AGE, GROWTH, REPRODUCTIVE BIOLOGY AND POPULATION DYNAMICS OF THE COMMON MEGRIM *LEPIDORHOMBUS WHIFFIAGONIS* (Walbaum, 1792) FROM OFF THE WEST COAST OF IRELAND

By

Stephen M. Robson B.Sc. (Hons.)

Degree of Doctor of Philosophy in Fisheries Biology Galway-Mayo Institute of Technology

Supervisor of Research Dr. Pauline A. King

Submitted to the Higher Education and Training Awards Council,

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This work is dedicated to my friends and family

Declaration

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Age, growth, reproductive biology and population dynamics of the common megrim Lepidorhombus whiffiagonis (Walbaum, 1792) from off the west coast of Ireland

Stephen M. Robson

ABSTRACT

A total of 4,964 common megrim *Lepidorhombus whiffiagonis*, were examined from commercial catches in Divisions VII_{b+c}, off the west coast of Ireland, between April 1997 and February 2001. A sex ratio of 31.8:1 females to males was recorded, with a higher percentage (15%) of fish being male at lengths <25cm TL, while no males were recorded >45cm TL.

The largest and oldest fish recorded was a 51.3cm TL female, aged 16 years and weighing 1012.61g. The smallest was a 15.1cm TL female, weighing just 18.24g. Females ranged in age from 2-16 years old, while the male age range was considerably smaller, that of 3-8 years old. Age at recruitment (t_r) was determined to be at age 6 years of age for both female and male fish. Values of 0.91 and 1.43 were recorded for total mortality (Z) for female and male respectively.

Three different growth models were used to describe the most accurate growth rates for the fish. Average values of 50.72cm for $L\infty$, 0.097 for K and -4.78 for t_0 were recorded for female fish, while $L\infty = 41.59$ cm, K = 0.138 and $t_0 = -3.062$ were determined for males. Yield per recruit curves revealed that optimum yield occurred at a fishing mortality (F) of 1.2 and 1.4 for female and male megrim respectively.

Five maturity stages were recorded for the species. Fecundity ranged from 26,522-640,523 oocytes. Megrim were determined to be total spawners, spawning once annually between January and early March. Estimates of 24.0cm TL and 25.0cm TL for $L_{50\%}$ were calculated for female and male histologically determined maturity at length. Maturity at age estimates for A_{50%} of 2 years and 2.5 years were recorded for female male fish respectively. An overall mean prevalence of atresia (Pa) of 63.5%, and relative intensity of atresia (Ia) of 24.2% was determined.

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CHAPTER ONE : PART 1. GENERAL INTRODUCTION

1.0 The common megrim Lepidorhombus whiffiagonis

The common megrim Lepidorhombus whiffiagonis (Walbaum, 1792) is a commercially exploited flatfish of the family Scopthalmidae. L. whiffiagonis occurs from Iceland (64°N) at its northernmost distribution, and extends as far south as Cape Bojador (26°N). It also occurs in the Mediterranean and Aegean Seas (Dando, 1970; Boon, 1984; Nielson, 1986; Poulard et al. 1993; Silva & Azevedo, 1994; Sanchez et al. 1998). It is primarily exploited by the Irish and EU demersal fleet off the west coast of Ireland, in Sub Area VI (Rockall and west of Scotland) and Sub Area VII and Divisions VIII ab.d+e (Celtic Sea and Bay of Biscay) (Fig. 1.). These two sub areas of megrim exploitation are regarded as two separate stocks are assessed individually (Anon., 2002). Megrim are usually caught as a bycatch in the mixed demersal fishery for prawns Nephrops norwegicus L., gadoid species, anglerfish (Lophius species) and ray (Raja species). Recently however the species has been targeted specifically by bottom trawlers, as regular whitefish and flatfish species become over-exploited (Fahy & Fannon, 1991). Megrim are mainly a deep-water fish, although occasionally and very rarely, is found at the surface and close inshore. They prefer soft muddy bottoms, from where they can predate on food items such as crustaceans and small species of fish (Wheeler, 1969).



Plate 1. Pair of common megrim Lepidorhombus whiffiagonis (Walbaum, 1792) caught in ICES Division VII_b off the west coast of Ireland during the present investigation.

1.1 Importance of megrim in Irish demersal fisheries

In 2002, the Irish demersal fleet reported total landings of 39,739 tonnes (live weight) of demersal fish species (Anon., 2003). This represents a small reduction on the 2001 landings of 42,378t. The most important species by weight were whiting (6,640t), orange roughy (4,646t), haddock (3,595t), anglerfish (2,828t) and megrim (2,760t). The total value of demersal fish landed in 2002 was ϵ 78.3 million, an increase of 14% on the 2000 value of ϵ 66.8 million (Anon., 2003). The most important species in terms of value were orange roughy (ϵ 13m), anglerfish (ϵ 9.2m), megrim (ϵ 8.2m), cod (ϵ 5.6m), whiting (ϵ 5.4m), haddock (ϵ 4.6m), sole (ϵ 3.9m) and hake (ϵ 2.2m) (Anon., 2003).



Figure 1. The ICES Divisions within Irish waters, with Sub Areas VII_b and VII_c highlighted in green. (Map courtesy of BIM)

1.2 ICES Division Sub Area VII Megrim Stock

The population of megrim caught and examined in this study are part of the stock in Sub Area VII. This area is combined with Divisions $VIII_{a,b,d+e}$ for the purposes of stock assessment, though the two areas have separate Total Allowable Catch (TAC) values. These areas correspond to the west of Ireland and the Celtic Sea (Sub Area VII) and the Bay of Biscay (Divisions VIII _{a,b,d+e}). The TAC for Sub Area VII in 2003 was 14,335t while the Irish quota for Sub Area VII TAC was 2,373t in

2003. The TAC for VIII_{a,b,d+e} in 2003 was 1,664t. The proposed TAC for 2004 is 18,099t and 2,101t in Sub Areas VII and VIII_{a,b,d+e} respectively. This equates to a proposed Irish quota of 2,996t in Sub Area VII in 2004. The economic value of the 2002 Irish quota was ϵ 6.6 million whilst the value of the 2002 Irish landings was ϵ 7.2 million (Anon., 2003). In recent years megrim has become an extremely important high value species for the Irish fishing industry, and is taken in mixed fisheries along with hake and anglerfish as well as *Nephrops*, cod and whiting (Anon., 2003).

Many other European countries compete for the available megrim stock in Sub Area VII. Spain and France dominate the fishery with almost 70% of the landings between them. In 2003, Ireland landed an estimated 15% of the total international landings, approximately 2,413t. The 2003 quota for Sub Area VII was divided between France (36.4%), Spain (30%), Ireland (16.6%), United Kingdom (14.3%) and Belgium (2.7%) (Fig. 2). The majority of UK landings of megrim are made by beam trawlers fishing in Divisions $VII_{e,f,g+h}$. Otter trawlers account for most of the Spanish landings from Sub Area VII exploiting a mixed fishery for anglerfish, hake and megrim on the continental shelf edge around the 200m contour to the south and west of Ireland. Megrim are a very valuable by-catch for Irish demersal trawlers from Killybegs, Rossaveal, Dunmore East, Castletownbere, Union Hall and other ports in SW Ireland. Irish megrim landings in Sub Area VII are largely by multi-purpose vessels fishing in Divisions $VII_{b,c,j+k}$ for gadoids as well as plaice, sole and anglerfish. In recent years megrim have also become important to the Irish beam trawl and twinrig fleets (Anon., 2003).



The value per tonne of these landings increased in 2003 (Anon., 2003). Irish landings in 2003 were similar to the 2003 Irish quota so any further reductions in the TAC will have a serious impact on the profitability of Irish vessels (Anon., 2003).

As with the landings of megrim in Sub Area VI, *L. whiffiagonis* is often caught in Sub Areas VII and Divisions VIII_{a,b,d+e} along with its close relative, the four spot megrim, *Lepidorhombus boscii*, though *L. whiffiagonis* constitutes the bulk of all Irish landings (Fahy & Fannon, 1991). Recent estimates on the contribution of *L. boscii* to the total Irish landings of megrim in Sub Area VII and Divisions VIII_{a,b,d+e} has been placed at 5% (Anon., 2003). Irish sampling indicates that catch rates of *L. boscii* are negligible in landings. Irish fishermen do not separate the two species. Due to the smaller average size, *L. boscii* are more common in discards, particularly in deeper waters (Anon., 2003).



