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The Ecology and Management of the European Grayling *Thymallus thymallus* (Linnaeus)

Interim Report

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CHAPTER 1

1 Overall aim

A collaborative research and development project between the Institute of Freshwater Ecology and the Environment Agency in the UK, to review the ecology, status and management of grayling in order to provide recommendations for future management of grayling fisheries in England and Wales.

2 Objectives

- To review grayling ecology, status and management practice in concentrating on England and Wales but including publishes literature from Europe and North America, where appropriate.
- To recommend best management practices on the basis of objective 1 and produce a guidance leaflet for internal and external circulation which promotes the key issues.
- To identify future information needs and propose and cost a programme of research and development to address these.

3 Achievements to date

Objective 1

- Reviewed 95% of all literature regarding grayling in Europe and North America to produce a near complete comprehensive literature review and reference list (see enclosed).

Objective 2

- Verbally contacted all Environment Agency Heads of Fisheries Depts. Followed up those which have grayling fisheries and relevant data, with individual letters (week commencing 18 October 1999) and a questionnaire (Appendix 1). Replies have come back from the following areas:

Name	*Area*
Jon Shelley	Northumbria
Tim Jacklin	Upper Trent
Andy Strevens	South Wessex
Paul Hyatt	Anglian (Northern)

Visits are being organised to the following offices: David Hopkins (Dales) and John Woolland (Upper Severn). Alan Starkie (Lower Severn) has acknowledged our letter.

- A meeting was arranged with Robin Mulholland (The Grayling Society Chairman), Anthony Wilson (The Grayling Research Trust Chairman) and Richard Cove (EA), to organise the distribution of a questionnaire (Appendix 2) and letter to the 900 members.

- Made contact with the relevant fisheries scientists in European countries outside the UK (week commencing 4 October). Replies from Germany, Lithuania, Latvia, Sweden and

Luxembourg to date. Have requested further details of grayling management programmes from Sweden, Germany and Latvia. Still awaiting replies from France, Italy, The Czech Republic, Denmark, Switzerland, Belgium, Slovakia, Austria and Norway.

- Received a large amount of information regarding grayling management practices in British Columbia and Alaska. Also identified contacts in Vancouver.

4 Future plans

Objective 2

- Collate data and questionnaire information received from EA contacts and chase those who have not replied by week ending 5 November 1999. Review information and commence formulation of management recommendations and identify future information needs.
- Collate questionnaire responses from the Grayling Society (closing data 30 November 1999).
- Chase European and North American contacts and review information as above.

Objective 3

- In view of information amassed from all contacts, locate areas of further research and development.

CHAPTER 2

1 Introduction

The European grayling, *Thymallus thymallus*, is a highly under-rated freshwater fish, particularly in the United Kingdom. As such, little scientific research has been conducted on its biology, ecology or specific management plans, in comparison to the related species, salmon, *Salmo salar* L. and brown trout, *Salmo trutta trutta* L. or the nearest relative to *T.thymallus*, the Arctic grayling, *Thymallus arcticus* (Walbaum), whose life history has been well documented in view of its high ranking by anglers, as a game fish. However, the importance of sound scientific research cannot be over stressed for this species, which can potentially provide an excellent fishery and source of income in salmonid depauparate rivers.

The aim of this report therefore, is to review all available information on the biology, ecology and management of the European grayling, *T. thymallus*, incorporating findings for *T. arcticus* to bridge subjects where the literature is scarce, and propose management strategies for *T. thymallus* in the United Kingdom.

2 General description

The European grayling, *T. thymallus*, used to belong to its own family, Thymallidae (Wheeler, 1969). It has only recently been re-included in the family Salmonidae (Wheeler, 1969). Historically, it has been regarded as a coarse fish in Britain and as a result, research on grayling biology and ecology has been quite limited.

The name grayling is at least five centuries old (Magee, 1993). *T. thymallus* originates from the faint smell of the herb thyme, which emanates from the flesh (Ibbotson, Pers. Comm.). The grayling has been described as 'The Lady of the River', however Table 1 indicates the many different names by which it is known throughout the rest of Europe.

The morphology of the grayling is well described by Northcote (1995). It is slightly flat-sided with a relatively small mouth. The upper jaw projects slightly beyond the lower jaw. Juvenile grayling are silvery/light green with bluish spots along the flanks, adults however, have a grey/green back, green sides and a white body. The distinguishing feature of the species, is the presence of a large dorsal fin, which has four to five rows of red and black spots (Cihar, 1998; Wheeler 1969). The fin varies in size and shape between males and females, producing notable sexual dimorphism within this species (Witkowski *et al.* 1984). The presence of the adipose fin groups the grayling taxonomically with the salmonids.

Both sexes show quite aggressive behaviour throughout the whole year. They tend to form schools outside the breeding season, in which each fish holds its own station, defending it as its own territory. During the spawning season, only the males defend their own territory and show pronounced aggression towards both sexes (Fabricius & Gustafson 1955).

T.thymallus is listed as protected species under Appendix III (Annex 5) of the EC Directive 78/659/EEC (www.ecnc, 1978) and of the Bern Convention on the Conservation of European Wildlife and Natural Habitats (www.ecnc.nl, 1978).

Table 1: The common names of *Thymallus thymallus* throughout Europe and America (www.fishbase.org.uk, 1999).

Common names of *T. thymallus*		
Common name	Used In	Language
Asch	Germany	German
Äsche	Austria	German
Äsche	Germany	German
European grayling	USA / England	English
Grayling	USA / England	English
Harjus	Finland	Finnish
Harr	Sweden	Swedish
Kharius	Belarus	Russian
Kharius	Latvia	Russian
Kharius	Russian Fed	Russian
Kharius	Ukraine	Russian
Kharous obyknovennyi	Russian Fed	Russian
Lipen obycajny	Czechoslovak	Slovak
Lipien europejski	Poland	Polish
Ombre	France	French
Ombre commun	Belgium	French
Ombre commun	France	French
Peixe-sombre	Portugal	Portuguese
Pénes pér	Hungary	Hungarian
Stalling	Denmark	Danish
Temolo	Italy	Italian
Temolo	Switzerland	Italian
Vlagzalm	Netherlands	Dutch

3 Distribution

The distribution of *Thymallus thymallus* is quite widespread; from west Wales, throughout Europe to the White Sea (Figure 1). It is found in the Northern Hemisphere, 40° - 70°N (Magee, 1993), at altitudes of up to 500m in the Alps and 1000m in the Carpathians (Northcote, 1995). *T. thymallus* is native to: Europe and the former USSR inland waters, the NE Atlantic, Mediterranean and Black Sea (www.fishbase.org.uk, 1999).

It is thought to have reached British rivers via the North Sea River before Britain became isolated from continental Europe (Woolland, 1986a). The distribution pattern is consistent with dispersal from a single refuge in the Danube basin, after the last glacial period when England was still joined to the continent and rivers of the East Coast of England and the mainstem shared with the Rhine. *T. thymallus* is absent in southern Europe, the north of Scandinavia and Ireland.

The grayling has been found in archaeological deposits in York, dating from the first to the twelfth century (Broughton, 1989). It is, therefore, likely that it is indigenous in the Yorkshire Ouse system. Grayling have been transferred from East Yorkshire to tributaries of the Ouse to replace populations which have been extinct by pollution (Magee, 1993). *T. thymallus* was introduced to Scotland in the 1800s (Northcote, 1995). In Wales, it is confined largely to the eastern rivers - the Dee, Severn and Wye. A small isolated population exists in the Teifi (Woolland, 1986a). The grayling is not indigenous to lakes however, it is found in two in the UK: the Gouthwaite Reservoir in Yorkshire and Llyn Tegid in Wales (Magee, 1993). It is generally a freshwater fish but also exists in brackish and marine environments (Table 2, page 5).

Table 2: The occurrence and status of European grayling *Thymallus thymallus* (ww.fishbase.org.uk, 1999).

Country	Fresh-water	Brackish	Salt-water	Status
Belarus	*			
Czech Republic	*			
Denmark	*	*	*	Protected. Minimum size limit of 33cm. Closed season 15th March – 15th May
Estonia	*	*	*	
Finland	*	*	*	Restricted although fairly common
France	*	*	*	Restricted. Vulnerable
Germany (FR)	*	*	*	Restricted Endangered in 1984
Hungary	*	*		
Italy	*	*	*	Scarce
Latvia	*	*	*	
Lithuania	*	*	*	
Republic of Moldova	*			
Netherlands	*	*	*	Fairly common in freshwater until 1885
Norway	*	*	*	
Poland	*	*	*	
Romania	*	*	*	
Russian Fed.	*	*	*	
Slovakia	*			
Sweden	*			Care demanding
Switzerland	*			Fairly common
UK	*	*	*	
Ukraine	*	*	*	
SFR of former Yugoslavia	*	*	*	

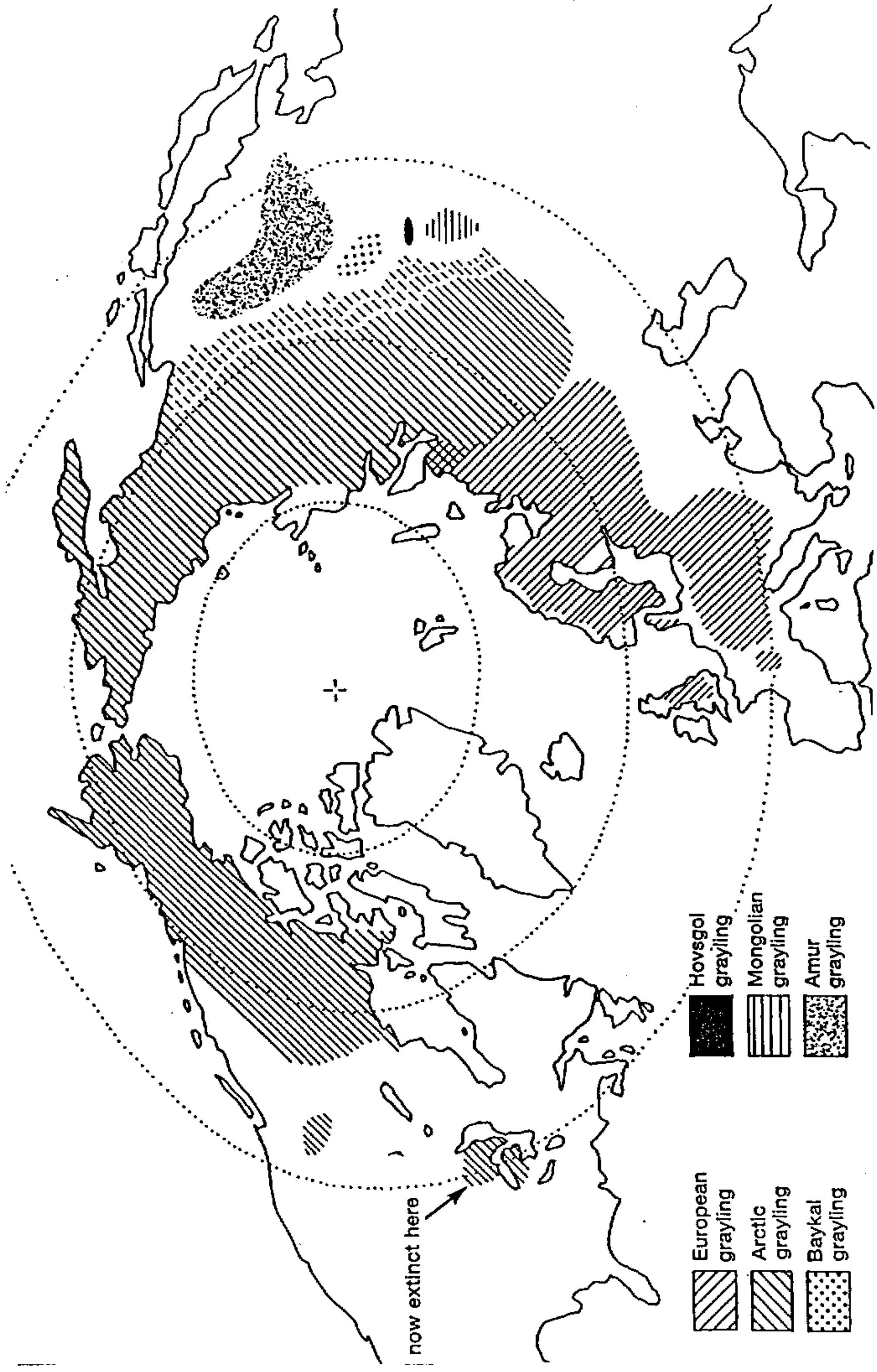


Figure 1. The worldwide distribution of *T. thymallus* and *T. arcticus* (Broughton, 1989).

The distribution of the Arctic grayling, *T. arcticus* as a holarctic species, extends throughout North America including northern Manitoba, Saskatchewan, Alberta, British Columbia, Northwest Territories, the Yukon and Alaska (Kreuger, 1981) (Figure 1). In addition, populations are found in Asia in Siberia, the former USSR, the Czech republic and Slovakia (www.fishbase.org.uk, 1999). *T. arcticus* is a native species to North America, Asia and the former USSR (www.fishbase.org.uk, 1999). It has been introduced to the inland waters of Europe (www.fishbase.org.uk, 1999).

4 Habitat requirements

Huet (1959) described rivers according to the type of physical, chemical and biological qualities associated with suitable habitat conditions for different fish species as shown in Table 3.

Table 3. The species zonation of rivers according to habitat type (Huet, 1959).

Zone	Definition
Trout	Steep, upland streams; water cool and well oxygenated; river bed of rock, boulder or pebbles.
Grayling	Further downstream, river wider, water cool and well oxygenated, gentle slope. Riffles and rapids separated by pools and runs.
Barbel	Further downstream, river wider, slight incline, riverbed is sandy/muddy silt. Water warmer and less well oxygenated.
Bream	Most downstream species, river widest, slight incline, riverbed is fine silt. Water warmer and less well oxygenated.

The grayling zone is characterised by rivers and larger, more rapidly flowing streams. The gradient is usually less than that of trout waters with riffles and rapids being separated by pools. Trout and grayling inhabit the more rapid stretches whereas the more lentic waters in between are occupied by cyprinids such as barbel and chub. The gradient is 10-30ft/mile.

The size of fish tends to increase as you go upstream; the upper stretches are dominated by adults whilst the juveniles are found in the lower stretches (Hughes, 1992). Such is true for the Arctic *grayling*.

Grayling favour certain physico-chemical conditions. These vary according to the life-stage (*cf.* Section 6.2 and: pp 12-15, 17-19), however these conditions can be summarised. The water quality requirements of grayling are similar to brown trout; cool, well oxygenated with a good sequence of pool, riffle, glide and run (Woolland, 1986a). They have a minimum oxygen requirement of 5 – 7ppm and an upper temperature tolerance of 18-25°C, preferring a maximum of 18°C (Woolland, 1986a). Although the environmental requirements are broader for grayling than brown trout, Woolland (1986a) has stated that grayling 'succumb' to pollution and higher temperatures more rapidly than trout. The suggested ranges of optimum, upper and lower temperatures for the European grayling are presented below (Table 4).

Table 4: The suggested optimum, upper and lower critical temperatures (°c) for grayling in Europe (Crisp, 1996).

Range	Temperature (°C)
Lower critical	0 – 4
Upper critical	>18
Optimum	4 - 18

Water depth is important in determining the distribution of freshwater fish. Table 5 represents depths favoured by different sized grayling.

Table 5. The water depth (cm) favoured by different sizes of grayling (cm) (Greenberg *et al*, 1996).

Fish size / cm	Depth / cm
2-8	105-180
9-18	45-90
19-50	75-165

Substrate is another important physical parameter determining grayling distribution (Table 6).

Table 6. The river bed substrate type favoured by different sized grayling (Greenberg *et al*, 1996).

Fish size (cm)	Substrate type
2-8	Sand/silt/gravel
9-18	Neutral
19-50	Preference for cobbles and boulders

Finally, water velocity contributes to grayling distribution. The preferred velocity of juveniles is <10cm/s whilst older, larger individuals prefer velocities of 20-50cm/s (Greenberg *et al.*, 1996).

Some information is known about the habitat requirements of the Arctic grayling by comparison. They prefer spring-fed, cool, clear streams, rivers or lakes but are also found in bog-fed streams in Alaska (Fish and Wildlife Service, 1985). *T. arcticus* are found almost exclusively in pools (Vascotto and Morrow, 1973). The mean current velocity inhabited by adult grayling is 0.26m/s (Kreuger, 1981) and the preferred oxygen saturation is approximately 7.2 mg/L (Nelson, 1954). Adult *T. arcticus* have been reported as tolerating temperatures of up to 20°C (LaPerriere and Carlson, 1973).

Habitat modelling has been explored using the Habitat Suitability Index (HSI) Model (Fish and Wildlife Service, 1985).

5 Reproduction

5.1 Fecundity

The European grayling is extremely fecund producing an average of 10000-31000 eggs/kg/hen (Janovic, 1964). In general, grayling egg size ranges between 2.5 and 3.5mm (Northcote, 1995). By the end of one month the larvae attain a length of 3cm which doubles after 2 months (Ibbotson, Pers. Comm.). They can reach up to 18cm by the end of their first year (Ibbotson, Pers. Comm).

