, see above).

Table 2. Variation between British and Irish populations of four mustelid species. * Mahalanobis distance between English and Irish specimens. ** Mahalanobis distance between Scottish and Irish specimens.

Species	Size	Wilks' Ω	F	P	D^2 (IE)*	D^2 (IS)**
Otter	In	0.313	2.86	0.0003	5.93	6.95
	Out	0.339	2.93	0.0003	4.80	6.95
Badger	In	0.562	6.89	0.0001	2.69	2.77
	Out	0.571	7.37	0.0001	2.65	2.73
Stoat	In	0.063	7.36	0.0001	18.10	22.50
	Out	0.084	6.87	0.0001	12.10	12.10
Mink	In	0.174	4.45	0.0001	11.08	10.98
	Out	0.175	4.99	0.0001	11.08	10.89

The separation between the stoat populations is greater than that between the mink, which in turn is greater than that between the otter and finally badger (as Wilks' Ω decreases with increasing separation, Table 2), thus supporting Hypothesis 2 (see above). The separation between the mink populations is greater than expected (by Hypothesis 3).

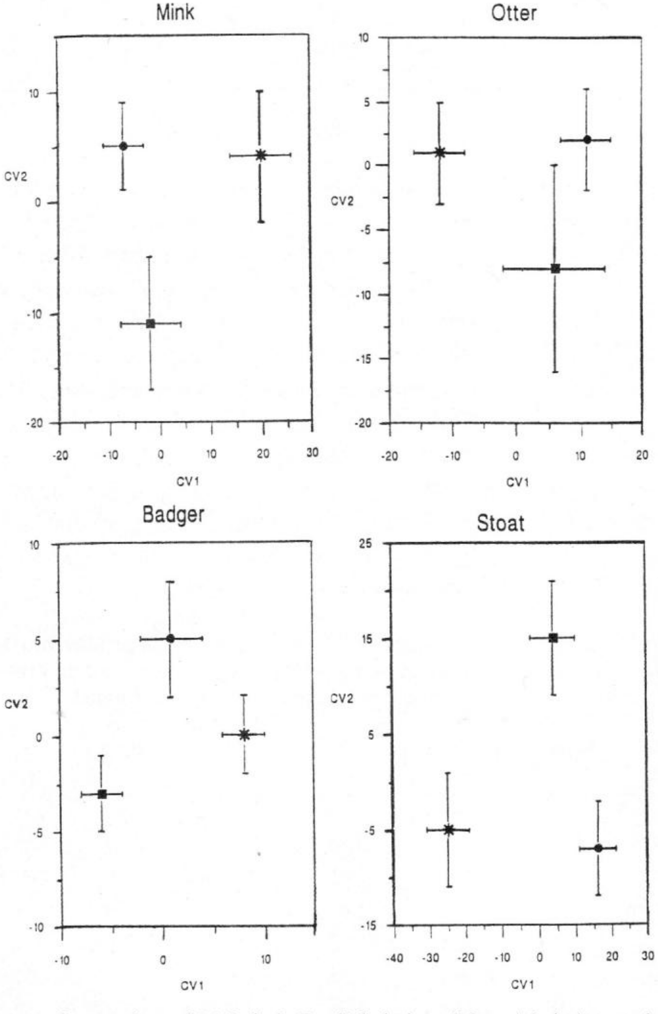

Figure 1. Separation of Irish (✱), English (■) and Scottish (●) samples of four mustelid species, on the basis of the two 'size-out' canonical variates obtained from an analysis of eleven cranial traits. Bars represent 95% confidence radii for the sample mean.

Discussion

Significant morphological differences between English, Scottish and Irish badger, otter, mink and stoat populations has been demonstrated. As was predicted above, the separation for a presumed glacial relict species (stoat) was greater than that for the other species, particularly when one considers 'shape' variation rather than size (which is particularly variable in the stoat; King, 1989). The mink populations are more distinct than predicted. The magnitude of this separation may be due to increased divergence caused by artificial selection while the mink were being ranched, or may be a product of the genetic diversity of the stock originally utilised on the ranches. The examination of the mink populations continues and in the near future this point will be addressed further. A study of the bank vole (*Clethrionomys glareolus* Schreber) would prove fruitful, given the species recent introduction to Ireland and the fact that it has not been interfered with by man.

It is of note that there is no archaeological evidence of many elements of the current fauna prior to the arrival of man. Whilst archeological data from Ireland is very scant, it is somewhat unusual that remains of large species, such as the otter, badger and fox have not been found prior to the late Mesolithic/Neolithic. The earliest reported occurrence in Ireland of the five native carnivores are as follows: fox, Neolithic; pine marten, early Christian; stoat, 33,500 years B.P. (Castlepook cave fauna); badger, Neolithic; and otter, Bronze/Iron age (Stuart *et al.*, 1985).

Given the above results, the theory of a recent origin for the otter and badger populations cannot be disproved. The timing of the putative landbridge just prior to, or during, the Nahanagan Stadial would have meant that colonists would have to contend with a mean annual air temperature in the region of -5^{O}C (Mitchell, 1986) while populations were becoming established. It is unlikely that woodland species, such as the badger or pine marten, would have survived such an adverse climate, with its unsuitable vegetation (Yalden, 1992).

As mentioned above, otters could have naturally colonized Ireland. Could man have introduced the badger (and perhaps the pine marten) to Ireland? A number of lines of evidence support this idea. Mustelids are, in general, valuable commodity species, and have in the past been transported by man from site to site. Clutton-Brock (1991) provides evidence of badgers being killed in a Neolithic site in Switzerland, whilst Griffiths (1991, 1993) details the recent use of badgers by man for food, clothing and indeed folk medicine and is of the belief that prehistoric man utilised badgers in a similar manner (H. I. Griffiths, pers. comm.). Fairley (1984) notes that the skins of foxes and martens were prized from early times. Furthermore, large-scale changes in the fauna of an island due to the arrival of man are not unknown; for example, the current mammalian fauna of Corsica is entirely of human origin, with most of the native species being exterminated shortly after the arrival of man (Vigne, 1992). Badgers are present on a number of the Mediterranean Islands, and it has been contended that the Cretean badgers are post-glacial introductions. Brown (1882) detailed a seventeenth century introduction of badgers to the Scottish island of Ailsa Craig. There is possible evidence for the introduction of live pine martens to the Orkney Isles during Neolithic times (Armour-Chelu, 1991) and Collins (1991) provides strong evidence for the introduction of the Island fox, *Urocyon littoralis* Baird, to Californian islands.

The sample sizes reported here are low. However, the collection of data is continuing on all the mustelid species and such morphologic data can usefully shed light on the past history of Irish mammals (Lynch, unpubl.). These studies hope to be extended to an examination of microgeographic variation, and thus examine the possibility of landbridge-aided colonization. However, the only means to provide a definite answer to this question is to ally morphological data with genetic analyses. An examination of genetic variation within the British Isles would allow an estimation of the time of divergence between Irish and British populations and tracing of the origin of the Irish populations. For example, a recent (in the region of 10,000 years) divergence between Irish and British stoat populations may be indicative of postglacial colonization *via* a landbridge, whereas a divergence time in the region of 40,000 years would be consistent with the refuge hypothesis presented above. Such work has the advantage that large numbers of specimens would not be required. In addition, with the advent of polymerase chain reaction techniques it is now possible to obtain short DNA segments from fossil and sub-fossil material for analysis using the highly sensitive technique of DNA fingerprinting (Hagelberg *et al.*, 1991).

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The biogeographical implications of the distribution and history of the strawberry tree, *Arbutus unedo*, in Ireland

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Summary

Arbutus unedo is essentially a Mediterranean shrub with a disjunct distribution up the Atlantic coast of Europe. In Ireland its distribution is concentrated in the southwest with an outlier population in the northwest near Sligo which represents the northern limit of this species. Its pollen is rarely preserved in lake and bog sediments due to poor dispersal. Temporal palynological data of *Arbutus* have been obtained by adopting the technique of fine spatial resolution pollen analysis. These palaeoecological data and historical sources are reviewed to elucidate the history of this species in Ireland. The impact of changing land use and climate on the distribution of *Arbutus* are considered from both historical and future perspectives.

Introduction

The distribution of *Arbutus unedo* L. in Europe illustrates that it is a Mediterranean-Atlantic species (Webb, 1983). *A. unedo* occurs widely in the Mediterranean region and has a disjunct distribution up the Atlantic coasts of France and Ireland reaching its most northern station at Lough Gill, Co. Sligo (Figure 1). In southern Europe *A. unedo* grows as a shrub and is most characteristic of the Maquis community which is maintained by regular burning (Sealy and Webb, 1950).

The distribution of *A. unedo* in Ireland may be divided into three distinct populations. The most significant population is at Killarney, Co. Kerry with a southern population at Glengarriff Co. Cork and the most northerly at Lough Gill Co. Sligo. To these may be added some smaller isolated populations in southwest Kerry and west Cork (Figure 1). In

Ireland individuals of *A. unedo* gain greater stature than in mainland Europe and the species grows as a tree of woodland edges and on open rocky ground (Sealy, 1949). This habitat preference illustrates its intolerance of shade and although trees are occasionally found within canopy oak wood in Killarney, they lack vigour and probably serve as indicators of formerly more open woodland (Mitchell, 1988). Its preference for woodland edge communities makes *A. unedo* a conspicuous feature of small wooded lake islands in Killarney and the Cloonee Lakes, Co. Kerry.

The distribution pattern of *A. unedo* in Ireland raises two fundamental questions related to its biogeography. Did this distribution pattern arise from spot introductions or does it represent the fragments of a formerly more widespread distribution? This paper will address these questions and assess the role of *A. unedo* in the past, present and future vegetation of Ireland.

The factors that restrict *A. unedo* in Ireland today must be considered as a prerequisite to addressing the questions above. Sealy and Webb (1950) have considered these factors in detail and so they will only be dealt with briefly here. *A. unedo* is particularly intolerant of shade and this high light requirement restricts the species to open habitats. The tree appears to thrive on a variety of substrata and moisture regimes but is particularly sensitive to frost (Sealy, 1949). This restricts its natural distribution to areas of Europe where mean January air temperatures are greater than 5°C (Figure 2).

Historical evidence

It is necessary to investigate the history of *A. unedo* in Ireland to answer the questions posed in the introduction. Historical records can provide valuable data but rarely date to earlier then the sixteenth century and tend to be of a qualitative rather than a quantitative nature. The earliest reference to *Arbutus* appears to be in *Bretha Comaithchesa* which is an old Irish legal document dating to the 8th century (Kelly, 1976). The export of *Arbutus* from Killarney to England is catalogued from 1568 (Scully, 1916). Evidence of a former, wider distribution comes from records of *Arbutus* growing on the islands at the head of the Kenmare estuary where it no longer grows today (Smith, 1756). There is further evidence from place names. Such data must be cautiously interpreted in view of potential ambiguities, corruptions and anglicisations of original Irish names. One potential site is Ardnacaithne (Smerwick) on the north Dingle coast which

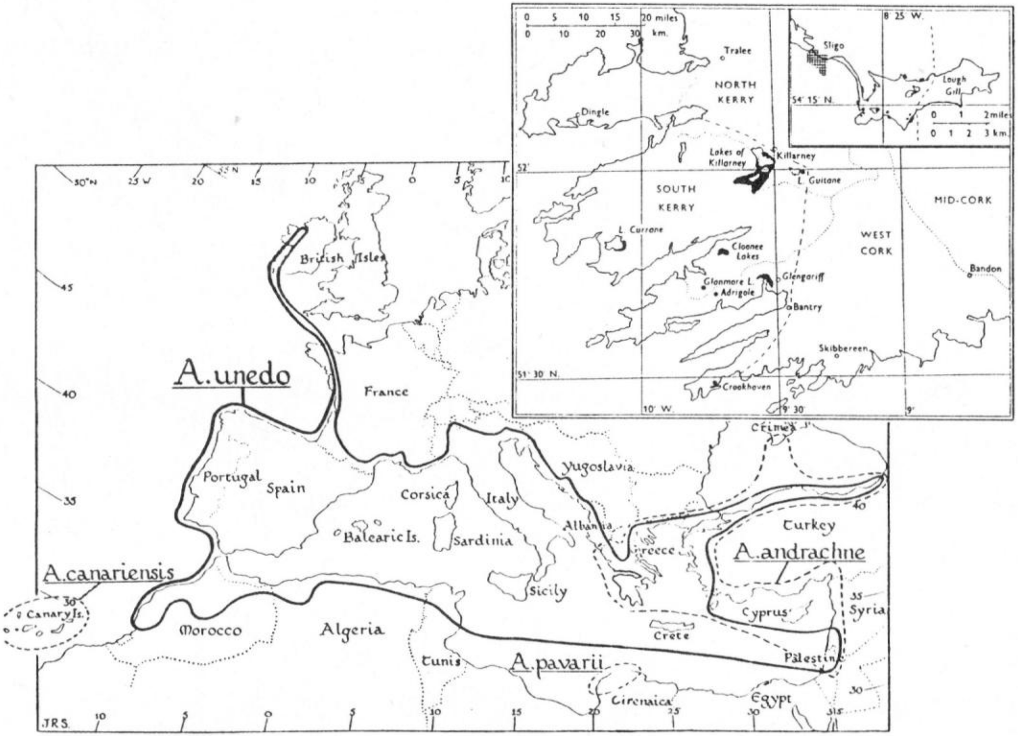

Figure 1. Distribution of *Arbutus* in Europe from Sealy (1949) and the distribution of *Arbutus unedo* in Ireland from Sealy and Webb (1950) (inset).

may be translated as "the height of the *Arbutus*" (Joyce, 1893). Ardnacaithne lies to the north of the present range of *A. unedo* in the southwest. No mention of *Arbutus* in Co. Sligo has been found in historical records before 1866.

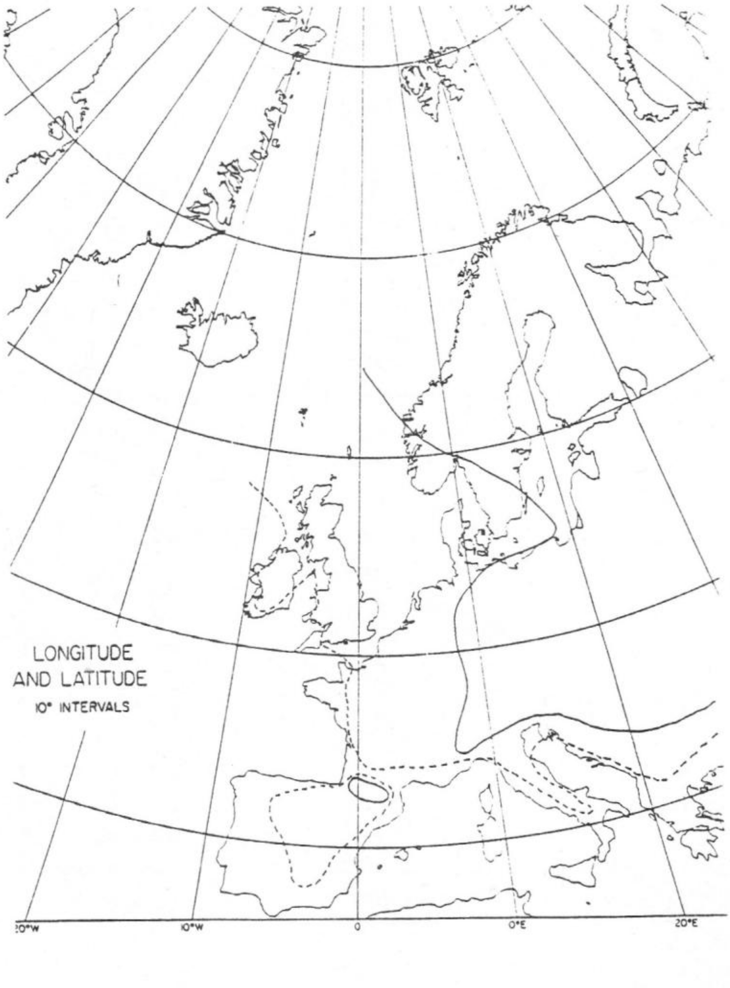

Figure 2. Mean January air temperature (5°C isotherm) for Europe today (broken line) and following a doubling of CO_2 (solid line).

Pollen evidence

A more objective assessment is gained through pollen analysis although *Arbutus* poses a few problems in this respect. *A. unedo* is entomophilous and so is not an abundant pollen producer nor is this pollen well dispersed. This feature is manifested by its rare occurrence in pollen diagrams. In addition, *A. unedo* pollen is not very distinct morphologically from some other Ericaceae under the light microscope and so definite identification is not always possible. Despite these difficulties there are fossil pollen records from both Killarney and Sligo that confirm the native status of the species at both locations. The oldest record is from Muckross in Killarney at 4000 years B.P. and the earliest record from Sligo is from Slish Wood at 1900 years B.P. (Dodson and Bradshaw, 1987). Although the Sligo date is more recent, it is still well before the establishment of monasteries in Ireland which were responsible for many early plant introductions into the country (Mitchell, 1986).

These data have established that *A. unedo* is native to Ireland. The pattern of its distribution therefore is unlikely to be due to isolated plantings. It is now necessary to assess the dynamics of *Arbutus* in the past in order to address the second question which was posed in the introduction.

It is possible to obtain temporal palynological data for *A. unedo* by applying standard palaeoecological techniques at a small spatial scale (Mitchell, 1988). Data from a number of Irish sites where this technique has been applied are summarized in Table 1. These data indicate that *Arbutus* was more abundant in the past at all seven sites than it is today. It may be concluded from this summary that *A. unedo* has gained its greatest abundance as a constituent of early secondary succession of western oak woods. It is therefore closely associated with woodland disturbance and often with burning. This interpretation of the pollen data is also supported by references to woodland disturbance and abundant *Arbutus* in the historical literature.

The question of whether *Arbutus* was more widespread in the past may be addressed by considering a link site between the two main centres of its distribution in southwest Ireland. Lough Inchiquin lies about equidistant between Glengarriff and Killarney. The lake is flanked by the impressive Uragh Wood which contains no *Arbutus* today but the vegetation of a small island (14 x 25 m) on the lake is currently dominated by *A. unedo*. Scully (1916) reports that *A. unedo* was growing on this island in 1866 and 1908. Several islands on the adjacent Cloonee lakes also support *Arbutus* but most of these have become infested with *Rhododendron ponticum*.

Table 1. Details of maximum values for *Arbutus unedo* in pollen diagrams

Site	Date (AD)	Vegetation dynamics	Charcoal	Source
Slish Mor	100	*Calluna* and *Quercus* rise	High	Dodson and Bradshaw (1987)
Slish Lake	190	*Calluna* rise, wood taxa fall	Low	Dodson and Bradshaw (1987)
Muckross	1750	Reduced wood cover	----	Vokes (1966)
Camillan	1750	Heathland and *Ilex* rise	High	Mitchell (1990)
Derrycunihy	1770	Open *Quercus* wood	High	Mitchell (1988)
Rough Island	1790	Grassland	High	Mitchell (1990)
Lough Inchiquin	1800	*Calluna* rise, *Quercus* fall	Low	This Paper

Pollen was prepared from a mor humus soil profile from the island on Lough Inchiquin and a summary diagram is presented in Figure 3 (for theory and methods see Bradshaw, 1988 and Mitchell, 1990). Both the extinction and reintroduction of *Pinus* are recorded in the diagram. Relative dates of 3090 years B.P. and 265 years B.P. respectively for these events may be applied by comparison with a radiocarbon dated pollen diagram from a site 15 km southwest of Lough Inchiquin (Lynch, 1981). It should be noted that although the percentage values of *Arbutus* pollen are generally low, this reflects the species' low pollen production and dispersal rather than its rarity in the past vegetation (Mitchell, 1988). Evidence for disturbance to the vegetation of this small island is clear at the base of the diagram and *Arbutus* responded accordingly. The maintenance of its

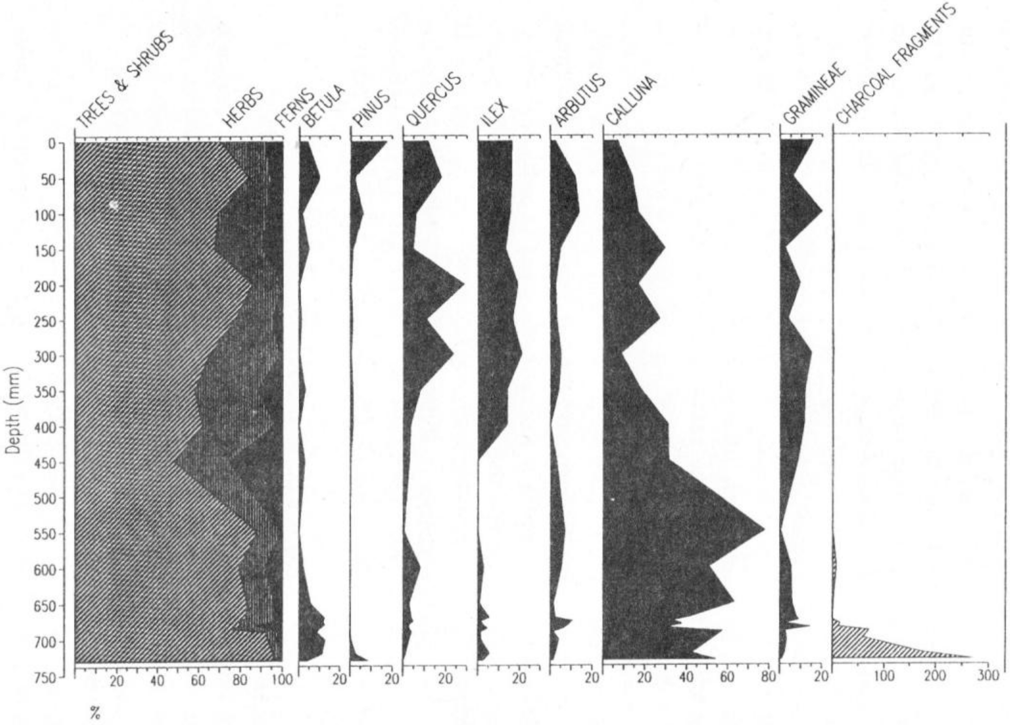

Figure 3. Percentage pollen diagram of selected taxa from the island on Lough Inchiquin, Co. Kerry.

importance throughout the subsequent period must be attributed to the ideal open habitat offered by the rocky edge of a small lake island. *A. unedo* must therefore be indigenous to this site and it has maintained its importance here throughout this 3000 year record.

A further exploration of this approach is to investigate likely sites where *A. unedo* is not found today. Hannon and Bradshaw (1989) have produced mor humus pollen diagrams from two small wooded lake islands in Connemara. These sites are about 120 km southwest of the Co. Sligo *A. unedo* population and about 160 km north of Killarney. The habitat is similar to that where *Arbutus* flourishes today in the southwest and the islands are west of the January 5^{o}C isotherm (Figure 2). Their pollen data provide a record of vegetation dynamics on the islands for the last one thousand years. The development of the present woodland vegetation on the islands was preceded by a period of disturbance with burning but at no point in the record was *A. unedo* pollen found. So although the successional pathway of the vegetation on the Connemara islands was almost the same as the Lough Inchiquin island, it did not include *A. unedo*. Before dismissing the possibility of *A. unedo* ever having grown between Killarney and Sligo it should be noted that these two small lake islands represent a drop in the ocean in terms of potential *A. unedo* sites between these two locations. The poor pollen representation of the taxon is an additional factor which is illustrated by its absence from some diagrams in Killarney (Mitchell, 1987). There are no data to support the past occurrence of *A. unedo* populations between Killarney and Sligo but there are also insufficient data to discount this possibility.

The future

It has been clearly demonstrated that, in the long term, climate is the determining factor in tree distribution in Europe (Huntley and Prentice, 1988; Huntley and Webb, 1989). The significant climatic factor restricting the distribution of *A. unedo* is mean January air temperatures of below 5^{o}C. The impact of shade from canopy trees or high levels of grazing such as those in the Killarney woods today may be considered as short-term phenomena when compared to climate. Future global climatic scenarios have been predicted from GCMs (General Circulation Models) and Warrick *et al.* (1990) have calculated predictions of European climate following a doubling of CO_2 based on output from four prevalent GCMs.

These data predict a significant spatial shift in the mean January 5°C isotherm in a north eastward direction across Europe (Figure 2). This then represents the potential future distribution of *A. unedo*. The interpretation of pollen data suggests that *Arbutus* plays a role as an early species in secondary successions to woodland (Table 1). The fragmented nature of European woodland provides ideal habitat as edge communities and therefore *A. unedo* is poised to expand its range. The fragmented distribution of the species in Ireland may hinder its spread due to the scarcity of seed source. However the fruits are eaten by a range of birds (Sealy and Webb, 1950) and so seed may be spread over considerable distances. It is also impossible to accurately predict how other plant and animal species will respond to rapid climatic change. Their interaction and future land use changes may hinder the migration of *A. unedo*.