The landings in 2002 were 17,400t, which was 2% higher than in 2001. Landings have been relatively stable, fluctuating around 17,000 t since 1990 (Fig. 3.).

As with the megrim from Sub Area VI, west of Scotland and Rockall, Irish sampling for the stocks of megrim in Sub Area VII and Divisions $VIII_{a,b,d+e}$ is supported through the EC funded Sampling Programme, which is required under the Data Collection Directives 1543/2000 and 1639/2001. The Marine Institute FSS also carried out an egg and larval survey in March 2000 and 2001. The preliminary results from this survey indicated that the continental shelf edge southwest of Ireland is an important spawning area for megrim (Anon., 2002). Fisheries Science Services (FSS)

sampling has also shown that the dominant year class in VII_g was age class 4, in VII_b age class 5 and age class 3 in VII_j .

There is a problem with discarding of small megrim which are retained in the 80mm mesh cod-ends. The FSS sampling programme suggests that about 29% of the total weight of megrim caught (60% by number) was discarded in 2000. About 43% of these were of landable size. The minimum landing size was reduced from 25 to 20cm for megrim in January 2000 in an attempt to reduce discarding. This reduction in the minimum landing size was part of a technical conservation measure (TCM) for the species (Anon., 2002). The selection pattern is poor for the Irish megrim fishery, which takes a disproportionate amount of small fish, and the FSS recommend that technical measures such as increases in mesh size to reduce the catches of small fish should be investigated. In the last three years, a decreasing trend in the discards of megrim has been observed. The estimation of discards in 2001 was the lowest in recent years. The discards decrease in 2000 and 2001 can be explained partly by the reduction in the minimum legal size and the use of larger mesh sizes due to the Northern Hake Emergency Plan (Anon., 2002). Though discarding in the Irish megrim fishery is being examined, only limited discard information is available for the French fleet fishing in these areas. However, small megrim are less valuable on the market and discarding continues to be a problem in this fishery (Anon., 2001b).



According to ICES, the megrim stock from Sub Area VII is harvested outside safe biological limits (Fig. 4.). The FSS estimate of F (0.39) for 2002 is above the proposed $F_{pa}=0.30$. Fishing mortality declined from the 1991 peak value until 1997, but has increased since then to above F_{pa} (Anon., 2003).

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The ICES medium term predictions suggest that fishing at current levels of exploitation will lead to a more than 95% probability of the spawning stock biomass (SSB) exceeding B_{pa} in 2007, at F_{pa} there is a 5% probability of SSB falling below B_{pa} in 2009. They also predict that there would be no loss in long term (yield per recruit) if the current fishing mortality rate was reduced to F_{max} . Such a reduction in fishing mortality would increase the expected spawning stock biomass per recruit to the order of 50% (Anon., 2002). The SSB decreased suddenly from about 80,000 t in the mid 1980's to about 60,000 t in 1989 (Fig. 5.). Since then SSB has remained fairly stable at about 60,000 t which is above B_{pa} = 55,000 t. The spawning stock biomass in 2003 was estimated at 82,400t. Spawning stock biomass was high from 1984 to 1988, then declined until 1990 and has been above B_{pa} since then. In the short term, spawning stock biomass is predicted to be decline in 2004 and 2005 at current fishing mortality (Anon., 2003).

Megrim are widely distributed over the whole of Sub Areas VII and VIII and are most abundant in the deeper waters of the continental shelf. Spawning takes place in these areas between January and April along the edge of the continental shelf to the southwest and west of the Ireland and the United Kingdom. Trawling surveys undertaken by research vessels indicated that 0-group megrim do not move far from the spawning grounds on the shelf edge during their first year (Anon., 2003).

According to the FSS, in order to be consistent with the precautionary approach, the management of the mixed fisheries taking megrim will be determined by measures to assist the recovery of hake. There are no explicit management

Chapter One: Introduction.

objectives or plan for these stocks, but measures need to be established and implemented for fisheries taking megrim (Anon., 2002). In the past mis-reporting has not been a problem in the megrim fishery in Sub Area VII and Divisions VIII_{a,b,d+e} as the TAC was not restrictive. During 2002, revised Irish commercial catch and effort data from logbooks was used to detail the assessment of the stocks. Revised data was also used from France for the years 2000 and 2001 by the ICES Working Group on Northern Shelf Demersal Stocks. The FSS carried out an age based analytical assessment using catch per unit effort from three commercial fleets and three surveys. Discard estimates were used but were considered incomplete as only Spain provided data.

Recruitment is estimated to be stable in the stock, especially recruitment at age 1 (Fig. 6.), with a peak in the 1998 and 2000 year classes. (Anon., 2003). Estimates of recruitment are very dependent on discard information. In 1998, high discard estimates from France resulted in a large estimate of recruitment into the spawning stock biomass (SSB) in 2000 (Anon., 2002).



Almost all megrim landed in Ireland are exported to Spain and France, as there is no local market for the species. The small amount not exported are eaten as table fish in Ireland, but usually under the name 'white sole'.

CHAPTER ONE : PART 2. PREVIOUS STUDIES

1.3:1 Previous megrim age and growth studies

There has been a considerable amount of work carried out on the growth of L. whiffiagonis in European waters.

Age determination of megrim was investigated by Peronnet & Rivoalen (1989) using caudal fin rays. Dawson (1990) presented the results of a preliminary analysis of an otolith exchange for *L. whiffiagonis* caught in the Celtic Sea. Following this otolith exchange, a first workshop was held in 1991, followed by a second in 1997, during which good agreement was obtained in age estimation (Anon., 1991; 1997).

Except for unpublished ageing studies undertaken by the Irish Marine Institute, studies on the growth of *L. whiffiagonis* in Ireland are very limited and there is no published information available on age and growth for the west coast of Ireland. There are only two published works on megrim growth in Ireland, Fahy & Fannon (1991), and Fahy & Glesson (1992). There is also a joint Irish and Scottish study on megrim and anglerfish which is unpublished (Anon., 2001a). Also of historical importance, is part of an unpublished PhD study by Tyndall (1980) which included megrim amongst other selected demersal species from Galway Bay.

The majority of megrim age and growth studies have been carried out in Spain. These extensive Spanish studies include Rodriquez & Iglesias (1985) in Sub Area VII; Moguedet & Perez (1988) also in Sub Area VII; Pineiro *et al.* (1993) from the north eastern Atlantic in ICES Divisions VII_{j-k}, VIII_{ab}, VIII_c and IX_a; Landa *et al.* (1996) also from the north east Atlantic; Perez (1998) in Sub Area VII and Divisions VII_c and IX_a; Santurtun *et al.* (1998a) in the Bay of Biscay, and Landa & Pineiro (2000) in the north eastern Atlantic.

In France, megrim growth has been studied extensively, the principal investigations being Conan *et al.* (1981), Aubin-Ottenheimer (1985) and Alperi (1990). Growth was also briefly looked at by Furnestin (1935) and Dwivedi (1964) in the Atlantic, North Sea and Mediterranean.

A preliminary study on the age and growth of both *L. whiffiagonis* and *L. boscii* from ICES Sub-area VII in the Celtic Sea was carried out by Dawson (1991a&b).

1.3:2 Previous Megrim Reproductive Studies

The only Irish reproductive study on megrim carried out, was part of an international study on megrim and anglerfish in ICES Division VI_a and VI_b and was jointly divided between Ireland and Scotland, with Ireland studying the megrim and Scotland, the anglerfish (Anon., 2001a).

Perez (1998) studied the biological parameters for *L. whiffiagonis* and *L. boscii* landings for Spanish vessels from the ICES Sub Area VII and Divisions VIII_c and IX_n. The reproductive biology of megrim was studied on fish from the Bay of Biscay during 1996-1997 by as part of biological study on the species (Santurtun *et al.* 1998a). The gonad histology and its development in megrim was also examined by Santurtun *et al.* (1998b) in Sub Areas VIII_{a,b+d}. The reproductive biology of *L. whiffiagonis* was studied by Furnestin (1935) in the Atlantic and North Sea.

Dwivedi (1964) published information on the reproductive biology of both species of megrim from the North Sea, Bay of Biscay and the Mediterranean. Aubin-Ottenheimer (1985) studied the biology of megrim from the Bay of Biscay in an unpublished PhD investigation which included a reproductive examination, though this information is unavailable for comparison.

The maturity and spawning distribution of *L. whiffiagonis* from the Celtic Sea, western Channel and the northern Bay of Biscay was examined by Dawson (1991c) from research vessel surveys carried out in March 1989 and 1990.