The fecundity of *T. arcticus* is dependant upon the size of the fish and the location (Armstrong, 1986). For example, Schallock (1966) demonstrated that Alaskan *T. arcticus* egg frequency varied between 1,700 for a specimen at 26.7cm and 12, 350 for one at 40cm and De Bruyn and McCart (1974) reported that egg frequency at three localities in the Yukon varied from 4,077 and 14, 429 per female.

5.2 Spawning

European grayling are spring spawners. Spawning occurs from the end of March (Parkinson *et al.* 1999) to the first half of June. (Clark, 1992; Eloranta, 1985; Gonczi, 1989; Kristiansen & Doving, 1996; Linloekken, 1993; Scott, 1985) or just after snowmelt in European countries (Peterson, 1968; Witkowski & Kowaleski, 1988). The Arctic grayling spawns later between late April and early July (Wojcik, 1954; Warner, 1955; Schallock, 1966; Roguski, 1967; Roguski and Tack, 1970; de Bruyn and McCart, 1974; Tack, 1974; Bendock, 1979).

The onset of spawning in both grayling genera, significantly correlates with climatic conditions (Witkowski & Kowalewski, 1988). Water temperature has been shown to affect the duration of migration and spawning (Witkowski & Kowalewski, 1988). With regards to *T. thymallus*, such temperatures range from 3 - 11°C, although temperatures as high as 14°C have been recorded in The Frome, Southwest England (Scott, 1985). The longest migration at a location, has been recorded as coinciding with the highest temperature and a full moon (Witkowski & Kowalewski, 1988). Other studies however, have determined that grayling were most active at a new moon

(Andreasson, 1973; Deelder, 1970; Johnson, 1982). Parkinson *et al.* (1999) discovered from radio-tagging studies, that fish mobility was significantly higher when water levels remained stable between consecutive days of surveying; in clear, decreasing water levels and on sunny days with high temperature variation.

In the case of *T. arcticus*, the rise in temperature leading to spring flooding has been shown to stimulate spawning (Armstrong, 1986). At 4°C, western Alaskan grayling spawn (Tack, 1973). This period often coincides with the turbid waters associated with spring flooding (de Bruyn and McCart, 1974). However, this is not universally the case for arctic grayling (Warner, 1955).
The European and Arctic grayling similarly ascend the rivers, migrating from the main river to a faster flowing tributary or from the sea to its natal stream, to spawn (Kristiansen & Dowving, 1996; Magee, 1993; Peterson, 1968; Witkowski & Kowalewski, 1988). Some populations are potamodrous, whereby they spend most of their lives in lake systems but ascend the tributaries in May/June when temperatures are greater than 5°C. They remain there for 10/15 days during spawning (Kristiansen & Doving, 1996).

5.3 Behaviour

Males arrive on the spawning ground several days before the females downstream (Fabriciuus & Gustafson, 1955). In some cases, males are present weeks before the females in order to increase their chances of securing a favourable territory and therefore increase their genetic fitness (Beauchamp, 1990). However, this is balanced with two additional factors; the higher risk of zygote dislodgement by additional, later spawners; and that females are rarely ready to mate so early in the season (Beauchamp, 1990). The males adopt and defend their territories, courting females approaching from downstream (Fabriciuus & Gustafson, 1955; Parkinson *et al.*, 1999; Persat & Zakariah, 1993; Poncin, 1994). The oldest and largest grayling spawn first (Witkowski & Kowaleski, 1988).

The sex ratio for European grayling has been found to change over the spawning season. During the first three days at the spawning sites, males dominate females by 3:1, decreasing mid-spawning to 1.5:1 (Witkowski & Kowaleski, 1988). Towards the end, the ratio equals out as fewer males ascend the river, until eventually the females are dominant (Witkowski & Kowaleski, 1988). An unequal ratio of 6:1 (males: females) exists in all grayling populations and it has been inferred that sex ratio could well be strongly influenced by angling pressure on females during the summer (Libosvarsky, 1967).

5.4 Courting display and spawning act (Fabricius & Gustafson, 1954).

Grayling exhibit aggressiveness throughout the whole year, however, such behaviour becomes more pronounced during the spawning season when males begin to defend territories. Females are only tolerated in male territories at the moment of spawning. Outside this period, they hide under overhanging vegetation, banks and behind stones.

The spawning act is very similar for both the European and Arctic grayling, however, there are subtle variations. Spawning is initiated by a vibrating display by the male. This motion enables the male to advertise his presence and attract females. The exact reasoning behind a female's choice of male is not clear, however, olfactory cues are thought to be important in addition to those regarding streambed stability, in view of the fact that spawning does not take place in a redd (Beauchamp, 1990).

The male hovers in the water, bending the caudal part of his body upwards so that the tail is lifted, he erects the dorsal and pelvic fins fully (in spasmodic and an almost twisted manner) and continues to perform vigorous and very rapid *trembling body movements*. When females are almost ready to spawn they become quite aggressive, attacking other individuals of both sexes and move several times towards the male that is usually situated on a gravel bank. This resident male often reacts aggressively. As the female ripens, she becomes less aggressive and approaches the male with her back arched and the dorsal fin pressed down, which suppresses male aggression. (In contrast, however, female *T. arcticus* erect their dorsal fin (Tack, 1971)). The male grayling approaches her and trembles. He does not erect his fins or bite in this courting act. Initially, the female flees but returns to complete the act. The males' trembling intensifies to a very quick vibration. He erects his fins to their fullest extent, tilts over on his side so that the female's back is covered with his large dorsal fin and part of his back. The caudal area is bent laterally, crossing over the tail of the female, pressing it down against the bottom. The bodies of the two fish form a cross shape. Vigorous flapping movements of the tail fin follow (more or less horizontally and close to the ground). The female begins trembling, supporting herself on her pelvics and bending the caudal part of her body very sharply and dorsoventrally, so that the anal fin is pressed against the ground whilst the tail and fore-part of her body are lifted. Very intense trembling movements occur at the caudal end of her body, to the extent that the adipose fin is buried beneath the gravel. Once this has reached a maximum, the female opens her mouth wide for several seconds. This is the stimulus for male orgasm. The male gapes and a joint orgasm follows. A sharp flick pushes the genital openings down deep where the eggs and milt are released. The duration of this is 14 seconds. Immediately after this, the male attacks the female who retaliates or flees. All European grayling spawning acts occur in the afternoon or evening as compared to those of *T. arcticus* which occur between 2000 hours and 0200 hours (Van Wyhe, 1962).

5.5 Spawning habitat

Grayling belong to a group of lithophils which hide their brood under gravel and do not guard the deposited eggs (Balon, 1975). European grayling differ from salmon and trout in that the redd (nest) is excavated by the male rather than the female (neither the male nor female Arctic grayling prepares a redd (Warner, 1955)). The male subsequently defends it as his own territory and, being promiscuous, spawns several times in it with different females (Cihar, 1998; Fabricius & Gustafson, 1955). Such promiscuity is of mutual benefit to both the male and female; the former increasing the genetic diversity of his offspring and the latter, again increasing progeny diversity but also by spreading her eggs, the female increases her chances of egg survival in the face of local impacts on the habitat (Beauchamp, 1990).

Site selection also differs in that salmon/trout choose redds towards the downstream end of pools (Hobbs, 1937; Stuart, 1953a) whereas in grayling, spawning takes place at the upstream end of a pool (Fabricius & Gustafson, 1955). The eggs are amber coloured (Cihar, 1998) and buried at much shallower depths than those of trout or salmon (Crisp, 1996). Studies of cumulative curves of ovulation of grayling in France, indicated that a decrease in water temperature during the spawning period reduces or inhibits the ovulation process (Maisse et al. 1987). Optimum spawning of the European grayling occurs at a constant temperature of >5 °C (Maisse et al. 1987), however the Arctic grayling spawns at temperatures of between 2 and 10°C (Tryon, 1947; Wojcik, 1954; Rawson, 1950; Warner, 1957; Kruse, 1959; Reed, 1964; Williams, 1968; Bishop, 1971; Netsch, 1975; Wells, 1968; Falk et al, 1982). The spawning period lasts between two and 24 days (Kratt and Smith, 1977).

Territory size is a function of the amount of visual isolation within a particular stretch of river. The greater the frequency of large rocks or logs, preventing grayling viewing each other, the more territories that particular area can support (Fabricius & Gustafson, 1955). The less favourable the selection of site, the more cramped the territories become, having a negative knock-on effect on spawning success. In addition, males become more aggressive and use up energy during interference with neighbouring males, in addition to driving females away (Beauchamp, 1990).

The mean size of a European grayling territory has been found to be $2.6m^2$ (Fabricius & Gustafson, 1955) with some as large as $5.2m^2$ (Crisp, 1996). Spawning sites tend to be oval in shape with the length of the longitudinal axis most likely related to the length of the 'host' fish (Sempeski & Gaudin, 1995a). Those of *T. arcticus* are commonly oval also and are between one and $10m^2$ (Tack, 1971).

In observations by Fabricius & Gustafson (1955), all spawning acts took place on gravel banks approximately 0.3 m^2 which were present in every territory. The spawning sites are easily identifiable as the substrate is very clean and forms small, oval light spots on the dark bottom of rivers. In addition, once eggs are laid, gravel is removed and depressions are notable in the substrate (Sempeski & Gaudin, 1995a). Grayling eggs are deposited under 5cm or less of fine gravel (2-3cm in the case of the Arctic grayling according to Van Wyhe (1962)). Such a depth is shallower than for trout eggs, which are also laid in coarser substrate. Grayling eggs are therefore more susceptible to being washed out by large floods (Woolland, 1986a). It has been suggested that these comparatively shallow nests result in greater exposure to daily fluctuations of light and temperature (Bardonnet & Gaudin, 1990). However, a limited oxygen supply is less likely to be a problem (Crisp, 1996).

5.6 Substrate

In the River Indalsalven in Sweden, *T. thymallus* eggs were found where the bottom substrate consisted predominantly of gravel (Gonczi, 1989) (Table 7). This is also the case for *T. arcticus* (Tack, 1971) for whom the common spawning gravel particle size is between 0.75 and 3.81 cm. No eggs have ever been located in sand or fine silt (Nelson, 1954).

Table 7. Percentage composition of bottom substrate on the spawning ground of grayling in the River Indalsalven, Sweden (Gonczi, 1989).

Substrate	Substrate size (cm)	Percentage (%)
Sand		5-15
Gravel	< 2	40-70
Small stones	2-10	20-30
Bigger stones	>10	Few

Sempeski and Gaudin (1995b) have suggested a predominance of fine and coarse gravel with fine pebble and fine gravel adjacent to the spawning site, very similar to that also described by Darchambeau & Poncin (1997).

T. arcticus usually spawns on gravel substrate similarly. The preferred areas are the transition regions bridging the lower end of a riffle and a pool (Bishop, 1951; Nelson, 1954). Spawning has never, in common with that of the European grayling, been reported as spawning over mud, silt or clay beds (Bishop, 1971 and Nelson, 1954).

5.7 Water velocity

The importance of water velocity relates to the maintenance of the eggs below the substrate surface. If velocity is high, the likelihood of egg dislodgement is increased. In addition, high flow rates could flush proceeding larval stages into areas where food abundance is sparse, or pools which are only accessible at high water (Clark, 1992). The temperature of the water may also be reduced as a result of mixing at high velocities which will slow the rate of egg development (Clark, 1992) and similarly, increased turbidity affects larval development by reducing feeding efficiency (Clark, 1992).

In general, a moderate velocity is required at spawning sites (Table 8), ranging from 20-90cm/s (Gonczi, 1989; Sempeski & Gaudin, 1995a). Resting pools are also essential at any site and the mean current velocity has been found to be much lower (13.7cm/s) in these pools (Sempeski & Gaudin, 1995a). *T.arcticus* male territories have been documented as having an average velocity of between 0.34 and 1.46 m/s (Kreuger, 1981).

Table 8: Velocities measured (cm/s) at spawning sites at the Rivers Pollon and River Suran, France (Sempeski & Gaudin, 1995a).

Position	Pollon (cm/s)	Suran (cm/s)
Mean velocity	47.8	47.7
Mean bottom velocity	37.2	33.7

5.8 Water depth

Depth is an important consideration during spawning in view of the fact that the eggs are buried and left to develop. The water must be deep enough to reduce the chance of being de-watered and exposed to lethally high temperatures (Beauchamp, 1990).

Water depth varies significantly from year to year and from site to site (Sempeski & Gaudin, 1995a) (Table 9). Darchambeau & Poncin (1997) found that most spawnings occurred at depths of 20-55cm in Belgium. Gonczi (1989) found a preference for mean depths of 36cm in Sweden. Alaskan Arctic grayling commonly spawned at a depth of 1 foot (Tack, 1971).

Table 9. The depths (cm) selected by European grayling as spawning sites at the River Pollon and the Suran, France (Sempeski & Gaudin, 1995a).

Selection	Depth (cm)	
	Pollon	Suran
Strongly selected	10 – 40	20-30
Avoided	<10 or >60	<10 or >40

5.9 New methods of studying spawning behaviour

It is possible that spawning may occur in different but unobservable conditions for example in turbid waters (Persat & Zakharia, 1993). Spawning produces noises related to the displacement of pebbles. These can be detected using a hydrophone (Persat & Zakharia, 1993) and can subsequently be interpreted using what has been termed the passive sonar equation (Urick, 1983). In one study by Persat & Zakharia (1993), a hydrophone was hung from a rod, 2m from the riverbank. Maximum activity was identified in the afternoon and minimum in the early morning. An acoustic method could well be viable in the investigation of spawning behaviour.

6.0 Unusual courting/spawning observations

Visual as well as acoustic and vibrational cues are extremely important in fish spawning behaviour (Persat & Zakharia, 1993; Satou *et al.* 1987; 1991). In the River Ourthe, Belgium, a large grayling was observed trying to spawn with a barbel (Poncin, 1994). The barbel was motionless, quite like the submissive female grayling. In addition, barbels produce a gravel noise, which may also have attracted the male grayling. Homosexual spawning attempts have also been reported (Fabricius & Gustafson, 1955). Hermaphroditism is rarely reported in Salmonidae, and until 1991, had never been documented in grayling. However, an hermaphrodite grayling was discovered in the River Nysa Klodzka, Lower Silesia, Poland

(Blachuta *et al.*, 1991), displaying both male and female gonads which were smaller than those of the true sex and a unique dorsal fin.

6.1 Hybridisation between grayling species

Shubin and Zakharov (1984) documented the presence of hybrids in some rivers of the polar and sub-polar Ural, which had developed between European and Arctic grayling in their secondary contact zone (Mayr, 1968). These hybrids were verified as being such by identification of the fractional composition of serum proteins in most cases but also on the basis of visible examination (Shubin and Zakharov, 1984).

6.2 Emergence

After spawning, the fertilised *T. thymallus* eggs remain in the gravel for approximately 177 degree-days (or 22 days at 8.05°C) after which they hatch (d'Hulstere & Philippart, 1982). The average hatching time of *T. arcticus* has been given as 186.24 degree-days at a mean temperature of 5.8°C (Kratt and Smith, 1977). However, individuals have been reported as hatching after 8 days at 15.5°C (124 degree-days) (Wojcik, 1955). Hatching in *T. thymallus* has been found to occur at an optimum temperature range of 7-11°C. Hatching time decreases with increasing temperature (Humpesch, 1985) and mortality at hatching has been stated as being 10% (d'Hulstere & Philippart, 1982). Mortality, of course, will be highly site specific and vary from year to year depending on both biotic and abiotic factors.

After 4-5 days in the gravel, feeding on their yolk sac, both European and Arctic fry emerge. This period of cover is required, as the embryos are unable to cope with water currents prior to becoming swim-up fry (Brown, 1938; Bishop, 1971). The fry begin feeding near the water surface even before the yolk sac has been fully absorbed (Kratt and Smith, 1977; Scott, 1985). Complete reabsorption of the yolk sac occurs after 12 days (156 degree-days) (Scott, 1985). Bardonnet & Gaudin (1991) have suggested emergence as being 10 days post-hatching (approximately 276-320°Days of incubation).

When the hatchlings first emerge their fork length size ranges from 15-19mm (Scott, 1985; *Sempeski & Gaudin*, 1995c). Emergence differs from other salmonids in that it is diurnal rather than nocturnal (Brannan, 1987; Elliott, 1986). The majority of grayling fry emerges with a peak at dawn (Bardonnet & Gaudin, 1990; Gaudin & Persat, 1985) but do not commence downstream displacement until nightfall (Bardonnet & Gaudin, 1990). Such nocturnal movement may be a predator-avoidance strategy (Godin, 1982; Gustafson-Marjanen & Dowse, 1983). Alternatively, prolonged presence in daylight may facilitate the familiarisation of the fry with their surroundings (Bardonnet & Gaudin, 1990). The display of maximum activity during the coldest hours is contrary to expected animal activity which usually increases with increasing temperature.