Conclusions

Analysis of pollen data indicates that *A. unedo* is indigenous to Ireland. In the southwest, *A. unedo* has been present for over 3000 years in both the main centre of its distribution and in outlier populations. The pollen data also illustrate that *A. unedo* was more abundant in the past and historical data suggest that it was more widespread. From these results it may be concluded that the present populations of *A. unedo* represent the fragments of a former, more widespread distribution. There are no pollen data to suggest that *Arbutus* grew north of Killarney thus providing a link with Sligo and the populations in the southwest. Seed dispersal by bird directly to Sligo cannot be discounted either.

Predicted climatic changes in Europe indicate that *A. unedo* will be able to expand its range both northward and eastwards. Such a range change will only be possible if seed can be effectively dispersed and recruitment of young trees is not hindered by biotic factors such as grazing.

Acknowledgements

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Ecological factors controlling the distribution of *Saxifraga spathularis* and *S. hirsuta* in Ireland

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Summary

The distribution of *Saxifraga spathularis* Brot. and *S. hirsuta* L. in Ireland is partly obscured by their frequent hybridization, which results in fertile progeny capable of segregation and backcrossing to parental species. Seed of both species germinated readily when exposed to diurnal temperature fluctuations; this is likely to ensure that seed only germinates when close to the surface of a substratum. Seedling recruitment in the field was favoured by the presence of moss, but many seedlings were subsequently overgrown by other bryophytes. *S. hirsuta* occurred only in damp shaded habitats, such as steep north facing cliffs or in woodland shade. *S. spathularis* exploited a wider range of habitats, and even occurred in relatively unshaded south facing slopes. This may reflect differences in both shade and desiccation tolerance between the two species. Competition from other vascular plants and bryophytes, and the ability of *S. spathularis* to exploit similar habitats, may explain the restricted distribution of *S. hirsuta* in Ireland, while the greater geographic range of *S. spathularis* may be explained by its broader ecological tolerances.

Introduction

Many native Irish plant species have interesting geographical distributions (see Webb, 1983), including the so-called 'Lusitanian' species that occur in the west of Ireland and in the western part of the Iberian peninsula, but are absent from Britain and most of France. *Saxifraga spathularis* Brot. and *S. hirsuta* L. are two closely related species with this type of distribution (Figure 1). *Saxifraga hirsuta* is the rarer of the two species in Ireland, and is restricted to counties Cork and Kerry. It always occurs close to the more widespread *S. spathularis*, which is widely scattered over western

Ireland, with outliers in counties Waterford and Wicklow. Elsewhere in Europe the two species are only sympatric in the Cantabrian mountains of north west Spain; the range of *S. hirsuta* extends east to the Pyrenees, while *S. spathularis* occurs further south and west into Portugal (Webb and Gornall, 1989).

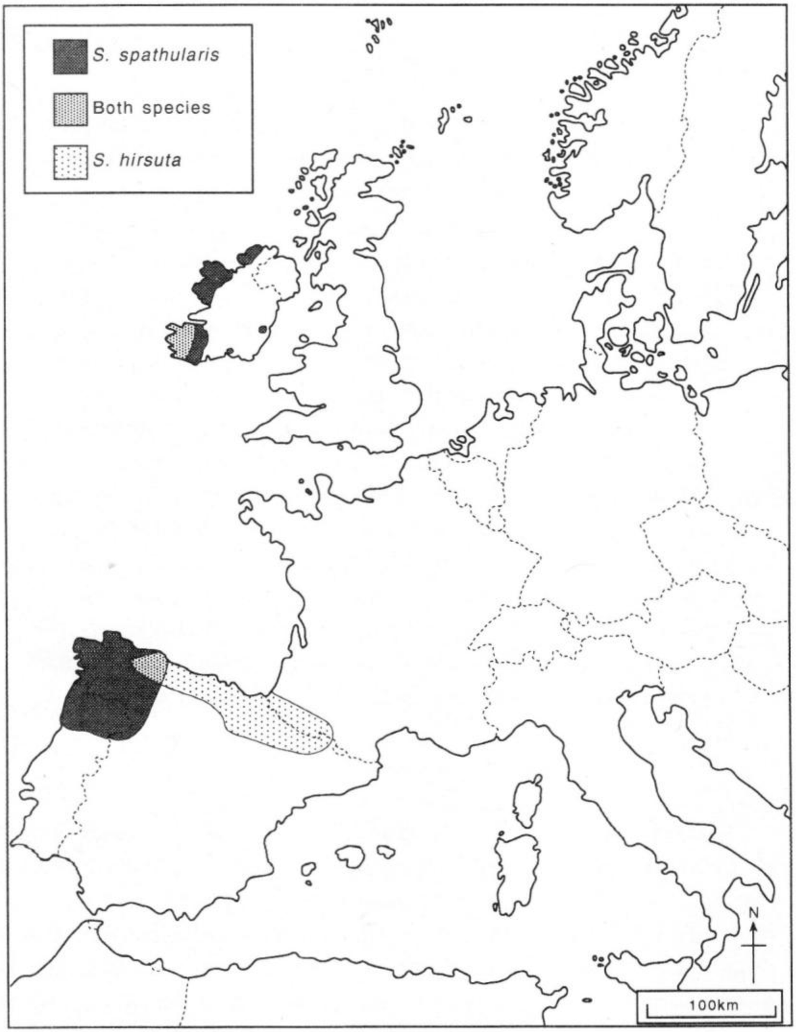

Figure 1. The distributions of *Saxifraga spathularis* and *S. hirsuta*.

The taxonomy of these two species was previously very confused (Webb, 1950). The species are best distinguished by leaf characters; *S. hirsuta* has rounded, hairy leaves with a crenate margin and thin hairy petioles, while *S. spathularis* has hairless, more serrate leaves with a cuneate base and broad flattened petioles. The two species are highly interfertile, and hybrids between them are frequent in Ireland. These hybrids are also fertile, and show a wide range of morphological variation (Scally, Parnell and Waldren, unpublished data). Indeed, if the two species did not occur outside Ireland, they would probably be considered as subspecies or varieties because the morphological variation in the hybrids completely spans the phenotypic differences between the parent species.

Hybrids occur outside the Irish range of *S. hirsuta*, as in Co. Galway and on Clare Island, Co. Mayo. It has been suggested that *S. hirsuta* formerly had a much wider geographic range than at present (Webb, 1950), but as there is no direct evidence for this, it is also possible that hybrids have spread beyond the initial sites of hybridization independently of the parent species. In Ireland, hybridization between the species has therefore not only led to taxonomic problems, but obscures the distribution of the parent species.

Ecological requirements are clearly of great importance in determining species distribution. Genetic isolation caused by differences in ecological tolerances may prevent certain interfertile species from coming into contact (Stace, 1975). The availability of intermediate habitats may determine the success and the pattern of morphological variation present if two species with differing ecological requirements should hybridise (Anderson, 1948). To date there have been few quantitative measurements of ecological tolerances or requirements of *S. spathularis* and *S. hirsuta*, although Rutledge (1983) reported differences between the two species in waterlogging and drought tolerance. Here we report some of our observations on seed germination, seedling establishment and response to shading; factors which are likely to be of great importance in determining the distribution of these species.

Methods

Seed was collected from the Blackstone Bridge, Kylemore and Valencia populations (for details of these and other populations, see Table 1) and germinated on moist filter paper in controlled temperature chambers, with a 14 hour daylength under constant (20°C) or fluctuating day (20°C) and night (15°C) temperature regimes. Seed germination and seedling establishment in the field were observed in the Kylemore Lough population between September 1989 and July 1990 using two permanent 50 x 50 cm quadrats. These were each subdivided into twenty-five 10 x 10 cm squares, and the number of seedlings and percentage cover of moss and liverworts periodically recorded. Seed production was estimated in this population by calculating the mean number of seeds produced per capsule and the mean number of capsules per panicle.

Table 1. Details of *Saxifraga* populations investigated. Vice counties (Co.) include South Kerry (SK), West Cork (WC), Wicklow (W), Waterford (WF).
* *Saxifraga* classes: S = *S. spathularis*; H = *S. hirsuta*; X = hybrid.

Location	Co.	Grid Ref.	Alt. (m)	*Saxifraga* present	Habitat
Connar Pass	SK	Q503053	300	S, H	Exposed cliff face
Foilclogh	SK	V504747	400	S, H, X	Rock outcrops
Valencia	SK	V405767	100	H	Woodland roadside
Derrycunihy	SK	V910813	45	S	Boulders in oak woodland
Blackstone Bridge	SK	V700861	22	S	Boulders in oak woodland
Torc Mountain	SK	V961837	320	H, X	Shaded rocks in open woodland
Muckross Lake	SK	V958847	30	H	Shaded rocks in open woodland
Derryvegall	WC	V668560	60	S, H, X	Oak woodland, retaining wall
Pass of Keimaniegh	WC	W104634	270	S, X	Exposed and shaded rocks
Glengarrif Woods	WC	V910564	30	H	Streamside in oak woodland
Lugnaquillia	W	T053931	450	S	Shaded rock gully
Coumshingaun	WF	S338111	350	S	Large boulders in stream

Photosynthetically active radiation (PAR; radiation between the wavelengths of 400 and 700 nm) was recorded for 12 Irish populations (Table 1) with a Li-Cor quantum sensor, and the ratio of red to far-red radiation (R:FR; 660 nm : 730 nm) with a Skye Instruments Red/Far-red meter. These measurements were made at 20 cm above the centre of at least ten individuals in each population. PAR was expressed as a percentage of the radiation measured simultaneously at an unshaded site adjacent to each population, as described elsewhere (Waldren *et al.*, 1989). R:FR suggests the amount of shading by plant canopies; chlorophyll absorbs red (660 nm) but not far-red (730 nm) radiation, therefore light reflected from or transmitted through a leaf canopy will be relatively enriched in far-red compared to red radiation

(Whitelam, 1988). R:FR values greater than unity suggests very little canopy shading, while dense leaf canopies may reduce R:FR to 0.3 or less. The aspect and slope of the sites in which individual plants were growing were also recorded.

Results and Discussion

Seed germination and seedling establishment

Some populations showed little or no germination in uniform temperature conditions, yet germination in the same populations was over 85% when subjected to day/night temperature fluctuations (Figure 2). This is likely to be a mechanism that ensures that only seed close to the substratum surface germinates and buried seed remains dormant, as diurnal temperature fluctuations decrease with depth through a soil profile (Fenner, 1985). Under optimal conditions of fluctuating temperature, 85 - 95 % of freshly collected seeds of both species germinated.

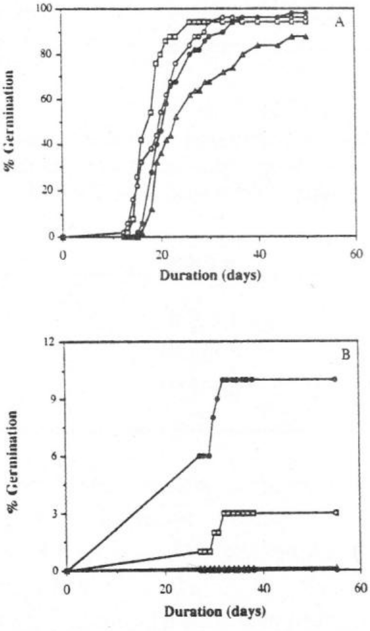

Figure 2. Seed germination of populations of *Saxifraga spathularis* and *S. hirsuta* in a growth cabinet with fluctuating day/night temperatures (**A**), and a similar cabinet with uniform temperatures (**B**). *S. spathularis* populations: Blackstone Bridge (squares, G), Valencia (hollow circles, E), Kylemore Lough (triangles, C); *S. hirsuta*: Valencia (solid circles, J).

Seed was copiously produced in the field. An estimated 4500 seeds were produced per flowering panicle in the Kylemore Lough *S. spathularis* population. Seed ripens in late July and early August, and is shaken from the dried capsules by wind action. Qualitative examination of other populations suggests that these observations are probably typical, but *S. hirsuta*, with generally smaller capsules, may produce a smaller quantity of seed compared to *S. spathularis*.

At Kylemore Lough, *S. spathularis* seeds germinated as soon as they were shed in late July, as predicted from the laboratory investigations. Large numbers of seedlings were recorded in late summer and early autumn in the permanent quadrats. The greatest numbers of seedlings were recorded in September 1989, when seedling number was highly correlated with the presence of moss (mainly *Campylopus atrovirens* De Not.; Table 2). The highest recorded density at this time was 195 seedlings in a 100 cm^2 subdivision. Seed gets trapped in the moss cushions, which provide a moist niche suitable for germination. The number of seedlings declines exponentially for the rest of the year (Figure 3), and although some seed continues to germinate through the winter, this is minimal compared to germination immediately after seed has been shed.

Table 2. Spearman's rank correlation coefficients for number of *Saxifraga spathularis* seedlings and the percentage cover of moss and liverworts at two sites near Kylemore Lough, Co. Galway. *** = $P < 0.001$ ns = $P > 0.10$

Seedling location	% Moss	% Liverwort
both sites	0.815 ***	-0.140 ns
site A	0.769 ***	0.660 ***
site B	0.697 ***	0.174 ns

The decline in seedling numbers was partly determined by amount of liverwort present. The dominant species, *Scapania* cf. *nemorea* (L.) Grolle, probably accounted for over 90% of the liverwort biomass. Liverwort cover increased markedly during winter with the actively growing *Scapania* wefts covering the *Saxifraga* seedlings. This was particularly apparent in site A for which liverwort cover (along with duration) was a significant predictor of the log of seedling numbers present (Table 3). Very few seedlings survive the first year. Those that do so grow very slowly, probably due to lack of nutrients in such a skeletal habitat. Therefore although seed germination benefited from the presence of moss, and to a lesser extent liverworts, subsequent seedling growth did not.

Table 3. Regression statistics for the effect of time *(T)* and % liverwort cover *(L)* on the natural logarithm of numbers of *Saxifraga spathularis* seedlings at Kylemore Lough, Co. Galway. Percent moss cover could not be significantly incorporated into either equation.

Site	Equation	Significance of regression	% Variance explained
A	$\mathrm{Ln(seedling)} = -0.0125T - 0.0058L + 7.546$	$P < 0.001$	99.94
B	$\mathrm{Ln(seedling)} = -0.0183T + 7.878$	$P < 0.001$	96.11

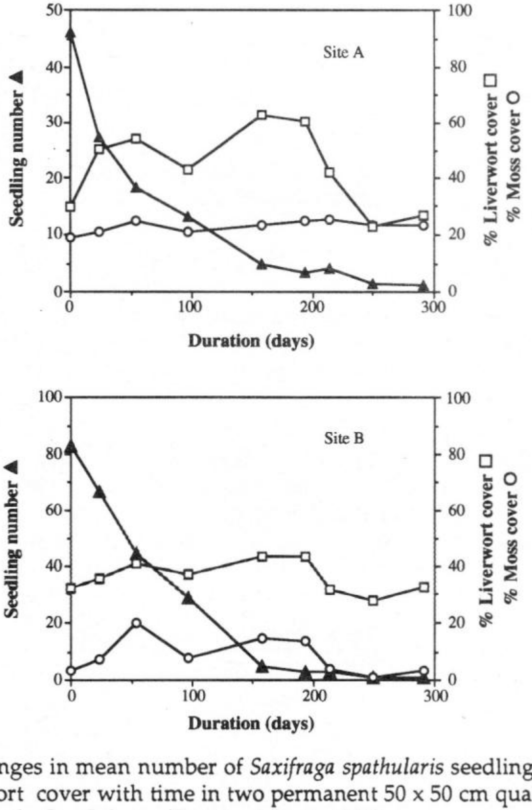

Figure 3. Changes in mean number of *Saxifraga spathularis* seedlings, % moss and % liverwort cover with time in two permanent 50 x 50 cm quadrats near Kylemore Lough, Co. Galway (Day 0 = 5 Sept., 1989).

Distribution and response to shading

Saxifraga hirsuta was more frequent than *S. spathularis* in low R:FR (Figure 4, Table 4). As might be expected, all sites with a low R:FR also had a low %PAR, because of shading by leaf canopies. *S. spathularis* sometimes occurred in woodland shade with low R:FR, notably at Blackstone Bridge and Derrycunihy. In both of these populations plants were growing on moss-covered boulders in woodland, quite different from the woodland habitats of *S. hirsuta* which were usually along streams or water seepages.

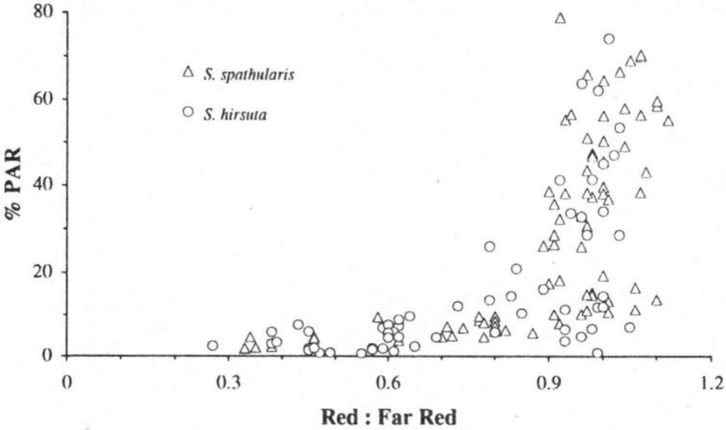

Figure 4. The ratio of red : far-red radiation and percent photosynthetically active radiation (%PAR) measured at 20 cm above the centre of *Saxifraga spathularis* and *S. hirsuta* individuals from various populations.

Table 4. Mean values of percent photosynthetically active radiation (%PAR) and red:far-red radiation (R/FR) measured over individuals of *Saxifraga spathularis* and *S. hirsuta* in various Irish populations. *P* is the probability level associated with the variance ratio calculated from these data, *n* the number of observations.

	S. spathularis	*S. hirsuta*	P
% PAR	27.6	15.3	< 0.001
R/FR	0.88	0.74	< 0.001
n	81	59	

Saxifraga hirsuta also occurred in high R:FR habitats, but was much less frequent than *S. spathularis* in unshaded sites with high %PAR and high R:FR (Figure 4, Table 4). Sites with low %PAR but with high R:FR are not shaded by leaf canopies but by the physical obstruction of rocks and cliff faces in the typically rocky habitats favoured by these species. These data suggest that *S. hirsuta* had a much stronger requirement for shading than *S. spathularis*, although it was of little importance whether this shading was biological (by leaf canopies) or physical (by rocks and overhangs).

Slope and aspect data also support the suggestions that *S. hirsuta* avoided unshaded sites (Figure 5). *S. hirsuta* rarely occurred on steep south facing slopes, and only did so under leaf canopies where the R:FR was lower than 0.7 (Figure 5a). However, *S. hirsuta* often occurred on very steep north-facing slopes, often in the absence of a leaf canopy (R:FR greater than 0.7); such sites would be shaded by the physical obstruction of the steeply sloping site. Steep north-facing slopes will rarely be exposed to direct sunlight, while steep south-facing slopes intercept the maximum amount of solar radiation (Pope and Lloyd, 1978).

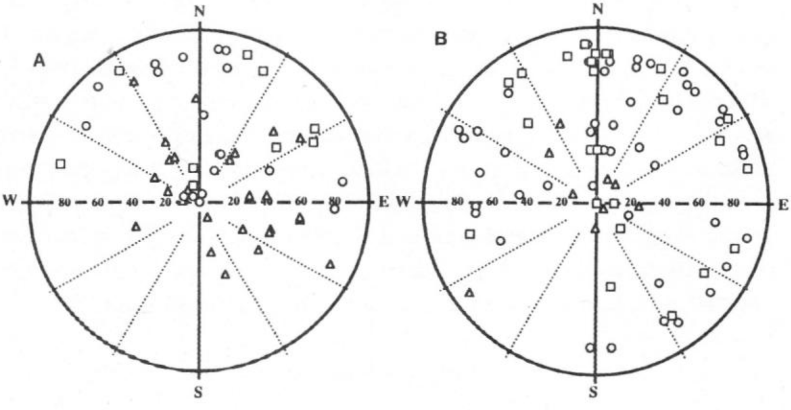

Figure 5. Slope (radius) and aspect (angle) for *Saxifraga hirsuta* (A) and *S. spathularis* (B) individuals growing in sites with < 0.7 (triangles, C), 0.7-1.0 (circles, E), and >1.0 (squares, G) red : far-red radiation.

Although *S. spathularis* was more frequent on north-facing slopes, it was also found on very steep south-facing slopes, some of which had a high R:FR and were not shaded by leaf canopies, and were therefore exposed to full sunlight (Figure 5b). This apparently wider ecological tolerance of *S. spathularis* may in part help to explain its wider geographical range within Ireland than *S. hirsuta*.

Both species produce large amounts of seed that has a high potential for germination. Given that individuals can spread vegetatively to cover a sizeable area, each individual may produce many flowering stems and therefore very large amounts of seed. Although primary seed dispersal is over short distances by the dried seeds being shaken from the the dehiscent capsules, secondary transport, for example by water flow, may move seeds to some distance from the parent plant. Many of the resulting seedlings are likely to be out-competed by other plants, but some are likely to survive in favourable niches. There seems to be no reason why both hybrid and parent seed should not be spread in this way, and so hybrid populations might occasionally arise independently of either parent.

Conclusions

In the Iberian Peninsula, different geographical distributions of *S. spathularis* and *S. hirsuta* keep them separated over much of their range, but in Ireland *S. hirsuta* is never found without hybrids and is rarely far from *S. spathularis*. Although the two species have slightly different environmental requirements, there is considerable overlap, and these differences are not marked enough to limit gene flow between the species. *S. spathularis* appears to have a wider ecological tolerance than *S. hirsuta*, which may account for its greater range and abundance in Ireland. *S. hirsuta* avoids unshaded sites more frequently than *S. spathularis*. This may be related to the greater drought tolerance of *S. spathularis* demonstrated experimentally by Rutledge (1983).

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Mayflies (Ephemeroptera) of the Corrib catchment, Ireland

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Summary

The general results of a survey of the distribution and abundance of ephemeropteran nymphs at 60 locations in the Corrib catchment area, western Ireland, are presented. A total of 25 species was recorded: *Siphlonurus lacustris* (Eaton), *Siphlonurus alternatus* (Say), *Baetis rhodani* (Pictet), *Baetis muticus* (L.), *Baetis vernus* (Curtis), *Baetis scambus* Eaton, *Baetis atribatinus* Eaton, *Centroptilum luteolum* (Müller), *Cloeon dipterum* (L.), *Cloeon simile* (Eaton), *Rhithrogena semicolorata* (Curtis), *Heptagenia lateralis* (Curtis), *Heptagenia sulphurea* (Müller), *Heptagenia fuscogrisea* (Retzius), *Ecdyonurus venosus* (Fabricius), *Ecdyonurus dispar* (Curtis), *Ecdyonurus insignis* (Eaton), *Leptophlebia vespertina* (L.), *Paraleptophlebia cincta* (Retzius), *Ephemerella ignita* (Poda), *Ephemera danica* Müller, *Caenis luctuosa* (Burmeister), *Caenis horaria* (L.), *Caenis rivulorum* (Eaton), *Caenis macrura* Stephens. Differences between the species assemblages occurring in lotic and lentic habitats, and sites in the oligotrophic western uplands and the eastern lowland limestone of the catchment are discussed. The general European distribution of the ephemeropteran species recorded in the Corrib catchment and geographic variations in life cycles is also discussed.

Introduction

The mayflies (Order: Ephemeroptera) are an ancient, and in many respects unusual, group of aquatic insects, which comprise over 2000 species world wide. Because of their limited flying power, mountain ranges and other physical barriers seem to effectively delineate distinct ephemeropteran assemblages throughout the world (Edmunds, 1972; Brittain, 1982). However, Ephemeroptera have been known to disperse passively by air currents (Johnson, 1969). There is little evidence to suggest that man plays a significant role in their dispersal. In fact, human influence on patterns of mayfly distribution seems to be largely of a negative nature. Biotic indices of organic pollution in rivers generally incorporate data on ephemeropteran abundances, as they are regarded as sensitive indicator species.

In their review of Irish Ephemeroptera, King and Halbert (1910) commented on the fact that the group was generally neglected at that time. The advent of reliable keys to the adults and nymphs (Macan, 1979; Elliott and Humpesch, 1983; Elliott *et al.*, 1988), and the numerous ecological studies of the order in Britain and continental Europe, have greately increased the scope for recording the distribution and ecology of Ireland's Ephemeroptera. In the present paper an account is given of the distribution, relative abundances and life cycles of Ephemeroptera in the Corrib catchment area, a major western Irish river basin, which includes a wide variety of aquatic habitat types. The relationships of this local ephemeropteran fauna to that of Ireland in general and to that of neighbouring Britain and continental Europe is discussed. In a future paper it is proposed to analyse further the habitat utilization by ephemeropteran nymphs in the Corrib system.