CHAPTER ONE : PART 2. PURPOSE OF STUDY

1.4 Purpose of the present study

There is no published information on the age, growth and reproductive biology for the common megrim *Lepidorhombus whiffiagonis* in Ireland. The only available data is for initial stock assessment purposes (Anon., 2001a, 2003; Fahy & Fannon, 1991; Fahy & Gleeson, 1992). Equally, there is very little known about the biology of megrim in Sub Areas VII_{b+e} and there is no information on the reproductive status of the species in this area. This reproductive status includes a lack of information on estimates of fecundity, length and age at first maturity, rates of atresia, oocyte dynamics, spawning period and type, and maturity assessments.

The aim of the current investigation is therefore to provide a detailed account of the biology of a previously unstudied population of the west coast of Ireland. The work will also provide a substantial baseline study for future similar studies on

Chapter One: Introduction.

megrim off the west coast. Results from this study will be compared with other megrim growth and reproductive studies throughout the rest of Europe.

Megrim are a commercially important flatfish species in Ireland with an annual value of approximately €7.5 million. It is therefore essential that concise and accurate research is carried out on its biology in order to allow sustainable exploitation of the resource and to maintain Irish megrim stocks within safe biological limits into the future. Understanding the biology of the common megrim off the west coast of Ireland in terms of its age, growth, reproductive strategies and population structure allows fisheries scientists, politicians, policy makers and fishermen to set practical total allowable catches (TAC's), quotas and exploitation levels for the stock.

As no work of this nature and level of detail has been carried out for the west coast of Ireland megrim population to date, this study will contribute enormously to the available information on megrim fished in Irish waters and thereby improve our understanding of the delicate dynamics of the species not only in Ireland, but also at a European level.

Chapter Two

Chapter Two : Part 1. Laboratory dissection

<u>Chapter Two : Part 2.</u> <u>Age and growth methods</u>

<u>Chapter Two : Part 3.</u> <u>Reproductive methods</u>

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<u>CHAPTER TWO: PART 1. SAMPLING & LABORATORY METHODS.</u> 2.0 General introduction

The materials and methods used in the study include the procedures from sampling and laboratory dissection, age determination and reproductive techniques including histology and fecundity analysis. Also presented here are the statistical calculations for various parameters such as growth, mortality and yield per recruit, as well as the statistical tests used.

2.0:1 Sampling procedure

A total of 4,964 common megrim, *Lepidorhombus whiffiagonis*, were examined during the present investigation. The fish were taken from catches landed at the commercial fishing port of Rossaveal, Co. Galway by fishing trawlers operated by members of the Galway and Aran Fishermen's Co-operative. Samples of megrim were taken monthly from April 1997 until March 2000, with an additional sample added during February 2001. A total of 29 monthly samples were obtained during this period. The fish were not frozen at the auction hall in Rossaveal, though they were packed in fish boxes which were covered in ice to retain a measure of freshness. At the laboratory, the megrim were preserved by freezing at -18°C pending further examination.

2.0.2 Fishing gear and sampling technique used

The fish were caught on prawn grounds (*Nephrops norvegicus* L.) off the west coast of Ireland in ICES Divisions VII_b mainly on fishing grounds behind the Aran Islands, and VII_c, particularly off the Porcupine Bank (Fig. 1.). The fish were caught at depths of approximately 100m, by commercial trawlers using an otter board bottom trawl with a standard mesh size of 80mm at the cod-end. Otter boards are the most developed method for keeping towed trawls open horizontally and first appeared in Ireland around 1885 (Von Brandt, 1984). A bottom trawl is constructed like a cone-shaped net that is towed by one or two boats, on the bottom. The body of the net ends in a codend, which retains the catch. Normally the net has two lateral wings extending forward from the opening (Fig. 7.). The mouth of the trawl is framed by a headline and a groundrope (Url. 1.). The headline rope usually has floats attached and serves to maintain the opening at the mouth of the net. The groundrope or footrope usually has tickler chains attached and is weighted. This is the part of the net that scrapes along the bottom of the sea bed and causes disturbance of the flatfish species present there.

The greater the number of tickler chains, the more efficient the net becomes for catching fish (Von Brandt, 1984).

Otterboard trawling is relatively simple in theory but quite difficult to operate in practice. The net is shot while the boat is moving forward while approximately 2.5 times the depth in metres of warp is released from the winches which insures that the net, bridles and doors reach the bottom and remain there at a favourable angle. The warp is released slowly and is braked at regular intervals to avoid the gear twisting or fouling while being shot (Power, 1998).

As the boat moves forward, the net begins to fish. Both otterboard doors are attached to the warp at an angle and as the boat moves forward, the hydrodynamic pull results in the spreading of the doors. As these are connected to the net, this also results in the spreading of the net wings. Both doors remain at an angle of approximately 45° to the horizontal direction of the moving fishing vessel. Equal strain on both sides of the otterboard doors is achieved by using backstraps made of fixed link heavy steel chain. It is this mechanism that separates the wings of the net. The doors scrape along the seabed, raising a dust cloud over the sediment. Targeted species are frightened by this and move away from the disturbed area. The two bridles are attached from the wings of the net to the otterboard doors and, when the net is fishing, they also form a dust cloud and a tapering angle from the doors to the mouth of the net. The fish are also frightened by the bridles and they are again turned back. The tapering of the bridles channels them into the mouth of the net. Towing speeds ranging from 1 to 7 knots (0.5-3.5 metres per second) are used, though more usually between 3 and 5 knots. Duration of a tow mainly depends on the expected density of fish, (whether the fish are aggregated or not), the shape of the bottom and the slope in the fishing area, from a few minutes (10-15), up to 10-12 hours (Url. 1.). After a tow of normally several hours duration, the net is hauled using powerful winches until the wings of the net are alongside the boat. The sheet end of the net is then brought alongside the boat, by means of a choking rope, the codend is lifted onboard using the lifting derrick and the fish are landed on deck (Power, 1998). The type of fishing vessels that use bottom trawls range in size from small, undecked boats, powered by outboard engines, up to large vessels with up to 8000 HP engines and weigh up to 3000 gross tonnes (Url. 1.).



Figure 7. Generalised diagram of bottom trawl with otter boards, towing warps, and codend. (Drawing courtesey of FAO)

2.0:3 Laboratory dissection

The megrim were defrosted overnight before dissection could begin. The examination of the fish began by recording morphometric parameters as presented in Fig. 8. below. Total length (TL) and standard length (SL) for each fish was measured to the nearest millimetre below. The body width (BW) was recorded by using a vernier calipers and measuring the width of the fish at a point on the lateral line where the bend in the line begins (Fig. 8.). This ensured that the body width was consistently measured at the same point with each individual megrim. Each fish was surface dried and weighed to the nearest gram on a AND FA-2000® top pan electronic balance. The fish were sexed by macroscopic examination of the gonads in situ. At this point the otoliths were removed from the head of the megrim. An incision was made across the head of the fish on the right hand side which exposed the pair of otoliths (Plate 2.). They could then be removed using a forceps and were immersed in water to remove surrounding membranes, cleaned and stored dry. The purpose of cleaning is to assist in the later ageing of the otolith. If the membranes are left on the otoliths, they harden and dry, and obscure the otolith surface making accurate age determination difficult. The otoliths were initially stored in paper envelopes which proved unsatisfactory until appropriate otolith boxes were obtained. These boxes were found to be extremely successful as otoliths could be stored quickly, easily recovered for ageing and most importantly, safely secured. The reproductive organs or gonads were then dissected and removed for further analyses.

The meristic and morphometric characteristics of megrim was examined *(see Appendix II)*, by determining the number of fin rays, vertebra and gill rakers as well as the body measurements of the fish (Fig. 8.). One hundred fish were examined in this manner, providing the first study of this nature for megrim in Ireland.



Figure 8. Drawing of the common megrim Lepidorhombus whiffiagonis. (Redrawn from Wheeler, 1969)



Plate 2. Pair of sagittal otoliths removed from the head of a 3 year old female L. whiffiagonis, measuring 23.9cm TL, caught in February 2001. Incision for otolith removal is visible just above the otoliths.

CHAPTER TWO: PART 2. GROWTH MATERIALS AND METHODS

2.1 General introduction

Otoliths or earstones are hard calcareous structures in the heads of teleosts or bony fishes and function as organs of balance. Although there are three pairs of otoliths altogether in each fish, only one pair are large enough to be of use in age determination. This pair is known as the sagittal otoliths.