6.3 The variation in habitat requirements, according to grayling developmental stage

It is clear that different life-stages of grayling require specific habitat types in order to survive. Three main habitat divisions have been identified in streams for the European grayling (Sempeski et al. 1998):

- The main channel: generally the middle of the stream with the fastest slow rate.
- The dead zone: marginal areas with the slowest flow rate.
- The transition zone: between the dead zone and main channel with an intermediate flow rate.

The distribution of grayling is related to current speed in view of the fact that the greater the fish size, the stronger the region of current they can occupy. Juveniles have been found to occupy areas where current speeds are approximately 50% of their median swimming capability (Scott, 1985). As grayling grow, their length and their mouth gape size increases. Their ability to detect and capture prey and to swim, increase, allowing them to inhabit a much wider spectrum of habitats. They can therefore minimise energy expenditure and maximise optimal fitness (Guma'a, 1978; Schmidt & O'Brien, 1982; Schmidt & Holbrook, 1984).

The hydrodynamic potential of any fish is very important for the colonisation of new habitats. A shift from the dead zone, to the transition, to the main channel corresponds to an increase in the square of the current velocity (Sagnes *et al.*, 1997). Thus, a shift in habitat with increasing size not only facilitates predator avoidance and foraging behaviour (Clark & Levy, 1988; Harvey, 1991; Schlosser, 1987) but also incorporates body shape and optimisation of hydrodynamic potential in relation to flow force (Sagnes *et al.*, 1997). Figure 2 gives a general outline of the shift in habitat type with increasing size and age of grayling. This is the case for both Arctic and European grayling.

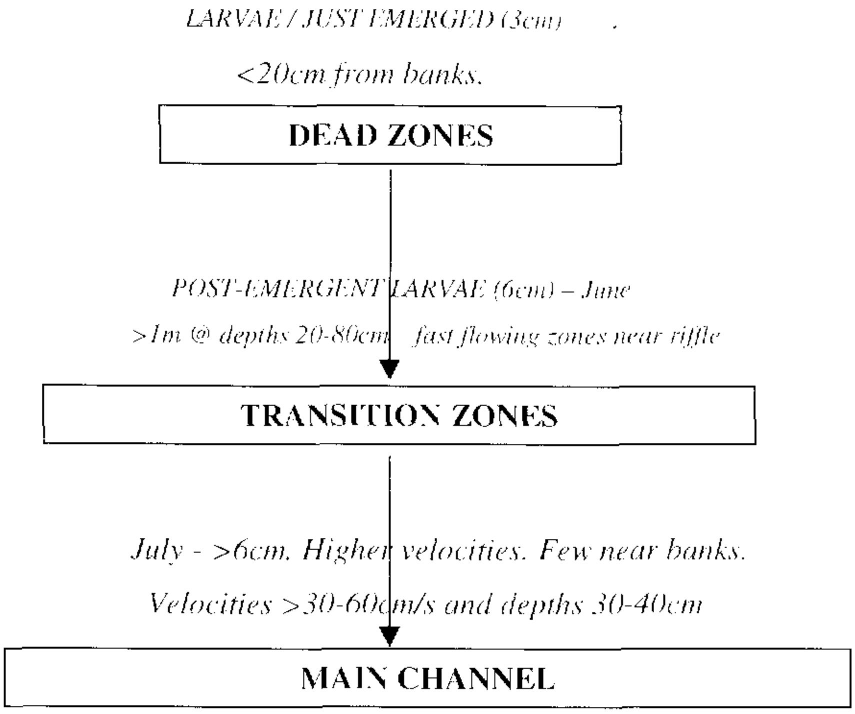


Figure 2. Shift in habitat type with different life-stages of grayling (Bardonnet *et al.*, 1991).

When larvae first emerge, they are relatively weak swimmers and tend to avoid habitats with steep banks or deep depths (Bardonnet *et al.*, 1991). They must learn quickly to locate food as the yolk sac is almost consumed and the oesophageal plug may not yet be removed, inhibiting feeding particularly if they are unable to fill their swim bladder (Bardonnet *et al.*, 1993). The larvae are also in a comparatively exposed habitat. It is, thus, the dead zones which provide a vital nursery habitat for fry in the first few weeks post-emergence as they reduce energy costs by minimising swimming activity and favouring the capture of drifting food particles (Sempeski & Gaudin, 1995c; Sempeski *et al.*, 1998). Such zones also aid predator avoidance and most likely will decrease the potential of encountering large fish such as brown trout or pike which would have difficulty swimming in water of less than 5cm depth (Sempeski *et al.*, 1998). Such is the case for Arctic grayling fry, which are also known to inhabit interstitial waters in between boulders (Kreuger, 1981). The fry stage is known to be the least temperature sensitive and are able to tolerate between 16.7 and 24.5 °C (LaPerriere and Carlson, 1973). They are in addition able to tolerate low oxygen tension of between 1.4 mg/L at 8°C to 1.8 mg/L at 20°C (Feldmuth and Eriksen, 1978). The mean current velocity inhabited by *T. arcticus* fry is 0.07m/s, increasing to 0.16m/s in older fry (Chislett and Stuart, 1979).

As the post-emergent fry grow (20-28 mm) (Scott, 1985), they move 1m or more away from the bank and to depths of between 20 and 80cm. These zones have a higher velocity, tending to be riffle and mid-channel areas (Bardonnet *et al.*, 1991). Larger fry will move to the transition zone, allowing the fish to observe and catch drifting prey in both the dead zone and main channel whilst remaining protected from strong currents, to minimise energy consumption (Bardonnet *et al.*, 1991; Sempeski *et al.*, 1998).

The distribution of grayling varies between night and day. As juveniles develop, they migrate during the day from the dead zone to the main channel. Once the grayling have attained 60mm or more they leave the marginal habitats. At night, all size classes have been observed in the dead zone and those 20-50mm in length were regularly distributed from the bank to the limit of the channel (Bardonnet & Gaudin, 1991). Behaviour also varies between night and day. Grayling feed in the water column and less frequently on the bottom during the day, whilst at night, they tend to rest on the bottom (Sempeski & Gaudin, 1995c).

In considering all of the information regarding the physical and chemical habitat requirements at each stage of the grayling life history, it is clear that in order for grayling to colonise an area a variety of habitats are required.

7 Foraging and diet

Food availability and the capacity to obtain it efficiently are vital if a species is to survive in a particular habitat (providing that all other parameters are suitable). For juvenile, inexperienced grayling, foraging can be perilous and is accompanied by high mortality rates, especially at the first feeding stage (Allen, 1951; Elliott, 1984).

Grayling larvae forage pelagically and feed on drift in the upper layers of the river. As juveniles, they tend to hold a benthic feeding station in the river channel within 5cm of the surface (Scott, 1985) and catch drifting invertebrates (Sempeski *et al.*, 1995). It is in the older stages that the grayling begin bottom feeding although they frequently rise to the surface to intercept floating prey (Peterson, 1968). Haugen & Rygg (1996a) have stated that grayling remained feeding in the upper layers until they attained a length of 150mm.

As previously discussed, the shift in habitat with lifestage is closely related to changes in foraging strategy. Feeding usually begins on first emergence to surface waters (Penaz, 1975). However, Arctic grayling have been documented as feeding four days post-hatching (Brown and Buck, 1939). As the fish grows, the mouth gape diameter increases, enabling the grayling to consume a greater variety of larger prey items (Sempeski & Gaudin, 1996). In addition, foraging efficiency increases with increasing age and size. In one study, it was discovered that foraging attempts of grayling larvae produced as many non-prey items as prey items (Drost, 1987; MacCrimmon and Twongo, 1980). Larvae do not usually move very far to intercept drifting prey, often less than 50% of their body length (Scott, 1985). Larvae of other salmonids, tend to feed on zoobenthos rather than drifting larvae (Maitland, 1965). The maximum feeding activity of grayling is at dawn and dusk although they also feed continuously during the day and not at all during the night (Scott, 1985). Arctic grayling feed predominantly in the day also (Reed, 1964).

The relationship between grayling dominance hierarchy within a population and the feeding position occupied by an individual, has been proven by Hughes (1992). He demonstrated that in a habitat where there was a difference in the desirability of feeding stations, the resident grayling population would compete and sort itself according to rank into such stations with the most dominant fish inhabiting the 'best' location (Hughes, 1992). The reason for this system of ranking is because grayling adults as drift feeders, select feeding positions which maximise their Net Energy Intake (NEI) (Hughes, 1992).

The type of prey consumed by grayling varies with age. In general, juveniles feed on chironomid larvae and microcrustacea such as copepods, whilst adults feed on chironomid pupae, ephemeroptera, simulidae and trichoptera (Scott, 1985). The number of prey items also differs with size; larger grayling consume more prey items (Sempeski & Gaudin, 1996). The feeding strategy adopted by juvenile graylings depends heavily on the physical attributes of their habitat. Seasonal variation also plays a significant role in the diet (Hellawell, 1971). Arctic grayling are active feeders during the summer (June and early July) (Reed, 1964).

The larvae of the European grayling have been found to specialise mainly on chironomid larvae irrespective of the diversity of invertebrates available (Carmie & Cuinat, 1984; Jennings, 1983; Scott, 1985; Sempeski *et al.*, 1995; Witkowski *et al.*, 1984; Woolland, 1987a). Although juveniles exhibited greater diversity in their consumption of copepods and oligochaetes, chironomid larvae and pupae still constituted more than 90% of prey ingested (Sempeski *et al.*, 1995b). This is also true of Arctic grayling larvae (Elliot, 1980, 1982). Such prey are energetically profitable at 5500cal/g dry weight (Maslin & Patee, 1981) and are easy to ingest, hence reducing energy expenditure in catching it. Other species such as oligochaetes and zooplankton are energetically costly to catch and hence, it is unfavourable for grayling to actively pursue such prey (Drenner *at al.*, 1978; Schmidt & O'Brien, 1982). However, in lake systems Arctic grayling have been reported as feeding on zooplankton (Evans and O'Brien, 1988). A search strategy has also been described for *T. arcticus*, allowing greater efficiency in the capture of such prey (Evans and O'Brien, 1988).

Trichoptera were also important for all ages with small caddis larvae such as *Agapetus* being consumed by juvenile grayling and larger prey including *Potamophylax*, by older grayling (Woolland, 1987a). Temperature can influence feeding activity. Woolland (1987a) found the greatest feeding activity at intermediate temperatures with maximum and minimum temperatures resulting in low feeding intensity.

Arctic grayling have similar feeding preference (Table 10). Individuals commonly ingest food found on the water surface or column but not the streambed (Vascotto, 1970; Vascotto and Morrow, 1973). However, in autumn, they have been reported as feeding on the bottom when drift is less prevalent (Morrow, 1980). In addition, bottom feeding is common in lakes (Wojcik, 1954; Yoshihara, 1972).

Table 10. A comparison of the recorded food ingested by the European and Arctic grayling.

Prey item	European grayling	Arctic grayling
Adult aquatic insects (caddis fly, mayfly, dipteran)	* (Scott, 1985)	* Juvenile and adult food (Van Wyhe, 1964; de Bruyn and McCart, 1974)
Larval aquatic insects (dipteran, caddis fly, mayfly, cladocera, trichoptera, ephemeropta)	* (Scott, 1985)	* Mostly fry food (Wojcik, 1953; Bishop, 1971; Yoshihara, 1972; Furniss, 1974, 1975)
Zooplankton	* (Drenner *at al.*, 1978; Schmidt & O'Brien, 1982)	* (Wojcik, 1954; Yoshihara, 1972)
Phytoplankton	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)
Gastropods	* (www.fishbase.org.uk, 1999)	* (Wojcik, 1954; Yoshihara, 1972)
Terrestrial invertebrates	* (Oligochaeta) (Drenner *at al.*, 1978; Schmidt & O'Brien, 1982).	* (Coleoptera) (Craig and Poulin, 1974; de Bruyn and McCart, 1974; Reed, 1964)
Salmon eggs	* (Hellawell, 1971)	* (Schallock, 1966; Alt, 1980)
Inconnu eggs (*Stenodus leucichthys*)		* (Alt, 1969)
Grayling eggs		* (Warner, 1958)

Table 10. A comparison of the recorded food ingested by the European and Arctic grayling (continued).

Cyprinid eggs	* (Hellawell, 1971)	
Sockeye salmon fry (*Onchorhynchus nerka*)	* (www.fishbase.org.uk, 1999)	* (Williams, 1969)
Nine-spine stickleback (*Pungitius pungitius*)		* (de Bruyn and McCart, 1974)
Mammals (shrews, lemmings)	* (www.fishbase.org.uk, 1999)	* (Reed, 1964; de Bruyn and McCart, 1974; Alt, 1980)
Birds	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)
Marine worms	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)
Marine crustaceans (isopods)	* (www.fishbase.org.uk, 1999)	* (Tack, 1980)
Cnidarians	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)
Echinoderms	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)
Cephalopods	* (www.fishbase.org.uk, 1999)	* (www.fishbase.org.uk, 1999)

Terrestrial invertebrates have been found to be an under utilised resource by grayling in the River Frome in England, with 4.3% by volume being consumed by 0+ grayling and 0-0.1% by volume in older age classes (Keay, 1990). However, an increase in terrestrial intake has been found elsewhere when aquatic insects were scarce (Dahl, 1962). Fish were generally not eaten but cyprinid and salmonid eggs were eaten during certain seasons (Hellawell, 1971). Studies carried out on the stomach contents of grayling from the River Test and Itchen, provided no evidence of predation on other fish species (Lemen, 1994). Gravel has been found in stomach contents which may be a deliberate act to help with food mastication, mistaken identification or in conjunction with the consumption of caddis cases (Keay, 1990).

There have been few studies investigating grayling interspecific feeding interactions. Wojcik (1954) reported that there was no competition between Arctic grayling, whitefish and lake charr for food. However, Pearse (1974) compared stomach contents for the same species and concluded that Arctic grayling and whitefish fed and therefore perhaps competed for, the same food.

8 Age and growth rate

The age of European and Arctic grayling and indeed all fish, is determined by examination of annulus formation on the scales (Woolland, 1987b). Scale formation takes place when grayling have attained a length of 33.5-37mm. They are initially laid down along the lateral line (Brown, 1943; Gustafson, 1948; Peterson, 1968). In the River Wylye, 0+ - 2+ scales were simple to read and indicated rapid growth of the species in the first two years (Pinder *et al.*, 1999). Beyond the age of five, it is reported to be difficult to read annuli as the growth rate slows and the annuli become very densely packed (Roguski and Winslow, 1969; Roguski and Tack, 1970; Engel, 1973). A comparison of the use of otoliths and scales as ageing tools, showed that interpretations of both give similar ages for fish aged 7 and 8, however, scales underestimated the ages of older fish (McCart et al, 1972; de Bruyn and McCart, 1974; Craig and Poulin, 1975). The reason for this being that otoliths constantly lay down clear annuli during the life of the fish, whereas scale annuli become denser with age (Nordeng, 1961). Hence, data involving older fish, which have been aged using scales, must be interpreted with caution.

The age at which grayling attain sexual maturity depends heavily on geographical location. For example, in the River Lugg, Herefordshire, European grayling did not reach sexual maturity until the end of the third year (2+ fish) (Hellawell, 1969). *T. arcticus* populations studies in Alaska matured between four and eight years (Tack, 1974). In the North Slope this extends to between six and nine years and the interior system four and six years (Tack, 1974).

However, maturity is more dependent upon size (Armstrong, 1986). In older *T. thymallus*, growth was most rapid from April to June with no further growth until November. Other studies have shown that growth was optimal from spring until autumn with little occurring in winter (Hellawell, 1969; 1975; Woolland, 1987b). Growth rate is most rapid in the first three years of life until the grayling are sexually mature. It then declines rapidly to a much lower, stable rate (Hellawell, 1969; Witkowski *et al.*, 1989). Growth rates of grayling vary throughout Europe. The English grayling appears to grow more in the first year than any other population studied.

There has been little documentation of the growth rates of first season *T. arcticus* juveniles (Armstrong, 1986). However, it is known that *T. arcticus* fry can attain a length of between 45 and 70mm in their first summer and 40mm in subsequent years to the age of VI (Craig and Poulin, 1975; Netsch, 1975). Such rates depend upon the time of hatching and hence the duration of the potential growing season (Armstrong, 1986). In addition, the location of the hatchlings, determining the availability of food and water temperature, affects growth (Armstrong, 1986). The majority of *T. arcticus* growth studies have focused on post-first year growth. Again this varies according to the system studied, although variation between systems in a similar geographical location is less (Armstrong, 1986). Growth rates are slowest, longevity is longer and individuals are generally smaller for grayling in northern Alaska. The opposite is true in southern Alaska (Kruse, 1959; Craig and Poulin, 1974; Armstrong, 1986). Growth takes place predominantly during the summer months and is one tenth of this for the rest of the year (Armstrong, 1986).

Males display faster growth rates than females in *T. thymallus* (Haughen & Rygg, 1996b; Huitfeldt-Kaas, 1927; Sφmme, 1935), this however, has not been found to be the case for *T. arcticus* for which growth rates are similar for both sexes (Tack, 1971, 1974; McCart et al, 1972; de Bruyn and McCart, 1974; Craig and Poulin, 1975).

