

Project 249

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Project 249

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R & D Project DO1.2  
Status of Rare Fish

Literature Review



NRA

National Rivers Authority

Institute of Freshwater Ecology  
February 1991

Status of Rare Fish Literature Review

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RA R&D Contract No. DO1.2

Environment Agency  
Information Centre  
Head Office

ENVIRONMENT AGENCY



128471

Research Contractor: Institute of Freshwater Ecology

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## 1. INTRODUCTION

The aim of this review as stated in Specific Objective 1 of the Terms of Reference of the project is "To review the extent of existing knowledge of whitefish ecology and genetic variability and of techniques for their artificial breeding and rearing". In addition, the Terms of Reference of the project also require that "This review should also identify other species which may be endangered in Britain and could be the subject of future research".

With respect to the latter objective, considerations of fish conservation are a relatively recent development and for a number of reasons lag behind most other areas of animal conservation (Tudge, 1990). This is particularly true of the U.K., with the result that the literature on rare British freshwater fishes per se is very restricted and is largely the product of the efforts of just one researcher, Peter S. Maitland. Thus, reviewing this field is relatively straightforward, with the major difficulty being the production of an objective rare species list for the present day.

In contrast, the whitefish (*Coregonus* spp.) literature now amounts to at least hundreds and probably thousands of articles. However, the vast majority of these publications originate from continental Europe and North America, usually with fishery themes, and so their conclusions are not all directly applicable or relevant to the present review.

A review of this nature could easily become too long and exhaustive to be of practical use for the purpose for which it is intended. Consequently, at all times the information reproduced here has been critically edited such that it meets the aim of the Overall Project Objectives in that it helps to "gather the information on ..... these fish which is necessary to safeguard their populations".

## 2. METHODS

This review was carried out through extensive use of the Freshwater Biological Association Library, together with the author's personal reprint collection and, most importantly, direct contacts with individuals currently working in relevant areas. The latter approach is particularly important with respect to breeding studies, where developments can be very rapid, and in assessing the current rarity status of British freshwater fishes. Several as yet unpublished manuscripts were thus made available during the course of this review.

Given the two major objectives, the review comprises two main parts. Firstly, British freshwater fishes are considered against a more general conservation background, and those which may now be considered rare are specified and their classification briefly justified. Secondly, a more detailed review of *Coregonus* biology is presented.

c. 380 *Coregonus* articles were consulted during the present work, of which approximately 150 are cited in this review. However, less than 50 of these are concerned with British coregonids, with approximately a further 20 covering the Irish *Coregonus autumnalis pollan*, and furthermore many of these works contain only limited references to these species. As a result, the review of *Coregonus* biology has been structured primarily on a subject rather than taxonomic basis, with major divisions being taxonomic relationships, ecology (occurrence, population biology, reproduction, feeding and seasonal distribution), variation and breeding.

In addition to the above published literature, there are also a number of unpublished Ph.D. theses dealing with the British coregonids. In recent years, the feeding, growth and reproductive physiology of the powan (*C. lavaretus*) have been studied by Pomeroy (1987), Brown (1989) and Rashid (1984) respectively, while the general biology of the gwyniad (*C. lavaretus*) was investigated some time ago by Haram (1968). The biology of the vendace (*C. albula*) and schelly (*C. lavaretus*) in the English Lake District were studied recently by Mubamba (1989).

Unfortunately, the literature search revealed only three publications from the above theses, these being Haram (1965) and Haram & Jones (1971) from Haram (1968) and Brown & Scott (1990) from Brown (1989), although more are probably currently in production from the later works. Of the latter, the work of Mubamba (1989) is particularly relevant to the current project and was read in full during this review. Publications from this work are known to be in preparation and Mubamba has been contacted concerning the future use of unpublished information, although his location in Zambia makes communication difficult. Given that the work remains as yet unpublished, this review does not present the findings of Mubamba (1989) in detail, but it does indicate those areas of English coregonid biology to which it might contribute in the future through either publications or personal communications, and which as a result may have a lower priority in the present research project.

### 3. RARE BRITISH FRESHWATER FISHES

#### 3.1 Conservation background

A useful discussion of current conservation ethos in Great Britain is given by Whitten (1990) within an article which also examines the present status of species protected by the Wildlife and Countryside Act, 1981, of which the only fishes are the vendace *Coregonus albula*, the whitefish (more specifically known as schelly, gwyniad or powan, and hereafter referred to as the schelly) *Coregonus lavaretus*, and the burbot *Lota lota*. The allis shad (*Alosa alosa*) is likely to receive such protection in the near future.

In terms of this Act, the species selected for protection are deemed to be "in danger of extinction in Great Britain or likely to become so endangered unless conservation measures are taken". The abundance of a species elsewhere (e.g. mainland Europe) is taken to be irrelevant in the selection process because its loss in Great Britain would be detrimental to the national natural heritage. This point is particularly important for freshwater fishes because none of the British species is endemic, including the rare ones some of which are in fact common elsewhere in Europe.

In conclusion, rarity in this review will be used in the sense of rare in Great Britain, rather than on a European or global basis, with the proviso that the species in question is native and has not been introduced by man.

#### 3.2 Rare species lists

The Wildlife and Countryside Act mentioned above constitutes a rare species list in itself, although it only contains three species of freshwater fishes (vendace, schelly and burbot) out of a native British freshwater fishes list which varies between 40 and 55 species depending on the inclusion criteria employed.

Table 1.1 presents the complete British freshwater fishes species list used in the current review, which is largely taken from Maitland (1974), with revisions given in Maitland (1990) and Maitland & Lyle (1990), and the addition of European status (defined below) from Lelek (1987). The inclusion of 'life-style' information is retained from Maitland's original table because of its importance in (a) determining the probability of British populations being genetically distinct from their European counterparts (this being more likely for purely freshwater forms), and (b) determining the fundamental nature and likely costs of future research and protective measures.

The terms used to describe British status, ranging from rare to common, have no precise definitions and their uses are justified in the species notes below. The European status terms are more precise, following a model published by the International Union for the Conservation of Nature in 1974, and are defined as follows.

Family	Species	Common name	Life-style	European status	British status
Petromyzontidae	<i>Petromyzon marinus</i>	Sea lamprey	Anad.	Vulner.	Common
	<i>Lampetra fluviatilis</i>	River lamprey	Anad.	Endang.	Common
	<i>Lampetra planeri</i>	Brook lamprey	Freshw.	Vulner.	Common
Acipenseridae	<i>Acipenser sturio</i>	Sturgeon	Anad.	Endang.	Rare
Channidae	<i>Allosa allosa allosa</i>	Alia shad	Estuar.	Endang.	Rare
	<i>Allosa fallax fallax</i>	Twiste shad	Estuar.	Endang.	Rare
Anguillidae	<i>Anguilla anguilla</i>	European eel	Catad.	Inter.-Vulner.	Common
Esoecidae	<i>Esox lucius</i>	Pike	Freshw.	Inter.-Vulner.	Common
Coregonidae	<i>Coregonus albula</i>	Vendace	Freshw.	Endang.	Rare
	<i>Coregonus lavaretus</i>	Schelly/ Ouzine/Powan	Freshw.	Endang.	Rare
	<i>Coregonus oxyrinchus</i>	Houting	Anad.	Endang.	Rare
Thymallidae	<i>Thymallus thymallus</i>	Grayling	Freshw.	Vulner.	Common
Salmonidae	<i>Salmo salar</i>	Atlantic salmon	Anad.	Endang.	Common
	<i>Salmo trutta trutta</i>	Sea trout	Anad.	Endang.	Common
	<i>Salmo trutta fario</i>	Brown trout	Freshw.	Vulner.	Common
	<i>Salvelinus alpinus</i>	Arctic char	Freshw.	Endang.	Rare
Osmorhynchidae	<i>Osmorhynchus eperlanus</i>	Smelt	Estuar.	Vulner.	Rare
Cyprinidae	<i>Cyprinus carpio</i>	Common carp	Freshw.	Vulner.-Endang.	Common
	<i>Abramis brama</i>	Common bream	Freshw.		Common
	<i>Alburnus alburnus</i>	Black	Freshw.	Inter.	Fairly common
	<i>Barbus barbus</i>	Barbel	Freshw.	Vulner.	Common
	<i>Blicca bjoerkna</i>	Silver bream	Freshw.	Inter.	Fairly common
	<i>Carassius auratus</i>	Ornamental carp	Freshw.	Rare-Vulner.	Fairly common
	<i>Gobio gobio</i>	Stone loach	Freshw.	Inter.-Rare	Common
	<i>Leuciscus cephalus</i>	Chub	Freshw.		Common
	<i>Leuciscus leuciscus</i>	Dace	Freshw.	Inter.-Vulner.	Common
	<i>Phoxinus phoxinus</i>	Minnow	Freshw.	Vulner.	Common
	<i>Rutilus rutilus</i>	Roach	Freshw.		Common
	<i>Scardinius erythrophthalmus</i>	Rudd	Freshw.	Vulner.	Common
	<i>Tinca tinca</i>	Tench	Freshw.	Inter.	Common
Cobitidae	<i>Cobitis taenia</i>	Spined loach	Freshw.	Rare	Fairly rare
	<i>Noemacheilus barbatulus</i>	Stone loach	Freshw.	Rare-Vulner.	Common
Gobiidae	<i>Lota lota</i>	Burbot	Freshw.	Rare-Inter.	Rare
Gasterosteidae	<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Freshw. and Estuar.	Inter.-Rare-Vulner.	Common
	<i>Pungitius pungitius</i>	Ten-spined stickleback	Freshw.	Inter.-Rare-Vulner.	Common
Cottidae	<i>Cottus gobio</i>	Bullhead	Freshw.	Vulner.	Common
Percidae	<i>Perca fluviatilis</i>	Burrowing perch	Freshw.		Common
	<i>Gymnocephalus cernuus</i>	Ruffe	Freshw.	Inter.	Fairly common
Mugilidae	<i>Cremno gyl labrosus</i>	Thick-tipped mullet	Estuar.		Common
	<i>Chelon ramada</i>	Thin-tipped mullet	Estuar.		Common
	<i>Chelon auratus</i>	Golden mullet	Estuar.		Un-common
Platypharidae	<i>Platichthys flesus</i>	Flounder	Estuar. and catad.	Rare-Vulner.	Common

Table 1.1

The native British freshwater fish fauna. Information on life-style and British status is taken from Maitland (1974), incorporating the revisions of Maitland (1990) and Maitland & Lyle (1990). Nomenclature and European status (definitions given in the text) are taken from Lelek (1987), with the exception of the family Mugilidae, for which Maitland's system is retained as no information is given for these species in Lelek's work. Abbreviations: Anad., anadromous; Catad., catadromous; Freshw., freshwater; Estuar., estuarine; Endang., endangered; Vulner., vulnerable; Inter., intermediate.



**Endangered:** All species, including those supposedly extinct, with only a "theoretical" chance of being re-established or re-introduced within the former range of their distribution area. This category includes threatened species which occur in one or two small localities, where their abundance is in addition very low.

**Vulnerable:** Taxa that are rare and very sensitive to environmental changes caused by man. Such species may be common in unsuitable habitats, where their presence depends on artificial hatching, stocking and management.

**Rare:** This category includes taxa which were never abundant but were permanently present in suitable biotopes, and species which are rare today, as their formerly large distribution areas are now reduced to a few remaining suitable biotopes.

**Intermediate:** Taxa which are common now, but which may be transferred to the categories Vulnerable or Rare if there is any further deterioration of their biotopes.

Table 1.1 shows that while only three species are currently protected under the Wildlife and Countryside Act, a total of nine British species is currently considered rare by Maitland (1990). These nine species are reproduced in Table 1.2 together with a further four species which can be considered potentially rare in Britain, and for which the European status varies from rare to intermediate.

Thus the British freshwater fishes considered to be rare or potentially rare for the purposes of this review are the sturgeon, allis shad, twaite shad, vendace, schelly, houting, Arctic charr, smelt, silver bream, crucian carp, rudd, spined loach and burbot. Of these 13 species, five have marine affinities (i.e. anadromous, catadromous or estuarine) while 8 have exclusively-freshwater distributions.

### 3.3 Brief species rarity notes

#### **Sturgeon *Acipenser sturio* Linnaeus, 1758**

Classified by Maitland (1990) as rare, and considered by Maitland & Lyle (1990b) to be only a rare vagrant. European status is endangered.