Otoliths are composed of calcium carbonate crystals embedded in an organic matrix. The organic material consists of layers of concentric shells. Opaque zones (light rings) are laid down during summer, and translucent / hyaline (dark rings) are formed during the winter months. Translucent zones appear dark and opaque zones light when viewed by reflected light against a black background (Caillet *et al.* 1986).



Plate 3. Close up of a sagittal otolith from a 6 year old female *L. whiffiagonis*, measuring 33.4cm TL, caught in September 1997. Annual growth bands as indicated by the yellow points are clearly visible.

2.1:1 Age determination

Age readings were taken by examining the otoliths under a Leica Zoom 2000[®] stereoscopic microscope, using reflected light against a black background with the whole otoliths laid flat and immersed in water. Water was used as the immersion medium for all ageing throughout the study. Leaving the otoliths to soak for several hours prior to ageing lessened the difficulty in ageing the larger otoliths. These

represented older fish and had normally more concentric rings present. The otoliths were placed in a glass petri dish before age determination could begin and the latter filled to three quarters level with water. Magnifications ranging from 3x to 10x were used on the stereoscopic microscope. When viewed under a low magnification, a series of successive concentric opaque and hyaline bands were noted radiating out to the otolith edge. Age was determined by counting the number of hyaline bands.



Plate 4. Pair of sagittal otoliths from a 3 year old female *L. whiffiagonis*, measuring 28.8cm TL, caught in September 1997. Annual growth bands indicated by yellow points, otolith nucleus indicated by red point.

Though both the opaque and translucent zones are used as annual marks, a completed annual ring is often defined as the interface between an inner translucent and outer opaque zone. As the new opaque zone is just being formed, it can be quite difficult to see. This could lead to it being overlooked, and the fish assigned to an incorrect year class. For this reason, an agreed birth date is often given for a species. This date generally coincides with the period when an annual band is formed. January 1st is widely used for flatfish species and was taken by this study as the notional birth date for megrim (Williams & Bedford, 1974).





2.1:2 Otolith marginal edge examination

The outer or marginal edges of all otoliths obtained were examined and determined either to be opaque or translucent. This was carried out by examining the otoliths under a Leica Zoom $2000^{\text{(B)}}$ stereoscopic microscope as in the manner used for age determination. As each seasonal band is laid down, *i.e.* an opaque band during the summer and a translucent band during the winter, the edge of the otolith changes from light to dark respectively. The percentage of opaque versus translucent marginal edges in each month's sample can be plotted against time. The resulting plot (see Figs. 31e. & f.) confirmed the theory that opaque zones are formed during the summer and that translucent zones are laid down during the winter months, thus presenting an annual growth cycle for megrim.

2.1:3 Otolith length measurements

The lengths of the removed otoliths were measured to examine the relationships between otolith length, and fish length and age. Each pair of sagittal otoliths were measured along their longest axis using a vernier calipers and the length measurement recorded. In instances of where one of the pair of otoliths were broken, only one length measurement was obtained. The mean length was then calculated for each pair of otoliths. The relationship between the total length (TL) of the fish and mean otolith length was determined, as well as the relationship between the age of the fish and mean otolith length. The relationship between the mean pair of otoliths was also determined, and the mean otolith length frequency distribution calculated.

2.1:4 Age frequency distributions

Age frequency distributions were constructed for the fish sampled in this investigation. The total number of fish present in each age class was determined, and the percentages present were then plotted in a histogram or frequency distribution. This was carried out for all male and female fish combined, as well as for males and females separately from the years 1997, 1998 and 1999. Finally, age frequency distributions were calculated for female fish only, from the months of January, February, April, October and November from each of the years investigated. These selected months were present in each of the consecutive years examined. No male fish were included in this monthly examination of age frequencies as too few were present in the monthly samples. From these age frequencies, it was possible to carry out both monthly and annual comparisons in age frequency.

2.1:5 Length frequency distributions

Length frequency distributions were calculated in a similar manner to that of the age frequencies. They were also determined for the same samples of fish as those used in the age frequencies. This allowed comparisons in length frequency distributions on a monthly basis as well as annually, for the species.

2.1:6 Length and weight regressions

The length-weight relationship represented by the formula $W = a.TL^b$ was log transformed to : $log_e a + b(log_e TL)$ where W = weight in grams and TL = total length in cm, and where b is an exponent with a value nearly always between 2 and 4, and often close to 3 (Ricker, 1971). The value of b = 3 indicates that the fish grows isometrically while values other than 3 indicate allometric growth : if b > 3, the fish becomes "heavier for its length" as it grows larger (Ricker, 1971). The variance (S^2) of the slope (b) was calculated using the equation of King (1995). The relationship between total length (TL) and standard length (SL) was also examined.

2.1:7 Catch curve construction

Catch curves were constructed for the all fish combined, and for female fish from 1997, 1998 and 1999. They were not calculated for male fish from these years as

too few males were present in the samples. A plot of the \log_e of numbers against ages was constructed resulting in a dome-shaped curve. The latter is commonly referred to as a catch curve (Gulland, 1985). From these catch curves a value of t_r was obtained. T_r or age of full recruitment corresponds to the age at which the fish theoretically enter the fishery or become fully susceptible to the fishing gear.

2.1:8 Mortality determination

The mortality co-efficients of Z (total mortality), M (natural mortality) and F (fishing mortality) as well as S (survivorship) were calculated for L. whiffiagonis. From the previously calculated catch curves, it was possible to estimate some of these mortality co-efficients. Since the age group representing the peak of the dome may or may not be totally vulnerable to the fishing gear, the portion of the descending leg used to estimate Z (the mortality co-efficient) is shifted one age group to the right of the dome (Gulland, 1985). From the catch curve, Z (the mortality co-efficient) was obtained. From this estimate of Z, a value for survivorship (S) was calculated using the following equation:

 $e^{(-Z)}$,

where e is the exponential function, and Z the value of total mortality. Natural mortality (M) was calculated by using the following equation:

-Ln (0.01)/ maximum age,

where maximum age corresponds to the oldest fish recorded in the sample. This equation follows the theory that natural mortality (M) is the mortality rate that reduces an unexploited cohort to 1% of its initial size over an entire lifetime. Fishing mortality (F) was determined by taking the value obtained for natural mortality (M) from the value calculated for Z, *i.e.* Z = M + F.

2.1:9 Growth determination

Growth calculations were carried out using several different methods, *i.e.* that of Rafail (1973), Ford (1933) Walford (1946) and Gulland-Holt (1959). Growth was determined for the total number of females and males separately, the total number of females and males combined, and finally for females only from the years 1997, 1998 and 1999. There were an insufficient number of male fish to determine growth for the above years separately. These were used to construct a Von Bertalanffy (1938) growth curve which is represented as $Lt = L\infty(1 - e^{-k(t-t_0)})$, where $L\infty$ is the maximum size that the fish would achieve if unaffected by fishing effort, predation,
disease and natural mortality; k is the rate at which the fish reaches the limiting size, and t_0 the age at which the fish is theoretically 0mm long. The mean lengths at age were determined for overall female and male fish separately, combined and from the years 1997, 1998 and 1999.

2.1:9:1 Rafail (1973) growth method

The first method of growth determination used to determine VBGPs (Von Bertalanffy growth parameters), was that of Rafail (1973) which entailed a simple and precise method for fitting a Von Bertalanffy (1938) growth curve. Using the mean lengths at age for the fish, the annual increments in growth or increase in length over the following year were obtained. The log_e of these annual increments were plotted against the age mid-points. The resulting slope gave a first estimate of K. Following this, the value for K could be used in the following equation :

$$L\infty = \frac{e^k \sum Lt - \sum Lt}{(n-1)(e^k - 1)},$$

to determine a first estimate of $L\infty$. This first estimate was then used in the equation :

$$Log_e(1-Lt/L\infty),$$

and plotted on a second graph against ages in years. The resulting slope gave a second and more accurate estimate of K. This new K value was then substituted into the equation for $L\infty$ to get a second and more accurate estimate of $L\infty$. The age at which the fish were theoretically 0mm in length (t₀) was determined by using the second estimate of K in the following equation:

$$t_0 = \frac{y - \text{int}\, ercept}{k}.$$

2.1:9:2 Gulland-Holt (1959) growth method

The VBGPs were also calculated using the method of Gulland-Holt (1949). The growth rate or annual increment were plotted against the median length of the fish. This gave $L\infty$ as the x-intercept and the slope as $1-e^{-k}$. This is presented in the following equation :