Growth rates depend on both biotic and abiotic factors (Witkowski *et al.*, 1989) of which temperature, river size and length of vegetation season are most influential (Persat & Patee, 1981; Witkowski *et al.*, 1984). At higher latitudes, fish grow more slowly. Hence, in central and Western Europe, growth rates are very high whilst in the Urals on the eastern edge of Europe, growth is slow (Witkowski *et al.*, 1989). Growth increases with increasing temperature up to a certain threshold value, which depends on the river system, after which, growth decreases. In France, this upper limit has been found to be 17°C (Persat & Patee, 1981).

Grayling exhibit a relatively short life span, in most cases reaching three or four years maximum (Witkowski *et al.*, 1989). In the River Bela, of the former Czechoslovakia, 90% of grayling were two and three year olds (Nagy, 1984). The oldest grayling found at Llyn Tegid and the River Dee in Wales were 6+ and 7+ (Woolland 1987b). The maximum recorded age elsewhere has been 7+ and 8+ although a grayling of ten years was recorded in Scandinavia and one of 13 in Yugoslavia (Somme, 1935; Woolland, 1987b). In Britain, they may live to up to nine years (Maitland & Campbell, 1992). For example, in the River Wharfe, Yorkshire, one grayling was caught that was older than its fourth summer (Axford, 1991). In general, the longer-lived populations are found mainly at higher latitudes (Cihar, 1998).

By comparison, the life span of the Arctic grayling varies according to geographical location. Ages of between seven and 11 years have been recorded for populations in Montana and Wyoming (Brown, 1938; Nelson, 1954; Curtis, 1977), whereas in Alaska, fish reach between 15 and 22 years of age (de Bruyn and McCart, 1974; Armstrong, 1986).

9 Population studies

The accurate estimation of grayling populations is difficult as spring flooding and the presence of ice remove the possibility of using weirs (Armstrong, 1986). Those studies which have been conducted, have focused on the annual survey of a stretch of water to yield a long term data set and some indication of population size. However, most of such studies have been made by electro-fishing which is selective towards fish larger than 150mm and hence an accurate assessment of the population is not obtained. The largest estimate of an Arctic grayling population was using hook and line. Roguski and Tack (1970) estimated a population of nearly 37,000 in a stream between Long Tangle and Lower Tangle Lake in Alaska. Other, smaller populations studies have been conducted in Alaska by: Paddock and Whitehead (1970), Siedelman and Cunningham (1972), Gwartney (1980).

10 Fish movements: Migration and homing

Grayling display various forms of movement and migration. These range from spawning migrations such as river to tributary, lake to tributary, sea to river, foraging trips, diel migrations and shifts in habitat with age. Often grayling make short-term foraging trips and return to a specific 'spot' in its own territory, occupying what is known as its home range. Movements are also seasonal (Table 11).

Table 11. Seasonal shifts in habitat (depth and position) of grayling (Greenberg et al, 1996).

Parameter	*Winter*	*Spring*	*Summer*	*Autumn*
Depth (m)	Moderate 1 2m	Large Shallows	Small Shallows	
Position	Shelter from currents e.g. depressions		More scattered All over esp. midstream	Back to lake, stream etc.
	Congregate in one *spot*	Spawning *migration*	Most in/near *spawning grounds*	

Netsch (1975) and Tack (1980) have extensively researched the migratory routes of Arctic grayling in Alaska. Tack (1980) stated that the sources of water supplying a river/stream determined its use by grayling (Table 12). The variety of systems utilised by grayling is a reflection of their spawning cycle in spring and summer and the fact that their fry mature rapidly allowing them to disperse from an area prior to isolation (Tack, 1980).

Table 12. The uses of river/stream systems, which differ in their source of water, by Arctic grayling (Tack, 1980).

Type of system	Use of water system
Glacier-fed	Overwintering, migratory route
Spring-fed	Feeding
Bog-fed	Spawning, feeding
Unsilted run-off	Spawning, feeding, overwintering

10.1 Homing

There are several different types of migrations in grayling:

- River (feed) - Tributaries (spawn)
- Lake (feed) - Tributaries (spawn)
- Sea (feed) - River (spawn)*

*Grayling can remain there for at least one year, all returning to the same stream/tributary for spawning and back to their own resident stream (Peterson, 1968).

10.11 Migrations and homing to spawning areas

The most notable migration is that of the adult male and female graylings, ascending the rivers to spawn. Homing is the ability of a fish to return to its natal river and is one method of ensuring reproductive isolation (Pavlov *et al.*, 1998) and a return to a river system with the environmental requirements suitable or optimal for that particular organism. Such movement is related to temperature and phases of the moon (Witkowski & Kowalseski, 1988). The most intense migratory response is associated with high temperatures and a full moon (Gustafson, 1949; Witkowski & Kowalseski, 1988). In the Arctic grayling, spawning migrations are associated with the rise in temperature to 1°C. This coincides with spring discharge (Tack, 1980). Such temperatures have been recorded during mid-April (southern Alaska) to early-June (Northern

Alaska) (Tack, 1980). *T. arcticus* has been recorded as travelling up to 150km to locate suitable spawning grounds (Nelson, 1954; Reed, 1964).

Witkowski & Kowaleski (1988) conducted mark-recapture surveys on European grayling and discovered that only 18.7% went back to spawn in their home stream. Pavlov *et al.* (1998), however, found that homing success varied with age (Table 13).

Table 13. The homing success (% returns) of different aged grayling (Pavlov et al, 1998).

Age of fish	% Homing success
0+	2.5% returned
2+	92.3% returned
2+ - 5+	57.7% returned
	17% overall strayed

Radio tracking has been used recently to study the spawning migration of the grayling in the Aisne River, Belgium (Parkinson *et al.*, 1999). Six fish were studied, all of which returned to the site where they had originally been captured. This has also been found in studies in Norway (Kristiansen, 1980) and Poland (Witkowski & Kowalseki, 1988). In the Aisne, all the fish displayed high fidelity to a precise pool-riffle sequence during the late winter/spring (Parkinson *et al.*, 1999). It has since been difficult to discover the exact mechanism controlling such homing behaviour but the use of pheromones as guidance cues has been suggested (Doving *et al.*, 1980).

Such homing abilities and spawning site fidelity have not as yet been confirmed for *T. arcticus*, however, this has been documented for homing to feeding sites and it therefore inferred that the same is the case for spawning sites (Tack, 1980). Overwintering grayling migrate to spawning areas in every case except in large unsilted rapid run-off rivers (Tack, 1980).

10.2 Feeding migrations

Adult grayling migrate from spawning to feeding grounds for the summer months, where food will be plentiful (Craig and Poulin, 1975). Feeding fidelity has been demonstrated in the Arctic grayling, in tributaries of the Tanana River in Alaska, where 99% of recaptured grayling were made in the same river as they were originally tagged (Tack, 1980). Such migrations vary according to age, the type of overwintering system and the type of spawning system (Armstrong, 1986). However, for the first year, Arctic grayling are thought to remain in their natal area to feed.

Migrating grayling travelling to unsilted rivers to feed, vary in their exact destination within the system according to age. For example, juveniles (1,2 and 3 years) tend to reside in the lower regions of rivers; pre-adult (4,5 and 6 years) occupy the mid-regions and the adults (7 and over) the uppermost regions (Armstrong, 1986).

The migrations to spring-fed systems are not as clearly defined as there are no overwintering or spawning populations in such areas and the origin of feeding migrations is therefore unknown. However, tagging studies have shown that most adults spawning in bog-fed systems migrate to those which are spring-fed (Armstrong, 1986).

10.3 Migrations to overwintering sites

Overwintering migration allows fish to reduce the chance of them being present in a body of water, which may freeze. In autumn, all ages of Arctic grayling leave the bog-fed and spring–fed tributaries which normally freeze up and migrate to predominantly groundwater streams (Armstrong, 1986). Some grayling have been reported as migrating as early as mid-July and conversely as late as December (Armstrong, 1986). Overwintering is also seen in lakes (Armstrong, 1986). Current velocities in overwintering sites are usually low (<0.15 m/s) (Kreuger, 1981) and dissolved oxygen varies between 0.6 and 4.8 mg/L (Bendock, 1980).

The distance, over which Arctic grayling will travel to reach their overwintering destination, varies greatly. For example, some populations will be resident adjacent to overwintering areas such as groundwater sources or lakes (Armstrong, 1986). However, certain individuals may cover between 130 and 160km (Armstrong, 1986).

10.4 Home ranges

Most stream fish fall into one of two categories:
a) A large static group which occupy a home range and hold a specific station in their territory, occasionally conducting foraging trips within a specified area around it.
b) Those which forage widely and do not appear to hold any particular territory. In the River Dee, Wales, fish have been found to move very little and occupy a home range (Woolland, 1986b). In the Llyn Tegid, Wales, home ranges were absent or they occupied non-specific areas, swimming randomly in a particular habitat which suited their requirements (Woolland, 1986b).

11 Comparison of grayling with other species

Although grayling are a member of the salmonidae, they are perceived as a coarse fish and the anglers' view of it can be somewhat divided and controversial. Some salmonid anglers consider the grayling to be vermin and have in view of this tried to eradicate it. Such an opinion is maintained, as they perceive the grayling to actively outcompete the salmon/trout fishery for food and habitat space. However, little work has been conducted to disprove such theories. In fact, recent studies have shown that habitat partitioning and a division of resources exists in streams where grayling and trout co-exist and an effective sympatry ensues.

In interspecific relationships, sympatry has been shown to induce competition (Everest & Chapman, 1972; Fauch & White, 1981; MacCrimmon et al., 1983) and where aggression towards each other is obvious, habitat segregation is essential (Greenberg *et al.*, 1996). However, a high degree of microhabitat segregation occurs between grayling (both Arctic and European) and brown trout. The list below gives details on different aspects of the ecology of grayling, salmon and brown trout:

- Female brown trout and salmon excavate the redd and maintain this territory during spawning. In grayling, however, it is the male which digs the nest and holds the spawning station (Cihar, 1998).
- Brown trout and salmon are autumn spawners whereas grayling are spring spawners (Clark, 1992; Crisp, 1996; Gonczi, 1989; Scott, 1985).
- Grayling eggs are buried at shallower depths than those of salmon or trout (Crisp, 1996).
- Emergence in brown trout and salmon is nocturnal (Gustafson-Marjanen & Dowse, 1983; Elliott, 1986) whilst in grayling it is diurnal (Gaudin & Persat, 1985).
- Emergence and displacement are shorter for grayling than salmon (Bardonnet *et al.* 1993).
- Brown trout prefer shallower water, nearer to instream cover than grayling (Woolland, 1988).
- Brown trout and salmon are common in pelagic areas whereas few grayling are found in pelagic zones. Grayling seem only to use the pelagic area in systems where interspecific competition for food is high. Most brown trout are found in the upper 8m of the benthic zone and more were caught in shallower water than grayling (Haughen & Rygg, 1996a).
- Larger grayling are more closely associated with the bottom than the brown trout (Woolland, 1988).
- Depth varies between size and species (Greenberg *et al.*, 1996) (Table 12).
- Substrate preferences varied between species (Greenberg *et al.*, 1996) (see Table 6, pg. 7).

Table 14. The depth of water (cm) favoured by different sized fishes (cm) of brown trout and grayling (Greenberg et al, 1996).

Fish size (cm)	Brown trout/cm	Grayling/cm
2-4	<45	105-180
9-18	30-60	45-90
20-50	60-135	75-165

- Grayling are found at lower current velocities (<10cm/s) as compared to all size classes of brown trout (Greenberg *et al.*, 1996).

- Juvenile grayling prefer velocities of <10cm/s whilst medium sized individuals preferred velocities of 20-50cm/s (Greenberg *et al.*, 1996).
- Brown trout were caught more frequently above coarse substrate than grayling (Haughen & Rygg, 1996).
- The probability of being caught over fine substrate increases with increasing length in brown trout whilst it decreases in grayling (Haughen & Rygg, 1996).
- Brown trout were seldom found near each other; >80% were singles and 0.5m or more apart from each other. Approximately 50% of grayling, however, were less than 0.5m apart from each other with 92% in groups (Greenberg *et al.*, 1996).
- The temperature tolerance range, varies between species (Table 14):

Table 15: Optimum, lower and upper critical temperatures for salmon, trout and grayling (Crisp, 1996).

	Temperature (°C)		
	S.salar (Salmon)	***S.trutta (Brown trout)***	***T.thymallus (Grayling)***
Lower critical	0 6	0 – 4	0 – 4
Upper critical	20 – 34	19 – 30	>18
Optimum	6 - 20	4 – 19	4 - 18

- There is more intraspecific competition between grayling than trout (Woolland, 1988).
- A narrow range of sizes of brown trout can be found under stones during the day. No grayling, however, have been located under stones (Greenberg *et al.*, 1996).
- The mouth gape of brown trout is larger than that of grayling (Haughen & Rygg, 1996b), leading to selection of smaller prey items by the latter (Northcote, 1995; Scott, 1985).
- Diet varies between trout and grayling; trout capture more aerial insect prey and grayling commonly ingest stoneflies, molluscs and crustaceans (Peterson, 1968; Woolland, 1987a).
- The consumption of surface food increases with age in trout. They are found in the mid-water and eat more aerial insects. In grayling, this decreases. Grayling are found closer to the bed and ingest fewer aerial invertebrates (Woolland, 1988).

- Grayling demonstrate a faster growth rate than trout in the first five growing seasons (males grow faster overall). However, growth declines markedly in the older age groups (Haughen & Rygg, 1996).
- Mortality increases with age in both species
- Post-stocking behaviour varies between species; trout tend to take cover within their habitat whilst grayling attempt to disperse from the area (Thorfve & Carlstein, 1998).
- The age range of the three species is very similar; 1+ - 12+ for salmon/brown trout and 1+ - 14+ for grayling (Northcote, 1995).
- There is no bias in the sex ratio of brown trout but in grayling there tends to be more females than males (Haughen & Rygg, 1996).

Although one species would probably benefit in the absence of the other, a mixed fish population allows much more efficient utilisation of all the resources available, ultimately resulting in enhanced productivity of a particular stream (Woolland, 1988). In one study of two chalk streams in Southwest England, the Bere Stream and The Mill Stream, it was found that different species of fish distributed themselves randomly (Prenda *et al.*, 1997). This could be a mechanism to minimise both intraspecific and interspecific competition (Fretwell & Lucas, 1969; Maitland, 1965). Habitat partitioning is a mechanism developed to facilitate species coexistence. This much easier to achieve in a stable environment as patterns of temperature and discharge are more constant. Degerman et al (Unpublished) conducted a study in Sweden, of brown trout and grayling 0+ yearlings in sympatry. They discovered that at the microhabitat level, some segregation between species had occurred and grayling tended to occupy the deeper water. Degerman (Unpublished) speculated that introducing grayling to brown trout streams would restrict habitat use by trout, (particularly in deeper waters) and indirectly the life history and biomass of the trout.

Some species often show similar feeding habits in the absence of the other. For example, in one study, Arctic char and brown trout showed similar feeding habits and occupied similar habitats when separate but when in sympatry, they showed a more specialised feeding regime (Svardson, 1976). It has often been assumed that when two species consume the same food, that which is ingested by one could be used by the other in their absence (Maitland, 1965). This would be more significant when food availability is low (Nilsson, 1967). Hence, it may be deduced from the data available, that grayling and other salmonids are able to coexist in sympatry.

12 Stocks, recruitment and populations

In the Chena River, Alaska, population size was estimated for the Arctic grayling employing the number of 2+ grayling in the lower 152km of the river. The parent stock was 5+, hence, a three year lag existed between egg deposition and recruitment and a two year lag between recruitment and spawning (Clark, 1992).

Both density dependent and density independent factors are involved in the determination of population size and dynamics. It has been found that density dependent mortality occurred at the highest levels of parent stock (Clark, 1992). Flow is a very important factor influencing year class strength. High flows produce a series of knock-on effects. For example, after spawning, high flows can disrupt the streambed, dislodging eggs (Vincent, 1962). In addition, high flows produce a decrease in temperature which consequently, may reduce growth and survival of larvae via delayed hatching and decreased metabolic processes (Walker, 1983). Biotic and abiotic factors also influence recruitment including competition, predation, disease and changes in physico-chemical parameters.

13 Identification of populations and individuals

It is possible to identify grayling using the black dots (Persat, 1982) which are present on the front half of the flanks (Duncker, 1960). Dots are not randomly distributed but positioned on dark lines separating two scale lines. Their position can be interpreted by using a specific computer programme and subsequently, individual fish dot patterns can be identified. The dots can also be used for identification at the population level (Persat, 1996).

14 Factors affecting grayling populations

In the UK, a marked decline in numbers of grayling has been recorded in many rivers for example the Lower Alwen, 1994-1996 (Ibbotson, Pers. Comm.). There has also been a similar decline in the number of brown trout over the last 10 years, the main cause of which is suggested to be predation by cormorants and goosanders (Cove, Pers. Comm). The Dee, despite being a notoriously good grayling fishery, has demonstrated a decline in the number of 1+ grayling in the Upper reaches and Llanderfel, producing a subsequent population imbalance (Dutton, Unpublished). A similar situation has arisen in the Alwen where a dramatic reduction in the young trout population has occurred since the mid-1980s (Ibottson, Pers. Comm. 1999).

