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

Interim Report

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Contents

Section	Title	Page number
Chapter 1: Progress Report		
1	Overall aim	1
2	Objectives	1
3	Achievements	1-2
4	Future plans	2
Chapter 2: Literature Review		
1	Introduction	3
2	General description	3-5
3	Distribution	6-9
4	Habitat requirements	9-11
5	Reproduction	12-23
5.1	Fecundity	12
5.2	Spawning	12-13
5.3	Behaviour	13-15
5.4	Courting display and spawning act	14-15
5.5	Spawning habitat	15-17
5.6	Substrate	17
5.7	Water velocity	18
5.8	Water depth	18-19
5.9	New methods of studying spawning behaviour	19
6.0	Unusual courting/spawning observations	19-20
6.1	Hybridisation between grayling species	20
6.2	Emergence	20-21
6.3	The variation in habitat requirements, according to grayling developmental stage	21-23
7	Foraging and diet	24-28
8	Age and growth rate	28-30
9	Population studies	30
10	Fish movements: Migration and homing	31-35
10.1	Homing	32
10.1.1	Migrations and homing to spawning areas	32-33
10.2	Feeding migrations	35
10.3	Migrations to overwintering sites	34-35
10.4	Home ranges	35
11	Comparison of grayling with other species	35-39
12	Stocks, recruitment and populations	39
13	Identification of populations and individuals	39
14	Factors affecting grayling populations	40
14.1	Indirect impacts	40
14.1.2	Habitat degradation	40-41
	Pipelines	
	Mining	
	Forestry	
14.1.3	Pollution	41-42



Contents continued.

Section	Title	Page number
14.14	Water abstraction	42-43
	Drainage and dredging	
	Recommendations for reducing the impacts of water abstraction	
14.15	Impoundment and barriers	44-45
	Hydro-electric dams	
	Roads and culverts	
14.2	Direct impacts	46
14.21	Culling	46
14.22	Stocking	46-49
14.23	Predators	49-50
14.24	Prey	50
14.25	Disease	50-51
14.26	Angling pressure	51-52
	References	53-77
	Appendices	
	Appendix 1	78-81
	Appendix 2	82-84



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:

<i>Name</i>	<i>Area</i>
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 depauperate 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 111 (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 <i>T. thymallus</i>		
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 obyčajny	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 15 th March – 15 th 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	*	*	*	