$$\Delta L / \Delta t = a + b L_{med}.$$

As the growth rate decreases with length, this plot has a negative slope b, which is used to estimate the parameter K. The intercept on the x-axis where growth is zero, is an estimate of L^{∞} and may be calculated as the negative of the y-axis intercept a, divided by the slope (King, 1995). The parameters of L^{∞} and K come from using the slope and intercept from the linear regression of the variables in the following way: $L\infty = -a/b$ and K = -b. Values for t₀ were calculated by use of the following equation from King (1995):

$$t_0 = t + (1/k)(Ln((L_{\infty} - Lt)/L_{\infty}))$$

2.1:9:3 Ford-Walford (1946) growth method

Finally, the VBGPs were determined by using the method of Ford-Walford. This plot is one of the simplest methods of estimating the parameters of the Von Bertalanffy (1938) equation. The Ford-Walford equation is of a linear form, and suggests that length at age $t(L_t)$ can be plotted against length at one year later (L_{t+1}) . The straight line fitting this data had a slope of $b = exp^{-k}$ and an intercept on the y-axis of $a = L\infty (1-exp^{-k})$. These were manipulated to estimate K and $L\infty$ as: $K = -\ln[b]$, $L\infty = a/(1-b)$. The Ford-Walford equation can be written as:

$$L_{((+\Delta)} = a + bL_t L_{(t+\Delta)}$$
 with $a = L \infty (1-b)$ and $b = e^{(-k\Delta t)}$.

The remaining parameter in the Von Bertalanffy (1938) growth equation t_0 , can only be estimated if length at a particular age is known (King, 1995). t_0 was estimated by using the following equation:

$$t_0 = \frac{y - \operatorname{int} ercept - \log_e L_{\infty}}{k}$$

2.1:9:4 Von Bertalanffy (1938) growth curves

Von Bertalanffy (1938) growth curves were determined for the total numbers of female and male fish separately, and females and males combined. They were also determined for female fish caught during 1997, 1998 and 1999. There were too few males present in the samples from these years to calculate growth curves separately for male fish. The growth curves were calculated by entering the Von Bertalanffy (1938) growth parameters of L ∞ , K and t₀ as obtained by using the growth methods of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946), into the Von Bertalanffy (1938) growth equation of :

$$Lt = L\infty(1 - e^{-k(t-t_0)}) ,$$

and substituting the value of t with the theoretical ages *i.e.* 1, 2, 3 *etc.* Once the lengths at each theoretical age were calculated, these were fitted over the data from which these curves were obtained. This provided growth curves for each of the groups

examined, females and males separately, combined, and females from 1997, 1998 and 1999.

2.1:10 Yield per recruit models

The yield per recruit can be defined as the estimated fishery yield from a given recruiting year class, once knowing growth rates, natural mortality and age at recruitment of a particular fish stock. The Beverton-Holt (1957) yield per recruit model used in this investigation was estimated using the following equation:

$$Y = \sum_{t_c}^{t_{\text{max}}} F_t N_t W_t$$

where t_c = age at first capture, t_{max} = maximum age of the cohort, F = instantaneous rate of fishing mortality, N = the number of individuals alive and W = the mean weights at age. The total yield per recruit for females overall, males overall, female and male fish combined, and for females from 1997, 1998 and 1999 was then calculated using the above equation for different values of F, the instantaneous coefficient of fishing mortality *i.e.* for F = 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2 and 1.4. From these, it was then possible to determine the optimum exploitation or fishing mortality level for each population group examined.

CHAPTER TWO : PART 3. REPRODUCTIVE METHODS AND MATERIALS

2.2 General introduction

The paired reproductive organs or gonads were dissected from the fish by cutting the surrounding membranes and connective tissue, and gently lifting the entire gonad from the reproductive cavity (*Plate 6.*).



Plate 6. Stage IV (pre-spawning & spawning) ovary in the gonadal cavity of a 4 year old female *L. whiffiagonis*, measuring 25.4cm TL.

2.2:1 Sex ratio determination

The gonads were sexed macroscopically and determined to be male (testis) or female (ovaries). The sex ratio for *L. whiffiagonis* was then calculated using the Chi square equation as follows:

$$\chi^{2} = \frac{(Observed - Expected)^{2}}{Expected} + \frac{(Observed - Expected)^{2}}{Expected}$$

The sex ratio was determined for female and male fish overall, as well as at varying length classes of <24.99cm TL, 25-34.99cm TL, 35-44.99cm TL and finally >45cm TL.

2.2:2 Macroscopic maturity assessment

The gonad was weighed on a top-pan electronic balance and the weight recorded to the nearest 0.1g. The colour of the gonad was noted and a macroscopic assessment of the maturity stage made (Tables 1. & 2.) (*Plates 7-12.*). The maturity stage of the ovaries and testes of the fish, refers to the degree of ripeness or how close an individual is to spawning (Caillet *et al.* 1986). These were described as follows:

Table 1. Male macroscopic maturity stages and maturity assessment.

Maturity stages for males	Description of Testes
Stage I (immature or virgin)	Testis very small (<3mm), tight against back of gut cavity, creamy white in colour, stringy in appearance, difficult to remove from fish.
Stage II (in maturation or resting)	Testis are roughly half full, creamy white in colour, gonad still small (<1cm), all sperm from ducts re-absorbed.
Stage III (mature)	Testis are full but not running under moderate pressure, creamy white in colour, gonad increasing in size(<1.5 cm).
Stage IV (pre-spawning & spawning)	Sperm can be extruded from the gonad with light pressure, creamy white in colour, testis at largest size (<2cm).
Stage V (post-spawning or spent)	Testis flabby in appearance, often red in places, little sperm left, creamy white colour, gonad size decreases (<1cm).



Plate 7. Testis from a Stage IV (pre-spawning & spawning) male L. whiffiagonis, measuring 25.4cm TL and aged at 6 years old.

Image of Ovary	Description of Ovary
	Stage I (immature or virgin) Ovaries very small, yellowish-orange in colour,
5 B	<4cm down the side of the body, gonad opaque.
and the second	Pictured ovary from a Stage I (immature or virgin)
7.415-2.	female L. whiffiagonis, measuring 25.0cm TL and aged at 3 years old.
1-11-1	Scale 30mm.
	Stage II (in maturation or resting)
	visible. >4cm down the side of the body, ovary
-	wall thin, gonad opaque.
	Pictured ovary from a Stage II (in maturation or
the second se	resting) female L. whiffiagonis, measuring 26.1cm TL and aged at 4 years old
and the second se	
The second s	Scale 30mm. Stage III (mature)
	Ovaries filling with eggs, generally about $\frac{1}{2}$ to $\frac{3}{4}$
and the second	the length of a full ovary, pinkish in colour, eggs
1 per	visible and opaque in appearance.
1 1 5 1 1 1 1	Pictured ovary from a Stage III (mature) female L.
	whiffiagonis, measuring 26.5cm TL and aged at 3
Strat	years one.
	Scale 30mm. Stage IV (pre-spawning & spawning)
and the second second	Ovaries full with eggs, body distended, eggs
	easily extruded under light pressure, ovary
A MARTINE CONTRACTOR	pinkish/grey in colour, eggs are translucent.
	Pictured ovary from a Stage IV (pre-spawning &
2000	TL and aged at 4 years old.
	Scale 30mm.
	Stage V (post-spawning or spent)
and the second second	Few eggs remaining, gonad stringy in
the second second	appearance, much slime in the ovaries, remaining
5	obe opuque, principin Brey obtour.
	Pictured ovary from a Stage V (post-spawning or
FR	spenij jemale L. wnijjlagonis, measuring 50.4cm IL and aged at 7 years old.
S Straw	Scale 30mm

Table 2. &	Plates 8-12.	Female macroscopic maturity stages.

The entire male gonad and a predetermined portion of the female gonad were then placed in a labelled universal of Bouin's fixative, for later histological examination. It was important to make the gross cut in approximately the same place on each gonad in order to maintain some consistency. An extra portion of the ovary was also removed from pre-spawning (Stage IV) female fish for fecundity studies and frozen at -18°C, pending further investigation. Only one male maturity photograph was obtained, that of a Stage IV (pre-spawning & spawning) as presented in *Plate 7*. above. This was due to a lack of male fish present in the samples.