The reasons for such declines in grayling populations, fall under two main headings; indirect and direct impacts.

14.1 Indirect impacts

14.12 Habitat degradation

Pipelines

Much of the research into the impacts of pipeline building programmes on grayling, has been conducted on Arctic species in British Colombia, the Yukon, Northwest territories and Alaska (Stewart et al. 1982; Steigenberger, 1974; Tripp and McCart, 1974; Elliott, 1980, respectively). In the latter study, grayling were demonstrated to be the most tolerant species of any, to crude oil pollution issuing from the pipelines (Elliott, 1980).

Mining

As with pipelines, there has been little research focusing on the impacts experienced by European grayling. Much of the studies of Arctic grayling have been conducted in the Yukon due to extensive mining activity in the Yukon Territory (Northcote, 1995). Simmons (1984) examined the effects on populations in Alaska and found that grayling exhibited gill damage, dietary deficiencies and a slower rate of maturation. The increased turbidity caused by mining gradually removed all grayling populations. The indirect loss of habitats was thought to contribute to this decline (Reynolds et al, 1989).

Forestry

The impact of the practice of log driving on grayling populations, has been documented in North America and Sweden only (Hubbs and Lager, 1958; Fabricius and Gustafson, 1955, respectively). When conducted during spawning or the larval development period of grayling, it has been known to cause whole populations to decline (Northcote, 1995).

14.13 Pollution

Land-use and its associated allochthonous inputs to rivers and streams, is critical in determining the physico-chemical parameters and biota of a system. The water chemistry and its quality are of prime importance for biodiversity in aquatic ecosystems. Most species have very precise requirements and failure to meet these results in decline or even complete eradication of the species. Such problems have become very common in recent years with increased industrialisation, agriculture and changing land-use.

Deterioration in water quality is one of the most significant factors influencing any fish population. As previously discussed, grayling require cool, well-oxygenated water with a good sequence of pool, riffle, glide and run. Although the range of environmental requirements is broader for grayling than brown trout, the grayling 'succumbs' to pollution and higher temperatures more quickly than trout (Woolland 1986a). Crisp (1996) has suggested ranges of optimum, lower and upper temperatures for European salmonids.

It has been documented that water pollution by chlorines, organomercury, acidification, PCBs, DDEs, has resulted in the decline of grayling populations in Europe (MacKay, 1970). The Douglas Water in Scotland was polluted with industrial detergent through drainage pipes in 1968, resulting in dead coarse fish adjacent to the outflow (MacKay, 1970). Tannery wastes had a similar devastating effect on juvenile fish, selectively eliminating them before the larger grayling.

by increasing suspended solids, free sulphides and the BOD (Stuart, 1953a). Rivers in Serbia suffered severe pollution in the late 1960s from industrial and domestic wastes, erosion, dam construction and intensive over-fishing resulting in the decline or disappearance of the species (Jankovic, 1978).

The effects of water pollution have not been well documented with respect to Arctic grayling.

14.14 Water abstraction.

Many grayling populations exist in regulated rivers, which contain important salmon and trout fisheries. However, in general, regulations of these rarely consider the impacts on the life history of grayling, which varies from salmon and trout. When water is abstracted, levels decrease and the available habitat for grayling is substantially reduced. In addition, flow rate can be affected to the detriment of the fish. The extraction process is known to have a much more direct impact on all biological organisms in rivers, with fish at all life-stages, as well as their invertebrate prey, being drawn into the pumps and destroyed (Magee, 1993). To date, little has been done to mitigate against this. However, it is not unreasonable to assume that specially designed filters could be fitted or some form of screening mechanism assembled to divert fish and other biota away from the pull of the abstraction pumps. Water abstraction for nuclear reactors can also affect downstream flow by causing it to be more irregular. Fluctuating levels can increase the risk of young fry being stranded and riverbed straightening can result in severe erosion of the bed, again limiting grayling habitat as well as invertebrate prey.

The more stable the environment, the less harmful the effect of floods by preventing the washing away of eggs laid in gravel, increasing the survival of invertebrates. Fish territory also increases due to higher minimum flows (Woolland, 1986a). The magnitude, timing and duration of regulated flows are of prime importance in determining suitable grayling habitat. Regulating water flows can act to stabilise the water levels and, consequently, the flow rate. Llyn Tegid, a lake in Wales, has its water level raised during the summer. This increases the area of shallow water which is young fry habitat, as well as increasing the food supply for these grayling (Woolland, 1986a).

Stream gradient is more important in structuring the fish community than differences in flow regimes. *Grayling and brown trout are found in higher abundance* where gradient is high. The transfer of water from a section of river has been found to affect grayling more than brown trout. This may be due to reduced recruitment as well as increased fishing pressure (Borgstroem & Loekensgard, 1984).

Drainage and dredging

Habitats are constantly lost from small tributaries by drainage. Dredging removes substrate essential for young fry and juveniles as well as invertebrate prey. This leads to destabilisation of bottom substrate, possibly dislodging very fine particulate matter, which would subsequently smother the gravel beds of spawning grayling.

An example of the impact drainage has on grayling, can be seen in the tributaries of the Arve river in France. Grayling used these areas as spawning grounds as they were protected from snow melt floods (Persat, 1996). However, the main river was dredged to build a highway and exploit gravel, producing huge erosional impacts. In addition, there are now only impassable waterfalls connecting the original river with it's tributaries impeding the passage of grayling spawners (Persat, 1996).

Recommendations for reducing the impacts of water abstraction

There are a number of measures, which could be taken to reduce the impacts of abstraction. These include prohibition of such activities during the following periods:

- Low flow when habitat is already reduced and oxygen levels are already low.
- The migration season or at specific times during migration for example at night.
- Specifics times of year such as the spawning season allowing the eggs and fry a better chance of success.
- Low flow for example in the summer.

14.15 Impoundment and barriers

The inhibition of grayling migration becomes important when considering spawning, feeding and overwintering sites; unless grayling are allowed to freely move, the population will die out.

Quite minor barriers can inhibit grayling mobility and the ability to colonise particular areas (Ibbotson, Pers.Comm.). This is particularly obvious where the distribution of a species comes to an abrupt halt at a weir. For example, at the Dorchester Weir on the River Frome in Dorset, there is a good head of grayling immediately below the weir but none above it (Ibbotson, Pers.Comm.).

Hydro-electric dams

Despite much effort which has been focused on mitigating against the adverse effects of hydro-electric dams such as fish passes, the recruitment of salmonids has been found to decrease and migration has been inhibited in some cases (Linloekken, 1993). Some fish have to migrate vast distances in order to feed. For example, in the Glomma River system, SE Norway, grayling and brown trout are said to travel 120km to feed (Linloekken, 1993). It is the large and very small members that may have difficulty in finding appropriate food. If migration is inhibited therefore, such grayling could starve.

The Genissiat dam on the Rhone in France was the first large dam to be created in a grayling area (Persat, 1996) in this country. It acted as a definite impediment to grayling migration upwards, in terms of the wall size and downwards for the fry, due to the size of the reservoir (Persat, 1996). The dam was in addition, a source of pollution as a result of it being emptied every three years, which impacted populations also. Recently, a final dam was added to the Rhone which has completely destroyed the remaining natural river course (Persat, 1996).

The discharge in a fishway, relative to the discharge through the turbine in the dam, is very important. Fish ascending the main river will regard the fishway as a tributary and avoid it if discharge is less than $1m^3/s$ (Linloekken, 1993). Consequently, they avoid this and keep going up the main river (Linloekken, 1993). It would, therefore, be recommended that these fish-passes be constructed at higher discharges.

The dams can also have an adverse effect on the habitat below. Streambeds can become very unstable as they are no longer fed with gravel from upstream and a shortage of fine gravel ensues (Klimgeman *et al.*, 1994). Eventually, a very coarse gravel bed will develop with adverse effects on spawning success.

There are also more subtle effects of dams on grayling populations. For example in the river Ain, (Persat, 1996) the populations dropped dramatically over 10 years due a change in the flow regime of the dam. This coincided with the development of nuclear plants as the dams are used to bridge gaps in the nuclear power generation (Persat, 1996). Flows would drop from 200 m^3/s to 12 m^3/s (Persat, 1996), increasing the risk of fry being stranded at low water.

Most of the research regarding the effects of habitat alterations on Arctic grayling, has focused on the development of dams for hydroelectric power (Northcote, 1995). Studies have demonstrated that such populations are vulnerable to invasions of piscivorous predators including pike and also to parasitic infestations (Lindsey, 1957). Withler (1959) also noted the impacts associated with the change in the population from a one of a riverine system to a reservoir, where spawning areas and general habitat availability would be scarce.

Roads and culverts

Culverts at road crossings are potential barriers to juvenile grayling, depending on the current velocity existing in the crossing (Northcote, 1995). This problem has however, only been researched with respect to Arctic grayling. Reports on impacts have been conducted in Alaska (Kane et al, 1989), Manitoba (Derksen, 1980) and the northwest territories (Dryden and Stein, 1975).

14.2 Direct impacts

14.21 Culling

The culling of grayling has been actively encouraged in certain parts of Great Britain as a result of their perception as vermin. Fish are removed by netting, electro-fishing and rod catching during the trout closed season. These are then used as food, disposed of by burying or translocated to areas depauparate of grayling. In general such practices are now less common.

14.22 Stocking

Although grayling are not globally threatened, they are in rapid decline and have been under the threat of extinction several times in their original habitat in certain European countries (Table 2). The reasons for this include the deterioration of water quality, eutrophication, acid rain, over-exploitation (sport fishing particularly in the case of the Arctic grayling) and the loss/destruction of habitat.

Providing that physico-chemical parameters are suitable for a grayling population to survive, stocking can be used as a management tool to enhance the population of grayling where they are rare or absent (Armstrong, 1986). There are a number of factors to take into consideration in attempting to ensure the successful stocking of a stream/river:

- Microhabitat availability.
- Interspecific interactions.
- Intraspecific interactions.
- Competition for food/space/territory, agonistic behaviour, predation, disease.
- Age at which the stocked fish are introduced.
- General state (health) of stocked fish.

The origin of the stock is also important. Stock which have come from a brood stock from a different river, may show an impaired homing ability in returning to their natal river; a mechanism, as already discussed, to ensure reproductive isolation and a habitat which demonstrates favourable or optimum conditions.

Predation is quite an important factor in stocking success as young grayling have been shown to have high mortality rates. In one experiment, stocked grayling were found in 18% of pike stomachs post-release into an experimental stream (Carlstein & Eriksson, 1996). This has been found similarly in the Arctic grayling (Armstrong, 1986), where little or no fry survived when pike were present.

It has been suggested by Henriksson & Muller (1979), that grayling of lake origin may be more susceptible to predation when in streams as they prefer the slower moving waters which are home to piscivore fish such as pike and perch. Lake releases however, were more successful than those into rivers, especially if predatory fish were minimal (Armstrong 1986). It also appears that stocked grayling take longer to acclimatise to their 'new situation' than brown trout. For example, grayling moved downstream after 14 days acclimation as opposed to only two for brown trout (Cresswell & Williams, 1983). Stocking a river system with grayling has been shown to result in a considerable loss of fish from the river close to where they were first released, regardless of their origin (Carlstein & Eriksson, 1996).

The size of stock can influence survival success. A study by Carlstein (1997) found a low recapture rate of fish with an initial lower size. These are likely to be predated upon by perch. A parallel finding was documented for Arctic grayling in the Delta Clearwater River (Tanana River drainage), whereby stocking was only found to be successful when fry were reared for three months prior to release (Armstrong, 1986).

Finally, it should be remembered that stocking can introduce disease to native wild populations. Infectious dermatitis (ASA) is common in the intensive rearing of grayling (Carlstein, 1997). Muzzall (1990) studied the parasites infecting a population of Arctic grayling stocked in lakes and streams in Michigan. He found that 66% of the stocked fish had parasites (listed in Section 15.8). Muzzall (1990) concluded that the reasons for such parasitic infections, related to the transfer of resident parasites in native and additional stocked salmonids and cyprinids, to the introduced grayling.

Although stocking appears to be a quick, simple way of restoring grayling populations in natural waters, there are undoubtedly risks associated with it. The stocked varieties are more than likely, from one brood stock and hence, weaknesses will invariably exist. Native and wild populations have established themselves in a particular area over a period of time through outbreeding and homing and hence specific survival mechanisms have been incorporated into their genotype. Once stocked members commence breeding with wild members, genetic diversity will be lost, weaker fish will be produced and an overall reduction in the genetic fitness of individuals and populations will ensue. Pleyer (1982) found that stocking with a desired species resulted in a reduction from 28% to 5% of the majority of native species in ten years. Another study by Hoffmann *et al.* (1995) found that intensive stocking with eels caused a severe reduction of Streber and grayling in the Upper Danube. The behaviour of stocked and wild populations also differs and can significantly interfere with their success (Kaya, 1989, 1990, 1991). As a consequence, it should be recommended that stocking be used in extreme situations, employing wild spawners collected from the stream/river to be stocked. Brood could be reared from these to be released together with the parents, in spring. Such a system has been used in a tributary of the Ain, France (Persat, 1996). Stocking will only work if the appropriate habitat is available, so conservation and enhancement of habitat is of prime importance before any stocking regime is undertaken.

The handling, transport and pre-treatment of the fish can affect the success of stocking. The stocking process could result in a high degree of disorientation, longer acclimatisation and increased susceptibility to predation and disease. However, stocked 1 year olds have been shown to demonstrate a high rate of downstream dispersal which may have been due to high stress levels from the above treatments (Carlstein & Eriksson, 1996; Thorfve & Carlstein, 1998). High stocking density has also been found to increase downstream dispersion from a site (Cowx, 1994). A lack of suitable/available habitat may exacerbate this migration (Thorfve & Carlstein, 1998).

It has been showed that an increased acclimation time before release appeared to reduce stress and post-stocking downstream dispersal *in the Arctic grayling* (Kaya & Jeanes, 1995; Cresswell & Williams, 1983).

Carmie et al (1987) carried out a detailed study of artificial spawning in *T. thymallus*. They outlined the exact procedure for artificial spawning and made a number of recommendations for the success of such a practice (Carmie et al, 1987):

- Fish should be chosen from wild populations, in May.
- The reproductive organs can be used for the first time in three-year-old fish.
- The only human intervention between spawning times occurs during feeding (three days every month), so as to minimise stress.

In addition, a further study by Maisse et al (1987) demonstrated that the best date on which to initiate artificial spawning was at approximately 130 °-days after the first of March. However, due to the lack of knowledge regarding the reproductive cycle of grayling and the external parameters controlling it, it is difficult to be certain of the first ovulation date (Maisse et al, 1987).

14.23 Predators

Predation is an inevitable part of any animal's life and an effective natural mechanism of population control. The grayling has a number of natural predators, which will obviously vary depending on where the grayling are found. Northcote (1993) has stated that there are at least 11 known piscivorous predators of Arctic grayling in British Colombian tributaries, the most dominant of which is the bull trout (*Salvelinus confluentus*) due to it's high abundance. In addition, predation by black bear, mink, river otter and osprey are thought account for Arctic grayling mortality in Northern America (Northcote, 1995). However, the literature regarding predation of *T. arcticus* is generally sparse.

Otters, other fish and terrestrial piscivorous birds such as the heron, kingfisher, cormorant and goosander commonly predate upon the European grayling (Northcote, 1995). Large piscivorous fish for example pike, perch and burbot, are all prime predators of smaller fish living in shallow habitats (Sempeski & Gaudin, 1995c). Stocked grayling have been found in 18% of pike stomachs in a first release experiment (Carlstein & Eriksson, 1996). Grayling migrating from lakes to rivers are more susceptible to predation as they prefer the slow moving waters where predatory fish are found (Henriksson & Muller, 1979). The appearance of cormorants during the winter 1995/1996, resulted in a decline of the grayling population of a 15km stretch of the River Lenne, N. Rhine Westphalia (Frenz *et al.*, 1997; Staub et al. 1998). Sempeski & Gaudin (1995c) have stated that: 'Predation risk has been recognised as the main factor influencing size-dependent segregation of individuals'.

14.24 Prey

The availability of suitable prey is essential if grayling are to exist in a particular area. Hence, a suitable habitat needs to be available for invertebrates. Many invertebrates are associated with aquatic plants. Magee (1992) has stated that the density of grayling/ha in the grayling zone seems to be related to the presence of aquatic plants. Dredging, active removal and increased herbicide use in particular areas, have lead to a reduction in aquatic plants. It may be postulated, therefore, that numbers of invertebrate prey could also decrease in such areas.

14.25 Disease

Where conditions are sub-optimal for example at low oxygen tension, high temperature or in polluted waters where in each case fish are stressed, the vulnerability of grayling to parasites and disease is increased. Under normal circumstances, grayling do not appear to be highly susceptible to disease. There have been no major outbreaks documented, other than a fungal disease in 1967 (Magee, 1993). Grayling are known to be host to cestode and nematode parasites as well as furunculosis caused by the fluke cercaria (Northcote, 1995). However, infectious dermatitis (ASA) is common in the intensive rearing of grayling (Carlstein, 1997).