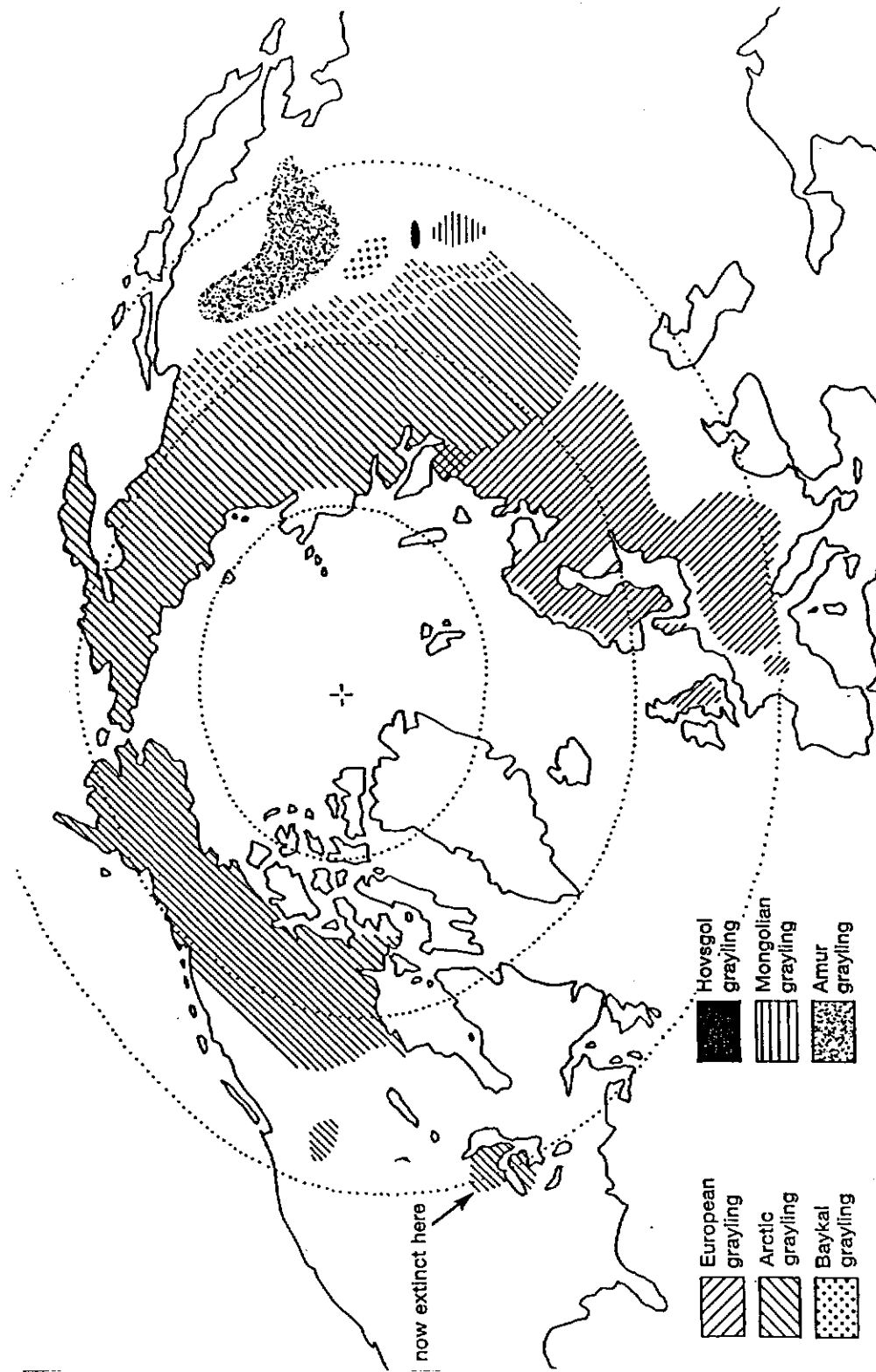


Figure 1. The worldwide distribution of *T. thymallus* and *T. arcticus* (Broughton, 1989).

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 (Wojeik, 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 & Dowling, 1996; Magee, 1993; Peterson, 1968; Witkowski & Kowalewski, 1988). Some populations are potamodorous, 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 & Dowling, 1996).

5.3 Behaviour

Males arrive on the spawning ground several days before the females downstream (Fabricius & 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 (Fabricius & 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 (Libosvsky, 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 pelvis 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 $>5^{\circ}\text{C}$ (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 ($2\text{-}3\text{cm}$ 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 (Gonczy, 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 (Gonczy, 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 (Urlick, 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). Bardonnnet & 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 flow 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.

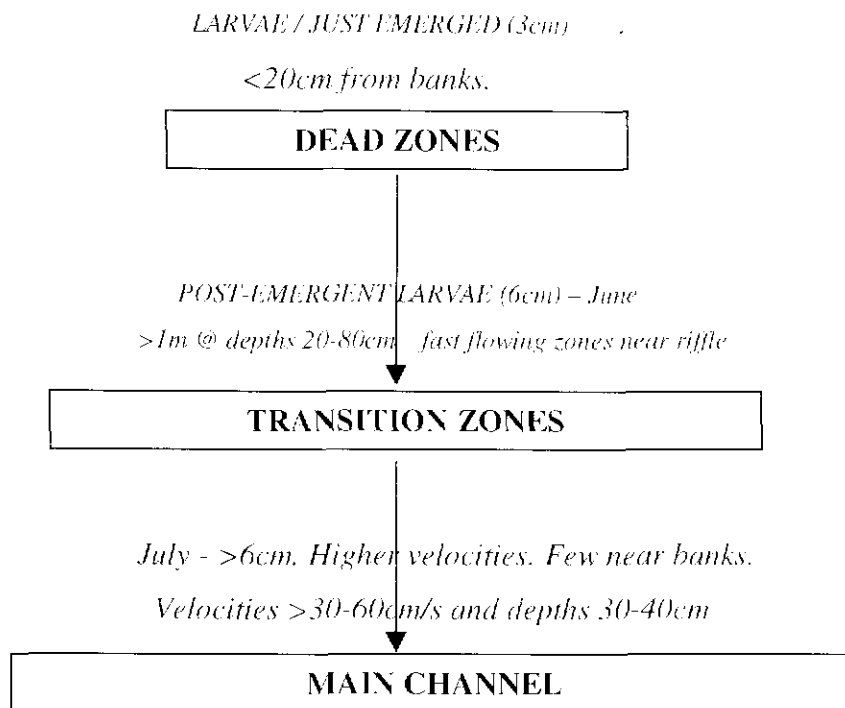


Figure 2. Shift in habitat type with different life-stages of grayling (Bardonnnet *et al.*, 1991).

When larvae first emerge, they are relatively weak swimmers and tend to avoid habitats with steep banks or deep depths (Bardonnnet *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 (Bardonnnet *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 (Bardonnnet *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 (Bardonnnet *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 (Bardonnnet & 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, simuliidae 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 (Hellowell, 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 *et 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 <i>at al.</i> , 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 <i>at al.</i> , 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 (<i>Stenodus leucichthys</i>)		* (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 (<i>Onchorhynchus nerka</i>)	* (www.fishbase.org.uk, 1999)	* (Williams, 1969)
Nine-spine stickleback (<i>Pungitius pungitius</i>)		* (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) (Hellowell, 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 (Hellowell, 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 (Hellowell, 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; Sømme, 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 Taek (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).

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

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 (Bardonnnet *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)		
	<i>S.salar</i> (Salmon)	<i>S.trutta</i> (Brown trout)	<i>T.thymallus</i> (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).