Study area

The Corrib catchment area has a surface area of a little over 3100 km^2, covering part of counties Mayo and Galway. Its three major lakes are Loughs Carra, Mask and Corrib, the latter of which is the second largest lake in Ireland. The drainage of the catchment runs southwards into Galway Bay (Figure 1). The three main lakes divide the system into two parts. The eastern limestone plain is drained by long meandering rivers with alkaline, nutrient rich water. In some places the limestone is karstic and underground drainage channels can connect surface waters via complex subterranean networks. The western upland area has a mixed geology and is drained by shorter spate rivers, which are generally acidic and nutrient poor (Figure 2).The course of some rivers runs from one geological substratum over another, resulting in intermediate water chemical and hydrological characteristics. The eastern lowland plain rises

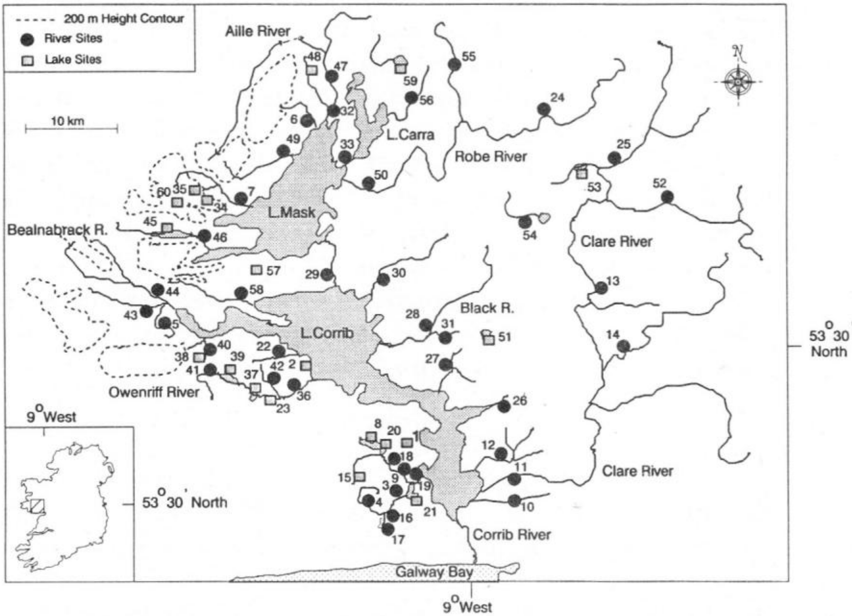

Figure 1. A map of the Corrib catchment area, with Ireland inset, indicating the locations of 60 sites at which Ephemeroptera were sampled.

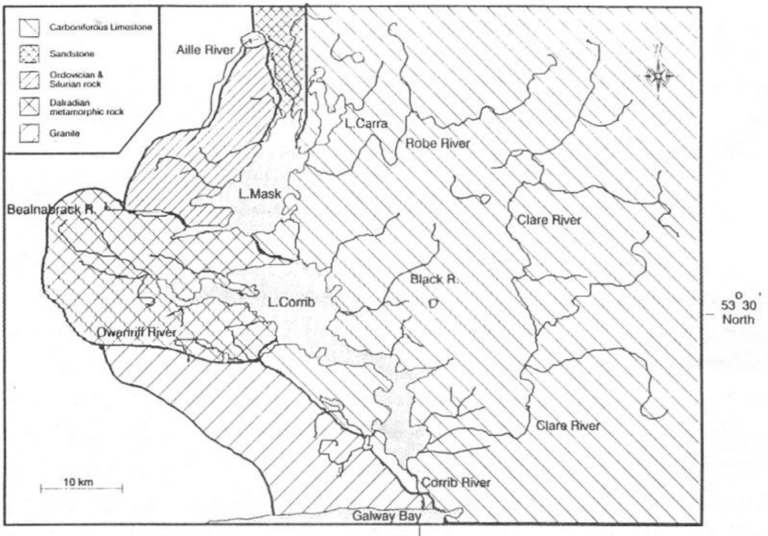

Figure 2. The geology of the Corrib catchment area.

gently to 122 m above sea level along its eastern boundary, while the western uplands rise to 670 m a.s.l.. The catchment has a temperate maritime climate and is under the moderating influence of the North Atlantic drift. Inland meteorological records show maximum air temperatures of above 20°C for 6.6% of days and minimum temperatures of below 0°C for 10% of days. Rainfall ranges from just over 1000 mm to just over 2500 mm per year in the catchment. The Corrib catchment area is predominantly an agricultural region with some industry near the larger centres of population (Galway city is the largest with around 40,000 inhabitants). Instances of pollution of freshwater habitats occur periodically, however, pollution and eutrophication have not as yet had a significant influence on the ecology of this catchment.

Methods

Ephemeropteran nymphs were collected from 20 lentic and 40 lotic locations in the catchment (Figure 1, Appendix 1). Two sets of samples were taken at nine locations, representing adjacent but contrasting habitats, thus giving a total of 69 sets of collections. Each of these were visited on four occasions, once per season. Five 2 m sweeps were taken through the habitat present at each site (silt/bottom debri, gravel/stones and aquatic vegetation) with a 25 cm square standard F.B.A. pondnet with a bag-depth of 30 cm and a mesh-size of 1.25 mm^2. The nymphs were sorted live in the field and preserved in alcohol for subsequent laboratory analysis. The species identifications were confirmed by Dr. J. P. O'Connor of the National Museum, Dublin and a representative set of material has been lodged in the museum collection.

Results

A total of 31,874 mayfly nymphs of 25 species were sampled during the present survey (Table 1). A small residual number of nymphs (0.2% of total), including damaged and very small specimens, could not be definitely identified, though some exhibited characteristics of two additional species namely *Leptophlebia marginata* (L.) and *Ecdyonurus torrentis* Kimmins. Because of the taxonomic uncertainties and small numbers involved, these were excluded from further statistical analysis. Frequencies of occurrence and overall abundance for the 25 ephemeropteran species recorded are given in Table 1. Details of the geographical distribution of each species within the Corrib catchment are given in Appendix 1.

Table 1. A checklist of Ephemeroptera species recorded in the Corrib catchment area, together with data on their frequencies of occurrence and overall abundances.

Species	Number of sites	Number of nymphs
Siphlonuridae		
(1) *Siphlonurus lacustris* Eaton	5	279
(2) *Siphlonurus alternatus* (Say)	2	11
Baetidae		
(3) *Baetis rhodani* (Pictet)	42	9438
(4) *Baetis muticus* (L.)	25	2251
(5) *Baetis vernus* Curtis	2	26
(6) *Baetis scambus* Eaton	17	1079
(7) *Baetis atrebatinus* Eaton	17	1021
(8) *Centroptilum luteolum* (Müller)	48	2899
(9) *Cloeon dipterum* (L.)	17	178
(10) *Cloeon simile* Eaton	42	1187
Heptageniidae		
(11) *Rhithrogena semicolorata* (Curtis)	10	277
(12) *Heptagenia lateralis* (Curtis)	7	121
(13) *Heptagenia sulphurea* (Müller)	13	534
(14) *Heptagenia fuscogrisea* (Retzius)	38	4844
(15) *Ecdyonurus venosus* (Fabricius)	13	199
(16) *Ecdyonurus dispar* (Curtis)	11	299
(17) *Ecdyonurus insignis* (Eaton)	3	3
Leptophlebiidae		
(18) *Leptophlebia vespertina* (L.)	54	2957
(19) *Paraleptophlebia cincta* (Retzius)	10	60
Ephemerelliidae		
(20) *Ephemerella ignita* (Poda)	34	2132
Ephemeridae		
(21) *Ephemera danica* Müller	17	114
Caenidae		
(22) *Caenis luctuosa* (Burmeister)	39	1516
(23) *Caenis horaria* (L.)	17	280
(24) *Caenis rivulorum* Eaton	14	76
(25) *Caenis macrura* Stephens	3	16

Leptophlebia vespertina (L.) was the most widespread species, but five other species (*Baetis rhodani* (Pictet), *Centroptilum luteolum* (Müller), *Cloeon simile* Eaton, *Heptagenia fuscogrisea* (Retzius), *Caenis* *luctuosa* (Burmeister)) also occurred in more than half the sites sampled. Likewise the species varied in relative abundance, with *B. rhodani* being the most numerous overall. When the relative abundances of species in the combined collections from lotic sites only and lentic sites only were analysed by examining the relationships between the $\log_{10}$ transformed abundances and rank order of abundance, they generally approach the geometric or niche pre-emption model (Figure 3). The total number of species recorded in the catchment appears to be a fairly complete inventory of its ephemeropteran fauna. Rarefraction curves summarizing the relationships between species richness and number of sites sampled, based on three randomisations of the site sampling sequence, are given for (a) all sites, (b) lotic sites only and (c) lentic sites only in Figure 4. These suggest that the number of sites need not exceed about 20 for the asymptotic cumulative number of species to be closely approached. In the case of the lentic sites the total number of species recorded was lower (N=18) than in the overall survey. However, all the species recorded in the catchment were found in at least some lotic habitats. The average number of species recorded per site was 7.2, but in the Dalgan River (location number 25) 18 species were recorded over the annual cycle of sampling. Five of the six sites at which more than 10 species were recorded (Appendix 1) were river sites in the eastern part of the catchment and the sixth, the River Aille (location number 32) was intermediate in respect of upstream geology and location within the catchment. The percentage frequency distributions for occurrence of ephemeropteran species for the 41 lotic and 28 lentic, and 34 eastern (alkaline) and 35 western (acidic), sites sampled are indicated in Figure 5. The ten most abundant species sampled (Figure 3a) illustrate the variation between species in respect of their frequency of occurrence in lotic versus lentic and eastern versus western catchment sites. Four (*H. fuscogrisea, L. vespertina, C. luteolum* and *C. luctuosa*) were more or less evenly distributed among these categories of sites. Four others (*B rhodani, Baetis muticus* (L.), *Ephemerella ignita* (Poda) and *C. simile*) though similarly distributed among eastern and western sites, differed in their distributions among lotic and lentic sites, with all but one (*C. simile*) showing preference for lotic habitats. *Baetis scambus* Eaton and *B. atrebatinus* Eaton, though strongly lotic in habitat preference, differed in respect of their utilization of eastern and western sites (Figure 5).

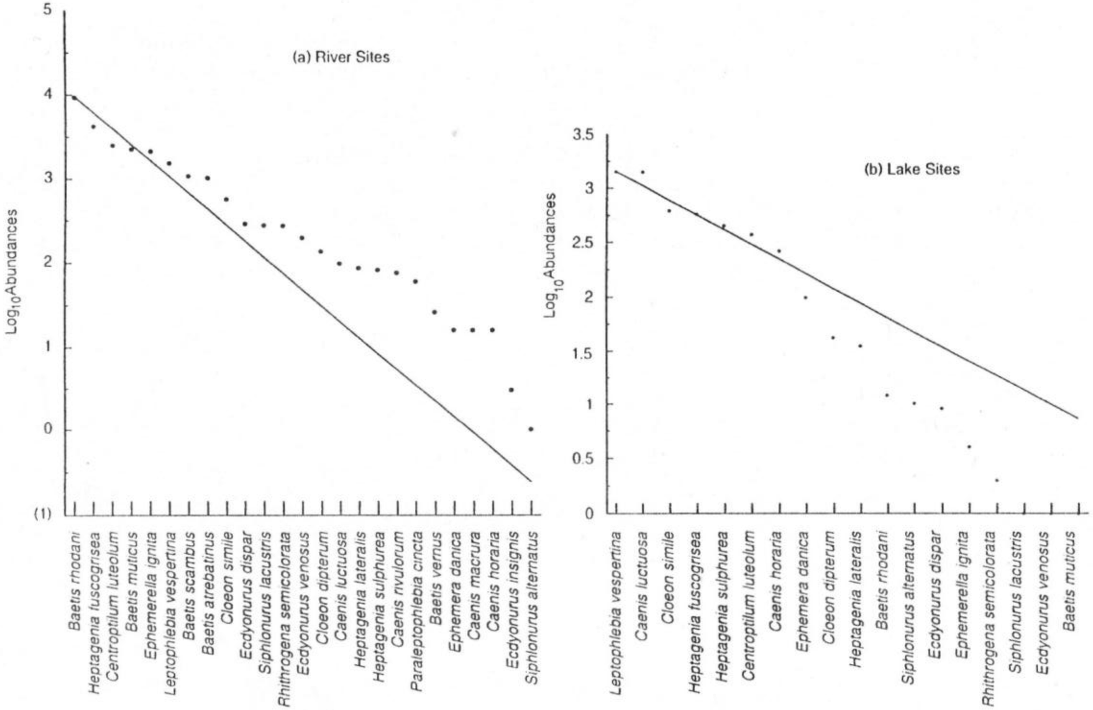

Figure 3. Relative abundances (Log$_{10}$ scale) of Corrib catchment Ephemeroptera plotted in decreasing order for (a) lotic sites and (b) lentic sites, showing their relationship with the Geometric model.

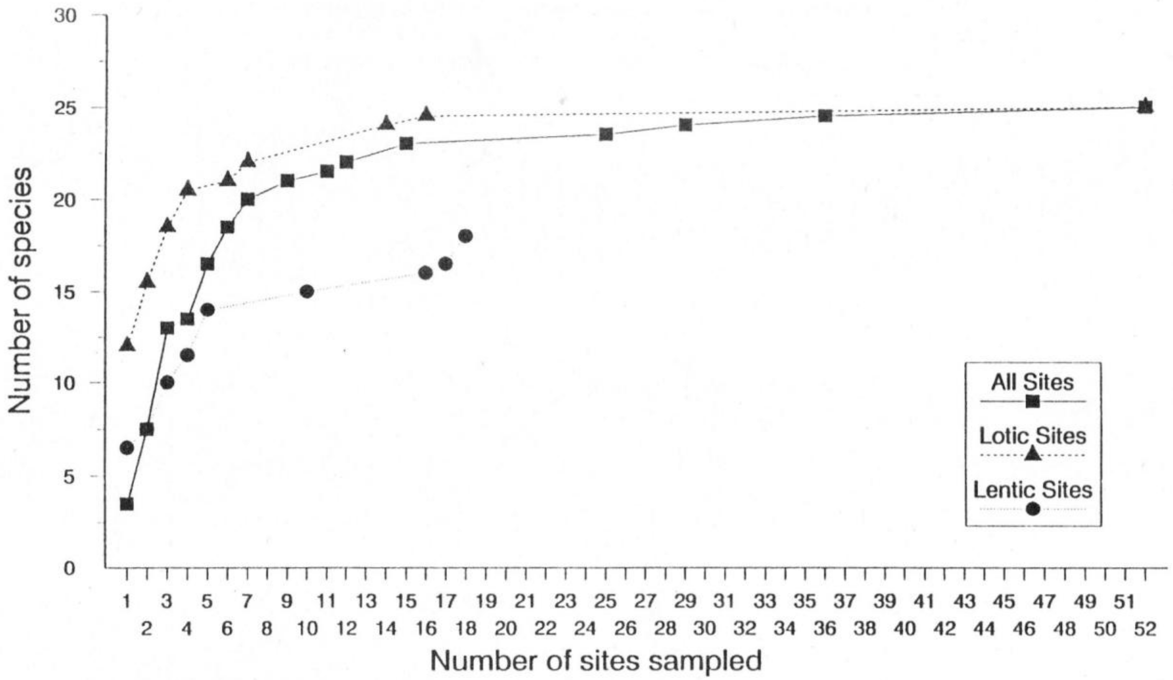

Figure 4. Rarefraction curves indicating the relationship between species richness and number of sites sampled.

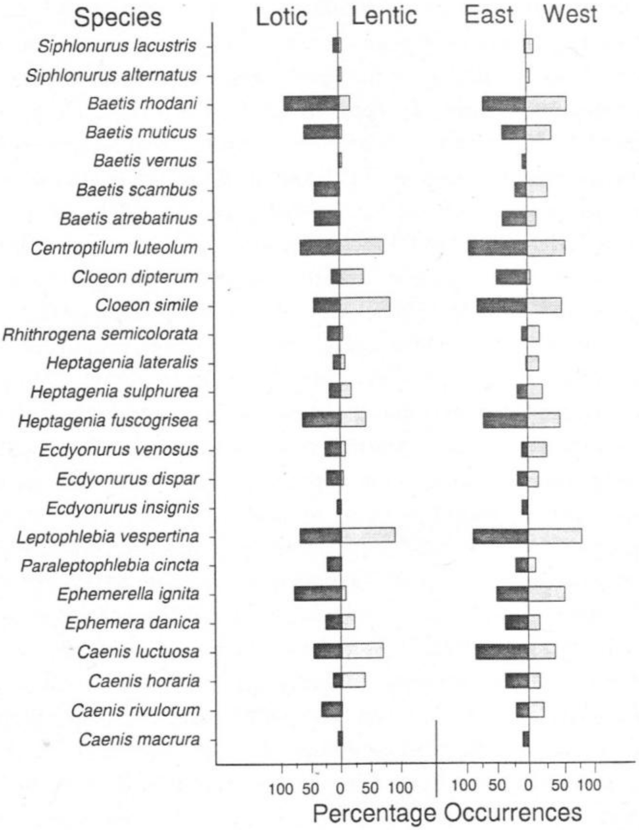

Figure 5. Relative occurrences of mayfly species in lotic and lentic and eastern and western sites in the Corrib catchment.

Discussion

The composition of Ireland's freshwater fauna reflects the variable extent to which the taxa have achieved post glacial recolonization, as well as the ecological factors associated with the countries latitudinal position and climate. Some taxa, such as the freshwater fishes, are greatly under represented in the Irish fauna in comparison to those of Britain and adjacent continental European regions (Wilson, 1986). However, when such comparisons are made in the context of the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) and account is taken of the relatively small area of the island of Ireland, a variety of freshwater macroinvertebrate taxa have been shown to be well represented in Ireland (McCarthy, 1986). In the case of the Ephemeroptera, there are apparently 34 species present in Ireland, as opposed to 47 in Britain and significantly larger numbers in adjacent continental countries. The percentage of the British ephemeropteran species (72%) present in Ireland is typical of many aquatic insect groups, including the Chironomidae (70%) (Murray and Ashe, 1983) and Trichoptera (73%) (O'Connor, 1978). In contrast, some taxa such as the even more poorly dispersing stoneflies (Plecoptera) are less well represented in Ireland (58%) whilst other groups such as the actively migrating waterboatmen (Corixidae) have a greater proportion of the British species (85%) (Costello, 1988; Tully *et al.*, 1991). There is no evidence to indicate that any of Ireland's Ephemeroptera have been introduced by man. Thus despite their limited power of flight, the majority of these insect species apparently have been able to, in the geological time scale (<10,000 yrs.) in question, disperse across marine zoogeographical barriers such as the Irish Sea. Speight (1986) reached a similar conclusion in respect of a variety of other insect orders in Ireland.

It appears that 25, and possibly 27, species of Ephemeroptera occur in the Corrib catchment area. This estimate of the species richness of the catchment's Ephemeroptera is probably quite accurate, because of the extensive (Figure 1) and seasonally repeated sampling undertaken. One limitation of the sampling technique was that no deeper than 2 m in water depth was sampled. However, this does not appear to have been of great significance. The sites were chosen so as to be representative of the full range of freshwater habitats and the rarefraction curves presented in Figure 4 indicate that most species would have been recorded if less than half the total number of sites had been included in the survey. The Corrib catchment area, though comprising less than 4% of the total land area of Ireland, is ecologically varied and contains a relatively diverse aquatic insect fauna. The proportion of the Irish species of Ephemeroptera recorded in the catchment area (74% and possibly 79%) is similar to the results obtained in comparable studies of the area's stoneflies (79%) and Corixidae (75%) (Costello *et al.*, 1984; Tully *et al.*, 1991). In each case the proportion exceeds that predictable in terms of species area relationships (MacArthur and Wilson, 1967). Thus it seems that insects such as these have had little difficulty in dispersing from one river catchment to another, once they had colonized the island. The diversity of aquatic insect life in the Corrib area reflects the varied topography, geology and habitat types that characterize it.

The relative abundances of the ephemeropteran species of the Corrib catchment can be effectively summarized by linear curves describing the relationships between $\log_{10}$ transformed data and ranked orders of abundance (Figure 3). Though the composition of the assemblages at the lotic and lentic sites differed, in each case the species abundance patterns corresponded broadly with what has been termed the geometric or niche pre-emption model. However, the ecological and biogeographic significance of this is not clear. Communities which are describable in terms of such geometric series are thought to be dominated by a single factor (Giller, 1984). Much evidence suggests that whilst early successional communities fit geometric models, so also can climax communities (Whittaker, 1975). Polluted marine benthic communities and assemblages of stream invertebrates which experienced severe flood conditions have been shown to fit the model (Gray, 1987; Twomey and Giller, 1991). However, notwithstanding the difficulties sometimes experienced in interpreting the ecological significance of species abundance patterns, such methods are useful ways of summarizing information of species composition, species richness and equitability and detecting changes in ecological communities (Ludwig and Reynolds, 1988).

The majority (15) of the ephemeropteran species recorded in the Corrib catchment area are widely distributed in Europe. However, *Siphlonurus alternatus* (Say), *H. fuscogrisea*, *L. vespertina*, *Paraleptophlebia cincta* (Retzius) and *Caenis rivulorum* Eaton are more typically northern/central European species, while *Rhithrogena semicolorata* (Curtis), *Heptagenia lateralis* (Curtis), *Ecdyonurus venosus* (Fabricius), *Ecdyonurus dispar* (Curtis) and *Ecdyonurus insignis* (Eaton) are southern/central European species (Illies, 1978). Differences in climatic factors and especially water temperatures, are reflected in the life histories of many species. The Corrib catchment area occupies a somewhat intermediate latitudinal position in Europe. European species such as *B. rhodani* and *B. muticus* which have univoltine life cycles in Scandinavia (Ulfstrand, 1968, 1969; Brittain, 1979) and trivoltine life cycles in the Pyrenees (Thibault, 1971; Benech, 1972) have bivoltine life cycles in the Corrib catchment area (authors unpubl.). Likewise *E. venosus*, which has a central and southern European distribution was found to have a univoltine life cycle in the Corrib catchment, while it can complete two life cycles per year in continental Europe. However, the maximum sizes of nymphs of this species recorded in the present study were up to 7 mm longer than those recorded in other European studies (Whitney, 1939; Hynes, 1961; Elliott, 1967; Thibault, 1971). Whelan (1980) described variations in the life cycle of *Ephemera danica* Müller populations in Irish lakes and attributed them to differences in lake temperature regimes and other environmental factors.

The relatively diverse ephemeropteran species assemblages encountered in the present study reflect both the natural dispersal abilities of these insects, as well as the variety of habitat available within the Corrib system. Many of the sites sampled were in near pristine condition. However, pollution sensitive species such as the Ephemeroptera and Plecoptera are increasingly under threat in Europe (Costello, 1988). Populations of these insects in Ireland are consequently acquiring an enhanced conservation status.

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Appendix 1. Site number (No.), national grid reference and name of the sampling locations used in this study, together with the mayfly species recorded at each. The species are numbered as in Table 1. Locations at which two sets of samples were taken are indicated by an asterix. L. = Lake or Lough; R. = River.