Whitfield (1999) studies the parasites of European grayling from the Itchen and Test in Hampshire. He found that all Test and Itchen fish carried at least one parasite. All parasites were identified as helminths, including *Crepidostomum farionis*, the nematode *Camallanus lacustris* and the acanthocephalan *Pomphorynchus laevis*. Older fish were generally found have a higher incidence of infection (Whitfield, 1999).

Muzzall (1990) studied the parasites infecting a population of grayling stocked in a number of streams and lakes in Michigan. He found that 66% of the 154 1+ fish were infected with one of the following: *Crepidostomum* sp., *Diplostomum* sp., *Ornithodiplostomum* sp., *Proteocephalus tenuissima*, *Spiroxys* sp., *Pomphorynchus bulbocolli* and *Trichophrya* sp. *Diplostomum* sp., *Ornithodiplostomum* sp. and *P. bulbocolli* were highly prevalent in three of the lakes (Muzzall, 1990), whilst *Trichophrya* sp. infected a high frequency of fish in two of the lakes ((Muzzall, 1990).

14.26 Angling pressure

Angling pressure is known to exert an influence on the grayling populations of different rivers. In any fisheries management strategy, the fishing effort, yield and catch per effort should be carefully monitored (Cowx, 1991). A negative correlation has been found between angling pressure and quotient of grayling/brown trout in catches. Grayling appear to be easier to catch than brown trout (Linloekken, 1995). In North Rena where the river was not disturbed by regulation, angling pressure was low. During the salmonid closed season, high frequencies of large grayling are caught. Angling pressure on females during the summer may produce a sex bias favouring males (Libosvarsky, 1967).

Although grayling are noted for being the 'Poor man's salmon', they are potentially of enormous economic value, even in top class salmonid fisheries. However, in order for such potential to be realised, the image of grayling must be changed.

Arctic grayling are reported as being highly vulnerable to angling, not least because of the ease with which they are caught (Northcote, 1995). As a result of this, grayling populations have been subject to severe over-fishing (Michiel, 1992; Nelson and Paetz, 1992).

REFERENCES

Andreasson, S. (1973). Seasonal changes in diel activity of *Cottus poecilopus* and *C. gobio* (Pisces) at the Arctic Circle. *Oikos*, **24**: 16-23.

Allen, K.R. (1951). The Horokiwi stream. A study of a trout population. *New Zealand Mar. Dept. Fish. Bull.* **10**. 1-238.

Alt, K. (1969). Taxonomy and ecology of the inconnu, *Stenodus leucichthys nelma*, in Alaska. *Biological Papers of the University of Alaska*. No. 12, 63pp.

Alt, K. (1980). Inventory and cataloguing of sport fish and sport fish waters of western Alaska. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1979-1980.* Project F-9-12, 21(G-I-P): 32-59.

Armstrong, R.H. (1986). A review of the Arctic grayling studies in Alaska, 1952-1982. *Biol. Pap. Univ. Alaska*. **23**, 3-17.

Axford, S. (1991). River Wharfe grayling. *Journal of the Grayling Society*. **Autumn**, 20-26.

Balon, E. (1975). Reproductive guilds of fishes: a proposal and definition. *J. Fish. Res. Board Can*. **32** (6), 821-864.

Bardonnet, A. & Gaudin, P. (1990) Diel pattern of first downstream post-emergence displacement in grayling, *Thymallus thymallus* (L., 1758). *Journal of Fish Biology*. **37**, 623-627.

Bardonnet, A., Gaudin, P. & Persat, H. (1991) Microhabitats and diet downstream migration of young grayling (*Thymallus thymallus L.*) *Freshwater Biology*. **26**, 365-376.

Bardonnet, A. & Gaudin, P. (1991). Influence of Daily variations of light and temperature on the emergence rhythm of Grayling fry (*Thymallus thymallus*). *Can. J. Fish. Aquat. Sci.* **48**, 1177-1180

Bardonnet, A., Gaudin, P., Grolet, O. & Thorpe, J. E. (1993) Diel rhythm of emergence and of first displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). *Journal of Fish Biology*. **43**, 755-762.

Beauchamp, D. A. (1990). Movements, habitat use and spawning strategies of Arctic grayling in a subalpine lake tributary. *Northwest Science*, **64** (4), 195-207.

Bendock, T. (1979). Inventory and cataloguing of arctic area waters. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1978-1979.* Project F-9-11, 20 (G-I-I). 64 pp.

Bendock, T. (1980). Inventory and cataloguing of Arctic area waters. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1979-1980.* **21** (G-I-I): 1-31.

Bishop, F. (1971). Observations on the spawning habits and fecundity of the Arctic grayling. *Prog. Fish-Cult.* 27:12-19.

Blachuta, J., Witkowski, A. & Kokurewicz, B. (1991). An hermaphrodite grayling, *Thymallus thymallus* (L.), from the Nysa Klodzka river (Lower Silesia, Poland). *Journal of Fish Biology*. **38**, 955-957.

Borgstroem, R. & Lockensgard, T. (1984). Influence of discharge and stream gradient of fish community composition in the regulated River Gloama, Norway. In: Regulated Rivers (from 2nd International Symposium on regulated streams, Oslo (Norway) 8th August 1982). Eds. Lillehammer, A. & A. Saltveit

Brännan, E. (1987). Influence of photoperiod and temperature on hatching and emergence of Baltic salmon (*Salmo salar*). *Can. J. Zool.* **65**, 1503-1508.

Brown, C. J. D. (1938). Observations on the life history and breeding habits of the Montana grayling. *Copeia* (**3**): 132-136.

Brown, C.J.D. (1943). Age and growth of Montana grayling. *Journ. Wildlife Management.* **7**, 353-364.

Brown, C. & Buck, G. (1939). When do trout and grayling fry begin to take food? *J. Wildl. Manage.* **3**(2): 134-140.

Broughton, R. (1989). *Grayling: The fourth game fish.* The Crowood Press. 224 p.

Carlstein, M. & Eriksson, L.O. (1996). Post-stocking dispersal of European grayling, *Thymallus thymallus* (L.) in a semi-natural experimental stream. *Fisheries Management and Ecology.* **3** (2) 143-155.

Carlstein, M. (1997). Effects of rearing technique and fish size on post-stocking feeding, growth and survival of European grayling, *Thymallus thymallus* (L.). *Fisheries Management and Ecology.* **4** (5) 391-404.

Carmie, H. & Cuinat, R. (1984). Elevage de l'Ombre commun. Premièrs résultats obtenus à la salmoniculture du Conseil Supérieur de la Pêche à Augerolles. *Rapp. CSP 6ème Dél Région (Auvergne Limousin). pp.19.*

Carmie, H., Morelet, B., Maisse, G., Jonard, L. & Cuinat, R. (1987). Observations sur la reproduction artificielle de L'Ombre commun (*Thymallus thymallus*). INRA-SCRIBE.

Chislett, G. & Stuart, K. (1979). Aspects of the life history of Arctic grayling in the Sekunka River drainage, British Columbia. *British Columbia Fish Wildl. Branch.* 110pp.

Čihař, J. (1998). Freshwater Fish. Blitz Editions.

Clark, R. A. (1992) Influence of stream flows and stock size on recruitment of Arctic Grayling (*Thymallus arcticus*) in the Chena river, Alaska.Can. *J. Fish. Sci.* **49**, 1027-1034.

Clark, C.W. & Levy, D.A. (1988). Diel vertical migrations by juvenile sockeye salmon and the anti-predation window. *Am. Nat.* **131**, 271-290.

Cowx, I.G. (1991). Catch effort sampling strategies conclusions and recommendations for management. In: *Catch Effort Sampling Strategies - Their Application in Freshwater Fisheries Management*. Ed. I.G. Cowx. Oxford: Fishing News Books, Blackwell Scientific Publications. pp. 404-413.

Cowx, I.G. (1994). Stocking strategies. *Fisheries Management and Ecology*. **1**, 15-30.

Craig, P.C., Poulin, V.A. (1974). Life history and movements of grayling (*Thymallus arcticus*) and juvenile Arctic Char (*Salvelinus alpinus*) in a small tundra stream tributary to the Kavik River, Alaska. In P. J. McCart, ed. Life histories of anadromous and fresh water fishes in the western Arctic. *Canadian Arctic Gas Study Ltd., Calgary, Biological Report Series* **20** (2). 54 pp.

Craig, P.C., Poulin, V.A. (1975) Movements and growth of Arctic Grayling (*Thymallus arcticus*) and juvenile Arctic Char (*Salvelinus alpinus*) in a small Arctic stream, Alaska.J. *Fish. Res. Board Can.* **32** (5).

Cresswell, R.C. & Williams, R. (1983). Post-stocking movements and recapture of hatchery-reared trout released into flowing waters – effect of prior acclimation to flow. *Journal of Fish Biology*. **23**, 265-276.

Crisp,D.T. (1996). Environmental requirements of common riverine European salmonid fish species in fresh water with particular reference to physical and chemical aspects. *Hydrobiologia*. **323**, 201-221.

Curtis, M. (1977). The biology and growth of Montana grayling (*Thymallus arcticus*), in Wyoming. *J. Colo.-Wyo. Acad. Sci.* 9 (1):9.

Dahl, J. (1962). Studies on the biology of Danish stream fishes. The food of grayling (*Thymallus thymallus*) in some Jutland streams. *Meddr. Danm. Fisk. –og Hauun-deis.* **3**, 1370-1373.

Darchambeau, F. & Poncin, P. (1997) Field observations of the spawning behaviour of European grayling. *Journal of Fish Biology*. **51**, 1066-1068.

De Bruyn, M. and McCart. (1974). Life history of the grayling (*Thymallus arcticus*) in Beaufort Sea drainages in the Yukon Territory. In P. J. McCart ed. *Fisheries research associated with proposed gas pipeline routes in Alaska, Yukon and Northwest Territories*. Canadian Arctic Study Ltd., Calgary, Biological Report Series, 15 (2). 39 pp.

Deedler, C. L. (1970). Factors affecting the migration of the silver eel in Dutch inland waters. *J. Cons. Perm. Int. Mer.*, **20**: 117-185.

Derksen, A. J. (1980). Evaluation of fish passage through culverts at the Goose Creek road crossing near Churchill, Manitoba, in April and May, 1977. *Manitoba Dept. Nat. Res., Winnipeg, Manuscript Rep.* No. 80-4. 114pp.

D'Hulstere, D. & Philippart, J.C. (1982). Observations sur le comportement d'eclosion et de post-eclosion chez l'ombre commun, *Thymallus thymallus (L.)*. Observations on the hatching and post-hatching behaviour of the European grayling, *Thymallus thymallus (L.)*. *Cah. Ehol. Appl.* **2** (1), 63-80.

Døving, K.B., Selset, R. & Thomnesen, G. (1980). Olfactory sensitivity to bile acids in salmonid fishes. *Acta physiol. Scand.* **108**, 123-131.

Drenner, R.W., Strickler, J.R. & O'Brien, W.J. (1978). Capture probablity: the role of zooplankton escape in the selective feeding of planktivorous fish. *J. Fish. Res. Board Can.* **35**, 1370-1373.

Drost, M.R. (1987). Relation between aiming and catch success in larval fishes. *Canadian Journal of Fisheries and Aquatic Sciences*. **44**, 304-315.

Duncker, G. (1960). Die Fische der Nordmark. *Abhandlunger des naturwissenschaftlichen Vereins Zu Hamburg, N.F.* Supplement, **1**, 432

Dryden, R. L. & Stein, J. N. (1975). Guidelines for the protection of the fish resources of the Northwest Territory during highway construction and operation. *Environment Canada, Fish. Mar. Serv., tech. Rep.* No. CEN/T-75-1.32pp.

Elliott, G. V. (1980). First interim report on the evaluation of stream crossings and effects of channel modifications on fishery resources along the route of the trans-Alaska pipeline. US Fish and Wildlife Service, Special Studies, Anchorage. 77 pp.

Elliott, G. V. (1982). Final report on the evaluation of stream crossings and effects of channel modifications on fishery resources along the route of the trans-Alaska pipeline. US Fish and Wildlife Service, Special Studies, Anchorage. 110 pp.

Elliott, J.M. (1984). Numerical changes and population regulation in young migratory trout, *Salmo trutta*, in a Lake District stream. *Journal of AnimalEcology*. **53**, 327-350.

Elliott, J.M. (1986). Spatial distribution and behaviour movements of migratory trout, *Salmo trutta*, in a Lake District stream. *Jn. of Animal Ecology*, **55**, 907-922.

Eloranta, A. (1985). Grayling (*Thymallus thymallus (L.)*) in the lower part of the Rautalampi watercourse, Finnish Lake District. *Verh. Internat. Verein. Limnol.* **22**, 2555-2559.

Engel, L. (1973). Inventory and cataloguing of Kenai Peninsula, Cook Inlet, and Prince William Sound drainages and fish stocks. Alaska Department of Fish and Game. Federal Aid in Fish Restoration. Annual Report of Progress, 1972-1973. Project F-9-5, 14 (G-I-C), 25 pp.

Evans, B.I. & O Brien, J. (1988) A re-evaluation of the search cycle of Planktivorous Arctic Grayling, *Thymallus arcticus. Can. J. Fish. Aquat. Sci. Vol.* **45**, pp187-192.

Everest, F.H. & Chapman, D.W. (1972). Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada.* **29**, 91-100.

Fabricius, E. & Gustafson, K.J. (1955) Observations on the spawning behaviour of the Grayling, *Thymallus thymallus* (L.). *Reports of the Drottningholm Freshwater Research Institute.* **36**, 75-103.

Falk, M. R., Roberge, M.M., Gillman, D. V., & Low, G. (1982). The Arctic grayling, Thymallus arcticus (Pallas), in Providence Creek, Northwest Territories, 1976-1979. *Canadian Manuscript Rep. Fish. Aqua. Sci. 1665. Western Region, Dept. Fish. Oceans, Winnipeg, Manitoba* R3T2N6. 27pp.

Fausch, K.D. & White, R.J. (1981). Competition between Brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences.* **38**, 1220-1227.

Feldmuth, C. R. & Eriksen, C. H. (1978). An hypothesis to explain the distribution of native trout in a drainage of Montana'a Big Hole River. *Verh. Interat. Verein. Limnol.* **20**: 2040-2044.

Fish and Wildlife Service. (1985). Habitat suitability index models and instream flow suitability curves: Arctic grayling riverine populations. *Biological Report* **82** (10.110). US Department of the Interior.

Frenz, C., Klinga, H. & Schuhmacher, H. (1997). Interim report on the factors affecting grayling (*Thymallus thymallus, L)* and brown trout (*Salmo trutta L.)* populations in the River Lenne (North Rhine – Westphalia): Habitats, cormorants and angling. (Zwischenbericht zur situation von pesche (*Thymallus thymallus L.)* und bachforelle (*Salmo trutta L.)* in der Lenne (NRW) – Lebensraum, kormorane und angelfischerei. *Nat – Landschaft.* **72** (9), 401-407.

Fretwell, S.D. & Lucas, H.L. Jr. (1969). On terrirorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheriologica.* **19**, 16-36.

Furniss, R. (1974). Inventory and cataloguing of arctic area waters. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance report.* 1973-1974. Project F-9-6, 15 (G-I-I). 45 pp.

Furniss, R. (1975). Inventory and cataloguing of arctic area waters. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance report.* 1974-1975. Project F-9-7, 16 (G-I-I). 47 pp.

Gaudin, P. & Persat, H. (1985). Rythmes d'émergence et de dévalaison des alevins d'ombre commun (*Thymallus thymallus*). Compte rendu hebdomadaire des Séances de l'Academie des Sciences, **301**, 843-846.

Godin, J.G.J. (1982). Migration of salmonid fishes during early life-history phases: daily and diurnal timing. In: *Salmon and trout migratory behaviour symposium (E.L. Brannon & E.O. Salo eds).* Seattle, WA: University of Washington Press. 22-51.

Gonzi, A.P. (1989). A study of physical parameters at the spawning sites of the European grayling (*Thymallus thymallus L.*). *Regulated rivers: Research and Management.* **3**, 221-224.

Greenberg, L., Svendsen, P. and Harby, A. (1996). Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in the River *Vojman, Swedan. Regul. Rivers: Res. Mgmt.* **12**, 287-303.

Guma'a, S.A. (1978). The food and feeding habits of young perch, *Perca fluviatilis*, in Windermere. *Freshwater Biology*. **8**, 177-187.

Gustafson, K.J. (1948) Movements and growth of grayling. *Report of the Institute of Freshwater research, Drottningholm*. **29**, 35-44.

Gustafson-Marjanen, K.I. & Dowse, H.B. (1983). Seasonal and diel patterns of emergence from the redd of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 813-817.

Gwartney, L. (1980). Inventory and cataloguing of the sport fish and sport fish waters of the Bristol Bay area. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1979-1980. Project F-9-12, **21** (G-I-E). 20pp.

Harvey, B.L. (1991). Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Oecologia*. **87**. 29-36.