2.2:3 Maturity ogive determination

Maturity ogives were constructed for female and male fish. These provided an estimate of first maturity at age and at length for L. whiffiagonis. From these maturity ogives, estimates of L25%, L50% and L75% as well as A25%, A50% and A75% were calculated for fish examined macroscopically and histologically. These values represent the lengths and ages at which 25%, 50% and 75% of the examined population are sexually mature respectively. In order to construct the maturity ogives, a definition of "mature" was required. It was decided to use the definitions used by previous studies of megrim maturity elsewhere, primarily those of Santurtun et al. (1998a) and Anon. (2001a), which stated that both macroscopic and histological Stages II - V were mature, whilst Stage I was defined as immature. By using data from the calculated maturity at length and age keys (Tables 25a-d. & 26a-d.) for female and male fish, the number of mature fish in each length and age class was determined. This number of mature fish was plotted as a percentage of the total number of individuals present, versus either length or age depending on which type of maturity ogive was being constructed. From the resulting plots, estimates of $L_{25\%}$, $L_{50\%}$ and $L_{75\%}$, and $A_{25\%},\,A_{50\%}$ and $A_{75\%}$ could be read from the x-axis.

2.3 Histology

The tissues were processed using standard histological procedures for wax histology (Bancroft & Stevens, 1977) and detailed as follows:

2.3:1 Fixation

The entire gonad was left in Bouin's fixative for 24 to 48 hours, before being preserved in 70% alcohol. The gonad can be left in this medium indefinitely until histological processing can begin. Thirty ovaries were randomly selected from each of the monthly samples while all male gonads in the samples were used for histological examination. A gross cut (5mm section) from the gonad was made and placed in a labelled tissue cassette. In this study gross cuts were made midway along the gonad length (*Plate 13.*). Labelling of the tissue cassette was made in pencil using a unique number for each section removed. The labelled cassettes were then stored in a container of 70% alcohol until processing could begin.



Plate 13. A Stage IV (pre-spawning & spawning) ovary from female L. whiffiagonis showing the 5mm thick histological gross cut midway down the gonad length. This female measured 27.4cm TL and was aged 5 years old. Gonad weight was 6.41g.

2.3:2 Processing

Processing was carried out at the histology laboratory of the Martin Ryan Marine Science Institute, National University of Ireland, Galway. The tissue cassettes were placed in a Shandon Citadel 2000[®] processor (*Plate 14.*) for a 24 hour period. Program A was used. This involved the tissue undergoing dehydration (approx. 8 hours and 40 minutes), clearing (8 hours) and impregnation (6 hours) as outlined in Table 3. below.

Vat	Program A	Processor Stages	Time
1	70% alcohol	(dehydration)	10 minutes
2	80% alcohol	(dehydration)	2 hours
3	90% alcohol	(dehydration)	2 hours
4	Absolute alcohol	(dehydration)	2 hours
5	Absolute alcohol	(dehydration)	2 hours
6	Absolute alcohol	(dehydration)	30 minutes
7	Mixture of absolute alcohol & H	istoclear II [®] (1:1 mix) (clearing)	2 hours
8	Histoclear II®	(clearing)	2 hours
9	Histoclear II®	(clearing)	2 hours
10	Histoclear II [®]	(clearing)	2 hours
11	Paraffin wax	(impregnation)	3 hours
12	Paraffin wax	(impregnation)	3 hours

Table 3. Histological processing stages of L. whiffiagonis gonads in processor.



Plate 14. Shandon Citadel 2000[®] processor used for histological tissue processing.

2.3:3 Dehydration

Dehydration involves the removal of water from the tissue and replacing it with alcohol. A series of graded alcohols was used. This prevented shrinkage of the tissue (caused by rapid dehydration). Following dehydration, the tissue underwent clearing or removal of the alcohol.

2.3:4 Clearing

The tissue was placed in several changes of a solvent or clearing agent. This solvent (Histoclear II^{\oplus}) is miscible with the paraffin wax which is the embedding medium. When the clearing was complete, the tissue underwent impregnation which involved placing the tissue in molten paraffin wax at 58°C. The impregnated tissue was then left in the molten wax in the processor until embedding could begin following the 24 hour period of processing.

Before embedding was carried out, the tissue cassettes were placed in a Gallenkamp[®] vacuum oven (*Plate 15.*) and brought up to a pressure of 600mm Hg for 30 minutes. This was to ensure that the tissue was fully impregnated with the paraffin wax.



Plate 15. Gallenkamp[®] vacuum oven used to fully impregnate tissue samples with paraffin wax at 600mm Hg for 30 minutes.

2.3:5 Embedding

Embedding was carried out on a Shandon Histocentre[®] (*Plate 16.*) and involved the tissue being embedded in a wax block. This was done by opening the cassette and placing the tissue in a metal mould together with molten wax and placing the tissue cassette on top. Molten wax was poured on top of the mould and allowed to solidify. The moulds were placed upon the cold plate of the embedding centre to harden. Once fully cooled, the moulds were removed and the wax blocks with tissue were stored. Before sectioning could take place, all of the wax blocks had to be cleaned. This was in order to remove excess wax from around the block which would foul the microtome and obscure the number on the cassette.



Plate 16. Shandon Histocentre[®] used to block out the tissue cassettes into wax moulds.

2.3:6 Sectioning

Sectioning was carried out on a Leica Jung RM2025[®] rotary microtome (*Plate* 17.). Each wax block containing the piece of gonadal tissue was attached to the microtome and sections of 5µm in thickness were cut. Tissues that were difficult to section were cut at a greater thickness, approximately 5-9µm. From each gonad, 3 sections or ribbons of tissue were taken, 1 was later stained while the other 2 were stored. The sections were floated out in a waterbath set at 45°C where any creases present in the section were removed. The sections were mounted on glass slides and secured using a BDH Gurr[®] glycerin albumen adhesive. The slides were then left to fully dry (on the waterbath sides) for approximately 30 minutes and then stored before undergoing staining.



Plate 17. Leica Jung RM2025[®] rotary microtome used to section gonadal tissue at approximately 5-8µm in thickness.

2.3:7 Staining

A Shandon Linistain GLX[®] (*Plate 18.*) was used to stain all slides. The tissues were stained using haematoxylin and eosin. Haematoxylin stains nuclei, cartilage and RNA blue, while eosin is a counterstain, staining only those structures not stained by the haematoxylin (Bancroft & Stevens, 1977). The chemicals used for the staining process are presented in Table 4. below. Directly following staining, a glass coverslip was mounted onto the slides using DPX[®], a recognised mountant for microscopy. This permanently preserves and protects the tissue and seals the slide indefinitely. The completed slides were left flat for several days in order to allow the DPX[®] to harden.



Plate 18. Shandon Linistain GLX[®] stainer used to stain the sectioned gonadal tissue with a haemotoxlylin and cosin stain.

Vat Number	Chemical Stage	Time in Vat
1	Histoclear II [®]	1 minute
2	Histoclear II [®]	1 minute
3	Histoclear II [®]	1 minute
4	Histoclear II®	1 minute
5	Absolute alcohol	1 minute
6	90% alcohol	1 minute
7	70% alcohol	1 minute
8	Distilled water	30 seconds
9	Haemotoxylin stain	1 minute
10	Haemotoxylin stain	1 minute
11	Haemotoxylin stain	1 minute
12	Haemotoxylin stain	1 minute
13	Distilled water	30 seconds
14	Distilled water	30 seconds
15	Tap water	2 minutes
16	Tap water	2 minutes
17	Tap water	2 minutes
18	Eosin stain	1 minute
19	Distilled water	30 seconds
20	70% alcohol	1 minute
21	90% alcohol	1 minute
22	Absolute alcohol	1 minute
23	Absolute alcohol	1 minute
24	Histoclear II®	2 minutes
25	Histoclear II [®]	2 minutes
26	Histoclear II®	2 minutes
27	Histoclear II [®]	2 minutes

A MOTO IL CHARTONIO GOOG LOI GLOUND DAMINING AN AND AN AND AN AND AN AND AN AND AN AND AND
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2.3:8 Histological maturity assessments

An Olympus CH-2[®] compound microscope was used to examine the prepared sections of gonads and to determine the histological maturity stages. This was carried out as a validation of the macroscopic maturity stages described earlier. Within the gonads, various developmental characteristics of oogensis and spermatogensis were observed and recorded, and used to determine the respective maturity stage. These are described for female and male fish in Tables 5. & 6. and *Plates 19-23. & 24-28.* respectively, as presented below.