#### **Allis shad *Alosa alosa alosa* (Linnaeus, 1758)**

Classified by Maitland (1990) as rare. European status is endangered. Although it can be caught seasonally in relatively large numbers off the coast of southern Ireland, no spawning population is known to exist in any river in the British Isles (Aprahamian & Aprahamian, 1990). Likely to become protected in the near future under the Wildlife and Countryside Act, 1981.

Family	Species	Common name	Life-style	European status	British status
Acipenseridae	<i>Acipenser sturio</i>	Sturgeon	Anad.	Endang.	Rare
Clupeidae	<i>Alosa alosa alosa</i>	Allis shad	Estuar.	Endang.	Rare
	<i>Alosa fallax fallax</i>	Twaite shad	Estuar.	Endang.	Rare
Coregonidae	<i>Coregonus albula</i>	Vendace	Freshw.	Endang.	Rare
	<i>Coregonus lavaretus</i>	Schelly/ Gwyniad/ Powan	Freshw.	Endang.	Rare
	<i>Coregonus oxyrhynchus</i>	Houting	Anad.	Endang.	Rare
Salmonidae	<i>Salvelinus alpinus</i>	Arctic charr	Freshw.	Endang.	Rare
Osmeridae	<i>Osmerus eperlanus</i>	Smelt	Estuar.	Vulner.	Rare
Cyprinidae	<i>Blicca bjoerkna</i>	Silver bream	Freshw.	Inter.	Fairly common
	<i>Carassius carassius</i>	Crucian carp	Freshw.	Rare-Vulner.	Fairly common
	<i>Scardinius erythrophthalmus</i>	Rudd	Freshw.	Vulner.	Common
Cobitidae	<i>Cobitis taenia</i>	Spined loach	Freshw.	Rare	Fairly rare
Gadidae	<i>Lota lota</i>	Burbot	Freshw.	Rare-Inter.	Rare

Table 1.2

List of British freshwater fishes considered to be rare or potentially rare for the purposes of this review. Further details, including origins of information, and justifications are given in the legend of Table 1.1 and the text.

**Twaiite shad *Alosa fallax fallax* Lacepede, 1800**

Classified by Maitland (1990) as rare. European status is endangered. Recorded from most coasts of the British Isles, sometimes in large numbers, although British spawning populations are confined to a few rivers which drain into the Bristol Channel (Aprahamian & Aprahamian, 1990).

**Vendace *Coregonus albula* Linnaeus, 1758**

Classified by Maitland (1990) as rare. European status is endangered. Only two British populations. Protected under the Wildlife and Countryside Act, 1981.

**Schelly/Powan/Gwyniad *Coregonus lavaretus* Linnaeus, 1758**

Classified by Maitland (1990) as rare. European status is endangered. Only six British populations are known to exist. Protected under the Wildlife and Countryside Act, 1981.

**Houting *Coregonus oxyrinchus* Linnaeus, 1758**

Classified by Maitland (1990) as rare. European status is endangered. No specimens have been seen around the coasts of Great Britain for many years (Maitland, 1990).

**Arctic charr *Salvelinus alpinus* (Linnaeus, 1758)**

Classified by Maitland (1990) as rare. European status is endangered. Although many independent populations are found in Britain, there has been a gradual loss over the last 200 years. Variation is so high within this species that even one lake may contain more than one race, each worthy of conservation.

**Smelt *Osmerus eperlanus* (Linnaeus, 1758)**

Classified by Maitland (1990) as rare. European status is vulnerable. It has been lost from several British estuaries in recent years due to pollution, although it has returned to the improved Thames (Maitland, 1990).

**Silver bream *Blicca bjoerkna* (Linnaeus, 1758)**

Classified by Maitland (1974) as fairly common. European status is intermediate. This species has a restricted British distribution (Maitland, 1972), primarily in central England, which now needs reviewing.

#### **Crucian carp *Carassius carassius* (Linnaeus, 1758)**

Classified by Maitland (1974) as fairly common. European status is rare-vulnerable. This species has a restricted British distribution (Maitland, 1972), primarily in south-east England, which now needs reviewing. While it is possible that this species is in fact introduced (Maitland, 1974), it was not listed as such by Wheeler & Maitland (1973) and so is assumed to be native.

#### **Rudd *Scardinius erythrophthalmus* (Linnaeus, 1758)**

Classified by Maitland (1974) as common. European status is vulnerable. This distribution of this species now urgently needs reviewing due to the loss of many populations, often in association with eutrophication.

#### **Spined loach *Cobitis taenia* Linnaeus, 1758**

Classified by Maitland (1974) as fairly rare. European status is rare. This species has a restricted British distribution (Maitland, 1972), primarily in central England, which now needs reviewing.

#### **Burbot *Lota lota* (Linnaeus, 1758)**

Classified by Maitland (1990) as rare. European status is rare-intermediate. Formerly found in the larger rivers of eastern England from Durham south to East Anglia, it is now believed to be extinct in Britain (Maitland, 1990) although unsubstantiated captures are still occasionally made.

### **3.4 Conclusions**

There are just three species of rare British freshwater fishes which are currently protected under the Wildlife and Countryside Act, 1981, these being the vendace, schelly and burbot, and the allis shad is likely to receive such protection in the near future. However, this review has shown that there are a number of other species which are also rare and require active conservation measures even though they do not yet enjoy such legislative protection.

Of the British freshwater fishes with marine affinities, a total of five species are now rare and should be considered for future research. These are the sturgeon, allis shad, twaite shad, houting and smelt. However, it must be acknowledged that because of their distributions, conservation work on such species would be expensive and have a low probability of success given our relative ignorance of their ecologies. Under the priority scheme of Whitten (1990), these species would score low given that research funds are limited.

Within the strictly freshwater species group there can be no doubt that the Arctic charr requires immediate conservation research programmes, and indeed some such work is already underway (Maitland & Lyle, 1990). Given the phenotypic and genotypic variability of this species (Partington & Mills, 1988), the preservation of only a few stocks would mean the irreversible loss of much genetic diversity. British populations of Arctic charr are of importance in a European context, where the species as a whole is endangered, and are particularly valuable for general population studies because, unusually for this widespread species, they are largely unexploited.

Finally, there is a group of freshwater species comprising the silver bream, crucian carp, rudd and spined loach which have always had a restricted British distribution and may now be becoming rarer. For example, many populations of rudd have thought to have been lost due to eutrophication, although published data on this trend are hard to find. The spined loach is in particular need of research given the paucity of studies so far carried out on this small and secretive species. In the first instance, a valuable starting point for future research on all of these fishes would be a study of their present distributions.

In summary, this review has shown that there is an imperative need for future conservation research on, in some order of urgency, the Arctic charr, spined loach, rudd, crucian carp and silver bream, in addition to the coregonid populations which will be investigated in the present project.

#### 4. *COREGONUS* BIOLOGY

##### 4.1 Taxonomic relationships

The taxonomy of the coregonids is probably more complicated than that of any other Eurasian freshwater fish genus (Lelek, 1987). However, recent electrophoretic studies have greatly clarified the situation, particularly with respect to the British species for which the taxonomy is now generally accepted to be as follows.

The scientific name of the British vendace is *Coregonus albula* Linnaeus, 1758, and it is thus conspecific with many other European coregonid populations. Although the vendace used to be considered to be conspecific with the Irish pollan (e.g. Maitland, 1972), this is no longer the case following the reclassification of the latter as a subspecies of *Coregonus autumnalis* (Pallas, 1811), which is not found elsewhere in Europe. The Irish pollan is thus *Coregonus autumnalis pollan* Thompson (Ferguson, *et al.* 1978). However, the vendace and the pollan do show many common features, particularly with respect to their ecologies.

The scientific name of the schelly (also known as the gwyniad and powan in Wales and Scotland respectively) is *Coregonus lavaretus* Linnaeus, 1758, which also has a number of subspecies elsewhere in Europe. The precise relationship of the schelly to these subspecies is at present unknown.

Acknowledging the above taxonomic relationships, this review is largely restricted in detail to *Coregonus albula*, *C. lavaretus* and *C. autumnalis pollan*, although reference is made to work on other species which is likely to be relevant to the aims of this project in more general terms.

##### 4.2 Ecology

###### 4.2.1 Occurrence

The genus *Coregonus* is widespread in the northern latitudes of the world, with representatives in Europe, Siberia and North America. Only three coregonid species are found naturally in Europe, these being *Coregonus albula*, *C. lavaretus* and a subspecies of *C. autumnalis*, but many more inhabit Siberian waters, including *C. autumnalis*, *C. chadary*, *C. muksun*, *C. nasus*, *C. peled*, *C. tugun* and *C. ussuriensis* (Resetnikov, 1988). Members of the latter group have now been introduced to various parts of Europe for commercial exploitation.

*Coregonus albula* is itself found in lakes east of the Elbe, in Sweden, Norway and Finland, in Lakes Ladoga and Onega, lakes in the upper Volga catchment area, in the Gulf of Bothnia, and in the Waginger and Tachen Lakes in Bavaria (Lelek, 1987). In addition, it has been introduced further south, particularly into man-made lakes in the U.S.S.R., France, Poland and Czechoslovakia (Lelek, *op. cit.*). Within Britain, the vendace is now found in only two lakes, Bassenthwaite and Derwentwater, in the

English Lake District. Populations used to occur in Scotland in the Castle Loch and Mill Loch, Lochmaben, but are now thought to be extinct (Maitland, 1990).

*Coregonus lavaretus* has a similar widespread distribution in the north of Europe and in Alpine Lakes (Lelek, 1987). Within Britain, *C. lavaretus* is found in Loch Lomond and Loch Eck in Scotland, where it is known as the powan, in Llyn Tegid (Lake Bala) in Wales where it is known as the gwyniad, and in the English Lake District where it is called the schelly. The latter area holds a total of at least three populations with relatively large stocks in Ullswater and Haweswater (Bagenal, 1970), and an undoubtedly smaller but still extant population in Red Tarn (Maitland *et al.*, 1990). Further populations may exist in Brotherswater, Loweswater (see Ellison, 1966) and other small water bodies in the Lake District, although these have not been confirmed in recent years.

The coregonids are stenothermic species with upper lethal temperature limits of adults in the region of 24° C (Alabaster & Lloyd, 1980), and are thus largely confined to cold, clear lakes and rivers. In addition to water temperature as a factor controlling their distribution (Bagenal, 1970), it is clear that the nutrient concentration of a water body also has a strong influence, even if it operates through indirect mechanisms. Although initial stages of the eutrophication of oligotrophic lakes can increase the growth rate and abundance of coregonids (Mills & Chalanchuk, 1988; Resetnikov, 1988), subsequent levels of eutrophication are considered to be a threat to both *C. albula* and *C. lavaretus* in Europe as a whole (Lelek, 1987). In Britain, the population of the former species in Castle Loch was almost certainly lost because of eutrophication by a sewage works (Maitland, 1990).

Deoxygenation of the water column (see Mills *et al.*, 1990) and particularly siltation of spawning grounds (Resetnikov, 1988; Sterligova *et al.*, 1988) are thought to be the main mechanisms through which eutrophication exerts its deleterious effects on *Coregonus* populations. It is worth noting that Hamrin (1986) found that *C. albula* in the field shows no avoidance of oxygen levels as low as 3 mg/l, and can even tolerate levels as low as 0.8 mg/l despite the fact that laboratory studies have found levels of 2 to 4 mg/l to be lethal. Hamrin (*op. cit.*) suggests that the discrepancy may be due to differential acclimation. However, the oxygen requirements of the eggs may be the crucial factor responsible for the survival or extinction of a population as Fluchter (1980) reports that the eggs of *C. lavaretus* require 8 mg/l of oxygen at 5° C. Increased rates of parasitism (Numann, 1972) and changes in the competitors and predators within the fish community (Sterligova *et al.*, 1988) may also be involved in the effects of eutrophication on *Coregonus* species.

The survival of the Irish pollan *Coregonus autumnalis pollan* in the very eutrophic Lough Neagh, where chlorophyll *a* levels frequently used to exceed 60 µg l<sup>-1</sup>, is probably due to the well-mixed nature of that lake and the use of inshore rocky areas as spawning grounds (Winfield & Wood, 1990). It is unlikely that coregonid populations would survive similar levels of eutrophication in stratified lakes.

#### 4.2.2 Population biology

##### General aspects

The population biology of *Coregonus* species has been relatively well studied, although almost always in association with commercial fisheries and thus on exploited populations in Europe and North America. Extrapolation to the unfished British populations must be performed with caution. Nevertheless, there are several aspects of coregonid population biology which are common to all populations.