No.	Grid ref.	Location name	Species present
*1	M230370	Chortachalla L.	3,8,9,10,22,23
2	M118456	Upper L. Corrib at Derreenmeel	8,13,16,18,21,22,23
3	M220310	L. Kip R. at main Rd	3,4,8,13,14,15,16,20,21,22
4	M187298	L.Kip R. at Keeagh	3,4,8,10,18,19,20,22,24
5	L962510	Shaugnessy bridge	1,3,12,14,15,18,20,24
6	M119726	Shrah bridge	3,4,6,11,15,16,20,24
7	M053628	Owenbrin R.	3,6,11,14,15,18,20,24
*8	M193373	Ross L. at Killanin	8,9,10,14,18,21,22
9	M222329	Canal near Moycullen	3,8,9,10,14,18,22
10	M320305	Drain on Galway Headford Rd	9,10,18
11	M321328	Clare R.at Headford Rd	7,8,10,14,18,20,22,23,24
12	M323350	Cregg R. at Headford Rd	3,7,8,10,14,18,19,20,22
13	M421538	Clare R. at Tuam	3,4,6,7,8,11,13,14,15,17,19,20,21, 22,24
14	M445469	Grange R. at Ballinderry	3,4,6,7,8,9,14,16,17,18,19,20,21, 22,23
15	M172325	Tawnybeg L.	2,9,10,18,23
16	M198285	L.Kip R. near L.Kip	3,8,10,13,14,18,19,20,23,24
17	M198284	L. Kip	8,10,18,22,23
18	M201354	Canal at Knockbane	1,3,7,8,9,10,14,18,22
19	M232325	Outflow from Ballyquirke L.	8,10,14,18,22,23
*20	M202358	Ross L. at Knockbane	8,9,10,14,18,21,22
*21	M227309	Ballyquirke L. at Clydagh	8,9,10,14,18,22,23
22	M099465	Stream at Gortdrishagh	3,4,11,12,15,16,20,24
*23	M064425	L. Agraffard	3,4,8,10,11,12,14,18,22,23
24	M364724	Robe R. at Castlemagarrett	3,4,6,7,8,14,18,19,20,24
25	M431676	Dalgan R. at Doonmacreena	3,4,6,7,8,11,12,13,14,16,17,18,19, 20,21,22,23,25
26	M318413	Kilroe R.	3,8,10,20,21
*27	M276450	Clooneen R.	3,7,8,10,18,22
28	M257490	Blackriver near Headford	3,4,10,20,22
29	M148553	R. at Cong	3,4,7,8,14,20,24
30	M194551	Cross R. at Cross	3,4,8,16,20,25

31	M262488	Blackriver tributary	3,4,7,14,18,20
32	M145738	Aille R. Cloon L./L.Mask	2,3,4,6,7,8,9,10,14,18,19, 20,21
33	M163680	Keel bridge	3,4,8,10,14,18,21,22
34	M010640	L. near L.Nadirkmore	8,18
35	M005642	L. Nadirkmore	18
36	M107426	Owenriff R.	3,4,6,7,8,10,18,20
*37	M054428	L. between L. Agraffard/L. Bofin	1,8,10,13,14,18,22
*38	M014457	Loughaunierin	8,10,18,22
*39	M029445	L. Bofin	3,8,10,13,14,18,22
40	M012471	Owenwee	3,4,6,7,8,14,18,20
41	M022447	Inflow into west L.Bofin	3,10,14,18,20
42	M084024	Bunowen R. at Glengowla	3,6,8,12,15,18,20,22,24
43	L963520	Failmore R.	3,4,6,11,12,14,15,16,20
44	L966527	Bealnabrack R. at Maam	1,3,4,6,8,10,14,16,18,20
45	L967598	L. Nafooey	3,8,12,13,14,15,18,20,21,22
46	M011587	Finny R. at Finny	3,4,6,11,13,15,20
47	M143761	Aille R.	3,4,6,7,8,14,18,20,21
48	M118775	L. Nacorralea	10,18
49	M098681	Glenshaul R.	3,4,6,11,15,20,22,24
50	M183642	Robe R. at Ballinrobe	3,7,8,9,10,14,18,22
51	M308488	L. Hackett	8,9,10,18,22,23
52	M500639	Sinking R. near Dunmore	3,4,5,6,7,8,11,13,14,18,20,21,24,25
53	M412673	Castlereagh L.	9,10,18,20,23
54	M365625	Stream near L.Altore	3,5,8,10,15,18,22
55	M263776	Stream at Curry	3,4,6,7,13,14,15,16,19,20,21,22,23,24
56	M225733	Mullingar bridge	3,4,8,13,16,18,20,22
57	M067556	L. Coolin	8,10,12,18,23
58	M040525	Dooghta R. at Cornamona	1,3,8,14,18,19,20,21,22
59	M211786	L. Frank	9,10,18,22,23
60	L971637	Pools on Maumtrasna Mtn.	18

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Distribution and seasonal abundance of *Arcitalitrus dorrieni*, a terrestrial crustacean introduced to Ireland

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Summary

A study was carried out on the distribution and reproductive ecology of *Arcitalitrus dorrieni* (Hunt) in the west of Ireland. The species is native to Australia but was introduced to this country. Our studies have shown that it is locally abundant, and reports the first records for Co. Mayo. In certain habitats, where *Rhododendron ponticum* L. predominates, numbers over 12000 m^{-2} were recorded. The animal is also found in grassland and coniferous woodland around Kylemore Lough, Co. Galway. Ovigerous females are present throughout the year, with a reproductive peak occurring in August - September.

Introduction

The Talitridae are the only family of amphipod crustaceans modified for terrestrial or semi-terrestrial life. Terrestrial species are commonly known as landhoppers and the semi-terrestrial species as beachfleas and sandhoppers. Over 200 species have been described in this family, almost half of which are landhoppers. Bousfield (1984) suggested that over 1000 terrestrial species remain to be described worldwide.

Landhoppers have an essentially Gondwanaland distribution, mainly occupying a nocturnal cryptozoic niche in the tropical forests of the Indo-Pacific region (Hurley, 1968). However, synanthropic dispersal has led to the establishment of several species in the Northern Hemisphere (Vader, 1972). One of these species, *Arcitalitrus dorrieni* (Hunt, 1925), was first described from specimens collected on the grounds of Tresco Abbey on the Scilly Isles in 1924. However, it is a native of Australia occurring from southern New South Wales to southern Queensland, and on the north island of New Zealand (Richardson, 1980). Introduction of the crustacean to Britain was probably associated with the importation of exotic plants to British nurseries and gardens (Moore and Spicer, 1986). Colonies are now located on the Isles of Scilly (Hunt, 1925; Sanderson, 1973; Richardson, 1980), Cornwall (Ingle, 1958, Murphy, 1973, 1974), on the island of Colonsay, Inner Hebrides (Moore and Spicer, 1986), Dorset and at the Royal Botanic Gardens at Kew (Richardson, 1980). In Ireland the species is known to occur in two regions, the area around Kylemore Lake, Co. Galway (Rawlinson, 1937) and in a garden centre at Stepaside, Co. Wicklow (O'Connor *et al.*, 1991). It is not known whether these colonies resulted from plant material brought from Australia or from Britain.

To date, very little detailed ecological work has been carried out on this species. The distributional records for Britain include some information on the habitats in which the particular colonies were found. Richardson (1980) and Moore and Spicer (1986) also included quantitative data on population abundance. Physiological data on the animal includes a study of the gill area relationships in seven talitrid amphipods, including *A. dorrieni* (Spicer and Taylor, 1986), aerial and aquatic oxygen consumption rates (Spicer and Taylor, 1987), and also work by Morritt (1987, 1988) on water loss and osmoregulation respectively.

This is the first ecological study on *A. dorrieni* in Ireland (apart from distributional records) and in this paper we describe the distribution and seasonal abundance of the species around Kylemore, Co. Galway.

Methods

Sampling methods

In order to assess the distribution of the animal, inspection of different sites was carried out at regular intervals. This process took two forms. The first involved carefully searching the litter layer and turning over any stones at the site. The presence or absence of the animal was noted accordingly. The second method involved the use of pitfall traps to get a more quantitative picture of the habitat preferences of the animal. Traps were placed in groups of four, at 1 m intervals, and collected after 5 weeks.

In the summer of 1991, two transects of pitfall traps were put in place in Connemara National Park. The first was placed on the lower northern slope of Diamond Hill (L731 570), a mixed habitat site of lowland blanket bog with some patches of bracken *Pteridium aquilinum* L., and *Molinia / Calluna* closer to the summit. The second was placed in an area of grassland on the lower northern slope of Benbaun (L765 569) near the N 59 road. Both transects were 800 m in length and ran up the mountain side. Four pitfall traps were placed in a circle at 100 m intervals, left for a total of 10 weeks and emptied twice, at intervals of 5 weeks.

In order to study the population dynamics of the animal, five quantitative samples were taken regularly from each of two sites, described below. These were collected with a metal box quadrat (16 x 16 cm), using a random sampling technique. The soil was sampled to a depth of 9 cm. The samples were placed in cardboard boxes and stored in paper bags for transport back to the laboratory. Sorting was done by hand, in a shallow white plastic tray, and the animals were preserved in 70% ethanol. Specimens were sexed and animal length was measured from the tip of the rostrum to the tip of the telson.

Study sites

Two sites were used to study the population dynamics of the animal. The first site is a pure stand of Lodgepole pine *Pinus contorta* var. *latifolia* S. Wats, in the Addergoole property of the Killary forest plantation (L733 581), Co. Galway. This was planted in 1969 and has no understorey. The litter layer has a mean thickness of 5 cm and the trees are planted on peat. The second site, at Tullywee Bridge (L731 588), Co. Galway, is 300 m from the first, but strikingly different. It is a mixed woodland of common beech *Fagus sylvatica* L., pedunculate oak *Quercus robur* L., and Scots pine *Pinus sylvestris* L.. The understorey is dominated by *Rhododendron ponticum* L. and the leaves of this plant make up a large proportion of the litter layer. Samples were always collected under these bushes. The soil at this site is sandy and there is no well developed organic layer.

Results

Distribution

Arcitalitrus dorrieni was recorded for the first time in five 10 km squares and its presence at Aasleagh Falls and in the Delphi Valley are the first records for County Mayo (Figure 1).

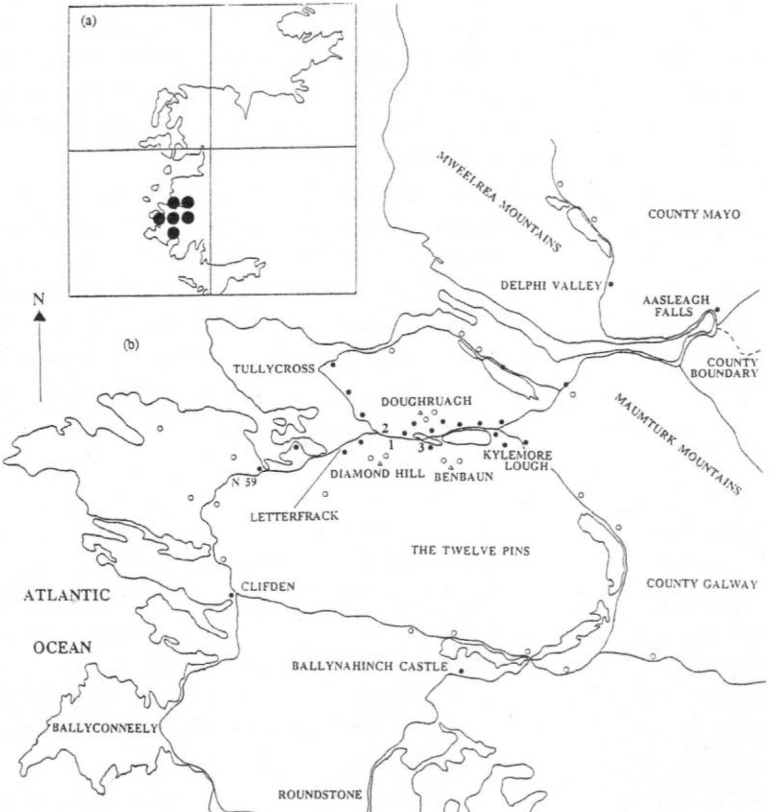

Figure 1. (a) Map showing location of *Arcitalitrus dorrieni* on a 10 km square basis. (b) Detail of part of county's Galway and Mayo showing the distribution of *A. dorrieni*. ● = *A. dorrieni* present, o = absent, 1 = Addergoole property, 2 = Tullywee Bridge, 3 = grassland site within the National Park.

The animal is locally abundant in the mixed woodland around Kylemore but the mosaic of different habitats in the area has resulted in its having quite a disjunct distribution. The presence of *A. dorrieni* in woods at Clifden and at Ballynahinch Castle could be the result of synanthropic dispersal and not due to natural colonization from Kylemore, as it was consistently absent from several open habitats between these different sites, namely, blanket bog, *Holcus / Juncus* grassland, and areas dominated by *Molinia / Calluna*. The animal was strongly associated with *Rhododendron ponticum* in the woods around Kylemore, and in fact, a common factor between many of the sites at which the animal was found was the presence of this plant. The animal was found under bracken *Pteridium aquilinum* and in grassland within the National Park (Table 1). Litter accumulation under hedges dominated by *Fuschia* along the road between Kylemore Lough and Letterfrack also harboured *A. dorrieni*. The results from the transects showed that the species is consistently absent from the *Molinia / Calluna* hilltops. The animal is present up to the treeline on Doughruagh mountain but it does not occur on the treeless upper slopes. A sitka spruce *Picea sitchensis* (Bongard) Carr. stand directly adjacent to the Addergoole pine stand appeared to be an unfavourable habitat for the animal. Pitfall traps set in both the sitka spruce and lodgepole pine woodland showed significantly more landhoppers in the lodgepole pine stand (ANOVA $F=22.93$, $P < .005$ for June; $F=124.45$, $P < .001$ for July; $F=24.14$, $P < .005$ for August; $F=39.67$, $P < .001$ for September). The absence of a suitable litter layer in sitka spruce woods could explain their avoidance of this habitat.

Table 1. Mean numbers ± 1 S.E. of *Arcitalitrus dorrieni* per pitfall trap (n=4, 35 trap days) at three sites in the Kylemore area between June and September 1991.

	June	July	August	September
sitka spruce	3 ± 1	4 ± 1	7 ± 3	8 ± 2
lodgepole pine	189 ± 39	78 ± 6	67 ± 12	114 ± 17
grassland	35 ± 10	60 ± 23	433 ± 120	240 ± 37

Population dynamics

The Tullywee Bridge site supported a higher average density of *A. dorrieni* than the Addergoole site (mean densities for March 1990 to October 1991 were 4336 and 2078 individuals m^{-2} respectively). Numbers at both study sites showed a clear seasonal pattern of change during the study period (Figure 2). Population density was at its maximum, after recruitment of young, in August-September. Ovigerous females were present year round in Tullywee Bridge samples. A high rate of mortality occurred, in both populations, during winter (Figure 2). In the Tullywee bridge site (Figure 2a) minimum levels are found in February of each year whereas in the Addergoole stand (Figure 2b) the population was at its lowest in June. The Tullywee bridge site showed a considerable decline from a maximum density of 12,172 m^{-2} in September 1990 to a maximum of 5187 m^{-2} in September 1991. It is not clear why this difference occurred.

The monthly changes in population structure for the Addergoole site are shown in Figure 3. Successive size class distributions show the change in numbers of animals in each size class attributable to growth. This is most clearly seen for the period March to November. The size class distributions for November and December are very similar suggesting that growth rates are low at that time of year. The population in June contains females just coming to reproductive size (7.5-8.0 mm). As a result, the population consists of a high proportion of juveniles by August.

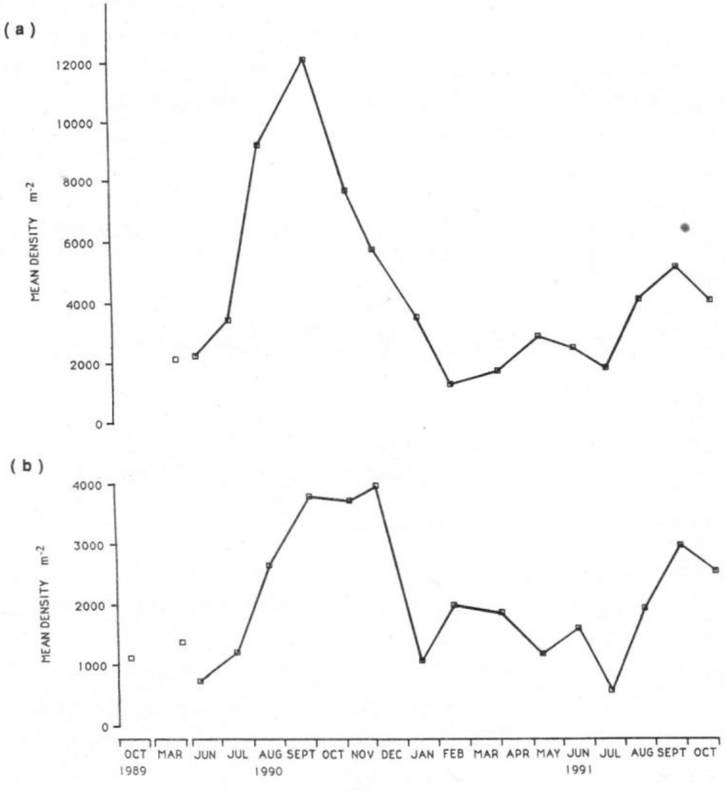

Figure 2. Mean population densities of *Arcitalitrus dorrieni* at (a) Tullywee Bridge and (b) the Addergoole pine site during the study period.

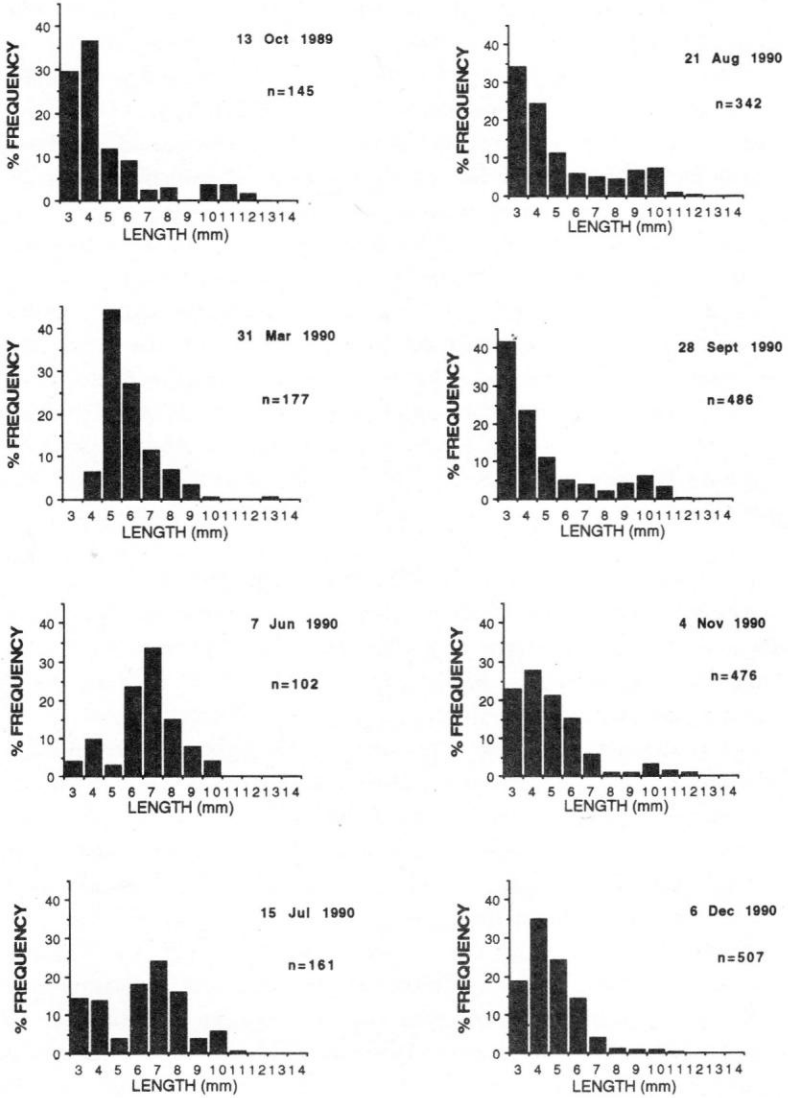

Figure 3. Size frequency distribution of the Addergoole pine population from October 1989 to December 1990.

Discussion

Richardson (1980) recorded a density of 2266 m^{-2} for *A. dorrieni* in Cornwall in December 1976 under the non-native species, *Dicksonia antarctica* Labill. Moore and Spicer (1986) found a maximum density of 680 m^{-2} in May 1985 for a population on the island of Colonsay. It is possible that the recorded densities at both Cornwall and Colonsay could have been higher had sampling occurred during the peak reproductive period of August -September. Because of the high population densities found under *D. antarctica*, Richardson (1980) speculated that it was the plant involved in the introduction of *A. dorrieni* from Australasia to Britain. Three reasons were given to support this suggestion, namely, the highest density of amphipods were found in the litter of this plant, the plant was transported intact, and the rough trunk of *D. antarctica* could have provided cavities to shelter the amphipod. In the present study, highest population densities were found under another non-native species, *Rhododendron ponticum*. However, it is unlikely that the amphipod was introduced to Ireland on this plant as it is not a native of Australia or New Zealand.

Friend and Richardson (1977, 1986) suggested that the diet of terrestrial amphipods is catholic, comprising decaying leaf litter. The discovery of the landhopper in a wide variety of different habitats, from grassland, to pine forestry, and mixed woodland certainly suggests that *A. dorrieni* has no highly specific food preferences. The population decline which occurred at both study sites during the December-January period is probably due to a climatic factor. Richardson (1980) suggested that climatic factors are limiting the ability of the species to further colonize Cornwall. The present study suggests that *A. dorrieni* has colonized most of the suitable wooded habitats around Kylemore. A factor which may limit further natural spread is the apparent unsuitability of open habitats for this species, namely *Holcus / Juncus* grassland, lowland blanket bog, and mountains where *Molinia / Calluna* is the dominant vegetation. The waterlogged nature of these areas and lack of litter accumulation are probably two important factors to be considered here. When the animal is found in grassland, it is usually in close proximity to a woodland site, with the population declining as one moves away from the wooded area. It is highly likely that the Twelve Bens, Mweelrea and Maumturk mountains, the lowland blanket bog around Ballyconneely and Roundstone and the

Holcus / Juncus grassland, which is an ubiquitous feature of this area, pose a considerable barrier to dispersal. However, the disjunct distribution of the landhopper in the region suggests that man will continue to be an agent of dispersal to other more favourable habitats.

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A review of Irish millipedes (Diplopoda)

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Summary

The results of past and recent surveys of millipedes in Ireland are reviewed, including a complete bibliography of publications referring to the occurrence of millipedes in Ireland. An up-to-date list of the species recorded in Ireland is given, with details of 17 species added to the Irish fauna since 1970, largely as a result of work by the British Myriapod Group. The significance of the Irish millipede fauna in relation to that of Britain and of continental Europe is assessed. Further co-ordinated surveys of millipedes in Ireland are recommended.

Introduction

Millipedes (Diplopoda) are a Class, divided into 3 Sub-classes in which there is a total of 14 Orders, with 10,000 described species (Blower, 1985). Hoffman (1979) suggested that an additional 70,000 species remain to be discovered or described. The group has a long evolutionary history going back to the Old Red (Devonian) Sandstone.

Millipedes form an important component of the decomposer community of soil and litter fauna in many ecosystems in temperate and tropical areas, but are absent from polar and tundra regions. Ireland, located at the extreme west of the Palaearctic region, has a small millipede fauna, all of which can be considered to have colonized the present land mass during the current (Littletonian) warm stage.

In the period from 1896 to 1919, 25 papers were published which summarized records of 25 species recorded in Ireland. After a gap of over 50 years, in which almost nothing was published, Petersen (1975) reviewed existing records and listed 21 species (plus one exotic and some unresolved problem species). However, the millipede fauna of Ireland is incompletely known and work by the British Myriapod Group (BMG), which began in the 1970s, has provided additional knowledge of the species which occur here.

This paper brings together all available published information, and the results of these recent surveys, to summarize knowledge of the occurrence of millipedes in Ireland. Some uncertainties remain about a number of the earlier records reviewed by Petersen (1975). First published records of 13 species added to the Irish list since 1919 are cited, in some cases with previously unpublished details, together with hitherto unpublished first records of a further four species.

Pre-1970 publications

Templeton (1836) published the first list of Irish millipedes and included definite records of five species and records of two further 'species' now split or regarded to be of uncertain status. Pocock (1893) published a list including 12 species of millipedes, eight of which were new to Ireland. This publication saw the beginning of a period of active work on the group by the Brade-Birks's, Brolemann, Carpenter, Foster, Jameson, Johnson and Selbie, with 26 publications (Table 1, Bibliography).

Table 1. Checklist of Irish millipedes (Diplopoda) citing first publications. Nomenclature and systematics follow Blower (1985). Species listed for the first time for Ireland in the present study (new to Ireland) also include the year of the original record.

Polyxenidae
Polyxenus lagurus (L.) - Pocock (1893)

Glomeridae
Glomeris marginata (Villers) - Templeton (1836)
Stygioglomeris crinita Brolemann - New to Ireland, 1983

Trachysphaeridae
Adenomeris gibbosa Mauries - Blower (1985)

Craspedosomatidae
Craspedosoma rawlinsii Leach - Selbie (1912)
Nanogona polydesmoides (Leach) - Pocock (1893)

Brachychaeteumatidae
Brachychaeteuma melanops Brade-Birks - Blower (1985)
Brachychaeteuma bagnalli Verhoeff - Jones (1992)

Chordeumatidae
Chordeuma proximum Ribaut - Jones (1992)
Melogona gallica (Latzel) - Blower (1985)
Melogona scutellare (Ribaut) - Blower (1985)

Nemasomatidae
Nemasoma varicorne C. L. Koch - Foster (1919)

Blaniulidae
Proteroiulus fuscus (Am Stein) - Pocock (1893)
Choneiulus palmatus (Nemec) - Blower (1985)
Blaniulus guttulatus (Fabricius) - Pocock (1893)
Archiboreoiulus pallidus (Brade-Birks) - Blower (1985)
Boreoiulus tenuis (Bigler) - English (1976)

Julidae
Ommatoiulus sabulosus (L.) - Pocock (1893)
Tachypodoiulus niger (Leach) - Pocock (1893)
Cylindroiulus londinensis (Leach) - Selbie (1912)
Cylindroiulus caeruleocinctus (Wood) - British Myriapod Group (1988)
Cylindroiulus vulnerarius (Berlese) - Blower (1985)
Cylindroiulus punctatus (Leach) - Templeton (1836)
Cylindroiulus latestriatus (Curtis) - Brade and Birks (1916)
Cylindroiulus britannicus (Verhoeff) - Broleman (1896)
Cylindroiulus parisiorum (Brolemann and Verhoeff) - new to Ireland, 1911
Julus scandinavius Latzel - Selbie (1912)
Ophyiulus pilosus (Newport) - Pocock (1893)
Leptoiulus belgicus (Latzel) - Irwin (1992)
Brachiulus pusillus (Leach) - Templeton (1836)

Polydesmidae
Polydesmus angustus Latzel - Templeton (1836)
Polydesmus inconstans Latzel - Jackson (1913)
Polydesmus gallicus Latzel - Pocock (1893)
Polydesmus denticulatus C. L. Koch - Selbie (1913a)
Brachydesmus superus Latzel - Pocock (1893)

Macrosternodesmidae
Macrosternodesmus palicola Brolemann - British Myriapod Group (1988)
Ophiodesmus albonanus (Latzel) - British Myriapod Group (1988)

Paradoxosomatidae
* *Oxidus gracilis* (C.L.Koch) - Foster (1919)
Stosatea italica (Latzel) - Blower (1985)

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* Exotic species recorded only from glasshouses.