Stage I (inmature or virgin) Mainly oogonia, chromatin nucleolus stage with Imm Pictured ovary from a Stage I (immature or virgin) female L. whiffiagonis, measuring 24.0cm TL and aged at 3 years old. Stage II (in maturation or resting) Oogonia, chromatin nucleolus stage, carly perinucleolar stage, lumen, early vitellogensis. Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage II (inmature) Oogonia, carly nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage II (indure) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage III (mature) Oogonia, carly nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage II (indure) female L. whiffiagonis, measuring 36.4 cm TL and aged at 8 years old. Scale Imm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, occyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning 28.0 cm TL and aged at 3 years old. Scale Imm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory foolicles, follicular atresia and atretic occytes.<	Image of Ovary	Description of Ovary
Pictured ovary from a Stage 1 (immature or virgin) female L. whiffiagonis, measuring 24.0cm TL and aged at 3 years old. Scale Imm. Stage II (in maturation or resting) Oogonia, chromatin nucleolus stage, early perinucleolar stage, lumen, early vitellogensis. Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 26.4cm TL and aged at 8 years old. Scale Imm. Stage I Imm Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenia oncytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenia and other immature stages, present, vitellogenia oncytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Oogonia, chromatin nucleolus stage, lumen, post-owulatory follicles, follicular atresia and atretic oocytes. Stage V (post-spawning or spent) Oogonia, TL and aged at 4 years old. Scale Imm.		Stage I (immature or virgin) Mainly oogonia, chromatin nucleolus stage with lumen.
Time Scale Imm. Stage II (in maturation or resting) Oogonia, chromatin nucleolus stage, early perinucleolar stage, lumen, early vitellogensis. Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage III (mature) Oogonia, early nucleous migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale Imm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old. Scale Imm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory form a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory form a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory form a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 33.3cm TL and aged at 4 years old.		Pictured ovary from a Stage I (immature or virgin) female L. whiffiagonis, measuring 24.0cm TL and aged at 3 years old.
Stage II (in maturation or resting) Oogonia, chromatin nucleolus stage, early perinucleolar stage, lumen, early vitellogensis. Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale Imm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Oogonia, ehromatin nucleolus stage, lumen, post-ovulatory folicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage IV (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent)	1 mm	Scale 1mm.
Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old. Scale Imm. Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale Imm. Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale Imm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) 28.0cm TL and aged at 3 years old. Scale Imm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale Imm.		Stage II (in maturation or resting) Oogonia, chromatin nucleolus stage, early perinucleolar stage, lumen, early vitellogensis.
Scale Imm. Stage III (mature) Oogonia, carly nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale Imm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old.		Pictured ovary from a Stage II (in maturation or resting) female L. whiffiagonis, measuring 27.8 cm TL and aged at 4 years old.
Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis, measuring 36.4cm TL and aged at 8 years old. Scale 1mm. Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic occytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic occytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) Scale 1mm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale 1mm.	- 1 mm	Scale 1mm.
Image: Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen. Pictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old. Scale Imm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale Imm.		Stage III (mature) Oogonia, early nucleus migration, vitellogensis, lumen, perinucleolar stage oocytes. Pictured ovary from a Stage III (mature) female L. whiffiagonis measuring 36 4cm TL and aged
Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen.Pictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old.Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 23.3cm TL and aged at 4 years old.Stage Imm.		at 8 years old. Scale 1mm.
ImmPictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old.Scale 1mm.Stage V (post-spawning or spent)Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale 1mm.		Stage IV (pre-spawning & spawning) Oogonia and other immature stages present, vitellogenic oocytes, migratory nucleus stage, oocyte hydration, lumen.
Scale 1mm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale 1mm.	1.mm	Pictured ovary from a Stage IV (pre-spawning & spawning) female L. whiffiagonis, measuring 28.0cm TL and aged at 3 years old.
A man		Scale 1mm. Stage V (post-spawning or spent) Oogonia, chromatin nucleolus stage, lumen, post-ovulatory follicles, follicular atresia and atretic oocytes. Pictured ovary from a Stage V (post-spawning or spent) female L. whiffiagonis, measuring 32.3cm TL and aged at 4 years old. Scale 1mm.

Table 5. & Plates 19-23. Female histological maturity stages.

Image of Testis	Description of Testis		
	Stage I (immature or virgin) Spermatogonia, with spermatocyte present, spermatozoids absent.		
	Pictured testes from a Stage I (immature or virgin) male L. whiffiagonis, measuring 28.0cm TL and aged at 4 years old.		
500 µm	Scale 500µm.		
	Stage II (in maturation or resting) Spermatogonia and spermatocyte present, few spermatozoids.		
	Pictured testes from a Stage II (in maturation or resting) male L. whiffiagonis, measuring 28.8cm TL and aged at 4 years old.		
1 mm	- Scale 1mm.		
	Stage III (mature) Spermatozoids predominant, spermatogonia and spermatocyte present only in the testis cortex.		
1 mm	Pictured testes from a Stage III (mature) male L. whiffiagonis, measuring 27.3cm TL and aged at 5 years old.		
1 4-8-184 VI.S. VI.S.	Scale 1mm. Stage IV (pre-spawning & spawning)		
	Spermatozoids predominant, very few spermatogonia.		
	Pictured testes from a Stage IV (pre-spawning or spawning) male L. whiffiagonis, measuring 25.0cm TL and aged at 4 years old.		
500 µm	Scale 500µm.		
	Stage V (post-spawning or spent)Emptyseminiferalducts,residualspermatozoids and few spermatogonia.		
	Pictured testes from a Stage V (post-spawning or spent) male L. whiffiagonis, measuring 31.9cm TL and aged at 6 years old.		
500 µm	Scale 500µm.		

Table 6. & Plates 24-28. Male histological maturity stages.

2.3:9 Oocyte dynamics

Image analysis was carried out using an Olympus CX41[®] compound microscope connected to a digital camera, an Olympus Camedia C-3040 Zoom[®], and the analySIS[®] 3.1 software package. Oocyte dynamics were determined on the prepared histological slides for female fish only, using of image analysis. Dynamics consisted of oocyte length measurements and determining an estimation of atresia.

For the oocyte length measurements, 5 slides of ovaries from each of the 5 maturity stages were examined. Using the image analysis software, a still image from each maturity stage was captured and 100 oocytes measured along their longest axis. Only oocytes with nuclei present were measured, *i.e.* to ensure that maximum oocyte diameters was recorded. Microscopic magnifications ranging from 40x to 400x were used depending on the image being examined. A total of 2,500 oocytes were measured and presented as percentage oocyte length frequency distributions.

From the slides, the incidence of atresia were recorded. This occurs when oocytes abort development and fail to be spawned from the ovary, and are reabsorbed back into the gonad. Atresia is important as it affects the estimated spawning potential of the stock (Witthames, 2000). As atresia goes through several phases, *i.e.* alpha (α) and beta (β), the occurrence of both types were counted for atresia estimation. Two estimates of atresia were carried out, the prevalence of atresia (Pa), defined as the proportion of females observed with atretic oocytes divided by the total number of normal and atretic vitellogenic oocytes in an individual female gonad when Pa > 0 (Kurita *et al.* 2003).

Ovaries from maturity Stage V (post-spawning or spent) fish were examined for the prevalence of atresia (Pa) by examining all prepared slides and noting the presence or absence of atretic oocytes in relation to the total number of fish in these maturity stages. The relative intensity of atresia (Ia) was determined by recording the amount of atretic oocytes in each ovary in relation to all oocytes present, both normal and atretic. This was carried out by examining individual Stage V females and capturing still images from several fields of view at 100x magnification. The number of fields of view ranged from 3 to 4, depending on the size of the particular ovary, so as to cover as large an area of the gonad as possible. All oocytes, both vitellogenic and atretic were counted, and the number of atretic oocytes calculated in proportion to the number of vitellogenic oocytes present.

2.4 Gonadosomatic Index

The gonadosomatic index (GSI) was calculated as follows:

$$GSI = \frac{W_{gon}}{W} * 100,$$

where W_{gon} = gonad weight in grams and W = weight of the fish in grams (Htun Han, 1978). The GSI is the percentage of the fish's total body weight that is composed of gonad. This percentage increases as the fish nears spawning time and drops off dramatically following spawning. From this, the period of spawning for the species can be determined (King, 1994).

2.5 Condition factor

The condition factor (CF) was calculated from the monthly samples, with female and male fish being combined. As with the gonadosomatic index, the sexes were not separated due to an absence of males from certain sampled months. The equation of $CF = W(g)/TL(cm)^3$, where W = weight in grams and TL = total length in centimetres, was used to determine the condition factor (Fulton, 1911).