Most coregonid species have relatively short life spans, often with few individuals older than age class 6+, and are relatively highly fecund. As a result they are often classified as r-specialists (see Hamrin, 1986). As is the case with most species of fish, growth rates are extremely plastic and dependent on environmental conditions. As a result, mean sizes of fish of equivalent ages not only vary between lakes but also between years in the same lake. Typical growth patterns can therefore be defined only in the vaguest of terms. Nevertheless, growth rates are usually quite high when compared with those of other freshwater fish and lengths well in excess of 100 mm are commonly attained during the first year of life. Recruitment is typically very variable which in conjunction with the low age class diversity leads to population fluctuations of considerable magnitude.

##### *Coregonus* species outside Britain

##### *Coregonus albula*

Coregonid population biology has probably been best investigated in *C. albula*, particularly in Finland where it supports many of the most important commercial fisheries in that country and has been exploited longer than it has been studied (Viljanen, 1986). As a result, the Finnish studies are almost all of heavily exploited populations in which fish of age-groups below 4+ typically constitute over 90% of the catch.

A review of the many population data which exist for Finnish *C. albula* populations is given by Viljanen (1986). Only the most general findings will be presented here as it is clear that coregonid population biology is extremely lake-specific, and even within a single lake the population parameters of the fish may change greatly between years. In central Finland, average lengths for 1+ fish are 110 mm, 2+ are 140 mm, 3+ are 160 mm, 4+ are 170 mm, and 5+ are 180 mm, while equivalent values for populations in southern Finland are 120 mm, 160 mm, 180 mm, 190 mm, and 200 mm.

Few estimates of mortality rates have been made because recruitment is extremely uneven and so estimates of survival and total mortality rates must be based on age composition data for many adjacent year classes. Viljanen (1986) argues that this procedure is of doubtful validity for *C. albula* in which mortality has been found to fluctuate according to age and year class. Thus catch curves cannot be legitimately



used to calculate mortality rates in this species, and such information must be obtained by comparisons within individual year classes. Viljanen (op. cit.) states that values for total mortality (Z) in Finland vary between 0.42 and 1.80, while fishing and natural mortalities fall in the ranges of 0.25 to 0.85 and 0.30 to 0.91 respectively.

In a detailed study of the *Coregonus* fisheries of Lake Pyhajarvi, Auvinen (1987) found values of Z for *C. albula* to be 0.97 in the heavily-fished Finnish areas and 0.42 in the lightly-fished Soviet areas. The *C. albula* population of this lake showed a strong year class every second year, a feature which is shown by many populations and will be returned to below.

A review of *C. albula* population biology in more eutrophic lakes in Poland is given by Luczynski (1986), although it must be remembered that these populations are usually heavily exploited and stocked. As in Finland, growth is confined to the summer months and 80 to 90% of the catches are composed of fish of age groups 1+, 2+ and 3+. A moderate growth rate for Polish *C. albula* populations results in 1+ being 129 mm in length (weight 20 g), 2+ being 183 mm (55 g), 3+ being 215 mm (85 g), 4+ being 242 mm (123 g), 5+ being 265 mm (157 g), and 6+ being 282 mm (179 g).

While information on population parameters such as that presented above is widely available for many exploited lakes, empirical studies of stock-recruitment relationships in *C. albula* are few in number because of the requirement for long time series. Valtonen & Marjomarki (1988) provide one such analysis using data on the annual sales of *C. albula* roe from the oligotrophic Lake Keitele in Finland during the period between 1913 and 1935. In the central lake, a clear relationship was found between recruitment and the parent stock, with greatest recruitment coming from the smallest stocks. A similar trend was found in the northern part of the lake, although here the relationship was more obscure due to long periods of recruitment failures probably induced by unfavourable weather conditions. Valtonen & Marjomarki (op. cit.) suggested that the main factor responsible for the relationship was food availability for the larvae when exogenous feeding commenced.

The above feeding hypothesis was developed further by Hamrin (1986) in a general review of *C. albula* ecology, with particular respect to several oligotrophic Swedish lakes. In all but one of these lakes, almost the whole population, excluding fry, was made up of only two age classes (1+ and 2+), while in the other lake just one age class (1+) made up more than 90% of the population. The fish in the different lakes reached between 100 and 150 mm in length during their first year, after which the length (but not the weight) increment decreased and the variation in growth rate between lakes increased. Thus, 4+ individuals from different lakes varied between 185 mm (45 g) and 250 mm (125 g). Fish typically matured as 1+, although maturation at 2+ was also recorded. Hamrin (op. cit.) suggested that this early maturation is an adaptation to the high mortality suffered by small fishes such as *C. albula* in the pelagic habitat.

Hamrin (op. cit.) found that the mortality of adult age classes varied between 50 and 100%, while for 0+ it often exceeded 95%, and as a result the population showed alternate years of good and poor recruitment typical of many *C. albula* stocks.

Hamrin argued that in lakes where physical factors such as high temperatures or low oxygen availabilities were not constraining factors, *C. albula* populations attain high densities and consequently deplete their zooplanktonic prey populations. The resulting severe intraspecific competition reduces the fecundity of mature females, which then through the stock-recruitment relationship results in a poor year class being produced. This in turn has less effect on the zooplankton of the following summer, which leads to higher fecundities and consequently a good year class, and thus the cycle begins again.

### *Coregonus lavaretus*

The population biology of *C. lavaretus* has not been as well studied as that of *C. albula*, particularly in Finland where it is not as important in commercial fisheries. *C. lavaretus* is more important in Poland, although here most of the populations are largely maintained by stocking as natural reproduction is often limited due to eutrophication.

Luczynski (1986) reviews the population biology of *C. lavaretus* in Polish fisheries and notes that the age structure of such populations is more diverse than that of *C. albula* populations, with 3+, 4+, 5+ and 6+ individuals all being important in the catches. A moderate growth rate for Polish *C. lavaretus* populations results in 1+ being 149 mm in length (weight 42 g), 2+ being 266 mm (235 g), 3+ being 336 mm (524 g), 4+ being 383 mm (811 g), 5+ being 414 mm (1034 g), 6+ being 431 mm (1149 g) and 7+ being 456 mm (1365 g).

The variability of growth rates in *C. lavaretus* is shown by three studies. Heese (1988) studied the growth of anadromous *C. lavaretus* in the Pomeranian Bay in Poland and found 1+ fish to be 218 mm in length and to maintain fast growth until age class 4+ when they were 483 mm, after which growth slowed down such that 10+ were 612 mm in length. In contrast, in Lake Walenstadt in Switzerland, Ruhle (1988) found 1+ individuals to be only 80 mm in length, with 2+, 3+ and 4+ being 180, 230 and 250 mm respectively. Turunen & Viljanen (1988) found a very similar growth for *C. lavaretus* in the oligotrophic Lake Suomunjarvi in Finland, where 1+ fish were 150 mm in length, 4+ were 250 mm, and 7+ were 300 mm.

Very few values of mortality rates in *C. lavaretus* have been published, in part for the same reasons as for *C. albula*. The study of Auvinen (1987) in Lake Pyhajarvi produced estimates of Z for *C. lavaretus* of 1.07 and 0.41 in the heavily-fished Finnish and lightly-fished Soviet areas respectively.

### *Coregonus autumnalis pollan*

The population biology of the pollan has been best studied in Lough Neagh, where it is exploited in a commercial fishery, with only a very limited amount of information being available for this coregonid in Lough Erne. Wilson (1984a) remarks that Lough Neagh pollan grow to a maximum length of 300 mm and live for up to five years, and cites evidence that a similar growth rate is shown in Lough Erne. As in

most *Coregonus* populations, growth is very rapid in the first two years of life such that 1+ and 2+ individuals are 140 mm and 240 mm in length respectively in Lough Neagh, with most growth occurring between March and October of each year when mid-lough temperatures exceed 10° C (Wilson & Pitcher, 1984b).

Unfortunately, catch statistics of the commercial fishery for pollan in Lough Neagh are not collected and so this source of information on population trends is unavailable. However, Wilson (1983) noted that a recruitment failure of the pollan in 1977 led to the virtual closure of the fishery in 1978, suggesting that the population in Lough Neagh shows the fluctuating population dynamics typical of coregonids elsewhere. Significant changes in the abundance of pollan in Lough Neagh have also been recorded in the 1980s (Winfield & Wood, 1990).

### *Coregonus* species in Britain

#### *Coregonus albula* (vendace)

No account of the population biology of the vendace of Bassenthwaite or Derwentwater has ever been published, although some information is given in Mubamba (1989) and may be published in the near future. While no detailed studies were made of the Lochmaben vendace prior to its extinction, Maitland (1966) suggested that this population probably had the smallest average individual lengths of the British and Irish coregonids as no records of fish larger than 230 mm had ever been made and adults were normally in the size range of 150 to 200 mm.

#### *Coregonus lavaretus* (schelly/powan/gwyniad)

##### Schelly

The population biology of the schelly in Haweswater and Ullswater was studied by Bagenal (1970).

In Haweswater, the spawning population of schelly was sampled solely as accidental captures of a water intake pipe, but nevertheless this gave extensive information on the growth rates of both sexes. Overall, 1+ fish were 70 mm in length, 2+ were 150 mm, 3+ were 240 mm, 4+ were 280 mm, 5+ were 310 mm, 6+ were 340 mm, 7+ were 340 mm, 8+ were 360 mm, and 9+, which were the oldest schelly found in the study, were 380 mm in length. Examples of recorded weights are 31 g for 2+, 208 g for 4+ and 508 g for 9+. Males tended to be slightly larger than females. The absence of a steady decrease in numbers with age suggested that year-class strength was not constant, and consequently survival rates could not be calculated.

The population biology of the schelly in Ullswater was investigated using gill nets which took individuals of age-groups 2+ to 8+. Overall, 1+ fish were 170 mm in

length, 2+ were 250 mm, 3+ were 250 mm, 4+ were 300 mm, 5+ were 320 mm, 6+ were 350 mm, 7+ were 360 mm, and 8+ were 380 mm in length.

Comparisons between the schelly of these two lakes reveals that the Ullswater fish are larger than those of the same age in Haweswater. The main difference between the growth rates occurs during the first three years, and particularly while the fish are still in their first year of life. The growth of fish older than 3+ was similar in the two lakes.

Mubamba (1989) also covers some aspects of the population biology of the schelly in Haweswater and Ullswater and this more recent information may be published in the near future.

Finally, some information is available for the small schelly population of Red Tarn. Maitland *et al.* (1990) captured 15 fish which were all mature individuals of a similar size, and had all shown a relatively slow growth rate. On the basis of back-calculations, it appears to take schelly at this site four years to reach a length of 150 mm, having attained a length of less than 50 mm before their first winter. Maitland *et al.* (op. cit.) conclude that schelly in Red Tarn probably do not mature before their 5th or 6th year if they spawn at a similar size to their conspecifics in Loch Lomond and Loch Eck.

#### Powan

Limited information is available on the population biology of the powan in either Loch Lomond or Loch Eck. Slack *et al.* (1957) noted that their samples from Loch Lomond contained powan which ranged in length between 150 and 420 mm, although the majority were between 260 mm and 340 mm in size. In summer, the average adult powan was 310 mm in length and weighed 230 g. The catches contained fish of age-groups 1+ to 10+, with 3+ and 4+ individuals predominating. No information on growth rates was presented.

Similar statistics are given in the study of powan reproduction in Loch Lomond by Maitland (1969), suggesting that the population biology of this species in this location was stable through the 1950s and 1960s. The size of spawning powan ranged between 200 and 350 mm, with the majority being between 260 and 310 mm and belonging to age-groups 3+ or 4+. Like the schelly in Haweswater, male powan were slightly larger than females, with average lengths of 272 and 266 mm respectively.

#### Gwyniad

No studies dealing specifically with the population biology of the gwyniad have ever been published. The only information available in the literature is given in the feeding study by Haram & Jones (1971) which states that all of the gwyniad examined in their catches were mature and between approximately 200 and 300 mm in length.