Perhaps the most tantalizing 'might have been' was the young Scot, C. M. Selbie (1890-1916), who took an active interest in myriapods as part of his duties at the National Museum of Ireland (NMI), under R. F. Scharff, and published four papers before enlisting at the outbreak of war in 1914. Like so many of his generation, his early promise ended tragically on the battlefield in Europe.

By the end of 1919, 25 species of millipede had apparently been recorded from Ireland, but there is doubt about the identity of species recorded as *Polydesmus edentulus* C. L. Koch and *Cylindroiulus luridus* (C. L. Koch) (Blower (1958) omitted them from his list); records of *Nopoiulus minutus sensu auct.* were misidentified (see below), and *Iulus luscus* Meinert is taxonomically undifferentiated.

Between 1920 and 1957 it appears that there were no publications relating to the occurrence of millipedes in Ireland, and only two were published between 1958 and 1970. Blower (1958) produced the first comprehensive key to 'British' species in which records from Ireland were included, based almost entirely on the earlier published records, and Richards (1961) published a few records from the Burren.

Publications from 1970 onwards

A review of the distribution of Irish millipedes by Petersen (1975) drew together information from publications, manuscript notes and maps and preserved material in NMI. This apparently comprehensive work included some determination or re-determination of material in the NMI collections and an incomplete survey of the literature. Petersen used the only available British key to species (Blower, 1958) for identifications, but apparently no other. For example, no continental literature, or a reliably identified voucher collection was used to aid with his identifications. Although it was an outstanding work when it was published, this earlier key (Blower, 1958) is now recognized to contain features which make it difficult for inexperienced workers to reliably identify several species.

Subsequent work on the NMI collections, by H. Enghoff (in Blower, 1985) and one of the present authors (CPF) has suggested that Petersen's review contains a number of misleading records. Any errors affecting the overall Irish list are corrected in this paper, but a full re-appraisal of the NMI collections remains to be prepared for publication.

Similar problems with the use of the key in Blower (1958) may have been encountered by English (1976) although her sole record of *Boreoiulus tenuis* (Bigler), new to Ireland, was confirmed by Blower (pers. comm.).

Most other publications have been by experienced people involved with the British Myriapod Group (see below), but there are three additional publications in the period since 1970. Hazelton (1974a, 1974b) summarized faunal recording in Irish cave systems in the 1960s, but all millipede records were of common and widespread species with identifications by F. A. Turk, an international expert on soil fauna. Healy (1977) included records of the characteristic dune species *Cylindroiulus latestriatus* (Curtis) from North Bull Island, Dublin.

British Myriapod Group Recording Scheme

The British Myriapod Group was formed in 1970 in association with the British Biological Records Centre (BRC) at Monks Wood. Most of the nearly 1700 post-1970 records from Ireland, now computerized on behalf of the Group at BRC, have been made by the authors, especially DD. Recording has covered both urban and countryside areas, with spatial referencing usually to the level of 1 km or 100 m squares of the Irish National Grid. Unlike some other surveys in Ireland, recording has not been limited to areas of known ecological importance, although many such sites have been covered *inter alia*.

The millipede fauna of Ireland

From published records and examination of specimens at NMI which are vouchers for some published records, there is evidence that up to 1919, a total of 22 species had been reliably recorded in Ireland and published (Table 1). Subsequent additions of 17 species to the Irish list are also summarized in Table 1.

In addition, four species which had been published, are now regarded to have been incorrectly identified. All records of *Nopoiulus kochii* (Gervais) (= *Nopoiulus venustus* (Meinert, exparte, *sensu* Schubart)) records refer to *Proteroiulus fuscus* (Enghoff) (in Blower, 1985). All extant specimens at NMI of *Cylindroiulus caeruleocinctus* (as part as *Cylindroiulus teutonicus/londinensis* group) (as listed by Petersen, 1975) refer to *Cylindroiulus latestriatus* or to C. *parisiorum* (Brolemann and Verhoeff) (CPF, present study). The nomenclatural complexities surrounding several species are considerable, but Blower (1985) clarified all relevant problems, except for the species identified by Johnson (1913) as *C. luridus* and *P. edentulus*. Petersen (1975) noted that specimens of these species have not survived (at NMI), but no attempt has yet been made to check if voucher specimens are present in the collection of the Ulster Museum.

The vice-county occurrence of millipedes in Ireland has been summarized in tables by Blower (1972), and British Myriapod Group (1988), and in the newsletters of the British Myriapod Group. These summaries perpetuate errors (at the vice county level) of identification in pre-1919 publications and almost certainly in Petersen (1975) and English (1976). Until the complete re-examination of the NMI collection by CPF is published, such tables must be regarded as containing some erroneous records. For this reason we have not included an updated vice-county table in this paper. Similarly, it has not been possible to incorporate any unvalidated pre-1970 records into the BMG dataset held at the BRC. For this reason the distribution map showing coverage of records (Figure 1) is limited almost entirely to post-1970 records collated and validated by BMG.

Status of millipedes in Ireland

The status of species is considered in two ways, in terms of being a constituent of the Irish fauna and in terms of being under threat from extinction.

All 39 species reliably recorded in Ireland to date will have arrived during the present (Littletonian) warm stage, that is within the last 10,000 years. One species, *Oxidus gracilis* (C. L. Koch), is known only from inside glasshouses and can therefore be considered to be a recent accidental introduction. For the remainder, one can only speculate as to their origin, but several are currently known mainly from synanthropic sites, especially around Dublin. However, this occurrence almost certainly reflects the recording effort by a few experienced recorders, especially the first author (DD). It is not unreasonable, therefore, to consider all the recorded species (except *O. gracilis)* as being native or naturalized in Ireland.

On present evidence, none of the species recorded in Ireland can be regarded to be nationally under threat. Knowledge is still fragmentary, even for apparently widespread species such as *Nanogona polydesmoides* (Leach). Several species (e.g. *Adenomeris gibbosa* Mauries, *Brachychaeteuma bagnalli* Verhoeff, *Cylindroiulus caeruleocinctus* (Wood) and *Cylindroiulus vulnerarius* (Berlene)) are known from only one or two sites, probably as a result of recorder effort. However, the sites from which they are known are highly disturbed or marginal land where development, such as building or landscaping, could occur at any time. In Britain, where knowledge is better, if somewhat patchy, only two species are regarded to be under threat and then only in the Red Data Book category K (Insufficiently Known) (Bratton, 1991). Neither of these species are known to occur in Ireland.

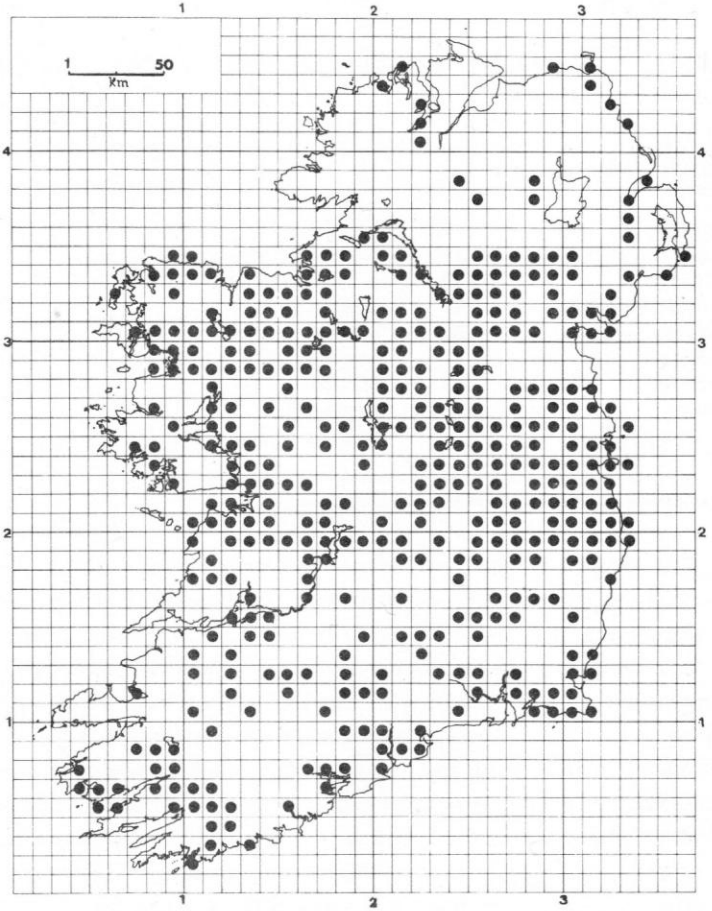

Figure 1. 10 km squares from which millipedes have been recorded in Ireland.

Comparison of the Irish millipede fauna with that of Britain and continental Europe

Comprehensive lists of the millipede faunas of several European countries have been published or are in preparation. Despite its geographically isolated position, Ireland now has a high total number of species when compared with those of other northwestern European countries (Table 2). How much this is a reflection of recorder effort is uncertain. Many of the additional 12 species found in Britain have a strongly southern/southeastern distribution there and are at the north of their range in Britain.

Table 2. Comparison of the millipede faunas of Ireland and other European countries.

Country	Number of species	Source
Ireland	38*	This paper
Britain	50*	Blower (1985)
Belgium	c.50	R. D. Kime (pers. comm.)
The Netherlands	45	Jeekel (1978)
Norway	28	Meidell (in Kime 1990b)
Denmark	37*	Enghoff (1974)
Germany	160	Schubart (1934)
France	250	Demange (1981)
Italy	470	Strasser and Minelli (1984)

* Excluding exotic species recorded only from glasshouses.

A recent European Invertebrate Survey publication (Kime, 1990a) summarized the geographical distribution in Europe of 50 species of millipede, including 21 species which are now known to occur in Ireland. Table 3 summarizes the distribution of 11 of the species included by Kime, comparing their distribution with that in Britain and 10 other western European countries. These species are widespread in Ireland and could be considered to be common and easily collected. What is perhaps surprising is the number of species which seem to have the centre, or a centre, of their distribution in Ireland and Britain. Notably *N. polydesmoides* is recorded only from Belgium and France, *Cylindroiulus britannicus* (Verhoeff) is recorded from less than 30-50 km squares in 7 other countries, *Ophyiulus pilosus* (Newport) is virtually absent from western continental Europe, and *Tachypodoiulus niger* (Leach) is a southern species, being absent from central Netherlands/Germany northwards.

In addition to the species listed in Table 3, three other species occurring in Ireland have very restricted distributions in Europe. Two are associated with mountain ranges, *Adenomeris gibbosa* (French Pyrenees) and *Melogona scutellare* (Ribaut) (French Pyrenees and French, Swiss and Italian Alps, but also in Britain), while *Chordeuma proximum* (Ribaut) is known only from Britain and France.

Table 3. Western European distribution of some species which are widespread in Ireland. Millipede distributions in Europe are summarized from Kime (1990a and pers. comm.). Key: GB = Great Britain, No = Norway, Sw = Sweden, D = Denmark, Ne = The Netherlands, G = Germany, B = Belgium, L = Luxembourg, F = France, Sp = Spain, P = Portugal.

	GB	No	Sw	D	Ne	G	B	L	F	Sp	P
Glomeris marginata	*	*	*	*	*	*	*	*	*	*	
Nanogona polydesmoides	*						*		*		
Proteroiulus fuscus	*	*	*	*	*	*	*	*	*		
Tachypodoiulus niger	*				*	*	*	*	*	*	
Cylindroiulus britannicus	*	*	*	*	*	*				*	*
Cylindroiulus latestriatus	*	*	*	*	*	*	*		*		*
Cylindroiulus punctatus	*	*	*	*	*	*	*	*	*	*	
Julus scandinavius	*	*	*	*	*	*	*	*	*		
Ophyiulus pilosus	*	*	*	*	*	*					
Polydesmus angustus	*				*	*	*	*	*	*	
Polydesmus coriaceus	*						*		*	*	*

Conclusions

Two periods of activity in recording the occurrence of millipedes in Ireland, in the 1890s to 1919 and since 1975, have led to the discovery of a total of 39 species. However, uncertainty remains about the true identity of some records from earlier this century. Non-intensive surveys since 1975 have added 16 species to the Irish list suggesting that the list may not yet be complete. For many species, particularly small, soil-dwelling species there are only scattered records which reflect the efforts of a few experienced recorders. Surveys should continue and the British Myriapod Group intends to encourage its members to carry out further surveys in Ireland.

Recent distribution records, have been summarized for most species by the British Myriapod Group (1988) at the scale of 10 km squares and subsequently by Kime (1990a) at the scale of 50 km squares. These summaries enable simple comparisons with the millipede faunas of Britain and other European countries. The Irish fauna includes several species which appear to be more common and widespread in Ireland and Britain than in continental Europe. Millipedes with an extreme western distribution, and which are common in Ireland, are not currently under threat, but the importance of these Irish populations should not be overlooked when considering species conservation in a wider European context.

Acknowledgements

We are grateful to members of the British Myriapod Group who have contributed Irish records to the BMG scheme, in particular N. M. Reardon and Dr A. J. Rundle. J. G. Blower has provided invaluable help over the years, especially with identification of specimens and advice on many points covered by this paper. D. T. Richardson also provided support for the scheme as overall organizer from 1984 to 1988. We are also grateful to R. D. Kime for advice on European distributions. At the Biological Records Centre, special thanks are due to D. M. Greene and J. C. M. Dring for data management.

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Appendix

Additions to the known millipede fauna of Ireland since 1970

Abbreviations: AGI = A. G. Irwin, AJR = A. J. Rundle, CPF = C. P. Fairhurst, DD = D. Doogue, JGB = J. G. Blower, ME = M. English, NMR = N. M. Reardon, PTH = P. T. Harding, REJ = R. E. Jones, RW = R. Welch.

Stygioglomeris crinita Brolemann
Kilkenny: Inistioge S63, 31.X.1983, Col: DD, Det: JGB.

Adenomeris gibbosa Mauries
Dublin: Ballygall, St Clare's Hospital, O1537, 28.IX.1979 & 18.XI.91, deserted garden, Col: DD, Det: JGB; Ballygall, Violet Hill Hospital O1637, XI.1979, Col & Det: DD: Lucan, Strawberry Beds Road O0235, garden of ruined house, 24.II.1981, Col and Det: DD. Blower (1985), British Myriapod Group (1988).

Brachychaeteuma bagnalli Verhoeff
Dublin: Ballygall, St Clare's Hospital, O1537, 29.XII.1978, deserted garden, Col: DD, Det: JGB, 18.XI.1979, Col and Det: DD. Lucan O0235, II.1980, Col: DD, Det: CPF. Blower (1985), Blower (1986), British Myriapod Group (1988).

Brachychaeteuma melanops Brade-Birks
Cork, West: Castletownshend W1831, 25.V.1982, garden, Col and Det: REJ. Baltimore W0426, 23.III.1991, garden, Col & Det: REJ. Jones (1992).

Chordeuma proximum Ribaut
Kerry, South: Cappamore V5664, 26.III.1991, mixed deciduous woodland, Col and Det: REJ. Jones (1992).

Melogona gallica (Latzel)
Wicklow: Glen of the Downs O21, 9.I.1983, Col: DD, Det: JGB. Blower (1985).

Melogona scutellare (Ribaut)
Sligo: east of Corbally G3125, 29.X.1978, open woodland, Col: DD, Det: CPF.
Kilkenny: Ballyrafton, near Dunmore S56, 1.XI.1983, Col: DD, Det: JGB. Blower (1985), British Myriapod Group (1988).

Choneiulus palmatus (Nemec)
Kildare: Kilcullen N8710, IX.1977, Col and Det: AJR.
Wicklow: Wicklow, The Murrough T3195, 14.VII.1979, rubbish dump, Col: DD, Det: JGB . Blower (1985), British Myriapod Group (1988).

Archiboreoiulus pallidus (Brade-Birks)

Dublin: Ballygall, St Clare's Hospital O1537, 6.XI.1976, deserted garden, Col: DD, Det: CPF.

Offaly: Moneyquid N3817, 27.VII.1977, roadside verge, Col and Det: DD.

Monaghan: Glaslough H7143, 21.IV.1979, open estate woodland, Col and Det: DD. Blower (1985), British Myriapod Group (1988).

Boreoiulus tenuis (Bigler)

Cork, East: Fota Island W7971, 11.III.75, Col: ME, Det: JGB. English (1976).

Subsequently recorded at more than 20 sites. Blower (1985), British Myriapod Group (1988).

Cylindroiulus caeruleocinctus (Wood)

Dublin: Glasnevin Hill O1738, 27.X.78, ruined house, Col: DD, Det: CPF. British Myriapod Group (1988).

Cylindroiulus vulnerarius (Berlese)

Dublin: Glasnevin Hill O1738, 27.X.1978, ruined house, Col: DD, Det: JGB. Blower (1985).

Cylindroiulus parisiorum (Brolemann and Verhoeff)

Antrim: Belfast, Botanic Gardens J37, 10.III.1911, Col: RW, Det: CPF.

Leptoiulus belgicus (Latzel)

Down: Cultra J4180, 11.VII.1989, garden, Col: AGI, Det: REJ. Irwin (1992).

Macrosternodesmus palicola Brolemann

Galway, North-east: Merlin Park M3325, 27.X.1978, open scrub woodland, Col and Det: CPF.

Tipperary, North: Killeen N0304, 26.X.1978, waste ground, Col and Det: CPF.

Kerry, South: Derrynane National Park V5158, 16.III.1991, sand dunes, Col and Det: REJ.

Kerry, North: near Kilgarvan V9972, 28.III.1991, garden, Col and Det: REJ.

British Myriapod Group (1988), Jones (1992).

Ophiodesmus albonanus (Latzel)

Cork, West: Reenadisert (Ballylickey) W0153, under stones by ruin near shore, VIII.1979, Col: DD, Det: JGB. Baltimore W0426, 23.III.1991, waste ground, Col and Det: REJ.

Kerry, North: near Kilgarvan V9972, 28.III.1991, garden, Col and Det: REJ.

British Myriapod Group (1988). Jones (1992).

Stosatea italica (Latzel)

Cork, East: Midleton W8873, IV.1976, town garden, Col: NMR, Det: CPF.

Waterford: near Youghal, Ardsalagh House X0981, dead wood on wall in woodland near river, VI.1977, Col: NMR, Det: PTH. British Myriapod Group (1988).

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A review of the summer phytoplankton distribution in Irish coastal waters: a biogeography related to physical oceanography

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Summary

Characteristic patterns in phytoplankton species dominance are evident in Irish coastal waters in summer. These patterns can be related to water column stability, in particular thermal stratification. The biogeographical distribution of phytoplankton in shelf waters around Ireland is described in relation to local physical processes such as stratification, tidal mixing and upwelling.

Introduction

The microscopic marine plants, or phytoplankton, have a central role in marine ecology in that they are responsible for nearly all primary production in the sea. Marine plankton, including the phytoplankton, have limited mobility in sea water in relation to water movements and conventional studies of their biogeography have related distributions to water masses. In common with most other micro-organisms phytoplankton generation times are short, typically in the region of 1-10 days (Harris, 1986). This poses a problem when relating phytoplankton biogeography to water masses whose advection has time-scales of the order of weeks during which populations can alter radically. The conventional approach is therefore of limited use in the explanation of phytoplankton distributions, although it has been successfully applied to larger planktonic organisms such as certain zooplankton whose growth patterns occur over longer time-scales (Bary, 1963). Around Ireland a small but regular proportion of species originate from oceanic realms far to the south and west of the country, being especially conspicuous in winter when concentrations of coastal species are low. Their presence is perhaps the only relic in our coastal flora of the Gulf Stream, and there is uncertainty as to whether their origin is from tropical regions of the north Atlantic further to the south.

Phytoplankton are photosynthetic; their viability in coastal waters relies on remaining in the upper few tens of metres of the water column due to the rapid vertical attenuation of light in sea water. For this reason, together with the similarity of vertical mixing time-scales and phytoplankton growth scales, vertical mixing is often far more important than horizontal advection when considering phytoplankton distributions.

Seasonal cycles in phytoplankton biomass for temperate areas are now well understood in general terms. Large mixing depths and low surface irradiance levels result in light limitation in winter. Increasing levels of irradiance and of vertical stability caused by warming of the surface layers through spring enables phytoplankton to bloom, after which the surface euphotic zone becomes depleted of nutrients. Nutrient replenishment of the surface layers from deeper water is inhibited due to the establishment of a seasonal thermocline across which diffusion rates are extremely low. Cooling of the surface layers in autumn results in increased mixing of the water column, and although a small autumn bloom may develop, decreasing levels of irradiance and increased surface mixing to depths below the euphotic zone quickly results in light limitation which persists through the winter. The water column may fail to stratify if tidal mixing is large relative to the water depth. In this situation light limitation can persist through summer if the water is mixed to depths below the euphotic zone.

Many phytoplankton encountered in Irish coastal waters fall into two main categories, the diatoms (Bacillariophyceae) and the dinoflagellates (Pyrrophyceae). In addition there is a third group, the microflagellates, whose taxonomy is ill-defined. This group consists of forms from various classes characterized by small size (1-5 μ diameter), flagellae and that they stain in Lugol's Iodine. Their biogeography is not well understood.

Diatoms are typically the first group to appear and constitute the majority of spring bloom material. With increasing stratification, however, other groups become dominant resulting in a high frequency of dinoflagellates in stratified waters in summer. Although to date this succession has not been explained satisfactorily in ecophysiological terms, the observational link between water column stability (i.e. stratification) and phytoplankton community composition is very strong (Tett and Edwards, 1984). Thus communities have been shown to occupy distinct niches on plots of stratification against another parameter such as growth potential, implicitly a function of light and nutrient availability (Margalef *et al.*, 1979), or depth scaled to irradiance (Pingree, 1978; Bowman *et al.*, 1981; Jones and Gowen, 1990) (Figure 1). The link between stratification and phytoplankton ecology therefore demands that any attempt at describing the summer phytoplankton biogeography must be preceded by a brief discussion of the physical oceanography.

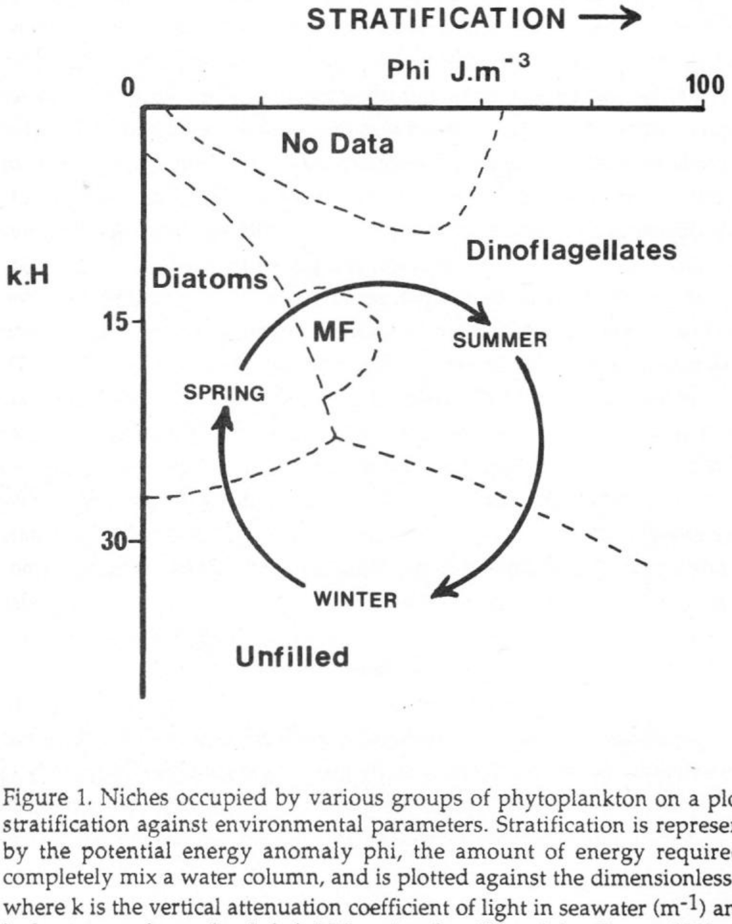

Figure 1. Niches occupied by various groups of phytoplankton on a plot of stratification against environmental parameters. Stratification is represented by the potential energy anomaly phi, the amount of energy required to completely mix a water column, and is plotted against the dimensionless k.H where k is the vertical attenuation coefficient of light in seawater (m^{-1}) and H is the water column depth (m). MF = microflagellates (after Tett and Edwards (1984) and Jones and Gowen (1990)).