Haugen, T.O., Rygg, T.A. (1996a) Food- and habitat-segregation in sympatric grayling and brown trout. *Journal of Fish Biology*. **49,** 301-318

Haugen, T.O. & Rygg, T.A. (1996b). Intra- and interspecific life history differences in sympatric grayling and brown trout in a Norwegian reservoir. *Journal of Fish Biology*. **48**, 964-978.

Hellawell, J.M. (1969) Age determination and growth of the Grayling, *Thymallus thymallus* (L.) of the River Lugg, Herefordshire. *Journal of Fish biology*. **1**, 373-382

Hellawell, J.M. (1971). The food of the grayling *Thymallus thymallus* (L.) of the River Lugg, Heredfordshire. *Journal of Fish Biology*, **3** (2) 187-197.

Henriksson, J. & Müller, K. (1979). Stream regulation in Swedan with some examples from Central Europe. In: J.V. Ward & J.A. Stanford (eds.) *The Ecology of Regulated streams*. New York & London: Plenure Press. pp. 183-199.

Hobbs, D. (1937). Natural reproduction of quinnat salmon, brown trout and rainbow trout in certain New Zealand waters. *Fish. Bull. New Zealand Marine Dept.* **6**, 1-104.

Hoffmann, R., Berg, R., Blank, S., Dehus, P., Gramm, R. & Rösch, R. (1995). Fische in Baden-Württenberg-Gefährdung und Schutz. *Min. für Ländlichen Raum, Ernährung, Landwirtschaft und Forster*. Baden-Württemberg, Stuttgart.

Hubbs, C. L. & Lagler, K. F. (1958). *Fishes of the Great Lakes Region.* Cranbrook Inst. Sci., Bull. No. 26, rev.edn. 213pp.

Huet, M. (1959). Profiles and biology of western European streams as related to fish management. *Trans. Amer. Fish Soc.*, **88**, 155-163.

Hughes, N.F.,(1992) Ranking of feeding positions by drift-feeding Arctic Grayling (*Thymallus arcticus*) in dominance hierarchies. *Can. J. Fish. Aquat. Sci.* **49**, 1994-1998.

Huitfeldt-Kaas, H. (1927). Studier over aldersforhalde og veksltyper hos norske ferskvannsfiskar. *Oslo.*

Humpesch, U.H. (1985). Gibt es optimale Wasswetemperatruen fuer die Erbruetung von Salmoniden und Thymallideneiern? (Is there an optimum temperature for hatching success of salmonid and grayling eggs?). *Oesterr. –Fisch.* **38** (10), 273-279.

Janovic, D. (1964). Synopsis of biological data on European grayling (*Thymallus thymallus* (Linnaeus) (1758)). *FAO Fish. Synop.* No. 24, F16/S24 (Rev. 1). 50pp.

Jankovic, D. (1978). Effects of anthropogenic factors on the zonal distribution of fishes in the Danube River System in Serbia (Yugoslavia). *Verhandlunger Internationale Vereinigung fur theoretische und ungewandte Limnologie.* **20** (4), 2150-2153.

Jennings, T.R. (1983). Survival, growth and food habits of young-of-the-year Arctic grayling stocked in barren, sub-arctic lakes. *Masters thesis,* University of Alaska, Fairbanks, Alaska, USA. pp. 68

Johnson, T. (1982). Seasonal migrations of anadromous fishes in a northern Swedish coastal stream. *Mon. Biol.*, **45**: 351-360.

Kane, D. L., Behlke, C. E., Basketfield, R. E., Giekek, R. E., McLean, R. F. & Travis, M. D. (1989). Hydrology, hydraulics and fish passage performance of Arctic grayling (*Thymallus arcticus)* at Fish Creek, Denali Highway near Cantiwell, Alaska. *Alaska Dept Transport. Public Facilities*, Rep. FHWA-AH-89-03. 180pp.

Kaya, C.M. (1989). Rheotaxis of young Arctic grayling from populations that spawn in inlet or outlet streams of a lake. *Transactions of the American Fisheries Society.* **118**, 474-481.

Kaya, C.M. (1990). Status report on fluvial Arctic grayling (*Thymallus arcticus*) In: *Montana. Helena, MT: Montana Dept. of Fish, Wildlife & Parks.* pp. 97.

Kaya, C.M. (1991). Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (*Thymallus arcticus*) and implications for the only remaining indigenous populations of fluvial Montana grayling. *Canadian Journal of Fisheries and Aquatic Sciences.* **48**, 53-59.

Kaya, C.M. & Jeanes, E.D. (1995). Retention of adaptive rheotactic behaviour by fluvial Arctic grayling. *Transactions of the American Fisheries Society*. **124**, 453-457.

Keay, I. S. (1990). *Some Aspects of the feeding ecology of grayling Thymallus thymallus L. in the River Frome*. Institute of Freshwater Ecology.

Klimgeman, P.C., Bravard, J.P. & Giuliani, Y. (1994). Les impacts morphodynamiques sur un cours d'eau soumis à un aménagement hydroélectrique à la dérivation: le Rhône en Chautagne (France). *Revue de Géographie de Lyon*. **69**, 73-87.

Kratt, L.F., Smith, R.J.F. (1977) A post-hatching sub-gravel stage in the life history of the Arctic grayling, *Thymallus arcticus*. *Transactions of the American Fisheries Society* **106** (3): 241-243.

Kratt, L.F., Smith, R.J.F. (1980) An analysis of the spawning behaviour of the arctic grayling *Thymallus arcticus* (Pallas) with observations on mating success. *Journal of Fish Biology*. **17**, 661-666.

Kreuger, S. W. (1981). Freshwater habitat relationships: Arctic grayling (*Thymallus arcticus*). *Alaska Dept. Fish Game*. 65pp.

Kristiansen, H. and Doving, K.B. (1996). The migration of spawning stocks of grayling. *Thymallus thymallus*, in Lake Mjosa, Norway. *Environmental Biology of Fishes*. **47**. 43-50.

Kruse, T. (1959). Grayling of Grebe Lake, Yellowstone National Park, Wyoming. *U. S. Fish and Wildlife Services Fisheries Bulletin*, **149**. 59: 305-351.

LaPerriere, J.D. & Carlson, R. F. (1973). Thermal tolerances of interior Alaskan Arctic grayling, *Thymallus arcticus*. *Inst. Water Resour.Rep*. IWR-46. Univ. Alaska, Fairbanks.

Lemen, H. (1994) ***A study to see whether Grayling (Thymallus thymallus) are selective feeders of invertebrates*****. A thesis submitted in partial fulfilment of the Higher National Diploma in fish farming/fish management.**

Libovárský, J. (1967). The spawning run of brown trout, *Salmo trutta m. fario L.*, and its analysis. *Zool. Listy*. 16, 73-86.

Lindsey, C. C. (1957). Possible effects of water diversions on fish distribution in British Colombia. *J. Fish. Res. Bd Can.* **14**, 651-668.

Linlokken, A. (1993). Efficiency of fishways and impacts of dams on the migration of grayling and brown trout in the Gomma River System, SE Norway. *Regulated Rivers Research and Management.* **8** (1 & 2), 145-153.

Linloekken, A. (1995). Angling pressure, yield and catch per effort of grayling, *Thymallus thymallus* (L.) and brown trout, *Salmo trutta* L. on the rivers Glomma and Rena, SE Norway. *Fisheries Management and Ecology.* **2** (4) 249-262.

MacCrimmon, H.R. & Twongo, T.K. (1980). Ontogeny of feeding behaviour in hatchery-reared rainbow trout, *Salmo gairdneri* Richardson. *Can. J. Zool.* **58**, 20-26.

MacCrimmon, H.R, Dickson, T.A. & Gibson, R.J. (1983). Implications of differences in emergent times on growth and behaviour of juvenile Atlantic salmon (*Salmo salar*) and brrok char (*Salvelinus fontinalis*) in sympatric stream population. *Naturaliste Canadien.* **110**, 379-384.

MacKay, D.W. (1970). Populations of trout and grayling in two Scottish rivers. *Journal of Fish Biology.* **2**, 39-45.

Magee, L. (1992). The grayling, an endangered species. *Bull. Yorkshire Naturalists Union.* **17**, 1-3.

Magee, L. (1993). A review of the grayling (*Thymallus thymallus*) in Yorkshire and some records of transfers of fish and ova. *Naturalist.* **118** (1007), 115-122.

Maisse, G., Carmie, H. and Jonard, L. (1987). Influence de la temperature sur l'ovulation de l'ombre commun *Thymallus thymallus*. *Bull. Fr. Peche Piscic.* **305**, 54-60.

Maitland, P.S. (1965). The feeding relationships of salmon, trout, minnows, stone loach and three-spined sticklebacks in the River Endrick, Scotland. *Journal of Animal Ecology*, **34**, 109-133.

Maitland, P.S. & Campbell, R.N. (1992). *Freshwater fishes of the British Isles.* London: Harper Collins, The New Naturalist, pp. 368.

Maslin, J.L. & Patee, E. (1981). La production du peuplement benthique d'une petite rivière: son évaluation par la méthode de Hynes, Coleman et Hamilton. *Arch. Hydrobiol.* **92**, 321-345.

Mayr, E. (1968). *Animal Species and Evolution (in Russia).* Mir Press, Moscow. 597pp.

McCart, P., Craig, P. and Bain, H. (1972). Report on fisheries investigations in the Sagavanirktok River and neighbouring drainages. Report to Alyeska Pipeline Service Company, Bellvue, WA. 170 pp.

Michiel, P. (1992). *Float trip grayling.* B.C. Outdoors (April), 40-42.

Morrow, J.E. (1980). *The freshwater fishes of Alaska.* Alaska North-west Publishing Co., Anchorage. 248 pp.

Muzzall, P.M. (1990). Parasites of Arctic grayling stocked into Michigan lakes. *Canadian Journal of Zoology*, **68**, 596-599.

Nagy, S. (1984). On the age, growth and food of grayling (*Thymallus thymallus L.*) in the River Bela (western Tatra mountains). Limnology of the Bela River/Limnologia Rieky Bela. Ertl.M. ed. *Laboratorium Rybarstva a Hydrobiologie Bratislava Czechoslovakia.* **4**, 301-326.

Nelson, P. H. (1954). Life history and management of the American grayling (*Thymallus signifer tricolor*) in Montana. *Journal of Wildlife Management*, 18:324-342.

Nelson, J. S. & Paetz, M. J. (1992). *The Fishes of Alberta*, 2nd edn. Edmonton: Univ. Alberta Press. 438pp.

Netsch, N. F. (1975). Fishery resources of waters along the routes of the Trans-Alaska Pipeline between Yukon River and Antigum Pass in north central Alaska. *U.S. Fish Wildl. Serv. Res. Publ.* **124**. 45pp.

Nilsson, N.A. (1967). Interactive segregation between fish species. In: *The biological basis of freshwater fish production* (Gerking, S.D. ed.). pp. 296-313. Oxford: Blackwell.

Nordeng, H. (1961). On the biology of char (*Salvelinus alpinus*) in Salangen, North Norway. Zoologi, 10: 67-121.

Northcote, T.G. (1993). A review of management and enhancement options for the Arctic grayling (*Thymallus arcticus*) with special reference to the Williston Reservoir watershed in British Colombia. *BC Min. Envt, Lands and Parks, Fish. Branch,Fish. Manage.Rep.*No. 101.69pp.

Northcote, T.G., (1995) Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). *Reviews in Fish Biology and Fisheries*. **5**. 141-194.

Paddock, D. & Whitehead, M. (1970). Inventory and cataloguing of the sport fish and sport fish waters of the Bristol Bay and lower Kuskokwim drainages. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress,* 1969-1970. Project F-9-2. **11** (12-A): 213-227.

Parkinson, D., Philippart, J.C. & Baras, E. (1999). A preliminary investigation of spawning migrations of grayling in a small stream as determined by radio-tracking. *Journal of Fish Biology*. **55**, 172-182.

Pavlov, D.S., Nezdolii, V.K., Ostrovskii, M.P. & Fomin, V.K. (1998). Homing in the grayling *Thymallus thymallus* in the basin of the Upper Volga. *Jn. Ichthyology Vopr. Ikhthiologie*. **38** (7), 552-553.

Pearse, G. A. (1974). A study of a typical spring-fed stream of interior Alaska. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report*. 1973-1974. Project F-9-6 (G-III-G). 49 pp.

Penaz, M. (1975). Early development of the grayling *Thymallus thymallus* (Linnaeus 1758). *Acta. Sci. Nat. Acad. Sci. Bohemoslov*. **9** (11), 3-35

Persat, H. (1982). Photographic identification of individual grayling, *Thymallus thymallus*, based on the deposition of black dots and scales. *Freshwater Biology*. **12**, 97-101.

Persat, H. (1996). *Threatened populations and conservation of the European grayling, Thymallus thymallus (L. 1758). Conservation of endangered freshwater fish in Europe*. Eds. A. Kirrchofer & D. Hefti. Basel Switzerland Birkhaeuser Verlag.

Persat, H. & Patee, E. (1981). The growth rate of young grayling in some French rivers. In: Sladecrk, ed *Proc. Internat. Assoc. Theoret. Appl. Limnology*. **21**, 1270-1275.

Persat, H., Zakharia, M. E. (1993) The detection of reproductive activity of the grayling *Thymallus thymallus* (L. 1758) by passive listening. *Arch. Hydrobiol.* **123** (4), 469-477.

Peterson, H.H. (1968) The Grayling, *Thymallus thymallus* (L.), of the Sundsvall Bay area. *Institute of freshwater research, Drottingholm*. **48**, 36-56.

Pinder, A., Ibbotson, A. & Sturgess, P. (1999). *Year Class Strengths and Recruitment in a Grayling Population.* Centre for Ecology and Hydrology. 43p.

Pleyer, G. (1982). Besatzmassnahmen und ihre Auswirkungen in einem als Angelgewässer genutzten Fluss. *Der Fischwirt.* **32**, 85-89.

Poncin, P. (1994). Field observations on a mating attempt of a spawning grayling, *Thymallus thymallus* with a feeding barbel, *Barbus barbus*. *Journal of Fish Biology.* **45**, 904-906.

Prenda, J., Armitage, P.D. & Grayston, A. (1997). Habitat use by the fish assemblages of two chalk streams. *Journal of Fish Biology.* **51**, 64-79.

Rawson, D. (1950). The grayling (*Thymallus signifer*) in northern Saskatchewan. *Can. Fish Cult.* 8pp.

Reed, R. (1964). Life History of migration patterns of Arctic grayling, Thymallus arcticus (Pallas), in the Tanana River drainage of Alaska. *Alaska Department of Fish and Game Research Report.* No. 2, 30pp.

Reynolds, J. B., Simmons, R. C. & Burkholder, A. R. (1989). Effects of placer mining discharge on health and food of Arctic grayling. *Water Resources Bulletin, Am. Resources Assoc.* **25**, 625-635.

Roguski, E. A. (1967). Inventory and cataloguing of the sport fish and sport fish waters in the interior of Alaska. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress,* 1966-1967. Project F-5-R-8, **8** (16-B):231-246.

Roguski, E. A. and Tack, S. L. (1970). Investigations of the Tanana River and Tangle Lakes grayling fisheries: Migratory and population study. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress,* 1969-1970. Project F-9-2, **11** (16-B): 17pp.

Roguski, E. A. and Winslow, P. (1969). Investigations of the Tanana River and Tangle Lakes grayling fisheries: Migratory and population study. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1968-1969. Project F-9-1, **10** (16-B): 333-351.

Sagnes, P., Gaudin, P., Statzner, B. (1997) Shifts in morphometrics and their relation to hydrodynamic potential and habitat use during grayling ontogenesis. *Journal of Fish biology*. **50**, 846-858.

Satou, M., Takeuchi, H., Takei, K., Hasegawa, T., Okumota, N. & Ueda, K. (1987). Involvement of vibrational and visual cues in eliciting spawning behaviour in male himé salmon (landlocked red salmon *Oncorhynchus nerka*). *Animal behaviour*, **35**, 1556-1558.

Satou, M., Takeuchi, H.A., Nishii, J., Tanabe, M., Kitamura, S., Kudo, Y. & Okumoto, N. (1991). Inter-sexual vubrational communication during spawning behaviour in the himé salmon (land-locked red salmon, *Oncorhynchus nerka*). In: *Reproductive physiology of fish*. Eds. Scott, A.P., Sumpler, J.P., Kime, D.E. & Rolfe, M.S.) Sheffield Fish Symposium 1991, pp. 185-187.

Schallock, E. (1966). *Grayling life history related to a hydroelectric development on the Chatanika River in interior Alaska*. MS Thesis, University of Alaska, Fairbanks. 113 pp.

Schlosser, I.J. (1987). The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, **68**, 651-659.

Schmidt, R.J. & Hoplbrook, S.J. (1984). Ontogeny of prey selection by black surfperch, *Embiotica jacksoni*) (Pisces: Embiotocidae): The roles of fish morphology, foraging behaviour and patch selection. *Mar. Ecol. Prog. Ser.* **18**, 225-239.

Schmidt, D. & O'Brien, W.J. (1982). Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). *Canadian Journal of Fisheries and Aquatic Sciences*. **39**, 475-482.