### 4.2.3 Reproduction

#### General aspects

Members of the genus *Coregonus* share a common basic reproductive biology, although there is considerable variation in the finer details. In general terms, reproduction is carried out in the late autumn or early winter when water temperatures drop below 7° C, typically following a migration to suitable spawning grounds which may be in deep water, shallow areas or even river mouths. Eggs typically hatch during the following spring, producing large numbers of larvae which then suffer high mortality over the next few weeks. Fecundity is usually relatively high when compared with other genera of freshwater fishes, particularly stream-dwelling salmonids, with most females producing thousands of eggs during each spawning season.

Before moving on to more species-specific reviews, it is worth noting here that the reproduction of all coregonids appears to be greatly impaired by changes to their spawning grounds. The effects of eutrophication have been particularly well documented for both *C. albula* and *C. lavaretus* in Poland (Wilkonska & Zuromska, 1982) and the U.S.S.R. (Sterligova *et al.*, 1988), with increased sedimentation of organic matter being the main agent of decline in both cases. Increased sedimentation was also found to reduce hatching success of *C. clupeaformis* in Southern Indian Lake, Manitoba, following the manipulation of the water level for hydro-electric purposes (Fudge & Bodaly, 1984), while unfavourable currents produced by gravel extraction had the same effect on a *Coregonus* species in Lake Lucerne, Switzerland (Meng & Muller, 1988). Clearly, *Coregonus* eggs are particularly susceptible to the effects of siltation during the eutrophication of a water body.

Reproduction, like most aspects of coregonid biology, has been best studied outside Britain, often on species which are not even found in this part of the world. Within the general framework described above, there is a great variation between species, lakes and even different years (Zuromska, 1982a), making detailed universal conclusions impossible. In addition, only limited parts of this body of knowledge are directly relevant to British coregonid populations, although given the paucity of published studies on the latter fishes, it is worth at least bearing in mind the results of work on other species. This approach is essential when considering the links which exist between reproduction and population dynamics. As mentioned earlier, such studies require very large data sets covering both fish populations and their environments over long time periods, and are completely lacking for the British coregonids. A few key examples of such investigations are reviewed below.

## *Coregonus* species outside Britain

### *Coregonus albula*

*C. albula* shows great adaptability in its reproductive biology. Both male and female *C. albula* may reach maturity as either 1+ or 2+, although 2+ predominate, and absolute fecundities can vary between approximately 5400 to 38 100 eggs per female depending on size but not age (Luczynski, 1986).

Both autumn- and spring-spawning populations are found, sometimes sympatrically (Airaksinen, 1968). Autumn-spawners are the most common (and include the British *C. albula*, see below), and in an extensive review, Zuromska (1982a) concluded that spawning begins when water temperatures fall to between 0.4 and 8° C, although for a given stock this temperature can vary significantly between years (e.g. from 3.5 to 7.3° C). As a consequence, the start of the spawning season varies greatly between populations, and even within a stock it can vary between years by up to two weeks.

The spawning grounds of autumn-spawning *C. albula* are located on the steep or gentle slopes of shorelines and islands, in the regions of underwater wells, or in river mouths. The sites used in a given lake are remarkably consistent from year to year, and are generally at depths of less than 10 m (in contrast to spring-spawners for which the depth is typically greater than 10 m). The substrate is usually hard, often with stones or gravel, and sometimes has vegetation present.

In the mesotrophic and eutrophic lakes studied by Zuromska (1982a), spawning began at temperatures between 5.0 and 8.0° C, and ended when they were between 2.5 and 6.0° C. Egg density on the sites was up to several hundred eggs per square metre, with some eggs laid on *Ceratophyllum demersum* or *Elodea canadensis*, and the hatching time was between four and five months. Further studies by Zuromska (1982b) showed that increased temperature was the greatest cause of egg mortality, particularly when temperatures exceeded 3° C for a long time. Egg mortality was also high in seasons with long periods below 2° C, and so for *C. albula* the optimum temperature for egg development was concluded to be between 1.2 and 7° C.

Despite the above effects of temperature on hatching success, both Auvinen (1988) and Valkeajarvi (1988) analysed extensive data sets and concluded that temperature was not the usual determinant of year class strength in *C. albula*, although exceptionally high temperatures may lead to the failure of a year class. Both authors found evidence that food availability was more often the major factor, and Auvinen (1988) specified that the first three weeks of the post-hatching life of the larvae were critical. It must be noted, however, that both of these studies of the effects of reproduction on population dynamics were carried out using data from oligotrophic or dystrophic lakes where food limitation might be expected to be of greater importance than in more eutrophic conditions (see *C. lavaretus* below).

### *Coregonus lavaretus*

The review given by Zuromska (1982a) also covers *C. lavaretus* in European waters. This species has many features in common with *C. albula*, including a great variety in reproductive biology over its range. However, one potentially important difference is that the upper temperatures for spawning in *C. lavaretus* seem to be lower than in *C. albula* (see below), and so this species tends to spawn later. *C. lavaretus* also tends to mature slightly later, with 3+ individuals dominating spawners, and absolute fecundities can vary between approximately 10 500 to 65 100 eggs per female (Luczynski, 1986).

While *C. lavaretus* may use sites less than 1 m in depth, it will use depths up to 10 m and thus may overlap with *C. albula*. Indeed, these two species share common spawning grounds in the mesotrophic Lake Pluszne and the eutrophic Lake Maroz studied by Zuromska (1982a). The substrate of spawning sites is usually hard, although eggs may also be deposited on plants.

The temperatures at which *C. lavaretus* start and finish spawning in Lakes Pluszne and Maroz are similar to the values given above for *C. albula*, although subsequent experimental studies on the eggs of these two species revealed important differences (Zuromska, 1982b). The optimum temperature range for *C. lavaretus* was found to be between 2 and 3° C, and thus significantly more restricted than that found for *C. albula* in the same experiments (1.2 and 7° C). Consequently, increased water temperatures are likely to have greater effects on *C. lavaretus* reproduction than on *C. albula*, although the implications for population dynamics are unclear.

The relationships between reproduction and population dynamics in *C. lavaretus* have been investigated by Salojarvi (1982) and Eckmann *et al.* (1988), with contrasting conclusions. Like the above *C. albula* studies, Salojarvi (1982) examined data from oligotrophic lakes and found that the key life stage was the first three weeks after hatching, and moreover that food limitation was the main agent responsible for the high mortality observed at this time. In contrast, Eckmann *et al.* (1988) concluded that zooplankton availability during spring had no significant influence on the year-class strength of *C. lavaretus* in Lake Constance. Variation in reproductive success over the period between 1962 and 1982 could, however, be largely attributed to meteorological conditions that lead to early thermal stratification in April. The authors were able to substantiate this conclusion with considerable evidence from both the field and laboratory.

One possible explanation for the above apparent discrepancy between the *C. lavaretus* studies lies in the trophic state of the different lakes studied. The 'food-controlled' populations studied by Salojarvi (1982) were all from oligotrophic lakes, while the 'temperature-controlled' population investigated by Eckmann *et al.* (1988) was from a eutrophic lake. The obvious possibility is that food was superabundant at all times in the more eutrophic lake. The validity of this explanation cannot be determined from the data given in the papers themselves and so it must remain just a hypothesis.

The main conclusion in the present context must be that the factors controlling the recruitment success of *C. lavaretus*, and possibly *C. albula*, can vary between lakes.

The elucidation of the relationships requires data of quality and quantity which are rarely available even for intensively fished European populations. Obviously, such studies will never be possible on the British coregonids and, while theoretically possible, have never been carried out on the only commercially-exploited coregonid in the British Isles, *Coregonus autumnalis pollan* in Ireland. However, other aspects of the reproductive biology of the pollan are worth reviewing because of the close similarity of the pollan and *C. albula*, and the similarity of the Irish and British climates.

### *Coregonus autumnalis pollan* (pollan)

The most comprehensive accounts of the reproduction of pollan have been published by Dabrowski (1981) and Wilson & Pitcher (1984a), and the former is used as the basis for this review. Like all recent work on the pollan, these studies were restricted to the pollan population of Lough Neagh, a lake which contrasts with the above European sites in being extremely eutrophic (see Winfield & Wood, 1990).

Pollan in Lough Neagh spawn almost exclusively during November and December, although Wilson & Pitcher (1984a) suggest that a spring spawning sub-population may be present. Males are the first to arrive on the spawning grounds, which are typically inshore rocky areas with a depth of 1 to 3 m. Dabrowski (1981) considers that a drop in temperature to 5° C initiates spawning, but Wilson & Pitcher (1984a) found evidence over a relatively longer study that decreasing day length is more important.

According to Wilson & Pitcher (1984a), both sexes usually mature as 2+ and fecundity is correlated with length and weight but not age, with females producing between 5000 and 12 000 eggs. In addition, specific fecundity was found to vary significantly between years from 37.1 to 42.9 eggs per g body weight. Interestingly, fecundity was higher in years when the stock was more abundant, which implies that density-dependent food limitation is not important in the pollan population of Lough Neagh.

Dabrowski (1981) first found newly-hatched larvae during the following February, but most seemed to hatch during March when densities in the water column approached one larvae per cubic metre. Larval growth was negligible during March but increased in April when the temperature increased from 6.9 to 11.4° C, which Dabrowski (op. cit.) suggests was responsible for this change. Thus in the eutrophic Lough Neagh, food limitation was apparently not important, a finding which conforms with other European studies in eutrophic lakes (see above). More unusually, dissolved oxygen was always present in high concentrations, sometimes approaching 100% saturation, due to the well-mixed nature of the Lough Neagh water column.

The only work published on other pollan populations this century was by Twomey (1956) on Lough Erne, although with respect to reproduction this paper presented little information other than confirming that this population also spawns in November and December, noting that most fish become mature as 1+, and giving the absolute



fecundities of two females 240 and 267 mm in length as 1628 and 1737 eggs respectively.

### *Coregonus* species in Britain

#### *Coregonus albula* (vendace)

No account of reproduction in the vendace of Bassenthwaite or Derwentwater has ever been published, although some information on fecundity and timing of spawning is given in Mubamba (1989). Accounts of reproduction in the vendace of Lochmaben prior to its recent extinction have also never been published, with the exception of a reference to an inshore spawning migration during the winter (Maitland, 1967).

#### *Coregonus lavaretus* (schelly/powan/gwyniad)

##### Schelly

The reproduction of the schelly in Haweswater and Ullswater was examined during studies of the general biology of this fish by Bagenal (1970).

Schelly in Haweswater were obtained solely as accidental captures of a water intake pipe. Consequently, sampling in this reservoir was spatially very restricted and no information was gathered on the location or nature of the spawning grounds, other than the obvious conclusion that one site is in the vicinity of the intake pipe. The spawning season was from mid January to mid February, with males maturing as 3+ and females as 4+.

Bagenal (op. cit.) sampled the schelly population in Ullswater by extensive gill netting operations, and hence more detailed information is available on the spawning grounds used in this lake. One spawning ground was located in the eastern side of Gowbarrow Bay west of Schelly Nab and inside an offshore bank. Inspection by a diver revealed the bottom to consist of a whitish clay covered by a layer of sand. There were a few scattered stones and patches covered with a growth of *Fontinalis antipyretica*. Schelly eggs were found on the stones and sand, but in greater abundance on and around the macrophytes.

Ullswater schelly shared a mid January to mid February spawning season with their conspecifics in Haweswater, although due to higher growth rates both males and females matured one year earlier as 2+ and 3+ respectively.

A very limited amount of information on the reproduction of the schelly in Haweswater and Ullswater is contained in Mubamba (1989).

## Powan

While no detailed account of the reproduction of powan in Loch Eck has yet been published, but see below for a brief account, such studies have been made on the population in Loch Lomond by Slack et al. (1957) and Maitland (1969). The latter publication is more extensive, covering the years 1953 to 1968, and is summarised briefly below.

Powan spawning grounds are usually areas of wave-washed gravel and small stones, often with associated macrophytes, in water of up to 5 m in depth. Males move onto these grounds at night towards the end of December, and then at the end of this month but mainly during January the females ripen and join them during dusk. Spawning thus occurs when the water temperature is below 5° C and the day length is short but increasing.

Spawning is complete by February and the adult population then disperses over the rest of the loch, but not before they are preyed upon extensively in certain parts of the lake by pike (*Esox lucius*). The eggs are also thought to suffer considerable mortality from trout (*Salmo trutta trutta* and *S. trutta fario*), powan, roach (*Rutilus rutilus*), *Asellus aquaticus* and larvae of the trichopteran *Phryganea*. Powan eggs require 525 degree-days to complete development, and thus most hatch in April.