Physical oceanography of Irish coastal waters in summer

Representative vertical distributions of temperature and nutrients for thermally stratified coastal waters are shown in Figure 2a. This level of stratification with surface-bottom temperature differences of up to 6°C would be typical of waters along the Atlantic shelf and Celtic Sea (e.g. Cooper, 1967). Towards the coastline, the sea-bed rises to the thermocline at around 35m; further inshore water is warm, vertically mixed and sparse in nutrients, typical of the large non-estuarine bays of the west coast such as Galway and Donegal. Over most of the Irish Sea the water is shallower and tidal streams are higher than those typical of the Celtic Sea and Atlantic shelf. Mixing resulting from tidal stirring is large enough to prevent development of the seasonal thermocline, except for a small area to the west of the Isle of Man (Figure 3), where depths up to 100 m or more may be found. Boundaries between tidally mixed and stratified waters are known as tidal fronts (Figure 2b) and their positions have been successfully predicted by physical models and confirmed by thermal infra-red remote sensing (Simpson, 1981). Tidal fronts (Figure 3) may be found at the southern (Celtic Sea Front) and northern (Islay Front) entrances to the Irish Sea, and bounding the patch of stratified water around the Lambay Deep (Irish Sea Front) (Simpson and Pingree, 1978). A different type of frontal system caused by variations in salinity bounds the western Atlantic shelf and follows the 200 m isobath (Huang *et al.*, 1991).

Stratification will be absent if upwelling occurs, a phenomenon describing the movement of deeper water to the surface. Upwelling areas are highly productive as nutrient rich water is brought into the euphotic layers thereby stimulating phytoplankton growth and they are generally driven by meteorology, notably wind direction. Upwelling is known to occur periodically around southwest Ireland (Figure 3), the area affected extending up to a few thousand km^2 (Raine *et al.*, 1990a).

Methods

Analytical methods for determining physical, chemical and biological parameters are outlined in Raine *et al.* (1990a). Phytoplankton nomenclature is in accordance with Dodge (1985) for dinoflagellates and Parke and Dixon (1976) for all other forms. In defining the regions below, the boundaries derived from the physical oceanographic studies of Dietrich (1950), Simpson (1976; 1981), Pingree *et al.* (1974), Pingree and Griffiths (1978), Holligan (1981) and Raine *et al.* (1990a) have been accepted. Field studies of phytoplankton distributions within these regions (Table 1) have been used to propose typical distribution patterns. Although further quantitative work is necessary to establish the generality of these patterns, it must be remembered that species dominance, rather than exclusive distributions, are being described.

The summer is defined as the warm months of June-September. This period was chosen, opposed to any other time of year, since phytoplankton are light-limited in winter, hence universally sparse around the coast, and it is not until after the spring bloom that fully stratified conditions may develop. Thus it is only in summer that the characteristic distribution of stratified and non-stratified waters around the Irish coast (Figure 3) is evident.

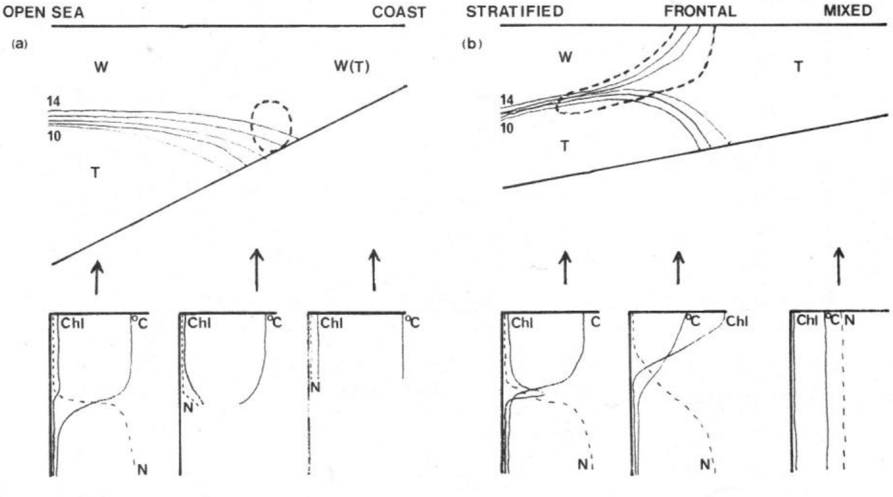

Figure 2. Representative isotherms (°C) for transects (a) running directly out from the coast towards stratified water and (b) across tidal fronts. Regions where enhanced biomass usually occur are enclosed by dashed lines. Inferred regimes are either wind-mixed (W) or tide-mixed (T). Underneath are typical vertical profiles of temperature (°C), nitrate (N) and phytoplankton biomass (Chl, chlorophyll concentration) at various points along the transects.

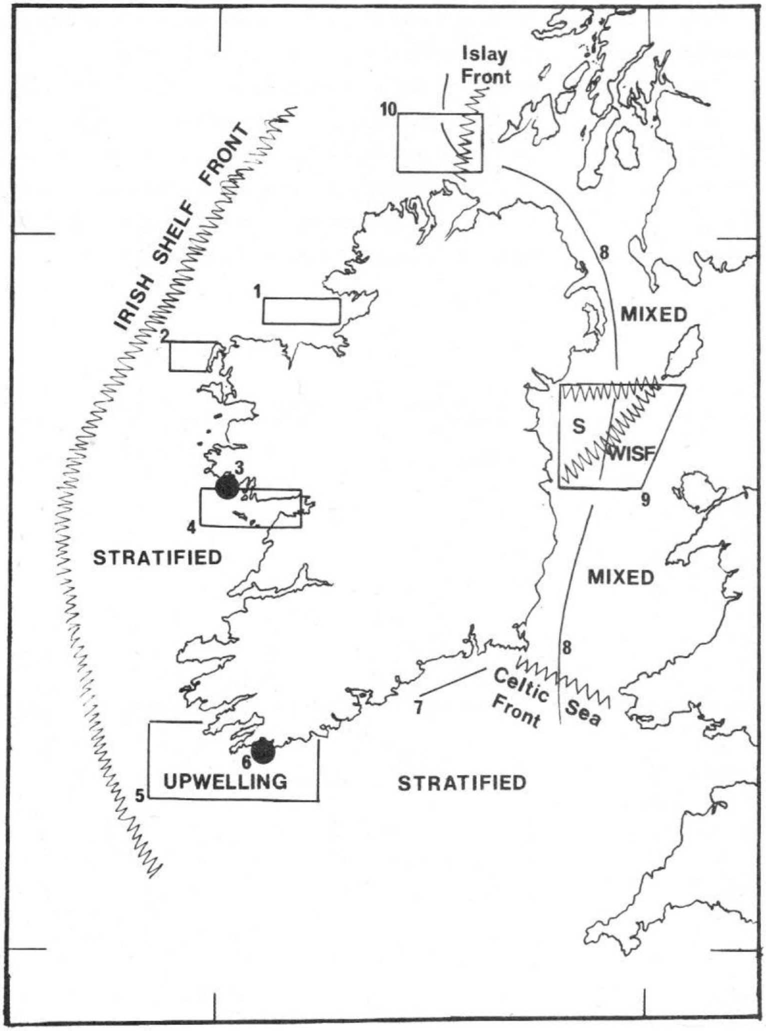

Figure 3. Map showing main physical features of Irish coastal waters in summer. Locations of detailed phytoplankton studies are marked, together with cruise tracks along which sampling took place; these are numbered anticlockwise and are listed in Table 1. Locations of fronts are denoted by dotted areas (WISF = Western Irish Sea Front). S = stratified water.

Table 1. Sources of information on phytoplankton distributions around Ireland utilized in the text, and the areas (Figure 3) to which they refer.

Atlantic region	
Raine, unpublished observations, August, 1988.	1
Raine, unpublished observations, August, 1988.	2
Roden (1984)	3
Oceanography Dept., University College, Galway unpublished observations 1975-1987	4
Southwest upwelling	
Holligan (1981)	5
Raine *et al*. (1990a, 1990b)	5
Roden *et al*. (1980, 1981)	6
Celtic sea	
Raine, unpublished observations, July, 1986.	7
Western Irish sea	
Richardson et al. (1985)	9
Raine, unpublished observations, June 1990.	9
Frontal regions	
Holligan *et al*. (1980)	8
Pingree *et al*. (1978)	10
Simpson *et al*. (1981)	10

Summer phytoplankton distributions around Ireland

In order to successfully describe summer phytoplankton distributions around Ireland, a series of geographical zones based on physical features described earlier is set out below. The choice is justified by our current understanding of phytoplankton ecology summarized earlier.

The Atlantic Shelf

The summer phytoplankton of the stratified Atlantic shelf can be divided into an early phase and a late phase. The temporal boundary between them occurs in mid-July and probably reflects the full development of the thermocline at around 35-40 m depth. In early summer occasional vertical mixing promotes a series of diatom blooms, in particular *Chaetoceros* spp. and

Rhizosolenia setigera, with virtually no dinoflagellates except possibly *Scripsiella* species. In the later phases these species do not occur and dinoflagellates, particularly *Ceratium* species, and the diatoms *Rhizosolenia alata* and *Leptocylindrus mediterraneus* are commonly found. In the inshore zone (Figure 2a) phytoplankton are very sparse and microflagellates are common. As summer progresses, the inshore zone extends as the thermocline deepens.

The Celtic Sea

This area has not been studied extensively, but there is no reason to suspect major differences from the pattern observed on the Atlantic shelf as these waters are fully stratified in summer (cf. work from the English Channel described by Holligan and Harbour, 1977; Maddock *et al.*, 1981). We are unaware of any detailed phytoplankton studies between Helvic Head and Courtmacsharry. Localized blooms nearshore do occur around the mouths of the larger estuaries as a result of nutrient inputs from the major rivers.

Western Irish Sea

The western Irish Sea stratifies in summer, yet the surface mixed layer is somewhat shallower than for the Atlantic or Celtic Sea shelf, with thermocline depths of only 20-30 m. The flora here contains a preponderance of microflagellates, particularly in early summer, with cell concentrations often in the range 10^6-$10^7.l^{-1}$. Some diatoms, in particular *Leptocylindrus danicus*, *L. minimum* and *Rhizosolenia delicatula*, are commonly found if not numerically dominant. The *Leptocylindrus* species are frequently associated with water in the proximity of frontal zones (Pingree *et al.*, 1978) as is the case here. *R. delicatula* is abundant on the mixed side of frontal zones, and is also recorded as constituting a large part of the spring bloom in the Western Irish Sea (Richardson *et al.*, 1985). The dinoflagellates *Scripsiella* sp. and *Prorocentrum micans* are common in June, and it may be inferred from published work that concentrations of these two organisms increase as summer progresses (Holligan *et al.*, 1980).

Mixed waters of the Irish Sea

Mixed waters to the south of the Western Irish Sea in early summer are generally rich in *Rhizosolenia delicatula*. Observations made in late summer to the north of the Celtic Sea front show the flora to be constituted mainly of microflagellates. It is presumed that these are the typical situations for the early and late summer respectively. A consequence of the absence of stratification is that due to low overall levels of available light the spring bloom never develops, summer growth is often light limited and consequently nutrients are always present. Towards the coastal boundaries of these mixed waters, where water depths are shallow, localized patches with a rich and varied flora may be found. These, however, are highly unpredictable in their floristic composition.

Fronts

The frontal boundaries between these major zones are themselves distinctive phytoplankton habitats with generally very high biomass levels. This is due to the combination of increased water column stability and the presence of nutrients in the euphotic zone (Figure 2b). The biomass is represented by large blooms of both diatoms and dinoflagellates, but frontal regions are renowned for exceptionally high concentrations of the dinoflagellate *Gyrodinium aureolum* (Pingree *et al.*, 1975; 1977), particularly on the stratified side of the front. This organism appears to be characteristic of the Celtic Sea front in summer (Holligan *et al.*, 1980). The Islay front to the north of Malin Head has consisted of both diatoms such as *R. delicatula* (Simpson *et al.*, 1979) and the dinoflagellates *Scripsiella* sp. (Simpson *et al.*, 1979), *Ceratium lineatum* (Holligan *et al.*, 1980) and *Gyrodinium aureolum* (Pingree *et al.*, 1978). Greater variability amongst the plankton at the Islay front is probably due to its proximity to salinity gradients associated with freshwater run-off into the Irish Sea and Firth of Clyde.

Southwest upwelling

The upwelling occurring in this region is highly variable in both its periodicity and magnitude (Raine *et al.*, 1990a). Events may prevail over time scales of several days or weeks, providing an alternation of conditions between upwelling and fully stratified (Roden, 1986). When absent, the water structure is very similar to that of the stratified Atlantic shelf whose flora would be typical of the region (Raine *et al.*, 1990b). When upwelling occurs to any extent diatoms flourish, particularly in the vicinity of the Fastnet Rock and along the south coast towards Courtmacsharry. Surface waters can be very cold (<11°C at 0 m inside Roaring Water Bay in mid-August) and typical spring bloom diatoms such as *Thalassiosira rotula/gravida, Lauderia borealis* and *Skeletonema costatum* can be surprisingly common. The more typical situation is intermediate between these two extremes and a variety of summer diatoms such as *Chaetoceros* spp., *Rhizosolenia setigera*, *R. hebetata* and *R. shrubsolei* are all common (Raine *et al.*, 1990a). As the water re-stratifies, the occurrence of dinoflagellates increases. The upwelling zone will be separated from the surrounding stratified water by a system of fronts, analogous in their flora to the tidal fronts described above. Their presence is possibly the origin of red tides of *Gyrodinium aureolum* recorded from the area in the past (Roden *et al.*, 1980, 1981).

Discussion

Although research into phytoplankton distributions around some parts of the Irish coast is as yet at a preliminary stage, nevertheless the link between water column stability and phytoplankton community composition already described holds for all areas visited, and for the present we assume that it is universal. Local detailed patterns may not always be consistent with this overall scheme but these have been in our experience the exception rather than the rule.

The biogeography of many marine organisms other than phytoplankton around the Irish coast may also be explained in terms of local physical processes rather than traditional associations with water masses. For example, due to upwelling areas being regions of high phytoplankton productivity, it is possible to explain the regular occurrence of baleen whales sited around southwest Ireland, as well as numerous colonies of seabirds including gannets and petrels situated in this area. Some hydroids (*Nemertesia antennina* and *N. ramosa*), which are confined to deeper waters at exposed sites on the west coast, are common and much larger in the southwest (Wood, 1988). Several Lusitanian species are quite uncommon here which may reflect the low water temperatures resulting from upwelling. Distribution maps of the urchin *Paracentrotus lividus*, the topshells *Gibbula umbilicalis* and *Monodonta lineata*, and the ratio of the summer breeding barnacle genus *Chthamalus* to the subarctic winter breeder *Semibalanus balanoides* (Southward and Crisp, 1954) around Ireland show clear associations with summer stratification conditions (Simpson, 1981).

Finally it must be considered whether this approach may be adapted to all coastal regions. The physical oceanography around Ireland is special in that a number of tidal fronts exist purely because of large tidal movements (Le Fevre, 1985). Additionally, the upwelling system off southwest Ireland appears to be unique amongst northwest European coastal processes. The area around southwestern Nova Scotia exhibits a complexity of tidal mixing and upwelling events (Fournier *et al.*, 1984) and may exhibit distributions analogous to those described above. This study suggests, however, that local physical processes are at least as important as more traditional empiricisms such as temperature and latitude when considering marine biogeography of coastal waters. Hopefully in time more information will become available to confirm or revise the description presented here.

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Possible influence of increases in mean sea temperature on Irish marine fauna and fisheries

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Summary

Should Irish mean sea temperatures rise, several species are likely to increase their numbers. These include pilchards and oysters which have been formerly abundant. Physiological responses such as promoted spawnings and increased growth of pre-recruits may result in increases in abundance of those species that inhabit, in particular, the shallow water fringe most influenced by insolation. Some non-native species may find conditions suitable for reproduction and develop populations, and in some cases may significantly compete with native species.

Introduction

Temperature is one of the most important physical characteristics determining the distribution of marine organisms. However, predicted changes as a result of global warming would also involve seasonal changes in rainfall and so localized changes in salinity and turbidity. Changes of mean sea level would have important effects on coastal lagoon systems, resulting in some new marine systems and greater rates of flushing of present embayments which in turn would also have an effect on sea temperature ranges. In this account possible influences of increases of mean sea temperature are discussed.

Since the last glaciation mean temperatures have fluctuated, with a climate optimum occurring from about 7000 to 5000 BP, a time when mean air temperatures attained values 2°C greater than at present (Lamb, 1965). Recent changes including a period of lower mean temperatures during the late 18th century, the little Ice Age, appear to have been global in extent. It is likely that mean temperatures will vary in the future as they have done for several thousand years. How these fluctuations are determined is by no means certain. Recent models predict increases of mean sea temperature (Houghton, 1991). The effect of such increases on some species as is discussed in this paper, with emphasis on range extensions of southern species.

In the English Channel and Celtic Sea variability of plankton has been described as being part of a long term "Russell" cycle (Cushing, 1982), and this may also be part of a worldwide phenomenon. Populations of most species are in a continuum of change, their abundance oscillating in accordance with physical and biological fluctuations and under the influence of man. The majority of changes in abundance and range probably escape our attention. However, dramatic changes in abundance are usually noticed and in some cases may result in changes of fishery landings. Kawasaki (1991) has shown landings of certain sardine species throughout the world have repeated and coinciding peaks of abundance. He suggests these fluctuations relate to changes in climate. Distributions of most marine organisms are incomplete, and extensions of range continue to be reported in biological journals. The completeness of biogeographical records is only as good as current taxonomy, the size and abundance of studied species, and the frequency of recorders. Relatively well known species are more likely to provide clear measurements of change, and these tend to be associated with fisheries. Future abundance and distributions of species may be predicted from past evidence and by knowledge of their physiological requirements and behaviour.

Likely changes of abundance based on historical evidence

Periods of higher mean sea-temperature over several years may provide conditions for some species to become more abundant. There is some evidence of former abundance of certain species in relation to higher sea temperatures. Two examples, pilchard and oysters are discussed.

The pilchard, *Sardina pilchardus* (Walbaum)

Records of pilchard on the Irish and English coasts date from 1591 when they were fished off Wexford (Went, 1943). This is a species subject to great fluctuations of abundance, and between these periods pilchard are either absent, or seldom captured. Pilchard, which form regular fisheries south of Ireland, and herring, *Clupea harengus* L., overlap ranges within

Irish waters. When pilchard are dominant, landings of herring often decrease. Southward *et al.* (1988) refer to this trend for English southwest coast landings since 1610 and they suggested that these fluctuations relate to small changes in climate. They found a relationship between pilchard abundance and air temperature records in Britain.

Went (1946) examined the history of the pilchard fishery in Ireland. He described 22 main landing sites ranging from Ardmore, Co. Waterford to Ballinskelligs, Co. Kerry and Co. Donegal. These records demonstrate that conditions have been favourable for pilchard fisheries in these areas. Some processing sites on the south coast dating back to 1611 still remain. Pilchards were pressed for the extraction of their oil which was used for lighting and cooking. Holes for the pressing beams were built into walls and cliff faces at these places.

Pilchard, when they appeared, occurred in great abundance. Went (1943) indicates Bantry owed its existence to this species in the 16th Century and for other ports the species was also a major economic asset. Pilchard were captured using a seine and two boats, one with ten men and another - the follower - with six. Fishing directions were given from the shore. These accounts, reported by Went, indicate that the pilchard came into shallow water and close to the shore in great abundance. The fishery took place from July until December or January.

In Irish waters there have been approximately seven major appearances since 1600 (1611-1689, 1726-1745, 1823-1824, 1833-1836,1869-1886, 1935-1943, 1955-1963, 1988-1991). The abundance of pilchards on the Cornish and Devon coasts, as reported in Southward *et al.* (1988), appeared approximately one month earlier to landings in Ireland, but occurred for similar durations (Went, 1946; Anon., 1869 - 1968). In the 1960's pilchard were captured off the Donegal coast. At this time the market for the species was poor and only part of the resource was exploited and reduced to fish meal.

Recently pilchard have again appeared off the west coast. These, although captured, have not been landed due to lack of demand. In the early 1980's pilchard eggs and larvae noticeably increased in the Celtic Sea (J. Molloy and E. Barnwall, pers. comm.). It is interesting to note that during this period the spawning times of herring became later, growth increased and stock size decreased (Molloy, 1984). Should there be a continued rise of sea temperature as has been predicted, pilchard may be expected to become more abundant in Irish waters.

The native oyster, *Ostrea edulis* L.

Oysters have been present in Ireland for thousands of years and are known from Pleistocene gravels (McMillan, 1964). Oysters were exploited in pre-historic times, almost certainly gathered in shallows or on the low shore. Their shells were cast to form mounds and indicate areas where oysters may have been formerly abundant. The oysters that resulted in the formation of shell middens, and recent oyster fisheries have both depended on natural spat production. Areas where only small numbers of oysters have been exploited in recent times, may have had greater numbers at some time in the past, as indicated by the presence of shell mounds. Local changes in topography such as sand bars and spits may have influenced oyster populations by altering hydrographic conditions. The majority of shell mounds were found to contain stone implements (Brunicardi, 1914), suggesting that many of these places were in use some thousands of years before now. There are several large oyster shell middens in the Forth valley, Scotland. One of these was dated as being occupied 4,000 to 2,000 years B.C. (Sloan, 1985). Some sites, such as those in Cork Harbour may have been in use until medieval times (O'Kelly, 1955).

Went (1962) gave an account of the distribution of the main oyster fisheries during and prior to their intensive exploitation over the last 150 years. However, shell middens appear in areas where there have been no recent records of oyster populations (Brunicardi, 1914). This suggests a difference in conditions for oysters since pre-historic times. Such a difference could also be explained by differences of mean sea temperatures in summer and its effect on oyster recruitment.

Shallow embayments, like Tralee Bay, develop high temperatures during sustained sunny periods. Once temperatures exceed 18°C large settlements normally take place and a good relationship between settlement intensity and sea temperatures has been found to exist over the period 1963 to 1973 ($r = 0.74$, $p = 0.01$) (Figure 1).

Should sea temperatures increase it is likely that consistent and intense settlements will take place in existing oyster areas and further that significant natural settlements of oysters will evolve elsewhere.

Likely changes of distribution and abundance based on current knowledge

Adult mullet, *Chelon labrosus* (Risso), are present on all coasts during summer but during winter appear only off the southwest coast. Where mullet spawn is not presently known, but their appearance on the southwest coast during the winter and spring may relate to this event. Hickling (1970) has suggested that they spawn in deeper water and according to Thompson (1963) may spawn in alternate years. In March to May, Kennedy and Fitzmaurice (1969) found specimens in spawning condition on the South coast. During April 1986 five ripe individuals, including three females oozing transparent eggs, were gill-netted at the entrance to Bantry Bay (pers. obs.).

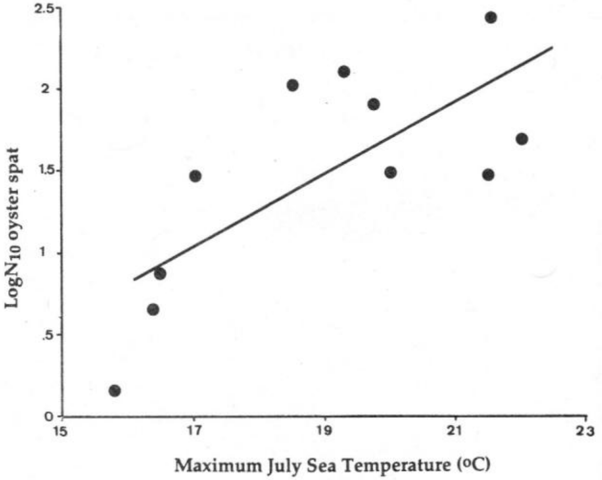

Figure 1. Relationship of mean numbers of individual oysters settled onto a standard unglazed plate, with maximum sea temperature (°C) recorded during July. Data is based on observations made in Tralee Bay and supplied by C. B. Duggan.

Chelon labrosus eggs and larvae have yet to be positively found in the northeast Atlantic (Russell, 1976). However, post-larvae are easily recognised and are often first noticed in small groups associated with drift at the sea surface. They appear inshore during July at Lough Hyne and form progressively larger shoals in the shallows where they remain until September-October. Variation of summer temperatures appears to have influenced mullet growth in Lough Hyne. 'O'- group mullet have an annual variation in size in August which relates to mean air temperatures from May to August ($r = 0.85$, $p = 0.01$) (Figure 2). Post-larval mullet are associated with the neuston. For this reason, air temperatures are likely to be of importance in determining their rate of growth, particularly during the time they appear in shallows and coastal ponds.