Scott, A. (1985). Distribution, growth and feeding of postemergent grayling *Thymallus thymallus* in an English river. *Transactions of the American fisheries society*, **114**, 525-531.

Sempeski, P. and Gaudin, P. (1995a) Habitat selection by grayling-I. Spawning habitats. *Journal of Fish Biology*, **47**, 256-265.

Sempeski, P. and Gaudin, P. (1995b) Habitat selection by grayling-II. Preliminary results on larval and juvenile daytime habitats. *Journal of Fish Biology*. **47**, 345-349

Sempeski, P. & Gaudin, P. (1995c) Size-related changes in diel distribution of young grayling (Thymallus thymallus). *Can. J. Fish. Aquat. Sci.* **52**, 1842-1848.

Sempeski, P., Gaudin, P., Persat, H. & Grolet, O. (1995) Diet selection in early-life stages of grayling (*Thymallus thymallus*). *Arch. Hydrobiol.* **32** (4), 437-452.

Sempeski, P. and Gaudin, G. (1996). Size-related shift in feeding strategy and prey-size selection in young grayling (*Thymallus thymallus*). *Can. J. Zool.* **74**, 1597-1603.

Sempeski, P. Gaudin, P. & Herouin, E. (1998) Experimental study of young grayling (*Thymallus thymallus*) physical habitat selection factors in an artificial stream. *Arch. Hydrobiol.* **141,** No.3 pp 321-332.

Shubin, P.N. & Zakharov, A. B. (1984). Hybridization between European Grayling, *Thymallus thymallus* and Arctic Grayling, *Thymallus arcticus*, in the contact zone of the species. *J. Ichthyol.* 24 (4), 159-163.

Siedelman, D. & Cunningham, P. (1972). Inventory and cataloguing of the sport fish and sport fish waters of the Bristol Bay area. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress,* 1971-1972. Project F-9-4, **13** (G-I-E): 67-83.

Simmons, R. C. (1984). *Effects of placer mining sedimentation on Arctic grayling of interior Alaska.* MSc thesis. University of Alaska, Fairbanks. 75pp.

Sømme, S. (1935). Verst og naering hos harr og ørret (*Thymallus thymallus* L. og *Salmo trutta* L.). *Nytt Magasin for Naturidenskapene*. **75**. 187-218.

Staub, E., Egloff, K., Kramer, A., & Walter, J. (1998) The effect of predation by wintering cormorants *Phalacrocorax carbo* on grayling, *Thymallus thymallus*, and trout (Salmonidae) populations: two case studies from Swiss rivers. Comment. *Journal of Applied Ecology*. **35**. 607-610.

Steigenberger, L.W. Birch, G. L., Bruce, P.G. & Robertson, R. A. (1974). *Northern Yukon Freshwater Fisheries Studies 1973.* Environmental-Social Committee Northern Pipelines. Task Force on Northern Oil Development, Rep. No. 74-20. 51pp.

Stewart, R. J., Mclenehan, R. E., Morgan, J.D. & Olmsted, W. R. (1982). *Ecological studies of Arctic grayling (Thymallus arcticus), Dolly Varden char (Salvelinus malama), and mountain whitefish (Prosopium williamsoni) in the Liard River drainage, B.C.E.V.S.* Consultants Ltd for Westcoast Transmission Company Ltd and Foothills Pipe Lines (North B.C.) Ltd. 99p.

Stuart, T.A. (1953a). Water currents through permeable gravels and their significance to spawning salmonids. *Nature*. **172**. 407-408.

Svärdson, G. (1976). Interspecific population dominance in fish communities of Scandinavian lakes. *Report of the institute of Freshwater Research, Drottningholm*. 55, 144-171.

Tack, S. L. (1971). Distribution, abundance and natural history of the Arctic grayling in the Tanana River drainage. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1970-1971. Project F-9-3. **12** (R-I). 35pp.

Tack, S. L. (1973). Distribution, abundance and natural history of the Arctic grayling in the Tanana River drainage. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1972-1973. Project F-9-5, **14** (R-I). 34pp.

Tack, S. L. (1974). Distribution, abundance and natural history of the Arctic grayling in the Tanana River drainage. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1973-1974. Project F-9-6, **15** (R-I). 52pp.

Tack, S. L. (1980). Migrations and distribution of the Arctic grayling in interior and arctic Alaska. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1990-1980. Project F-9-12, **21** (R-I). 32pp.

Thorfve, S. & Carlstein, M. (1998). Post-stocking behaviour of hatchery-reared European grayling, *Thymallus thymallus* (L.) and brown trout, *Salmo trutta L.*, in a semi-natural stream. *Fisheries Management and Ecology*. **5**, 2, 147-159.

Tripp, D. B. & McCart, P. J. (1974). Life histories of grayling (*Thymallus arcticus*) and longnose suckers (*Catostomus catostomus*) in the Donelly River System, Northwest Territories. In Life Histories of Anadromous and Freshwater Fish in the Western Arctic. Canadian Arctic Gas Study Limited, Calgary, Alberta. *Biol. Rep. Ser.* Vol. **20** (1), 1-50pp.

Tryon, C. (1947). The Montana grayling. *Prog. Fish. Cult.* **9**(3): 136-142.

Urick, R.J. (1983). Principle of underwater sound. McGraw Hill, New York, pp.425.

Van Wyhe, G. (1962). Inventory and cataloguing of sport fish and sport fish waters of the Copper River and Prince William Sound drainages. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress*, 1961-1962. Project F-5-R-3, **3** (11-A): 227-243.

Vascotto, G. L. (1970). *Summer ecology and behaviour of the grayling of McManus Creek, Alaska.* MS Thesis, University of Alaska.

Vascotto, G. L. and Morrow, J. E. (1973). Behaviour of the Arctic grayling, *Thymallus arcticus*, in McManus Creek, Alaska. *Biological Papers of the University of Alaska.* No. **13**: 29-38.

Vincent, R.E. (1962). Biogeographical and ecological factors contributing to the decline of the Arctic grayling, *Thymallus arcticus* (Pallas), in Michigan and Montana. *PhD_Thesis. University of Michigan, Ann. Arbor MI.* Univ. Microfilms Internatl., Ann Arbor, MI, pp. 169.

Walker, R.J. (1983). Growth of young-of-the-year salmonids in the Chena River, Alaska. *MS. Thesis, University of Alaska, Fairbanks, Fairbanks, AK*, pp. 148.

Warner, G. W. (1955). Spawning habits of grayling in interior Alaska. *U.S. Fish and Game Service and Alaska Game Commission, Federal Aid in Fish Restoration, Quarterly Progress Report.* Project F-1-R-5, Work Plan E, Job No. 1, **5**(2). 10pp.

Warner, G. W. (1957). Game fish investigations of Alaska: Environmental studies of grayling as related to spawning, migration and distribution. *Q. Prog. Rep. , Alaska Dept. Fish Game, Proj.* F-001-R-06, Work Plan C, Job 4.

Warner, G. W. (1958). Environmental studies of grayling in Alaska. *U.S. Fish and Game Service and Alaska Game Commission, Federal Aid in Fish Restoration, Quarterly Progress Report.* Project F-1-R-7, Work Plan C, Job 3b, **7**(3). 14pp.

Wells, J. D. (1968). Grayling investigations on Tolsona and Moose Lakes. *Sport fish investigations of Alaska. Alaska Dept. Fish Game.* Proj. F-5-R-9, Job 14-B, rep. 14-B.

Wheeler, A. (1969). *The Fishes of the British Isles and Northwest Europe.* Macmillan, London. 613p.

Whitfield, T. (1999) The Helminth Parasites of Grayling (*Thymallus thymallus*) from the rivers Test and Itchen, Hampshire. A Comparative Study. .*A dissertation submitted in partial fulfilment of the requirements of the B.Sc. in Aquaculture and Fishery Management.*

Williams, F. T. (1968). Grayling investigations on Tolsona and Moose Lakes. Sport fish and investigations of Alaska. *Alaska Department of Fish and Game.* Project F-5-R-9, Job 14-B. Rep. 14-B.

Williams, F. T. (1969). Grayling investigations on Tolsona and Moose Lakes. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress,* 1968-1969. Project F-9-1. **10** (14-B): 291-300.

Withler, I. L. (1959). Fisheries problems associated with development of the Peace River and its upper tributaries for hydroelectric purposes. *British Colombia Fish and Wildlife Branch, Fish. Manage.* Rep. No. 31. 19pp.

Witkowski, A., Kowalewski, M. & Korkurewicz, B. (1984). Grayling. *Warsaw Pañstwowe Wydawnictwo Rolnicze I Lesne.* (in Polish).

Witkowski, A. & Kowalewski, M. (1988) Migration and structure of spawning population of the European grayling, *Thymallus thymallus* (L.) in the Dunajec basin. *Arch. Hydrobiol.* **112** (2), 279-297.

Witkowski, A., Blachuta, J., Kokurewicz, B. & Kowalewski, M. (1989). Changes of gonadosomatic index in *Thymallus thymallus (L.)* in annual cycle. *Acta Ichthyologica et Piscatoria.* **19**, 21-28.

Wojcik, F. (1953). Migration, growth rate and food habits of grayling in the Little Salcha River near Fairbanks, Alaska. *U.S. Fish and Game Service and Alaska Game Commission, Federal Aid in Fish Restoration, Quarterly Progress Report,* Project F-1-R-2, Work Plan 3, Job 1, 2. 6pp.

Wojcik, F. (1954). Spawning habits of grayling in interior Alaska. *U.S. Fish and Game Service and Alaska Game Commission, Federal Aid in Fish Restoration, Quarterly Progress Report.* Project F-1-R-4, 4(1). 3pp.

Wojcik, F. (1955). *Life history and management of the grayling in interior Alaska.* MS Thesis. University of Alaska, Fairbanks. 54pp.

Woolland, J. & Jones, S. (1975). Studies on grayling, *Thymallus thymallus*, in Llyn Tegid and the Upper River Dee, N. Wales. 1. Age and Growth. *J. Fish Biology*. **7**, 749-773.

Woolland, J.V. (1986a). Grayling in the Welsh Dee. *Journal of the Grayling Society*. **Spring**, 17-20.

Woolland, J.V. (1986b). Grayling in the Welsh Dee Part 2. Movements. *Journal of the Grayling Society*. **Autumn**,. 35-37.

Woolland, J.V. (1987a). Grayling in the Welsh Dee Part 3, Feeding. *Journal of the Grayling Society*. **Spring**, 15-20.

Woolland, J.V. (1987b). Grayling in the Welsh Dee Part 4, Age and Growth. *Journal of the Grayling Society*. **Autumn**,. 33-38.

Woolland, J.V. (1988). The feeding relationships of grayling and trout in the Welsh Dee. *Journal of the Grayling Society*, **Spring**, 28-29.

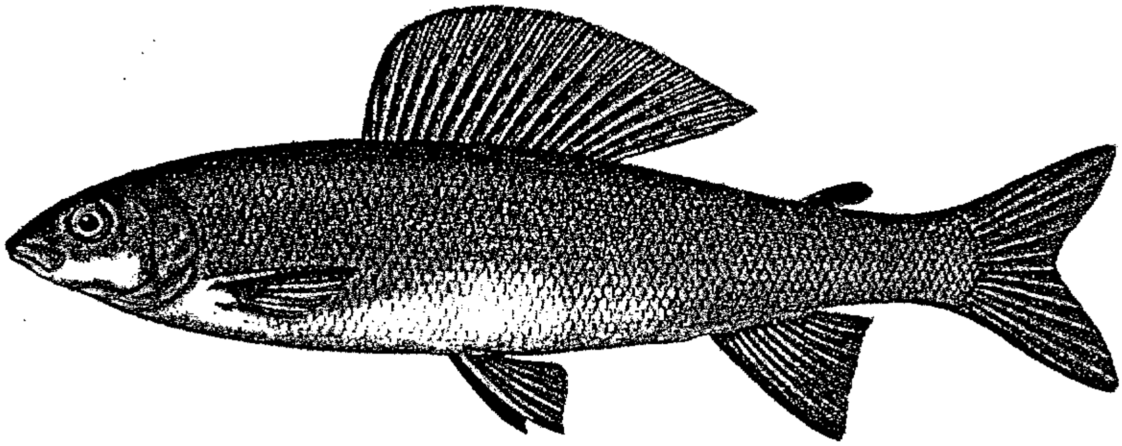
WWW.ecnc.nl/doc/europe/legislat/bernapp3.html (1978).

WWW.fishbase.org.uk. (1999).

Yoshihara, H. T. (1972). Monitoring and evaluation of arctic waters with emphasis on the North Slope drainages. *Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress.* Project F-9-4, 13 (G-II-A): 1-49.

Appendix 1.

GRAYLING RESEARCH QUESTIONNAIRE



Name:

Job title:

Environment Agency Area:

Appendix 1 continued...

How highly are grayling valued as a fishery resource in your area (please tick)?

High value	
Low value	
Not at all	

Appendix 1 continued......

What do you believe are the key issues affecting grayling populations in your area (please place in order of importance, 1 being the most important and 12 the least)?

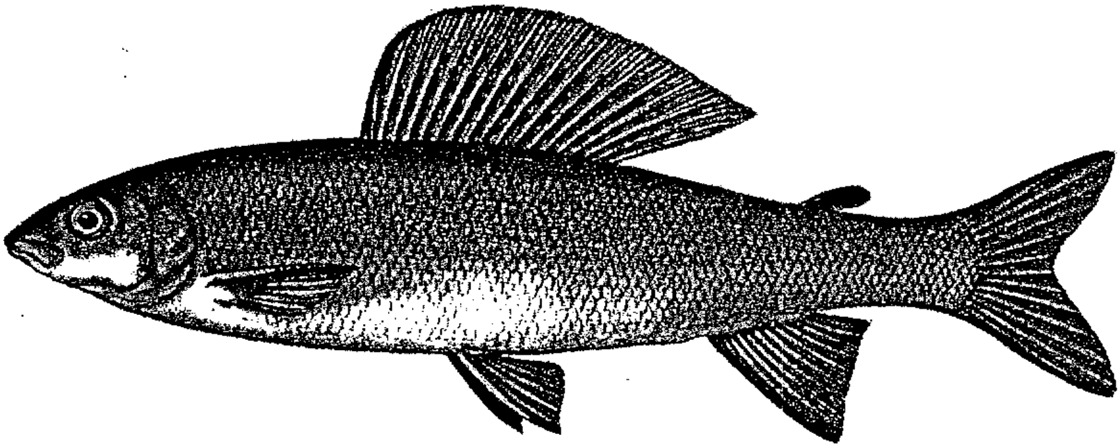
Re-introductions where grayling no longer exist Comments:	**No.**
Transplantations and introductions Comments:	**No.**
Disease and parasites Comments:	**No.**
Removal and/or culling Comments:	**No.**
Predation (fish, birds and mammals) Comments:	**No.**
Competition with other species Comments:	**No.**
Barriers to migration Comments:	**No.**
Water abstraction/regulation/transfer or other water resource management Comments:	**No.**
Pollution Comments:	**No.**
Habitat degradation Comments:	**No.**
Angling restrictions (methods, closed seasons etc.) Comments:	**No.**
Angling pressure Comments:	**No.**
Other Comments:	**No.**

What in your view, would be the most useful issues on which to receive management guidance (please place in order of importance, 1 being the most important and 7 the least)?

Habitat management Comments:	**No.**
Removal and culling Comments:	**No.**
Re-introductions (where grayling no longer exist) Comments:	**No.**
Transplantations and introductions Comments:	**No.**
Angling restrictions (methods, closed seasons etc.) Comments:	**No.**
Grayling as a financial asset/fishery resource Comments:	**No.**
Monitoring Comments:	**No.**
Other Comments:	**No.**

Appendix 2.

GRAYLING RESEARCH QUESTIONNAIRE



Name:
Rivers fished:
Grayling Society Area:

Appendix 2 continued……

What do you believe are the key issues affecting grayling populations in your area (please place in order of importance, 1 being the most important and 12 the least)?

Re-introductions where grayling no longer exist Comments:	**No.**
Transplantations and introductions Comments:	**No.**
Disease and parasites Comments:	**No.**
Removal and/or culling Comments:	**No.**
Predation (fish, birds and mammals) Comments:	**No.**
Competition with other species Comments:	**No.**
Barriers to migration Comments:	**No.**
Water abstraction/regulation/transfer or other water resource management Comments:	**No.**
Pollution Comments:	**No.**
Habitat degradation Comments:	**No.**
Angling restrictions (methods, closed seasons etc.) Comments:	**No.**
Angling pressure Comments:	**No.**
Other Comments:	**No.**

What in your view, would be the most useful issues on which to receive management guidance (please place in order of importance, 1 being the most important and 7 the least)?

Habitat management Comments:	**No.**
Removal and culling Comments:	**No.**
Re-introductions (where grayling no longer exist) Comments:	**No.**
Transplantations and introductions Comments:	**No.**
Angling restrictions (methods, closed seasons etc.) Comments:	**No.**
Grayling as a financial asset/fishery resource Comments:	**No.**
Monitoring Comments:	**No.**
Other Comments:	**No.**

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