The sex ratio probably approaches 1:1 in the population overall, but on the spawning grounds males outnumber females by more than 9:1. The size of spawning fish ranges from 20 to 35 cm, although it is mainly in the range of 26 to 31 cm with males being slightly larger than females. Most spawning fish were 3+ or 4+, with much smaller numbers of 2+, 5+ and 6+. Older fish were extremely rare. In 1966, the average length of a spawning female was 27.2 cm and average weight was 246 g. The average fresh ovary weight was 36 g, while the number of eggs per female ranged from 2000 to 11 000.

With regard to the powan of Loch Eck, Brown & Scott (1990) give some brief details of the physiology of reproduction. In the context of the current review, it is worth noting that these authors found the beginning of spawning in Loch Lomond to have begun consistently within two weeks of the winter solstice for the past 10 years, while variation of up to one month has been recorded in Loch Eck.

## Gwyniad

No account of reproduction in the gwyniad of Llyn Tegid has ever been published.

#### 4.2.4 Feeding

##### General aspects

Given the widespread distribution of the coregonids, it is inevitable that their feeding ecology is also diverse. As a result, Jacobsen (1982) in a review of this subject concluded that few generalities apply to the group as a whole. Consequently, the present review is restricted to the species *Coregonus albula*, *C. lavaretus* and *C. autumnalis pollan*. Individuals of these three species usually consume zooplankton and/or macroinvertebrates, with the occurrence of other prey types such as fish or plants being extremely infrequent. More specific information is presented below for each species.

Remarkably little has been published concerning the competitive interactions for food resources of coregonids with other fish species. Lindstrom (1989) considered the potential for competition between *Coregonus* spp. and Arctic charr (*Salvelinus alpinus*), although no evidence for it was presented, and Tikkanen *et al.* (1988) found little dietary overlap between a *Coregonus* sp. and perch (*Perca fluviatilis*). In contrast, there is good evidence of intraspecific competition for food within *C. albula* populations (see below).

The paucity of studies of interspecific competition may be due in part to the fact that communities including *Coregonus* spp. are often of low diversity and so the opportunity for competition with other fishes may be limited. It is interesting to note, however, that Hammar (1988) concluded that small pelagic *Coregonus* spp. may suffer from competition with the invertebrate *Mysis relicta* for cladoceran zooplankton, including *Daphnia* and *Bosmina* spp. As the diet of *Mysis relicta* is very similar to that of young fishes such as the cyprinid roach (*Rutilus rutilus*) (see Cryer *et al.*, 1986), it is very likely that *Coregonus* spp. will compete with such fish under appropriate environmental conditions.

The established interaction between *Coregonus* spp. and *Mysis relicta* is only one way in which these fish interact with the rest of the freshwater ecosystem. Like many other species of fish, in recent years coregonids have been the subject of several studies investigating their roles in aquatic systems. Lang & Lang (1986) found that predation pressure from a *Coregonus* sp. in Lake Joux, Switzerland, influenced the zooplankton populations of the lake, which in turn led to changes in the phytoplankton. Experiments using a subspecies of *Coregonus lavaretus* in enclosures in Lake Suwa, Japan, showed similar effects on plankton populations, and also effects on nutrient concentrations (Hanazoto *et al.*, 1990; Iwakuma *et al.*, 1990). The stocking of *C. lavaretus* into the hypertrophic Hjarbaek Fjord in Denmark may have produced changes in both the plankton and benthos communities (Rasmussen, 1990).

Clearly, coregonids can play very important roles in the functioning of lake ecosystems and studies of this very complex area of limnology are only just beginning. At present it is impossible to know the full implications of the introduction of a coregonid to a new water body. This deduction, while being frustratingly inconclusive, is of great importance for both fisheries management and

conservation. It adds a new dimension to the issue of selecting new water bodies to be stocked with threatened coregonids as the threat may simply be transferred to other components of the lake ecosystem, or even the nature of the lake as a whole.

### *Coregonus* species outside Britain

#### *Coregonus albula*

The diets of both young and mature *C. albula* have been studied in detail in Europe, as have their links with recruitment success and hence population dynamics.

Auvinen (1988) investigated the diet of larval *C. albula* in the mesotrophic Lake Pyhajarvi, Finland, where this species supports an important commercial fishery. Following hatching in May, exogenous feeding begins while the yolk sac is still attached and the larvae are only 8 mm long. The first food is usually Rotifera, but copepod nauplii may also be taken at this time. The first Cladocera appear in the diet when the larvae are 10 mm in length and increase in importance when they reach 13 to 15 mm, beyond which they dominate the diet.

The importance of feeding conditions of larvae for year-class strength was noted earlier and Auvinen (op. cit.) found a clear relationship between diet composition and the success of recruitment. When the larvae were 10 to 14 mm long, the density of Cladocera was higher in years with good year-classes and the larvae began to feed on these larger zooplankton at a smaller size, with a corresponding decrease in the use of rotifers. Thus, when the larvae began feeding on Cladocera when only 10 to 11 mm long, the resulting year-class was stronger. Year-class strength in *C. albula* in this lake at least depends strongly on the feeding ecology of larvae during the first three weeks after hatching.

Sarvala *et al.* (1988) also studied the diet of larval *C. albula* in Lake Pyhajarvi, although their study followed the fish through their first summer and also investigated *C. lavaretus* of similar size (see below). The first food of *C. albula* was again cyclopoid nauplii and copepodids, calanoid nauplii and rotifers. Copepods usually remained the dominant food through May, with an increasing contribution from cladocerans. *Bosmina longirostris*, *B. coregoni* and *Holopedium* were important, with lower numbers of *Daphnia* spp. Rotifers were only important when Cladocera were scarce.

The diet of young *C. albula* was also investigated by Huusko *et al.* (1988) from first feeding in May through to the end of August when a length of 100 mm was reached. The study sites were two Finnish oligotrophic lakes, Lake Lentua which is in a natural state and Lake Ontojarvi which has been regulated with a fluctuation of 4.4 m since 1951. However, no significant differences in *C. albula* diet were found between the two lakes.

Feeding started a few days after the larvae came into the littoral in May when one week old and 9 mm in length. The water temperature was 6 to 8° C and the yolk sac

was gone after a further 10 days. The first food items were usually copepod nauplii or copepodites and rotifers, especially *Synchaeta* spp. Spores, phytoplankton and pollen were also found. Cladocerans including *Holopedium gibberum*, *Bosmina coregoni* and *Polyphemus pediculus* soon came into the diet and dominated it by the end of the littoral phase.

After the fry moved to the pelagic zone in July at a length of 13 to 15 mm, Cladocera species dominated the diet with *Bosmina coregoni*, *Daphnia cristata*, *Polyphemus pediculus* and *Diaphanosoma brachyurum*. In July, they also took emerging pupae and adult chironomids and other species.

The most comprehensive account of the diet, and other aspects, of adult *C. albula* is given by Hamrin (1986) in a study covering five oligotrophic and mesotrophic lakes in Sweden. Foraging was usually restricted to dusk and dawn in all of the lakes and in July in the stratified mesotrophic Lake Ivosjon, the adult *C. albula* migrated to the epilimnion in the afternoon and consumed *Daphnia* spp. and to some extent *Bosmina coregoni*. After dark they returned to the hypolimnion and foraged on *Bosmina coregoni*. During the autumn when there was no stratification, the adult *C. albula* foraged during dusk and daytime mainly in midwater areas. *Bosmina coregoni* was thus the dominant food species between May and August, when feeding was most intense, while in April and October/November the diet was dominated by copepods. In early June, copepodites were important together with *Bosmina coregoni*.

Hamrin (op. cit.) considered *C. albula* to be an obligate planktivore, with all size classes between 20 and 200 mm consuming largely the same species of zooplankton, although other prey types are very occasionally taken. This high dietary overlap between age classes can result in severe intraspecific competition (Hamrin & Persson, 1986), which in turn can bring about oscillations in population abundance as described earlier.

### *Coregonus lavaretus*

The feeding ecology of *C. lavaretus* was reviewed extensively by Jacobsen (1982). The main food of the youngest fry is copepods, although small macroinvertebrates may also be taken. In general, fry prefer *Cyclops* to *Diaptomus*, *Bosmina* and *Daphnia*. Older fry feed more frequently on cladocerans, often *Bosmina* and *Daphnia*. During the summer, when most growth occurs, older *C. lavaretus* feed almost exclusively on zooplankton, preferring *Daphnia* and *Bosmina* to copepods. Jacobsen (op. cit.) states that little is known about the winter diet of *C. lavaretus*, when feeding levels are reduced.

As mentioned above, the diet of larval *C. lavaretus* was studied in the mesotrophic Lake Pyhajarvi, Finland, by Sarvala *et al.* (1988). Newly-hatched *C. lavaretus* consumed largely the same food as *C. albula*, i.e. cyclopoid copepodids and calanoid and cyclopoid nauplii. However, rotifers were almost entirely lacking in *C. lavaretus*. In larger *C. lavaretus*, the importance of chironomid larvae and pupae and littoral or benthic cladocerans was higher, and that of *Holopedium* lower than in *C. albula*. Cyclopoid copepodids and adults were relatively more important for *C. lavaretus*,

especially towards the end of the summer. In general, *C. lavaretus* tended to feed on larger prey items than *C. albula*.

The diet of adult *C. lavaretus* in two Finnish oligotrophic lakes was studied by Heikinheimo-Schmid (1985) in Lake Anattijarvi, which is unregulated, and Lake Kiantajarvi which has been regulated with a fluctuation of 4 m since 1964. In Lake Anattijarvi, the most important prey were fish eggs in spring, benthic macroinvertebrates in summer and late autumn, and zooplankton in the early autumn. In the regulated Lake Kiantajarvi, zooplankton dominated the diet of *C. lavaretus* in summer but benthic macroinvertebrates increased in importance in autumn, although molluscs and large insect larvae and nymphs were rarely consumed. Heikinheimo-Schmid (op. cit.) concluded that benthic macroinvertebrates were usually important in the diet of *C. lavaretus*, but that their availability was very restricted in the regulated lake.

### *Coregonus autumnalis pollan*

The most comprehensive accounts of feeding in pollan have been published by Dabrowski *et al.* (1984) and Wilson (1984b), and like all recent work these studies were restricted to the pollan population of Lough Neagh. Wilson (1984a) briefly summarises the very limited diet work which has been carried out on other populations, although it all suffers from extremely limited sample sizes and so is not presented in this review.

Dabrowski *et al.* (1984) studied the diet of pollan alevins and fry over the period between March and July. The first food of alevins was dominated by nauplii and copepodites, but larger copepods dominated once the alevins had reached weights of 20 mg. By the middle of May, fish weighed 45 mg and their diets contained *Daphnia longispina*. Benthic invertebrates (including *Chironomus* sp. larvae) were found in fish greater than 1.4 g in weight. By July, the fish had become mainly bottom feeders.

Wilson (1984b) presents a detailed account of the diet of mature (2+ and older) pollan throughout the year, with some information on 0+ and 1+ individuals. Feeding intensity of adults was highest in the warmer months of the year, when between May and September the fish ate primarily *Daphnia* spp. For the rest of the year, the pollan fed largely on benthic animals, mainly chironomid larvae, with the exception of April when large numbers of chironomid pupae were taken.

When feeding on the benthos the adult pollan apparently showed little selectivity, with *Chironomus anthracinus* dominating the diet. *Gammarus tigranus*, *Valvata* sp. and *Pisidium* sp. were also taken in small amounts. When feeding on zooplankton, both *Daphnia hyalina* and *D. longispina* were taken in large numbers, but *Cyclops* and other copepods were much less frequent.

The diets of late 0+ and 1+ pollan, which ranged in length from approximately 50 to 150 mm, were similar to those of the adults. However, the food of the fry was found to be significantly different. The first young-of-the-year were caught in June when

they were 30 to 50 mm in length and feeding mainly on *Daphnia*, although *Cyclops* and small chironomids (probably *Procladius*) were also taken. Larger fry took *Bythotrephes longimanus*.

### *Coregonus* species in Britain

#### *Coregonus albula* (vendace)

No account of feeding in the vendace of Bassenthwaite or Derwentwater has ever been published, although detailed and extensive work on adults is to be found in Mubamba (1989) and is currently being prepared for publication. Accounts of feeding in the vendace of Lochmaben prior to its recent extinction have also never been published.