According to Kennedy and Fitzmaurice (1969), mullet growth is slow, variable, influenced by water temperature, and ceases in November until May or June of the following year. Survival may be promoted by entering the winter at a large size. In a related mullet species in the Black Sea, *Liza saliens* (Risso), those entering the winter at a size greater than 1g have a greater rate of survival (Kulikova *et al.*, 1986). According to Kennedy and Fitzmaurice (1969), *C. labrosus* are active feeders at temperatures above 10°C, but inactive and cease feeding below 8°C. Increases in sea temperature should promote a longer duration of faster growth, promote survival and could result in individuals spawning annually from a younger age.

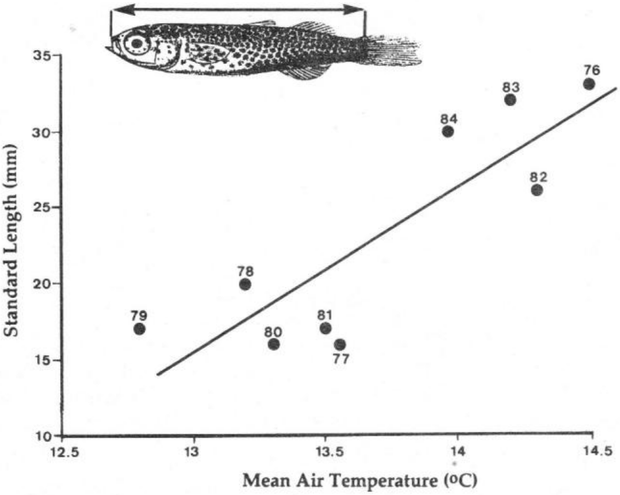

Figure 2. The largest modal size of young grey mullet captured in the shallows of Lough Hyne during August are related to mean air temperature (°C) for the period May to August (Valentia Observatory data). Years of collection are indicated.

Bass, *Dicentrarchus labrax* (L.), spawn on the southwest to southeast Irish coasts (Kennedy and Fitzmaurice, 1972) with the majority of 'O' group fish occuring on the southeast coast. This species occurs inshore for much of its life and is likely to be subject to the annual variations in air temperature. Although at the edge of its range in Ireland bass are found on all Irish coasts becoming less frequent to the north. Growth and spawning time according to Kennedy and Fitzmaurice (1972) is influenced by sea temperature, with faster growth and greater year class strength appearing in years with sunny summers. Bass may be expected to become more abundant on the south coast and to become more frequent in areas to the north.

Similarly, sea temperatures may also influence growth and recruitment of more southerly distributed species. Examples of these are garfish, *Belone belone* (L.), whose post-larvae appear on the south coast during warm summers (Minchin, 1984b), red mullet, *Mullus surmuletus* L., whose 'O' Group stages are known only from the southern Irish Sea and south coast (Minchin, 1987a) and red gurnard, *Aspitrigla cuculus* (L.), which, although present on all Irish coasts, its youngest year class is known only from the south coast (P. Connolly, pers. comm.; pers. obs.).

Strandings of large bones of cuttlefish *Sepia officinalis* L. appear on all Irish coasts, but these are more frequent in the southeast where both large and small bones can be found together (Figure 3). These two modes probably represent two year classes and their proximity to a spawning population. Commercial landings from the Celtic Sea were made in 1990 and Dingle in February 1991. Should this species breed in Irish waters it may be expected to increase its abundance and range.

Young longfin-tuna, *Thunnus alalunga* (Bonnaterre) migrations are associated with the 17°C isotherm which extends progressively northward to areas offshore, southwest or west of the Irish coast during the summer. The most northward extent of these migrations varies according to the progression of this warmer water in each year. Records of sea surface temperature, gathered by satellite, are provided for use by French vessels involved in this fishery (Piquion, 1985). Other species are associated with these tuna movements, including the bonitos *Sarda sarda* (Bloch) and *Katsuwonus pelamis* (L.). Ray's bream, *Brama brama* (Bonnaterre), although often associated with tuna, is not as dependent on these temperatures and can be found to range northwards to near the Faroes (Hoydal and Reinart, 1973). Increases in temperature would probably result in more northerly progressions of these species than in present years, and landings of them may thus increase.

Trigger fish, *Balistes carolinensis* Gmelin, are distributed throughout the central Atlantic, have been reported more frequently from Irish waters, (Went, 1978) and in greater numbers during the last decade. It is not clear whether this increase is due to population expansion off the west African coast or from some other cause. Although further numbers may continue to appear in future years, it is unlikely this species will form breeding populations in Irish waters. According to Luther and Fiedler (1976) they die once sea temperatures fall below 12°C, and in Ireland these temperatures fall below this during the autumn.

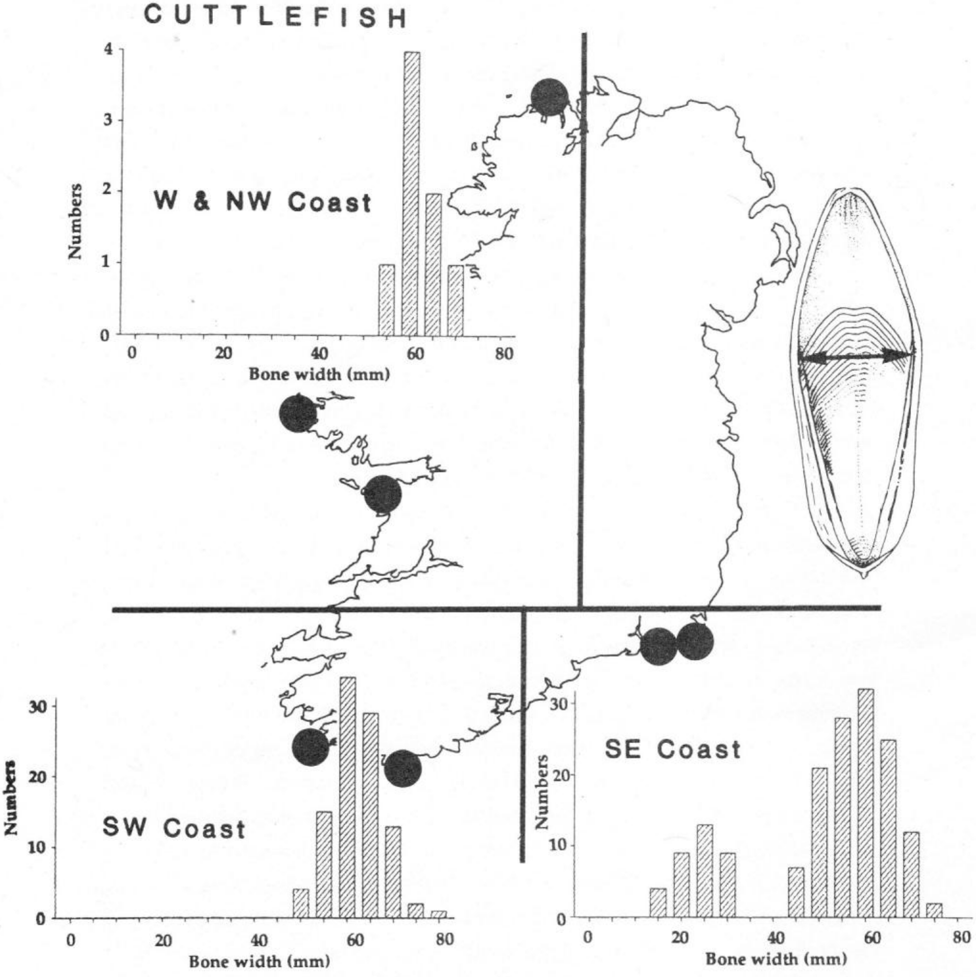

Figure 3. Size frequency distributions of cuttlefish 'bones' collected from the shore during 1991. Maximum width of 'bone', the measurement used in this study is also shown. 'Bones' collected per hour were: southeast coast 34, southwest coast 12, west and northwest coasts <1.

Increases in sea temperature may result in the appearance of some pest species. Range extensions by the eagle ray, *Myliobatis aquila* (L.), which can consume large quantities of oysters in France (Korringa, 1976), and the gilt-head sea-bream, *Sparus aurata* L., have implications for mollusc cultivation and diversity of the benthos.

Spawning in many invertebrates is synchronised by elevations of temperature and the sea-star *Marthasterias glacialis* (L.), common in shallow bays, is an example of this. This sea-star spawns within highly localised areas during moderate onshore winds on afternoons of sunny days (Minchin, 1987b). With increases in mean temperature, spawnings may become more frequent and lead to increased recruitment.

The sea-urchin, *Paracentrotus lividus* (Lamarck), spawns frequently during warm summers at Lough Hyne, and the echinopluteus stage appears in the plankton during July and August (pers. obs.). With increases of sea temperature further spawnings may result in increased settlements and promoted biomass. Exploitation of this species has reduced some populations to levels where fishing is not presently possible, however, with further knowledge of cultivation techniques some populations may become restocked by sowings of young urchins which then may contribute to natural settlements. Should summer sea temperatures increase, opportunities for the range expansion of this species may take place.

Range extensions resulting from the activities of man

The Pacific oyster, *Crassostrea gigas* (Thunberg), was introduced to Ireland to supplement the high demand for oysters. It was thought to be unable to spawn in Irish waters. However spat resulting from a natural settlement in 1990 were found during July 1991 in Donegal Bay (C. B. Duggan, pers. comm.). The exotic Pacific clam, *Ruditapes philippinarum* (Adams and Reeve), is also widely cultivated in Ireland and may also be capable of spawning to produce settlements, should sea temperatures rise.

Many exotic species are known to have been accidentally introduced to Ireland, these include: the Korean sea squirt *Styela clava* Herdman, the tube worm *Mercierella enigmatica* Fauvel; the parasitic copepod *Mytilicola intestinalis* Steuer; and the slipper limpet *Crepidula fornicata* (L.). These were introduced either with transfers of oysters or with shipping.

Transfers of fouling organisms may continue to take place, but risks from this source were significantly reduced as a result of effective biocide paint preparations such as organotin paints. Many ports in Ireland have a fully marine or estuarine environment, and as ports in many areas of the world are moving downriver towards more marine conditions, the possibilities for transfer become more likely.

The transfer of ship's ballast water between biological provinces is currently an area of concern. As shipping becomes more efficient and journeys become shorter there will probably be an increase in the survival of transferred biota. This may result in further transfers of exotic organisms and the establishment of new populations. There is evidence that the cysts of toxic and other algal species are transferred by means of ballast water (Hallegraeff and Bolch, 1991, 1992). Algal blooms, previously unknown in various parts of the world, have appeared and the species responsible may have been transferred there by shipping (Maclean, 1989). Some blooms are toxic and can result in mortalities of marine organisms, but more usually toxins become stored in shellfish which renders them unsuitable for consumption.

Non-toxic blooms can also result in significant mortalities of marine organisms. Morrison *et al.* (1991) report the collapse of a diatom bloom causing deoxygenation of the sea floor in an area where herring eggs had been recently spawned. These eggs, laid on the sea floor, were covered with the decomposing algae and suffered a high mortality. A similar event took place in Bantry Bay, between Whiddy Island and Shot head, during May 1989 and may have been due to the collapse of an algal bloom. Benthic macrofauna, notably the Dublin Bay prawn *Nephrops norvegicus* (L.), the scallop *Pecten maximus* (L.) and the burrowing urchin *Echinocardium cordatum* Pennant, suffered high mortalities. Diving observations at the time suggest that this may have been due to oxygen depletion. Increases in temperature may give rise to similar events in bays and inlets. Warmer water contains less dissolved oxygen yet at the same time there is a greater demand for oxygen by ectothermic organisms which may exceed the supply available.

Man may modify populations by exploitation, in particular those that have a high value such as *P. lividus* or those that are large late maturing species such as the common skate, *Raja batis* L. This skate is presently extinct in the Irish Sea (Brander, 1981) and is seldom found elsewhere in harbours and bays where they were formerly common.

Should sea temperatures increase, opportunities for the cultivation of bass, sole *Solea vulgaris* Quensel and turbot *Psetta maxima* (L.) may evolve and replace salmonid cultivation on the southwest and western coasts. Sea temperature increases would also greatly benefit oyster cultivation. Ponds presently used for the spawning and settlement of spat, on account of the higher water temperatures contained within them when compared with the sea, are likely to become more widespread.

To enable monitoring in the future, it will be neccessary to have an accurate account of present conditions so that changes can be measured. For example, it will be neccessary to have:

1. Accurate statistics of each species landed. It is unfortunate that landings of many different species are combined;

2. A regular sequence of measurements of sea temperatures about the Irish coast. Lightship station records for the early part of this centuary formed useful data sets, these are no longer kept because lightships have been decommissioned. Sea temperature records from Malin Head and offshore rarely reflect conditions found in Irish bays;

3. Reference areas where annual biological observations can be made. Although Lough Hyne, Galway Bay and Strangford Lough are well studied there are few phenological records kept;

It is unlikely that faunal changes, should they take place in the future, will evolve and mirror the composition of more southern communities. The complex ecological interrelationships cannot spontaneously evolve in Ireland once physical conditions become suitable. Many species are sedentary, have short planktonic lives and so those forms living some distance to the south of Ireland may never appear unaided. In addition should they extend their ranges to Ireland the establishment of these as well as other normally associated species may take considerable time and may be modified considerably by the introduction of cosmopolitan species by shipping.

Acknowledgements

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Trigger fish in Irish waters: a biogeographical review

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Summary

The trigger fish (*Balistes capriscus* Gmelin, 1789) has exhibited a phenomenal increase in abundance in Irish waters during recent years. A biogeographical survey of the species' distribution and abundance in other regions of the North and South Atlantic indicated that the trigger fish has also been increasing in these areas. It is possible that changes in global climate and/or oceanographical conditions may have influenced the recent increase in trigger fish abundance. The trigger fish may be a useful indicator species for monitoring such changes.

Introduction

The trigger fish, *Balistes capriscus* Gmelin, 1789, is found on both sides of the North and South Atlantic. In the Western Atlantic it ranges from Nova Scotia southwards through the Gulf of Mexico to Argentina (Briggs, 1958; Moore, 1967). In the Eastern Atlantic it has been recorded from as far north as Scotland (Dobson, 1984) and southwards to Angola. It is common around the Azores, the Canary and Madeira Islands, and in the Mediterranean but it is rare in the Black Sea (Tortonese, 1986).

In 1949 Went considered *B. capriscus* as "rare" in Irish waters; only six records are known up to that date. However, by 1976, Went and Kennedy regarded the species as "scarce" rather than "rare" due to a large increase in records during the early 1970's (Went, 1978). By 1985, the species appeared to have become a regular summer and autumn time visitor (Quigley, 1985). However, during the last three years, a phenomenal increase in trigger fish abundance occurred in Irish waters. Between 1989 and 1991, a total of 184 specimens were recorded, representing at least 53.6% of the total number of specimens documented since the species was first reported in 1845 (Quigley *et al.*, 1993).

Possible reasons for the recent increase in trigger fish abundance in Irish waters are here examined in relation to observed changes in the species' biogeographical range in other regions of the Atlantic Ocean.

Methods

The status of *B. capriscus* in Irish waters was reviewed by collating and analyzing all known records of the species. The database includes details on a total of 343 published and unpublished records. In order to obtain up-to-date information on the current distribution and abundance of trigger fish, both within and beyond its known range, data was sought from an extensive number of foreign museums and marine biology institutes. Respondents are referred to in the text and acknowledgements.

Results

Trigger fish in Irish waters

Prior to 1958, only six records of *B. capriscus* are known from Irish waters. However, between 1958 and 1991, a total of 339 specimens were recorded (Figure 1). Went (1978) reviewed records up to 1976, while Quigley (1985) updated the records to 1984, and Quigley *et al.* (1993) subsequently reviewed records up to 1991. Although there have been large fluctuations in the annual numbers of specimens recorded, there would appear to have been two main cycles of abundance during the last two decades together with a phenomenal increase in records during the last three years. Over 53% of the total number of specimens recorded since 1845 were reported between 1989 and 1991 when summer seawater temperatures were noticeably warmer (Figure 1).

The monthly frequency of occurrence of *B. capriscus* in Irish waters is shown in Figure 2. The influx of trigger fish would appear to occur in August before sea temperatures decline. However, the pattern of monthly frequency occurrence may vary from year to year depending on sea water temperatures.

The vast majority of specimens were recorded from the west and southwest coasts, while the species was only rarely recorded from the east and northeast coasts.

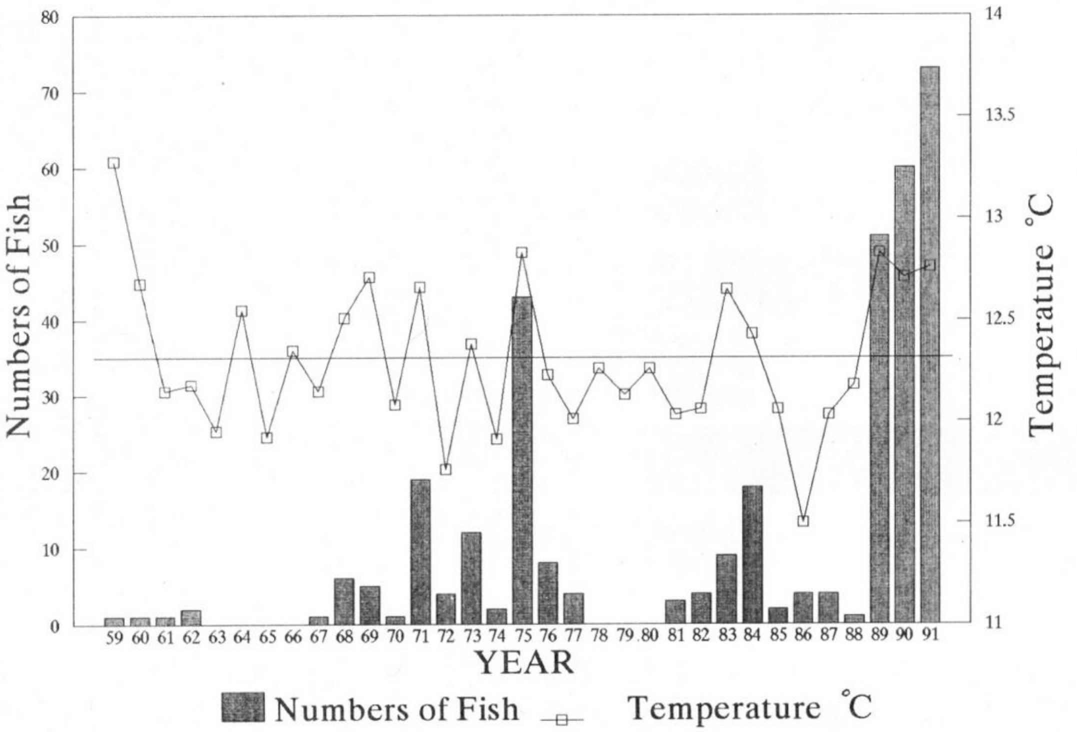

Figure 1. Annual numbers of trigger fish (*Balistes capriscus*) in Irish waters, together with the annual mean seawater temperature (July - December) at Malin Head, Co. Donegal.

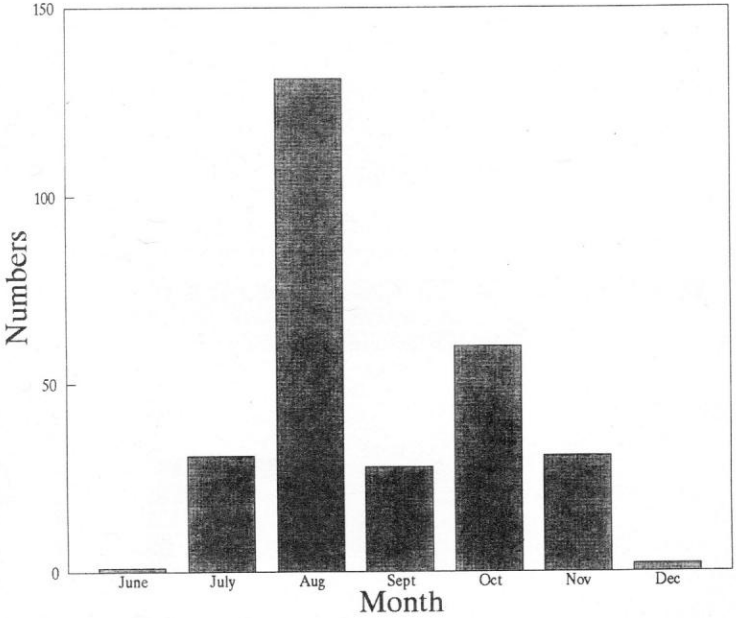

Figure 2. Monthly frequency occurrence of trigger fish (*Balistes capriscus*) in Irish waters.

Table 1. Length and weight statistics of trigger fish captured in Irish waters. T.L. = total body length; Wt. = total (wet) body weight; N = number of fish examined.

	T. L. (cm)	Wt. (g)
Mean	35.3	887.6
Minimum	18.0	120.0
Maximum	49.5	2267.9
S. D. (±)	7.0	400.0
N	88	96

The range, mean, and standard deviation (SD) of observed total lengths (T.L.) and weights (Wt.) are summarized in Table 1. The majority (74%) of the trigger fish were found to be within a relatively narrow length range (30-45 cm); only 7.4% were greater than 45 cm. However, the same fish exhibited wide variation in weight at any given length (Figure 3). This probably reflects size variation due to age, sex and maturation levels. Indeed, a specimen captured in October 1989 off the southwest coast was found to be close to spawning (Witthames, pers. comm.). Furthermore, Johnson and Saloman (1984) found wide variation in length at age and overlays of length ranges between ages in trigger fish from the Gulf of Mexico.

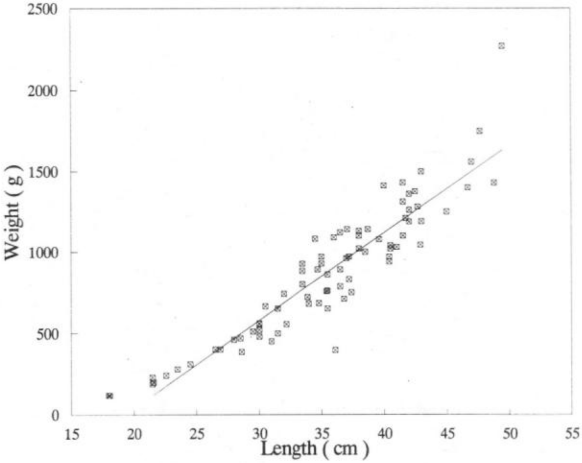

Figure 3. Relationship of body weight with length for trigger fish in Irish waters.

About 21% of the specimens were sighted by scuba divers in recent years, particularly in rocky areas off the southwest coast (Table 2). The species has also been captured by anglers more frequently in recent years. Although approximately equal numbers of specimens were captured by demersal trawls and pelagic drift nets in offshore waters, the majority of specimens were taken in inshore waters by other demersal methods (Table 2). The relatively high frequency of captures in lobster pots might suggest that the species has a habit of scavenging or is attracted to the imprisoned crustaceans.

A significant proportion of the specimens were found stranded, particularly towards the end of the season (October to December). Since it has been reported that trigger fish become dormant at temperatures below 15°C (Dobson, 1984), and that death occurs at temperatures below 12°C (Luther and Fiedler, 1976), it seems likely that the species becomes disorientated, eventually dies and gets stranded as temperatures fall below critical levels, usually in October. It therefore seems unlikely that the species could survive all year round in Irish waters at current ambient sea temperatures.

Table 2. Capture methods of Irish trigger fish.

Method	Number	%
Sighted	65	20.8
Rod & Line	44	14.1
Trawl	40	12.8
Drift Net	37	11.8
Lobster Pot	36	11.5
Trammel Net	32	10.2
Stranded	28	8.9
Seine Net	21	6.7
Hand Net	4	1.3
Speared	3	1.0
Salmon Weir	2	0.6
Bag Net	1	0.3
Total:	313	100.0

Trigger fish in other northern European waters

In 1969 Wheeler considered the trigger fish as rare in northern European waters, particularly north of the English Channel and the southwest Irish coast. However, in late summer it occurred almost annually to the south of this area but there was nothing to suggest that it was resident in these waters. Indeed, all the evidence indicated a northward movement with the summertime warming of the sea.

During the 1960's and 1970's the trigger fish appeared to increase in both frequency and range in British waters (Blacker, 1964, 1973; Dobson, 1984; Wheeler and Blacker, 1972; Wheeler *et al.*, 1975). Indeed, during the 1970's, the species occurred in numbers in the North Sea (Blacker, 1981) and penetrated even into the Thames estuary (Andrews and Wheeler, 1985). During the same period, the species was recorded from the coasts of Denmark (Neilsen, pers. comm.), Holland (de Groot, 1973), and Belgium (De Clerck, 1975). By 1978, Wheeler considered that the trigger fish appeared to make regular annual migrations into northern European waters, where its relative abundance varied from year to year.

During the 1980's and early 1990's trigger fish numbers appeared to increase further. In 1983, two specimens were recorded from the Dutch coast (de Groot, 1986), while in 1984, several specimens were recorded from as far north as Scotland (Dobson, 1984). Large numbers of trigger fish were also captured by anglers off the southwest coast of England in 1984 and 1989 (Anon, 1984; Cooling, 1989). During 1991, trigger fish appear to have occurred more frequently than usual in UK waters, particularly in the west and northwest of Scotland (Gill, 1991; Gordon and Stenhouse, pers. comm.). In 1991, Wheeler (pers. comm.) remarked that "the trigger fish had become so common in English waters that it is probably the most striking change in the fauna this century." Indeed, based on unsubstantiated reports on the occurrence of very small "young" trigger fish, Wheeler (pers. comm.) speculated that the species may be "breeding quite close to our coasts (perhaps in Biscay)."