#### *Coregonus lavaretus* (schelly/powan/gwyniad)

##### Schelly

The diets of the schelly in its three known sites, i.e. Ullswater, Haweswater and Red Tarn have been described by Bagenal (1966), Swynnerton & Worthington (1940) and Maitland *et al.* (1990) respectively, although all three studies were very limited. Limited information is also found in Mubamba (1989).

Bagenal (1966) briefly described the schelly in Ullswater as being mainly a plankton feeder, with snails, midge larvae and schelly eggs also occasionally being taken. No further details were given.

Swynnerton & Worthington (1940) described the diet of ten schelly ranging between approximately 200 and 240 mm taken from Haweswater in July 1938 before the lake was impounded. The diet was dominated by small Crustacea including *Bosmina*, but it also contained large numbers of copepods, mainly *Cyclops* but also some *Diaptomus*. Of the Cladocera, only *Leptodora* among the large predators had been eaten, but also taken were *Eurycercus*, *Alona*, *Sida*, molluscs (*Valvata piscinalis*) and *Hydracarina*. The authors concluded that the schelly were feeding near the bottom of the lake and in and around plants, although they also obviously also fed in open water at times.

Maitland *et al.* (1990) described the diet of schelly in Red Tarn from one sampling visit which ran over 31st May and 1st June 1989 and caught 15 mature specimens. The diet was dominated by planktonic Crustacea (mainly *Bosmina* and *Cyclops*), with smaller quantities of detritus, chironomids, gastropods and a few other items.

## Powan

The only published account of feeding in the powan of Loch Lomond and Loch Eck is given by Slack *et al.* (1957), although this area was also the subject of the thesis of Pomeroy (1987).

Investigation of the diet in Loch Lomond involved the examination of over 700 fish ranging from 1+ to 10+, although 3+ and 4+ dominated the sample. Between June and November, the diet was dominated by plankton, particularly the cladocerans *Bosmina obtusirostris* and *Daphnia hyalina*. *Bythotrephes* and the copepods *Diaptomus* and *Cyclops* were also taken, as were small numbers of macroinvertebrates. During the winter, feeding switched to principally benthic animals including chironomid larvae, *Asellus* and *Lymnaea*. Powan eggs were consumed during the spawning season. Like the pollan, the powan showed much reduced feeding rates between December and April.

Rearing studies using fish originating from Loch Lomond showed that the larvae prefer *Diaptomus* to *Bosmina*, even when the latter prey type was more abundant.

In Loch Eck, a small sample size of 17 powan ranging between approximately 220 and 270 mm was taken in September. The diet of these fish was dominated by planktonic crustaceans with *Bythotrephes* making up 75% by volume, and *Bosmina obtusirostris*, *Diaphanosoma brachyurum* and *Diaptomus gracilis* also being taken. One fish contained *Pisidium*, but this was the only benthic food found.

## Gwyniad

The diet of the gwyniad in Llyn Tegid was described by Dunn (1954) and in more detail by Haram & Jones (1971). The study performed by Dunn (op. cit.) was carried out before the water level of the lake became subject to greater fluctuations, while that of Haram & Jones (op. cit.) was undertaken after this significant change. Unfortunately, Dunn's sampling was very restricted, amounting to only eight fish, and so while it showed that the gwyniad at that time consumed both planktonic and benthic prey, a robust comparison with the later findings is not possible.

The sampling of Haram & Jones (1971) was much more extensive, and the subsequent examinations were more detailed. Feeding rates of adult fish (approximately 200 to 300 mm) were low from January to April, but increased in summer and remained high until December.

From December through to July, the gwyniad fed largely on the bottom of the lake, with chironomid larvae, *Pisidium* and detritus common in the diet. Ostracods, Ceratopogonids, Hydracarinae and *Asellus* were found infrequently, while powan eggs were taken in February.

Between August and November, the gwyniad foraged more widely with prey being taken from the lake surface and midwater in addition to the bottom. Copepods were found in numbers in the diet between December and March, and from June onwards.



Cladocera were taken from August to November, while chironomid pupae were only consumed in July and August.

#### 4.2.5 Seasonal distribution

##### General aspects

Numerous authors have remarked upon the extensive nature of migrations shown by various *Coregonus* species, which consequently have dramatic seasonal shifts in their distributions. A variety of abiotic and biotic factors are thought to be responsible for these migrations, although the major movements are associated with feeding and spawning. Specific spawning migrations were reviewed earlier and so will only be mentioned briefly in this section of the review. While most of these migrations are restricted to within the lake, some species outside Britain may enter river systems or even the sea during the course of a year. Because of this diversity, the present review is again restricted to the species *Coregonus albula*, *C. lavaretus* and *C. autumnalis pollan*, although it must still be remembered that these investigations have been performed in lakes much larger than those inhabited by coregonids in Britain, and thus findings are not always directly applicable to the latter populations.

##### *Coregonus* species outside Britain

##### *Coregonus albula*

The distribution of *C. albula* has been studied for all life stages from newly-hatched larvae through to the mature adult, and a clear pattern of seasonal and ontogenetic changes has emerged.

Bagge & Hakkari (1987) first found newly-hatched larvae of 6 to 7 mm in length in the pelagic zone of Lake Paijanne, Finland, immediately after ice-break. The young *C. albula* were patchily distributed throughout their first year of life, particularly when they moved to the littoral zone at a length of 17 to 18 mm in the second week of June. In contrast, Auvinen (1988) found newly-hatched *C. albula* larvae in dense schools in areas of the littoral zone only 20 to 60 cm in depth of the oligotrophic Lake Pyhajarvi, Finland, in May. After three to four weeks in these areas, the young fish reached 20 to 25 mm in length and moved out to the pelagic zone.

Naesje *et al.* (1986) made a detailed study of habitat use by 0+ *C. albula*, and *C. lavaretus*, in Lake Mjosa, a large lake in Norway with a maximum depth of 449 m. In this lake, both coregonids spawn in an inflowing river and the larvae subsequently drift into the lake proper where they aggregate along the shoreline and begin exogenous feeding. Both species stay in this zone until the end of July, often in mixed shoals. From August onwards, *C. albula* abandoned the littoral areas for the pelagic zone at depths of 15 to 30 m.

Studies by Dembinski (1971) and Hamrin (1986) also investigated habitat use by 0+ *C. albula*, although in both of these works the distribution of adults was also recorded.

Dembinski (1971) looked at the distribution of *C. albula* in several Polish lakes with depths of approximately 40 m, using an echo-sounder and netting techniques. In May and April, *C. albula* were found at depths between 5 and 40 m, while in other months the upper occurrence range by night descended together with the thermocline. For example, in July this depth was 10 m, in September 15 m, and in October 20 m. Thus, during stratification *C. albula* were usually restricted to the hypolimnion at a depth of 20 to 35 m where they schooled during the day and dispersed at night. In the winter they were not found in water cooler than 2° C.

From August, 0+ were also taken in the mid-water together with older *C. albula*. In September, when older individuals were concentrated at the bottom of the lake, 0+ congregated in the upper hypolimnion at 15 to 25 m depth where oxygen levels were relatively higher (4.6 to 3.0 mg/l against 2.6 mg/l). In October, the older *C. albula* also moved off the bottom to a higher layer of depth 20 to 30 m which had a relatively higher oxygen concentration than the bottom (2.2 to 1.6 mg/l against 1.3 to 1.0 mg/l). At this time most 0+ were found at 20 to 25 m depth where oxygen levels were in the range of 2.2 to 1.8 mg/l. During the autumn and spring overturns, 1+ *C. albula* could be found between the surface and bottom of the lake, while 0+ at these times were restricted to 20 to 25 m depth.

Hamrin (1986) also used a combination of echo-sounder and nets to investigate the seasonal distribution of *C. albula* in six Swedish lakes, all of which were oligotrophic except for one which was mesotrophic and in which maximum depths ranged from 18 to 50 m. Adults concentrated in the hypolimnion whenever stratification existed, although a few fish were found in the epilimnion if the temperature was below 18° C. Like in the Polish lakes reviewed above, adults were not concentrated in deep water during the autumn mixes, but in contrast to the above lakes, Hamrin never found hypolimnetic oxygen concentrations below 4 mg/l. In the homiothermic hypolimnion of one lake, adult *C. albula* were most abundant at the upper and most illuminated part. Throughout the year, catches were highest from dusk to dawn, with highest values during the first part of this period. Daytime catches were always low.

Echo-sounding allowed the observation of changes in the seasonal and diel vertical distributions of 0+ *C. albula*, although the patterns observed differed greatly between the lakes. Generally, 0+ were more abundant than adults in the metalimnion, while the reverse was true in the hypolimnion. During the night, this upper layer of 0+ migrated up to the epilimnion (temperature between 15 and 19° C) while the adults stayed within the hypo- and metalimnion (temperature 13 to 15° C). The 0+ thus experienced a temperature change of up to 10° C during their diel vertical migration. Hamrin suggested that predation pressure was at least partly responsible for these differing vertical migration patterns.

The distribution of adult *C. albula* has been studied in several investigations of Finnish lakes by Jurvelius and colleagues, the findings of two of which are summarised here. Jurvelius & Heikkinen (1988) used an echo-sounder to study the

diel and seasonal distribution of *C. albula* in the oligotrophic Lake Paasivesi which has a mean depth of 21 m and a maximum depth of over 50 m. From May to August, *C. albula* were mainly found at 10 to 30 m depths, but began to descend in August such that by October they were found at depths of between 10 and 60 m. In all months the fish tended to stay higher in the water column by night than by day. Very similar behaviour was shown by *C. albula* in Lake Karljalan Pyhajarvi (Jurvelius *et al.*, 1988).

### *Coregonus lavaretus*

The seasonal distribution of *C. lavaretus* has been less studied than that of *C. albula*, although as stated above Naesje *et al.* (1986) provide a comparison of 0+ of both species in the same water body, Lake Mjosa in Norway which has a maximum depth of 449 m. In this lake, both coregonids spawn in an inflowing river and the larvae subsequently drift into the lake proper where they aggregate along the shoreline and begin exogenous feeding. Both species stay in this zone until the end of July, often in mixed shoals. From August onwards, *C. albula* abandons the littoral areas for the pelagic zone, but *C. lavaretus* stays in the littoral areas through the summer.

The distribution of older *C. lavaretus* was investigated using gill nets by Hessen *et al.* (1986) in the incipient mesotrophic Lake Tyrifjorden in Norway which has a mean depth of 114 m and a maximum depth of 295 m. Catches of *C. lavaretus* in the upper pelagic zone increased from May to a maximum in July, and then decreased rapidly in August and September concurrently with increasing catches in the deeper layers. Differences between the distributions of smaller and larger fish, with the former tending to avoid the open pelagic, were thought to be due to differential predation pressure.

In summary, *C. lavaretus* is less of a pelagic specialist than *C. albula*, although distributions obviously vary greatly between lakes.

### *Coregonus autumnalis pollan*

All studies of the distribution of pollan have been restricted to Lough Neagh, which as a shallow, unstratified, eutrophic lake (Winfield & Wood, 1990) is a very atypical coregonid habitat.

The distribution of larvae has been briefly studied by Dabrowski (1981) who reported that newly-hatched pollan were first found in February at a distance of 100 to 200 m offshore where the water column was 1 to 3 m deep. Larger numbers were found in April but they were still associated with a known spawning ground. Further studies revealed that pollan fry change from pelagic to benthic feeding in July (Dabrowski, 1982).

The spawning migration of adult pollan from offshore to inshore areas was described above (Dabrowski, 1981), and Wilson (1984a) reports that adult pollan also undertake

complex seasonal and diel vertical and horizontal migrations in association with feeding activities.

### *Coregonus* species in Britain

#### *Coregonus albula* (vendace)

No account of seasonal distribution in the vendace of Bassenthwaite or Derwentwater has ever been published, although some work on adults is to be found in Mubamba (1989) and may be published in the near future. Thus, the only published account of distribution of *C. albula* in Britain is of the vendace of Lochmaben by Maitland (1967) prior to its recent extinction.

Maitland (1967) studied the distribution of the vendace in Mill Loch which is a small lake of 13 ha, with a mean depth of 6.3 m and a maximum depth of 16.8 m. While eels, perch, pike and roach were found mostly around the edges during the summer, the vendace was in contrast largely restricted to the deeper waters, particularly the 15 m basin. During daylight the vendace was found to stay mainly in mid-water at depths greater than 5 m, although fish moved up to the surface at dusk where they stayed until dawn.

#### *Coregonus lavaretus* (schelly/powan/gwyniad)

##### Schelly

The account of the biology of the schelly in Haweswater and Ullswater by Bagenal (1970) includes references to distributions. The schelly sampled from Haweswater were drawn down a pipe which was itself 18.3 m below the water surface when the reservoir was full, corresponding to a position 10.7 m above the original lake surface, with the bulk of the fish being taken between the 15th of January and 15th of February each year in association with the spawning season. It is unknown whether the schelly have retained old spawning grounds which are now in over 30.5 m of water, or have moved to new grounds. Nothing has been published concerning other aspects of the distribution of schelly in Haweswater.

In Ullswater, Bagenal (1970) gives the location of an inshore spawning ground in Gowbarrow Bay, but again nothing is known about the summer feeding migrations of the schelly in this lake with the exception of the observation that floating nets are inefficient in their capture.

A very limited account of the distribution of the small population of schelly in Red Tarn, which is 9.8 ha in extent and has a maximum depth of 26 m, is given by Maitland *et al.* (1990). One 24 hour sampling session over May 31st and June 1st revealed schelly close to the bottom of the lake in deep water.

## Powan

Maitland (1969) states that the powan of Loch Lomond shows regular diel and seasonal migrations connected with feeding or reproduction. Outside the breeding season, adult powan stay deep in the water bottom, including on the bottom in the littoral and sublittoral or at depths of 20 to 30 m in deeper water. At dusk they move into shallower water, often coming up to the surface and in to the edge of littoral areas to feed. The reverse movement occurs at dawn.

In addition, Maitland (1967) remarked that the distributions and migrations of the powan in Loch Lomond and Loch Eck are similar to those described above for the vendace in Mill Loch, although no details were given.

## Gwyniad

No accounts of the distribution of the gwyniad in Llyn Tegid have ever been published, although Haram & Jones (1971) note that this coregonid shows complex diurnal and seasonal patterns of migration which change with both sex and age.

### 4.3 Variation

#### 4.3.1 General aspects

The genus *Coregonus* is renowned for the high degree of morphological variation shown by its members, a phenomenon which is partly responsible for the present state of uncertainty over the taxonomic relationships of many populations. In addition, it is clear that isolating mechanisms within the coregonids are poor and, coupled with many introductions for fishery purposes, have led to the formation of many 'hybrids' throughout the geographical range of these fishes (Svardson, 1979).

Attempts to classify coregonids in the past were dominated by morphological approaches examining the phenotype, but in more recent years researchers have increasingly turned to starch gel electrophoresis to assess enzyme and thus genotypic variation more directly. In addition, the last two years have also seen the publication of a few electrophoretic investigations of mitochondrial DNA, although this technique has not yet been widely employed in coregonid research.

#### 4.3.2 Phenotypic variation

The major morphological feature used in coregonid taxonomy has been the number of gill rakers (see for example Svardson, 1979). However, the variation found in this parameter, while having a large genetic component, is also strongly influenced by the environment. In particular, there are strong links between gill raker morphology and diet (Kliewer, 1970), and thus with growth and other aspects of population biology.

Lindsey (1981) made a detailed study of gill raker numbers in the North American *Coregonus clupeaformis* and the principles of his findings probably also apply to European populations. It was found that characters which apparently render a given stock distinctive may in fact vary with the presence or absence of other fish species in the lake, particularly in the case of gill raker numbers. In the face of this kind of variability it is not surprising that coregonid taxonomy has only relatively recently begun to be clarified. Kristofferson & Clayton (1990) were able to identify several subpopulations of *C. clupeaformis* in Lake Winnipeg only after making a total of 23 morphological measurements, 8 meristic counts, and extensive electrophoretic examination of enzymes (see below). A combination of morphological examination and electrophoretic techniques was also used by Ihssen *et al.* (1981) in a study of five allopatric stocks of *C. clupeaformis* in the Great Lakes Region of Canada. One important finding of this study was that a significant part of the morphometric variation among the stocks was in fact related to differences in growth rates.

No similarly exhaustive examinations of *Coregonus* morphology have been published for British populations, although some information is given in Mubamba (1989). However, morphological variation is clearly present in the *C. lavaretus* populations as Slack *et al.* (1957) report the presence of a supernumerary pelvic fin in approximately 1% of the powan of Loch Lomond and Bagenal (1970) gives a similar level of occurrence (1.4%) in the schelly of Ullswater but notes that this feature is absent from the schelly of Haweswater. Slack *et al.* (op. cit.) also state that the *C. wartmanni* of Lac de Thoun in Switzerland also show a supernumerary pelvic fin in about 1% of individuals.

#### 4.3.2 Genotypic variation

The application of starch gel electrophoresis to the study of genetic variation and relationships in coregonids during the 1970s clarified many aspects of these problems. The work was largely pioneered by examination of the enzyme systems of *C. clupeaformis* in North America, and more recent work on subpopulations of this species using this technique was mentioned above (Ihssen *et al.*, 1981; Kristofferson & Clayton, 1990).

In Europe, electrophoresis has been used extensively for interspecific comparisons to resolve outstanding questions of coregonid taxonomy, including that of the British populations. Ferguson (1974) investigated the relationships of vendace from Bassenthwaite, schelly from Haweswater, powan from Loch Lomond, gwyniad from Llyn Tegid and pollan from Lough Neagh and Lough Erne. Electrophoresis of enzymes showed that three *Coregonus* species are present in the British Isles, as defined in detail earlier in this review. However, neither the study of Ferguson (1974) nor the later one of Ferguson *et al.* (1978) investigated intraspecific relationships among the coregonids from different sites in Britain. Some such information is available for both vendace and schelly in Mubamba (1989), although it is derived from very small sample sizes.

Within-species variation was investigated in the *C. albula* populations of Finland by Vuorinen *et al.* (1981) and Vuorinen (1984). High levels of genetic polymorphism

were found in both studies, with about 50% of the enzyme loci studied being polymorphic, resulting in extensive genetic heterogeneity among the populations. The genetic basis of this variation was established by the electrophoretic examination of hybrids between *C. albula* and *C. lavaretus* (Vuorinen & Piironen, 1984), which showed that a number of alleles segregated in a simple Mendelian fashion.

A subsequent examination of variation in nine populations of the *C. lavaretus* complex in central Europe revealed a much lower level of genetic diversity (Vuorinen *et al.*, 1986). However, Vuorinen *et al.* (op. cit.) note that electrophoresis detects only a part of the genetic variability of a population. Therefore, the observation of only slight genetic differences does not exclude the existence of adaptive genetic differences between populations.

In the late 1980s, the technique of mitochondrial DNA electrophoresis was first applied to *Coregonus* species. Shields *et al.* (1990) used the technique to confirm that dwarf and normal-sized ciscoes in Ten Mile Lake, Minnesota, are conspecific *C. artedii*, while Bernatchez & Dodson (1990) used it to investigate genetic structuring in anadromous *C. artedii*. The only application using a European coregonid population found during this review was by Bernatchez *et al.* (1989) who compared mitochondrial DNA variability in anadromous European *C. lavaretus* with that in North American *C. clupeaformis* and concluded that the severity of population bottlenecks related to Pleistocene glaciation events may be largely responsible for the level of variability observed in present populations.

Bernatchez *et al.* (op. cit.) also commented on the failure to date of mitochondrial DNA studies to discriminate between stocks in many temperate fish species. They suggested that currently used analyses are insufficient to permit the discrimination of mitochondrial DNA genotypes differing solely by the accumulation of mutations over a period of 18 000 years or less. However, they did conclude that stocks can be discriminated by the differential distribution frequencies of mitochondrial DNA lineages that predate the genetic isolation of populations.

#### 4.4 Breeding

##### 4.4.1 General aspects

The breeding and rearing of *Coregonus* has a long history, dating back to the early part of this century (Bodaly, 1986; Salojarvi, 1986), although it is only in very recent years that major breakthroughs have been made. Almost all of this work has been carried out with the aim of the efficient production of large number of fish for stocking in commercial fisheries, rather than for nature conservation.

In a review of *Coregonus* rearing techniques of the late 1970s, Fluchter (1980), writing from a German viewpoint, noted that the production of most coregonid fisheries was limited by the supply of larvae, and thus their propagation and stocking held great potential. At that time, the major rearing problem to be solved was the feeding of newly-hatched larvae. Most coregonid production was carried out using

live zooplankton as food in pond or cage systems, an approach which precluded the true intensification of the production process. Artificial diets available at the time resulted in poor survival of the larvae, often with high levels of deformities, although feeding was much less of a problem once the larvae were longer than 18 to 20 mm and had metamorphosed into young adults.

Further reviews of coregonid rearing were produced a few years later by Luczynski (1986), Salojarvi (1986), Viljanen (1986), and Bodaly (1986). Production of *C. albula* and *C. lavaretus* in Poland was still based on feeding with live zooplankton in ponds and cages (Luczynski, 1986), as it was for these two species in Finland (Viljanen, 1986 and Salojarvi, 1986 respectively). The same technique was also used in Canada for the production of *C. clupeaformis*, although a large project investigating the use of new artificial diets was in its early stages (Bodaly, 1986). The need to produce fingerlings for stocking was becoming increasingly clear from the often poor results of stocking with eggs or larvae (Luczynski, 1986).

The last two years have seen the first publications of successful, large-scale rearing of coregonid larvae on exclusively artificial diets. This important advance has been made with both European and North American species and will be reviewed in detail below.

#### 4.4.2 Conservation aspects

As noted above, the vast majority of studies of coregonid rearing have been carried out on fishery grounds and so have understandably concentrated on the low-cost, large-scale production of fish, with little consideration of nature conservation aspects. The latter concerns mainly centre around the preservation of genetic diversity within a reared or supplemented population.

While questions of minimum viable population sizes have been investigated by ecologists for some time, few definite conclusions have been reached. Whitten (1990) considers this aspect of conservation work, although he does not arrive at any firm conclusions or guidelines. In the conservation-motivated introduction work of Maitland & Lyle (1990), attempts to maximise genetic diversity of the introduced fish were made by taking sexual products from as many parents as possible. Similarly, conservation rearing work on the unique *C. clupeaformis* population of Lake Simcoe in Canada, although carried out in large part for the benefit of a recreational fishery, has also attempted to maximise diversity by taking eggs from several spawning grounds (Harris, in press).

#### 4.4.3 Practical aspects

##### Recent advances

As outlined above, the history of coregonid rearing around the world has seen a shift from semi-natural pond based systems using zooplankton as food, through to cages of



various kinds exploiting the same natural but limited diet, and finally to largely or exclusively artificial diets in tanks. The rearing project involving the *C. clupeaformis* of Lake Simcoe in Canada has been central in these developments.

Drouin *et al.* (1986) investigated several diets using the *C. clupeaformis* of Lake Simcoe, including live *Artemia salina* nauplii and artificial starter food developed for trout. This study revealed that live food could be completely removed from the diet of larvae by substitution with decapsulated, lyophilised *Artemia* cysts. This technique produced survival rates of greater than 93% such that after seven weeks and at a weight of 140 mg the young coregonids could be moved on to a standard trout starter food. Additional rearing to yearling size was accomplished easily using trout feed, with mortalities being kept to less than 3% and fish weighing 50 g available for stocking at 14 months of age.

Rearing research has continued with this *C. clupeaformis* population, resulting in the first large-scale, fully-intensive production of a coregonid using only artificial food (Harris, in press). Husbandry techniques have been refined over the years of this research project and many artificial diets have been evaluated, many of which were accepted by the larvae but led to high incidences of scoliosis, incomplete opercular development, and/or lower jaw deformities when the diet was not supplemented with *Artemia*. In 1987, trials were carried out using Fry Feed Kyowa-B (FFKB) made by Kyowa Hakko Kogyo of Tokyo, Japan. This diet was found to give excellent growth and survival greater than 95% without significant levels of deformity, even with no supplementation by *Artemia*, and has now been adopted as the standard production diet.

In Europe, Koskela (1988) reported some success in rearing *C. muksun* larvae on experimental artificial diets with final survival figures of between 64 and 78%. However, Koskela (pers. comm.) recommends that these diets are supplemented with *Artemia* to avoid problems with incorrect development of operculae.

### *Coregonus albula*

The rearing of *C. albula* has been carried out extensively in Poland for some years and is reviewed by Luczynski (1986). Spawning adults are gill netted in the autumn and stripped at the lakeside. The eggs are fertilised and water hardened before being transported to hatcheries where survival to hatching is 60 to 85%. During incubation, eggs are treated to prevent fungal attacks and any dead ones are removed at frequent intervals. Larvae are usually stocked into lakes several days after hatching, although the benefits of rearing them to fingerling size are appreciated. Delayed hatching techniques are sometimes used so that larvae are stocked under better zooplankton conditions.