In northern European waters, trigger fish have not been recorded from Germany (Karrer, pers. comm.), Latvia (Uzars, pers. comm.), Estonia (Aps, pers. comm.), Russia (Sazonov, pers. comm.), Finland (Koli, pers. comm.), Sweden (Kullander, pers. comm.), or Iceland (Petersen, pers. comm.).

Trigger fish in southern European waters and the Mediterranean Sea

In 1976, the trigger fish was regarded as rare north of the Gulf of Gascony in southwest France (Harambillet *et al.*, 1976). However, during the 1960's, 1970's and 1980's, the species was recorded with increasing frequency as far north as northwest France (Lebeurier, 1971, 1972; Le Gall, 1970; Quéro, 1973; Gueguen *et al.*, 1975; Quéro *et al.*, 1976, 1986; Delmas *et al.*, 1986).

Unfortunately, very little information was available regarding the current status of *B. capriscus* in Spanish or Portuguese waters. Although Quéro (1973) alluded to "the usual occurrence of the species during the summer months on the northern coast of Spain", there are recent unconfirmed reports that the species may be increasing in abundance off the Portuguese coast and around the Azores (Saldanha, pers. comm.).

Tortonese (1986) regarded the trigger fish as common in the Mediterranean. Although the species is also common in the southern Adriatic Sea, it is regarded as very rare in the northern areas, and only occurs in some years in the middle Adriatic in the region of Split (Croatia). The last such occurrence was recorded in 1986/87 when some specimens were caught near the islands of Zadar, Kornati and Losinj (Pallaoro, pers. comm.). In 1969 and again in 1978, specimens were reported from the extreme north of the Adriatic in the Gulf of Venice (Boldrin and Rallo, 1980).

Trigger fish in West African waters

Up to 1970, the trigger fish was considered to be a relatively rare species in West African waters (Caverivière *et al*., 1980). However, between 1971 and 1980 a great increase in trigger fish abundance occurred sequentially in the waters between Ghana and Mauritania. Proliferation began off Ghana in late 1971 and early 1972; off Togo and Ivory Coast in March 1972; off Guinea, Guinea Bissau and Sierra Leone from March 1974 to September 1976; off Senegal in 1978 and 1979; and off Mauritania in 1980 (Caverivière, 1982, 1991). Although the species was always regarded as common around the Madeira Islands, off the coast of Morocco, there was no evidence of any major change in abundance during the above period (Maul, pers. comm.).

A comparison between catches of nine different species of fish taken off Ghana in 1976 showed that the trigger fish was 1,003 times more abundant than in the period 1962-65 (Pupyshev, 1982). Indeed, the total trigger fish biomass was estimated at over one million tonnes, which represented more than half the total fish biomass on the continental shelf between Cape Verde (Senegal) and Nigeria (Caverivière, 1982, 1991). A further survey carried out along the coasts of Guinea, Sierra Leone and Guinea Bissau during November/December 1978 found that trigger fish accounted for 60% of the total estimated fish biomass of 730,000 tonnes (Marchal *et al*., 1979).

Afterwards, in 1986, a net decrease in abundance, without any relationship to exploitation, was noted in the whole area, while significant quantities of trigger fish were found further south off Gabon and Congo (Caverivière, 1991). However, in 1987 there was some evidence that the species was beginning to increase in abundance again off Ivory Coast (Oliver *et al*., 1987). More recently, however, the abundance of trigger fish off the West African coast decreased sharply in 1989 and current stocks are reported to be 2-3 orders lower than they were during the period of maximum proliferation (Sazonov, pers. comm.).

The following multifactorial hypothesis was put forward by Binet (1982) in order to explain the dramatic proliferation in trigger fish abundance off the West African coast:

1. Prior to the trigger fish population explosion in 1972, the sardine (*Sardinella aurita* Valenciennes) supported a very important, albeit extremely variable, fishery off the West African coast. Annual catches usually ranged from 8,000 to 40,000 tonnes, but in 1972, 94,000 tonnes was harvested, causing a spectacular decrease in catch during the following years. It was not until 1976 that the stock appeared to recover.

2. Coastal oceanographic observations (temperatures and zooplankton biomass) together with terrestrial hydrological data (river flows) recorded in Ivory Coast since 1966 were used in the study of the sardine fishery collapse. Between 1971 and 1978 a change in the ecosystem appeared to coincide with the Sahalian drought, a decrease in zooplankton biomass, and the collapse in the sardine fishery, together with the sudden increase in trigger fish abundance .

3. The collapse in the sardine fishery was thought to be due to over-exploitation of juveniles during 1972, followed by a period of adverse weather conditions for the sardine larvae. The sardine is a stenohaline species, migrating towards the surface and the shore during periods of upwelling. In 1972 the drought probably reduced the amount of inshore estuarine water and this in turn may have resulted in the exceptional availability of sardine which finally led to the catastrophic over-fishing of this species in that year.

Caverivière (1991) speculated that the collapse of the sardine fishery may have favoured, in some unknown way, the proliferation of the trigger fish population. The reproductive capacity and parental strategy of the trigger fish, particularly its relatively high fecundity and the protection it provides for its eggs, may also have contributed to the species rapid proliferation.

Trigger fish in North American waters

In 1966, Leim and Scott reported that *B. capriscus* was found occasionally as far north as Nova Scotia (Canada). However, in 1988, Scott and Scott extended the northward range of the species following the capture of a specimen off Newfoundland (50 39'N 57 18'W) in September 1983. Although the remains of another specimen was found near Halifax (Nova Scotia) in 1990, the species is still generally regarded as exotic in this area (Silvert, pers. comm.).

Prior to 1979, the trigger fish was regarded as rare in New York waters. However, between 1979 and 1981, several specimens were captured off Long Island by both lobster fishermen and anglers (Briggs *et al.*, 1985). More recently, anglers recorded exceptional catches in the same area: 5,500 specimens in 1988; 30,000 specimens in 1989; and 8,900 specimens in 1990. Although the trigger fish is now regarded as a regular summer and autumn addition to the state's fish fauna, commercial catches during the same period appeared to be relatively low and the species does not appear to be common north of Cape Cod (Massachusetts, USA) or east of Long Island (Briggs, pers. comm.).

Further south, autumn trawling surveys off North Carolina indicated that trigger fish have been gradually increasing in numbers since 1984, with a dramatic increase in 1990. In general, the species is found north of Cape Hatteras in the autumn when seawater temperatures are warmer, whereas, in spring, when the water is cooler, the species stays to the south of this area (Kostovick, pers. comm.).

In 1968, Bohlke and Chaplin could find only a single specimen of trigger fish from the Bahamas (southwest Florida). However, in recent years the species has come to represent one of the most abundant fish resources subjected to exploitation off Panama City (northeast Florida) in the northeastern Gulf of Mexico (Johnson and Saloman, 1984). The increase in demand for the species was reflected in the dramatic increase in commercial landings on the west coast of Florida between 1967 (7.7t) and 1977 (26.7t).

Trigger fish in South American waters

A comparison between the results of trawl surveys carried out in southern Brazilian waters during 1970 and 1980, showed an increase in the distribution and abundance of *B. capriscus* (de Lema *et al.*, 1975; Matsuura and Katsuragawa, 1981). Although the reason for the emergence of the trigger fish population is not yet clarified, some researchers attributed it to the resistance of the species to polluted environments.

Further south, in 1981, the species was captured in unusually large numbers between 34° and 37°S during research cruises off the coastal waters of Uruguay and Argentina (Garcia and Menni, 1982; Cousseau, pers. comm.).

Conclusions

It is clear from the biogeographical review that *B. capriscus* has been extending its range and abundance on both sides of the North and South Atlantic during recent decades. The phenomenal increase in trigger fish abundance in Irish waters would appear to be part of this overall trend.

The greater geographical range and general abundance of trigger fish may be related to changes in climate and/or oceanographical conditions (Quigley, 1985). Indeed, the occurrence of the species was shown to be related to the presence of warm seawater temperatures off the coast of northern France (Quéro, 1973).

Global temperatures, for example, have risen by about 0.5°C this century (Sweeney, 1989). Indeed, the exceptionally high temperatures experienced during the last three years only continued the pattern set in the

1980's which was the warmest decade of the century. Although the thermal dominance of the 1980's on a global scale was not reflected as dramatically here in Ireland (McWilliams, 1992), there was a significant increase in mean seawater temperatures during the last five years (Figure 1). It is interesting to observe the close correlation between peaks in trigger fish abundance and above average seawater temperatures.

However, it is less clear, at this stage, whether the trigger fish found in Irish waters are derived from either eastern or western Atlantic stocks. It may be more difficult, on account of the prevailing northeast Atlantic currents together with the species relatively feeble swimming powers, for the trigger fish to get into northern European waters from the Iberian Peninsula than it is for them to recruit from mid-Atlantic stocks around the Azores.

The results of a comparative analysis of morphometric characters of trigger fish from the sub-regions of Guinea Bissau and Sierra Leone with individuals from the sub-regions of the southern part of the Gulf of Guinea and the open part of the Atlantic Ocean, indicated that significant differences existed between them (Sazonov and Galaktionova, 1987). A similar study would need to be carried out on Irish and western Atlantic stocks in order to confirm their origin.

Although exotic species such as trigger fish may be of little or no commercial value in Irish waters, their status needs to be evaluated on a continuous basis because it is becoming increasingly apparent that uncommon species, and particularly those on the edge of their distribution, can be essential indicators of environmental change (Swaby and Potts, 1990).

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Climate change and the future for the cockle *Cerastoderma edule* in Dublin Bay- an exercise in prediction modelling

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Summary

The cockle, *Cerastoderma edule,* is a typical littoral species of Dublin Bay. It is present in just less than 50% of the intertidal and contributes around 60% of the total macrofaunal biomass. This pre-eminence seems to be a position it has held over the centuries. However, the predicted global climate change will alter the environment of the cockle, firstly through an altered temperature regime and secondly through a rise in sea level. Rises in sea level will mean an overall reduction in intertidal area, with a consequent reduction in the cockle population. Rises in temperature, while unlikely to be directly lethal, may promote instability in the population with cycles of scarcity and abundance. Other possible effects, particularly system change such as increased predation or changes in inter- and intra-specific competition, are expected to take place but are very much more difficult to assess.

Introduction

The cockle, *Cerastoderma edule* (L.), is one of the most prominent species in Dublin Bay. Wilson (1982, 1983a) found it distributed throughout the intertidal from the Bull Island lagoons out to low water mark at Sandymount and Dollymount strands (Figure 1). Highest densities, and greatest biomass were recorded close to mid-shore (Wilson, 1982). This is similar to observations made elsewhere in Germany and the Netherlands (Dankers and Beukema, 1975).

Cerastoderma edule is one of the species nominated under the European Community Concerted Action on Science and Technology (COST) 647 intertidal group programme for long-term monitoring. A synthesis of data, including data from Dublin Bay, on population structure and fluctuations in recruitment and density has recently been published (Ducrotoy *et al.*, 1991). This synthesis pointed out the great annual variability in densities of C. *edule* at many European locations. However, populations in Dublin Bay never seemed to attain densities of some thousands per metre square reported elsewhere, nor did they seem to be subject to the same magnitude of changes in population density (Ducrotoy *et al.*, 1991).

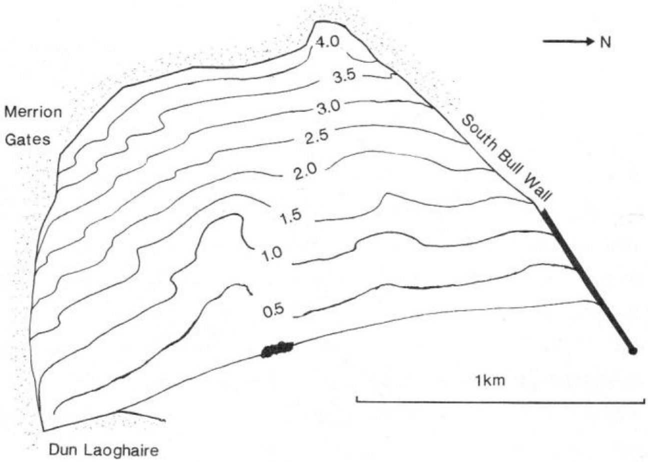

Figure 1. Depth contours (m above Chart Datum) of the South Bull, Dublin Bay.

Until the fishery was prohibited for reasons of public health, Dublin Bay sustained an admittedly small commercial fishery for cockles up to the beginning of this century (West *et al.*, 1978). The populations of the south Bull were re-surveyed by West *et al.* from 1970 to 1972 who concluded that there had been little change in their abundance since commercial times and that the population could still maintain a fishery of around 20 tonnes per annum. However, they (West *et al.*, 1978) did point out that densities were very low for a commercial operation.

The fishery terminated due to sewage contamination. Studies of pollution in Dublin Bay in cockles and the other biota in Dublin Bay has received considerable attention in the last ten years or so (e.g. Wilson, 1983b; Wilson *et al.*, 1990). More recently, public attention has been focussed on another threat to coastal ecosystems, namely the possible impacts of climate change. Various, and wildly differing, scenarios have been predicted (Beukema *et al.*, 1990; McWilliams, 1992), but overall there is some agreement that there may be a general warming of 2°C and a concomitant rise in sea level of 50 cm by the year 2050 and up to 1.0 m by 2100.

In this paper, the possible effects of climate change, in particular sea level rise, on distribution and densities of C. *edule* are examined, taking the South Bull in Dublin Bay as an example.

Methods

The distribution map for C. *edule* produced by Wilson (1982, 1983a) was used along with height contours for the south Bull. The tidal height observations were fed into ARCINFO Geographical Information System (GIS) system and a regularized map generated (Figure 1). The system also generated a tidal height for each station sampled by Wilson (1983a) and this data in turn was used to calculate the relationship between density and tidal height.

Two models of the relationship of cockle density with shore level were set up. The first model averaged the cockle density over the areas enclosed by the depth contours from which the following equation was derived

$$\text{Density}\quad 0.25\text{m}^{-2} = -5.66 + 15.55\ \text{TH} - 3.16\ \text{TH}^2 \text{..........(a)}$$

where TH = contour height above Chart Datum in metres. The second model regressed the individual data for each site sampled, using the cockle density at each site with the height of each site generated from the GIS map. This relationship could be expressed

$$\text{Density}\quad 0.25\text{m}^{-2} = -18.96 + 21.92\ \text{TH} - 3.61\ \text{TH}^2 \text{..........(b)}$$

where TH = site height above chart datum in metres. These equations were then used to examine the density/tidal height relationship and to generate the cockle population densities under scenarios of gradually increasing sea level.

Results and Discussion

Solving equations (a) and (b) above for tidal height gives maximum densities of C. *edule* at +2.46 m and +3.03 m respectively. Mean sea level

(MSL) in Dublin Bay is around +2.5 m, so the optimum shore height for the cockle would seem to be about MSL or slightly above, depending on the relationship used. This observation agrees well with that of Dankers and Beukema (1975), who concluded that the cockle attains its maximum densities around +0.8 m in the Wadden Sea where the MSL is about +0.9m.

The landward limits of the south Bull are fixed by sea-walls except for a small gap at Merrion gates. Presently, high spring tides reach these walls, leaving little possibility of a landward extension with an overall rise in sea level.

As sea level rises, and assuming that there will be no redistribution of sediments, the extent of the intertidal zone will diminish. Table 1 and Figure 2 show the projected reductions corresponding to rises of 20 cm, 50 cm and 100 cm respectively with reductions in the extent covered by the different contours. Depending on the extent of the rise, some contours are reduced, while others remain relatively unaffected, with the upper levels progressively reduced as sea level rises. The reduction of intertidal area, by up to 50% in some cases, will reduce the habitat for C. *edule* but because of the differential reduction in the areas falling within predicted contours, the effect on overall C. *edule* numbers is difficult to assess. Table 2 shows the estimated reduction in total numbers of C. *edule* under different sea level rise projections using models (a) and (b).

Table 1. Areas (km^2) falling within height contours (expressed as metres above Lowest Astronomical Tide which approximates to chart datum) under different sea level rise scenarios.

Sea level rise (cm)	Contour (m)								Total area (km^2)
	<1.0	1.5	2.0	2.5	3.0	3.5	4.0	>4.5	
Present (0.0)	2.11	1.65	1.48	0.90	0.84	0.74	0.66	0.36	8.74
+20	2.70	1.32	1.37	0.67	0.95	0.61	0.58	0.19	8.39
+50	1.65	1.48	0.90	0.84	0.74	0.66	0.36		6.63
+100	1.48	0.90	0.84	0.74	0.66	0.36			4.98

Model (a) of course gives the actual numbers for the present, but model (b), as can be seen from Table 2, gives a very close estimate of the cockle population numbers. Over the expected range of sea level rise, both models give roughly the same numbers. Should there be a rise in sea level of 1.0 m the cockle population on the south Bull would be almost halved.

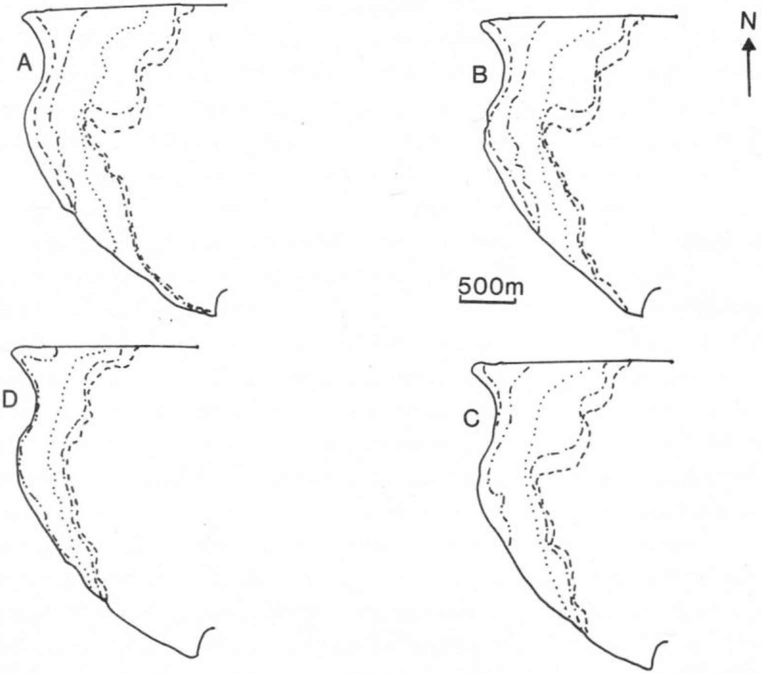

Figure 2. Depth zones (- - - 0.0m; -·-·- 1.0m; ····· 2.0m ; -··-··- 3.0m; —·—·— 4.0m) on the South Bull under different sea level rise scenarios: (A) at present; (B) +20 cm; (C) +50 cm; (D) +100 cm. See also Tables 1, 2.

Table 2. Numbers (x 10^6) of *Cerastoderma edule* on the south Bull under different sea level rise scenarios (nc - not calculated).

Sea level rise (cm)	Model (a)	Model (b)
Present (0.0)	224.5	235.4
+10	nc	223.6
+20	204.3	212.6
+50	186.2	176.5
+100	135.1	121.8

The results shown in Figure 2 are based on model (a) which was slightly the more conservative and for which the optimum tidal height more closely matched that (MSL) reported elsewhere. The shift of the population up the shore can be clearly seen.

In addition to the cockle population the other intertidal fauna will be affected and the effects will clearly vary according to the species and its preferred height. However, it would seem that even under this scenario, the system itself would continue to function, albeit in a somewhat altered form. More serious could be the effects on the bird populations, which will not only suffer reduced feeding areas and a significant drop in prey, but also in all probability their high tide roosting areas, which are severely restricted in the south Bay due to the urbanization, may disappear entirely.

It is difficult to determine the effects of increased temperatures on cockle populations in Dublin Bay. Ansell *et al.* (1981) have shown that the upper thermal lethal limit for *C. edule* was around 30°C and that this limit was not significantly altered by acclimation. *C. edule* is distributed along the length of the European Atlantic coast including areas where there are much higher temperatures than those in Dublin Bay. Accordingly, a temperature rise of a couple of degrees is extremely unlikely to result in direct mortality.

Indirect effects of increased temperature are more difficult to assess. The temperature at which burrowing is inhibited (around 28°C) is rather less than the lethal temperature (around 30°C) (Ansell *et al.*, 1981), but as with the lethal limit, it is difficult to see that *C. edule* would be directly affected. More subtle effects have been suggested by Wilson and Elkaim (1991) for *Tellina tenuis* and *T. fabula*, which, like the cockle, are found in the Dublin Bay intertidal. These effects include a general shift in the population down the shore, in which case the impact of sea level rise and temperature increase may be antagonistic; a tendency toward a different life style and in particular toward a smaller maximum size and toward younger and more frequent spawning; and the possibility in a shift in the pattern of predation from vertebrates such as fish or birds to invertebrates such as predatory gastropods.

For a number of years now, long-term monitoring data on the cockle, and other selected species, has been gathered under the EC COST 647 programme. A preliminary attempt to bring together this cockle data and to relate changes to anthropogenic or environmental variables was presented by Ducrotoy *et al.* (1991). In this synthesis, the main factors in the fluctuations of the cockle populations were identified as severe winters and eutrophication. In fact Dublin Bay was rather exceptional in that there did not seem to be any large fluctuations in cockle populations as reported at the other European sites. The same trend was found in *Macoma balthica* (Desprez *et al.*, 1990) and the explanation may be the small temperature range in Dublin Bay. Any change in this climate pattern may thus have consequences out of all relation to the magnitude of the change in absolute terms.

There are temporal changes in the cockle populations in Dublin Bay (Figure 3). Data from West *et al.* (1978) from 1971 and 1972 suggest very low population densities, a situation remarked upon at the time by West *et al.* (1978), who concluded that it had been the extent of the cockle beds rather than the density which had sustained the traditional fishery for so long. West *et al.* (1978) used a 6 mm mesh rather than a 1 mm mesh used in the later work, but even so it is improbable that this alone explains the different results.

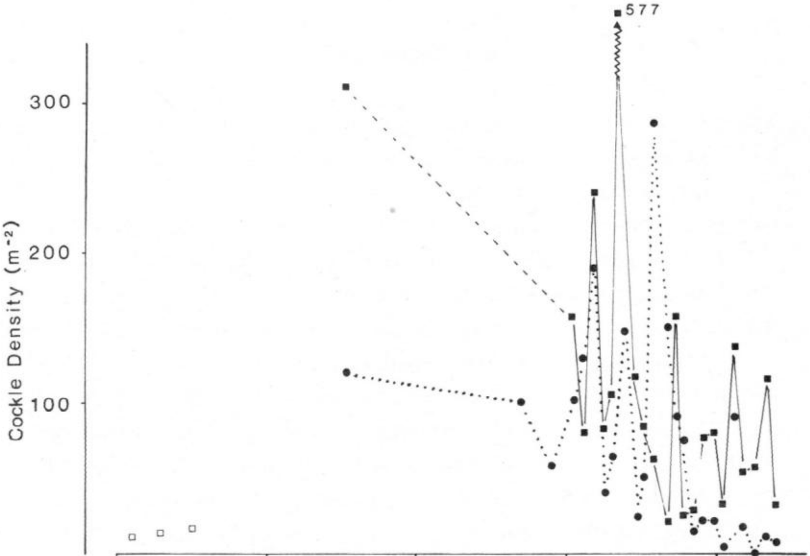

Figure 3. Change from 1970 to 1991 in cockle densities at two sites in Dublin Bay, the south Bull (squares) and Bull Island (dots); open symbols denote data from West *et al.* (1978).

From a peak in the late 1970s and early 1980s (Figure 3) numbers declined to low levels at both Bull Island and the South Bull. Densities have fallen close to and once to zero in the last three years at Bull Island.It is tempting to ascribe the very low numbers in 1989 and 1990 to the covering of the mud-flat by algal mats (mainly *Enteromorpha* spp.), which were particularly dense in those years (Jeffrey *et al.*, 1990). The decline on the South Bull is less easily explained. The summers of 1989 and 1990 were exceptional, yet so were 1976 and 1977, when very high densities were recorded. There may be some link with bird densities, and in particular the oystercatcher, which is an avid feeder on the cockle. Oystercatcher numbers were particularly high in the mid 1980s, but have almost halved since then (B. Madden, Botany Dept., TCD, pers. comm.) and, although the oystercatcher will shift to other food items if the cockle is not present (Desprez *et al.*, in press) the decline of the two species may be related.

The future of the cockle in Dublin Bay is uncertain. Although it is unlikely that it will disappear from the Bay, its numbers and its distribution are expected to be significantly reduced due to rising sea level and this will change the whole character of the Bay .

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