Viljanen (1986) states that similar rearing programmes are used for *C. albula* in Finland, although details of husbandry procedures are not given.

### *Coregonus lavaretus*

In Finland, the rearing of *C. lavaretus* fingerlings for stocking began at the end of the last century, although mass production did not start until the 1960s (Salojarvi, 1986). Since this time, millions of fingerlings have been produced on diets of zooplankton in semi-natural ponds.

Mamcarz & Nowak (1987) describe the latest advance in cage technology for *C. lavaretus* rearing in Polish ponds where natural zooplankton populations are again used as the main food supply. The major problem with such apparatus has been the need to retain the small larvae while allowing free entry of zooplankton to the cage, but the authors show that this can be overcome by using lights to exploit the positive phototaxis of *C. lavaretus* larvae.

The usefulness of frozen zooplankton as a food for *C. lavaretus* was investigated by Kleifeld-Kriebitz & Rosch (1987). Within 10 weeks of beginning to feed, the larvae had reached 30 mm in length and had an average dry weight of 22 mg, with survival over this period being 45%. The larvae were successfully switched to an artificial diet once a length of 40 mm had been attained.

*C. lavaretus* larvae were reared exclusively on experimental artificial diets based on yeast and freeze-dried liver or diets supplemented with freeze-dried cod muscle or roe by Dabrowski & Poczczynski (1988), again with a later switch to a standard trout feed.

Finally, Rosch (1988) reports the results of feeding two forms of *C. lavaretus* from Lake Constance on a new commercially available artificial diet, Tetra 200 manufactured by Tetra-Werke of Melle, Germany. The inshore-spawning 'gangfisch' showed a survival of 80% and grew to an average weight of 46 mg after 45 days, while the offshore-spawning 'blaufelchen' showed a survival of 50% and grew to 19 mg after 35 days.

#### 4.4.4 *Coregonus* species in Britain

##### *Coregonus albula* (vendace)

No detailed accounts of the rearing of vendace in Britain have been published. Maitland & Lyle (1990) successfully hatched eggs obtained from Bassenthwaite in 1988 and introduced most of the young to new sites in Scotland, as well as retaining some to rear to maturity in an attempt to obtain further supplies of eggs without recourse to the parent population. However, no information was given on the techniques employed, nor on the survival and numbers of young produced.

An account of vendace rearing on a small scale is given by Mubamba (1989), although this study was purely experimental and sustained very high larval losses.

## *Coregonus lavaretus* (schelly/powan/gwyniad)

### Schelly

The only published account of rearing of schelly is given by Bagenal (1970), although again this was an experimental investigation and used the eggs of just one female from Ullswater. After being taken in a gill net in early January, the female was stripped at the lakeside and the fertilised eggs then transported to the laboratory.

Some of the eggs were used for rearing purposes while the rest were used to investigate the effects of temperature on hatching success. Total egg mortality was experienced at 10° C, with high mortality at 8° C. Incubation at 6° C, which was probably near to the temperature of Ullswater at the time, and 4° C resulted in much higher hatching levels with the former temperature producing first hatchings in late March.

The eggs in the rearing study were successfully hatched in running Windermere water and the resulting larvae fed on a mixture of live *Artemia salina* and dried *Daphnia*, before being given a commercial trout food in their later stages. In this way, some schelly were successfully raised to maturity.

### Powan

Slack *et al.* (1957) evidently reared powan from Loch Lomond from eggs to beyond metamorphosis during a study of their development, although no details of the husbandry procedures were given.

The Loch Lomond powan was also the main population used by Maitland (1967) in a study of artificial fertilisation and rearing of *C. lavaretus* eggs in Britain, although the resulting larvae were apparently not raised. Adults were taken by gill netting before being stripped in the standard way for salmonids.

More recently, Maitland & Lyle (1990) have reared powan originating from Loch Lomond to maturity in ponds and artificial tanks, although again no details were given of the husbandry procedures or the numbers of fish produced.

### Gwyniad

No accounts of rearing gwyniad from Llyn Tegid have been published.

#### 4.5 Conclusions

Members of the genus *Coregonus* have been extensively studied in mainland Europe and elsewhere, but the number of publications dealing with the British populations is relatively small. While the main body of this review is in essence itself a series of conclusions, a few more specific statements can be made about the British populations in a conservation context.

Firstly, it is possible that the full distribution of coregonids in Britain is not yet fully appreciated. The continued existence of the schelly in Red Tarn was confirmed only recently and populations may also occur in Brotherswater, Loweswater and other small water bodies in the Lake District. The conservation value of such populations would be extremely high.

Information on the population biology of coregonids in Britain is poor when compared with populations elsewhere, although this situation is to be expected given the absence of commercial fisheries. Populations of *Coregonus* in mainland Europe show rapid and dramatic changes in recruitment, abundance and growth, characteristics which make investigations of their population dynamics very difficult even over long study periods. Detailed analysis of the mechanisms of coregonid population dynamics is impossible over a three year period. However, the development of a non-destructive method of monitoring the absolute abundances of the British species would be invaluable.

The basic details of coregonid reproduction in the British Isles are known and a more precise knowledge of the timing of spawning, fecundities, etc. is of questionable value for their conservation, particularly when the numbers of fish which must be killed are taken into account (see below). However, knowledge of the numbers and locations of spawning grounds would be useful, particularly in the more eutrophic lakes where they may be under threat.

The diets of all known *Coregonus* populations in Britain have been studied to greater or lesser extents, although not all of this work has yet been published. However, most investigations have been confined to adults and very little is known about the diets of larvae and juveniles. Given that competitive interactions with other fishes, if they occur at all, are more likely during the first few months of life, and the established importance of feeding conditions in the first few weeks after hatching, this is an extremely important area of coregonid biology.

Very little is known about the seasonal distributions of British coregonids, particularly in relation to the effects of eutrophication which have been shown to be important in mainland Europe. For coregonids in such environments, deoxygenation is often coupled with the threat of lethally high temperatures and is a major problem to be considered in their conservation. The extrapolation of laboratory studies to nature has been found to be difficult and so such relationships are best studied in the field. Several of the British coregonid populations are likely to suffer from restricted habitat use due to eutrophication.

No studies have been made of intraspecific variation in the British coregonids. However, variation clearly does exist at least phenotypically in the schelly in terms of

the supernumerary pelvic fin. Given the phenotypic plasticity of members of the genus *Coregonus*, it is likely that an assessment of intraspecific variation will be more successful if pursued through electrophoretic rather than biometric techniques.

Finally, very little has been published on the artificial breeding and rearing of coregonids in the British Isles. However, significant advances have been made in this field in Europe and North America in recent years with the result that the production of fingerling coregonids on an exclusively artificial diet is now a possibility. Such commercially-developed methods can probably be modified for use in the relatively small-scale production of British coregonids for stock supplementation, although experimental trials with the British populations have not been carried out.

## 5. CONCLUDING REMARKS

In addition to the three species of British freshwater fishes protected by the Wildlife and Countryside Act, 1981, several further species are acknowledged as rare or are potentially rare. While some of these species, such as the Arctic charr, are already the subjects of some conservation research, this is not the case with fish such as the spined loach, rudd, crucian carp and silver bream. No studies of the distributions of these species have been published since the early 1970s, although some populations are known to have declined or even to have been lost entirely.

The British coregonids have been relatively little studied, although something is known of most aspects of their ecologies with the exceptions of their present seasonal distributions in relation to environmental factors, such as levels of dissolved oxygen, and their absolute abundances. Given our ignorance of the latter area of coregonid ecology, the taking of large sample sizes by destructive methods would be reckless and is rightly forbidden by the Nature Conservancy Council.

The above restriction imposes considerable restraints on the nature of research that can be undertaken on the British populations given the destructive nature of standard large lake fishing techniques, particularly for delicate species such as coregonids. However, recent developments in echo-sounding technology hold much promise for the study of coregonid population biology, and may also contribute to the assessment of their seasonal distributions in relation to oxygen, temperature and other environmental parameters. The latter factors probably pose the greatest threat to the continued survival of the British coregonid populations.

## 6. ACKNOWLEDGEMENTS

Kenneth Harris, Roland Rosch and Juha Koskela kindly provided advice and unpublished manuscripts on the rearing of coregonids. Jurgen Hartmann and Cathy Hill gave useful directions for the literature search, while the staff of the FBA Library made it all possible.

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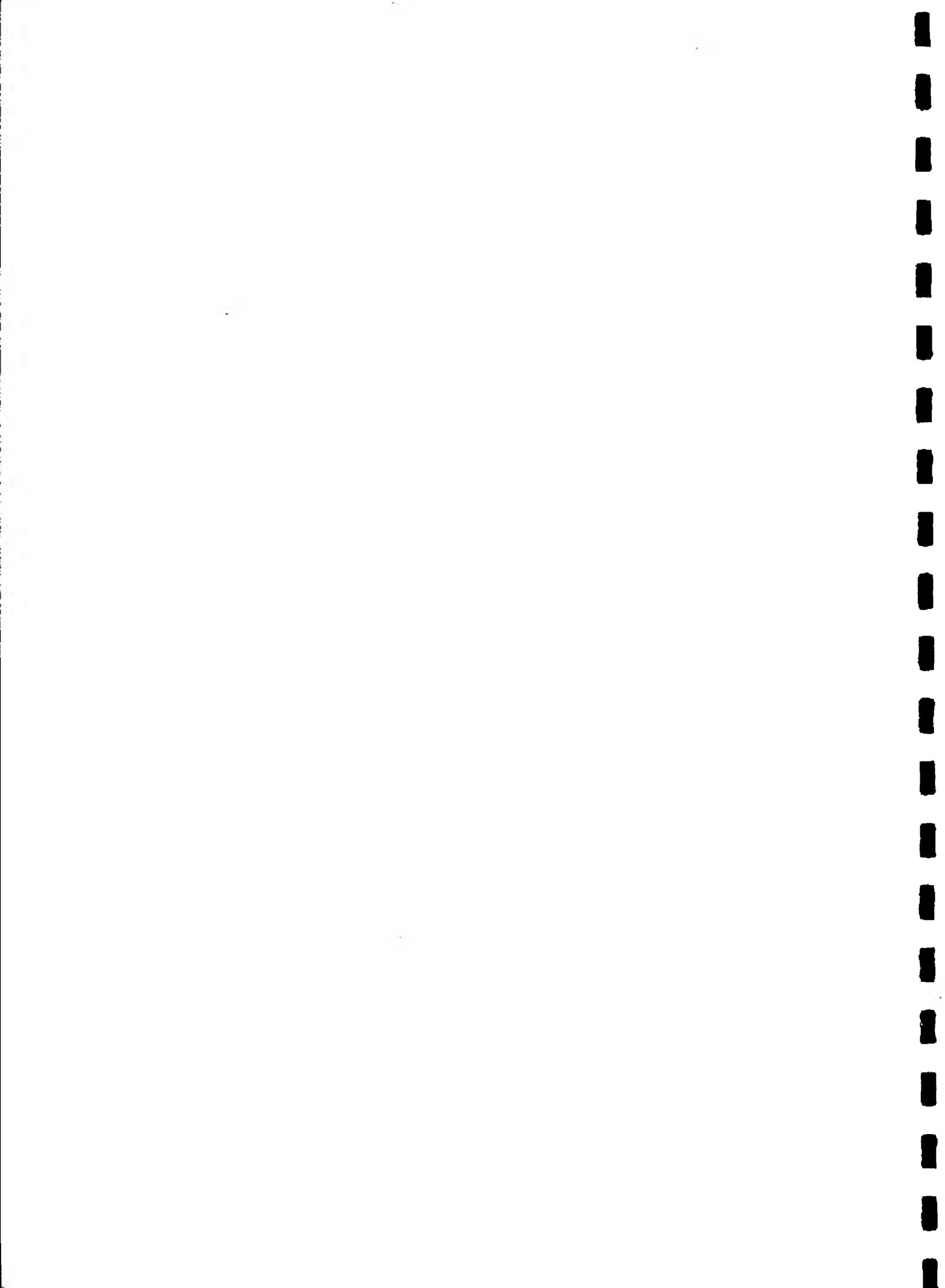
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