2.6 Fecundity

Fecundity was carried out on Stage IV (pre-spawning) ovaries only. This maturity stage was used as the formation of the eggs was complete, but none had been delivered or spawned. This was confirmed by the absence of clear or hydrated eggs in the ovaries. Following defrosting at -18° C, a subsample of 0.5g was removed and weighed from the gonad and placed in a labelled universal of Gilson's Fluid, which was used to dissolve the membranes between the eggs so they could be counted at a later time. Gilson's Fluid is composed of equal parts of glacial acetic acid, chloroform and 60% ethanol, and does not cause overhardening of the eggs. It loosens them from the surrounding ovarian tissue, though this process may require several days to a few weeks to occur. During this period the eggs harden sufficiently to be counted effectively (Caillet *et al.* 1986). The universals were shaken vigorously at frequent intervals to ensure that the eggs were fully separated. Once the eggs were separated, the Gilson's Fluid was removed from the universals and replaced with water until counting could take place.



Plate 29. Oocytes from a Stage IV (pre-spawning) female *L. whiffiagonis* on a Sedgewick Rafter[®] counting cell. This female measured 25.7cm TL and was aged 4 years old.

Counting was carried out on a Sedgewick Rafter[®] counting cell viewed under an Olympus CH-2[®] compound microscope at 40x magnification. Due to the tedious and time consuming nature of carrying out oocyte total counts, a variant of the gravimetric subsampling method was used. This particular method was taken from Horwood et al. (1986) who used it to determine the fecundity of plaice (Pleuronectes platessa L.). The eggs to be counted were cleaned in water to remove all remnants of the Gilson's Fluid and also any debris present with the eggs. The eggs were then rinsed into a small plastic jar with pinhole perforations in its base. Excess moisture was removed by resting the jar in a plastic funnel connected to a vacuum pump via a water trap. The suction from the pump was sufficient to extract moisture without damaging the eggs. Once all the moisture was removed from the eggs, a subsample was taken and weighed on an analytical balance. This subsample was then placed on the Sedgewick Rafter[®] counting cell and the eggs counted. The total number was estimated by raising the sample weight to the total weight. Following total counts on the same samples, trials showed that the total variation due to counting and raising was approximately 3.8%. The absolute fecundity (AF) which is the number of vitellogenic oocytes in the ovary prior to spawning (Anward, 1998), was determined by counting the number of oocytes in the subsample and then calculating the overall

number present in the entire gonad. The following equation was used to calculate the absolute fecundity:

$$AF = \frac{W_{gon}}{W_{sub}} * N_{sub},$$

where W_{gon} = gonad weight in grams, W_{sub} = weight of subsample in grams and N_{sub} = numbers of eggs in subsample. Following calculation of absolute fecundity (AF), estimates of relative fecundity (RF) which is defined as the number of oocytes per kilogram of bodyweight (Anward, 1998), was determined. This was carried out by dividing 1000g by the mean ovary weights of the samples and multiplying by the mean absolute fecundity from the samples.

Oocyte diameters were taken from 5 randomly selected eggs in each fecundity sample. These were converted from eye-piece units to real measurement units and used to construct an oocyte percentage length frequency distribution. Once fecundity was determined, the relationships between fecundity (F) and total length (TL), weight (W), age (A)and gonad weight (GW) were examined and described by the following equations : $F = a.TL^b$, replacing the TL with the parameter being regressed with fecundity, *i.e.* W, A and GW. A percentage oocyte length frequency distribution was then constructed to examine oocyte lengths from each fecundity sample. Mean fecundity was also calculated for each of the three monthly fecundity samples and presented in a frequency distribution.



Plate 30. Oocytes of varying diameter from a Stage IV (pre-spawning) female L. whiffiagonis on a Sedgewick Rafter[®] counting cell. The 1mm² counting cells are clearly visible underneath the oocytes.

CHAPTER TWO : PART 4. STATISTICAL TESTS

2.7 General introduction

A range of statistical tests were carried out on the data obtained during the present investigation. These ranged from the Chi^2 statistics, analysis of variance (ANOVA), *F*-test for normality to Student's *T*-test for distribution. Other statistical methods were used to analyse data such as percentage frequency distributions, mean values, modes, standard deviation, 95% confidence intervals, and regression analysis. 2.7:1 *Analysis of variance (ANOVA)*

Analysis of variance (ANOVA) was carried out to examine if differences occurred between mean values obtained during the investigation. It was used during the determination of the mean lengths and weights at age for female and male *L. whiffiagonis* as well as to examine if differences occurred between the theoretical lengths determined following the use of the three different growth methods. The theoretical lengths calculated by use of the growth methods of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946) were tested to see if differences occurred between the methods and also between overall female and male fish, combined females and males, and female fish from 1997, 1998 and 1999. Finally, ANOVA was used to examine if differences occurred between the population groups for total yield per recruit determination.

2.7:2 F-test for normality

A series of *F*-tests were carried out between the population groups of overall female and male fish, and between females from 1997, 1998 and 1999, in order to determine if the recorded data was normally distributed. The parameters of total length and age were examined using the *F*-tests. Once it was established that the data was normally distributed, Student's *T*-test could be carried out to examine if differences existed between the population groups in terms of distribution.

2.7:3 Student's T-test for distribution

The same population groups examined for the F-tests were subjected to a Student's T-test (assuming equal variances) for distribution. This type of T-test assumes that the means of both data sets are equal and is referred to as a homoscedastic T-test (Fowler & Cohen, 1995).

Chapter Three

<u>Chapter Three : Part 1.</u> Sampling, length & weight results

Chapter Three : Part 2. Age and growth results

<u>Chapter Three : Part 3.</u> <u>Reproductive results</u>

Contents of Chapter Three : Results

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PART 1. SAMPLING, LENGTH & WEIGHT RESULTS

3.0 General introduction

During the investigation, a total of 4,964 *Lepidorhombus whiffiagonis* were examined. From this sample of fish, only one was excluded from the statistical analysis due to a missing caudal/tail fin. A summary of the months and fish sampled are presented in Table 7.

No. of Months Sampled	Year	Month	Total No. of Fish Captured	No. of Females Captured	No. of Males Captured
1	1997	April	81	65	16
2	1997	May	170	170	0
3	1997	June	50	46	4
4	1997	July	139	138	1
5	1997	August	192	190	2
6	1997	September	163	159	4
7	1997	October	235	230	5
8	1997	November	92	89	3
9	1997	December	78	78	0
10	1998	January	144	126	18
11	1998	February	187	172	15
12	1998	April	146	144	2
13	1998	October	117	113	4
14	1998	November	170	168	2
15	1998	December	279	271	8
16	1999	January	160	158	2
17	1999	February	157	154	3
18	1999	March	369	365	4
19	1999	April	531	524	7
20	1999	May	284	276	8
21	1999	June	202	198	4
22	1999	July	129	129	0
23	1999	August	161	149	12
24	1999	September	119	109	10
25	1999	October	85	84	1
26	1999	November	89	86	3
27	2000	January	98	97	1
28	2000	March	221	212	9
29	2001	February	116	113	3
Total			4964	4813	151

Table 7. Summary of months sampled and number of fish captured during investigation.

3.0:1 Samples

A total of 29 monthly samples were collected during the investigation. The number of females (Fig. 9a.) in the samples ranged from 46 fish in June 1997 to 524 in April 1999, with a mean number of 195.96 fish (\pm s.d. 97.937) per sample. The number of males (Fig. 9b.) ranged from 0 fish in May 1997, December 1997 and July 1999 to 18 fish in January 1998, with the males having a mean number of 5.20 fish (\pm s.d. 4.930) per sample.



3.0:2 Length frequencies

For all percentage length frequency distributions, male and female fish are presented separately on the same graph. The overall percentage length frequency distribution for all samples combined is shown in Fig. 10. The largest percentage of females (11.76%) was recorded within the length class of 29-29.99cm TL, while the largest percentage of males (16.5%) was found within the slightly smaller length class of 27-27.99cm TL. The largest fish recorded was a female measuring 53.2cm TL, while the largest male fish was 40.0cm TL. The smallest male and female fish measured 16.9cm TL and 15.1cm TL respectively. All specimens of greater than 40.0cm TL were female.

Percentage length frequency distributions were calculated for fish captured in years 1997, 1998 and 1999 and the results presented in Figs. 11a-c. and Table 8a. below. In 1997 (Fig. 11a.), the largest percentage (11.59%) of females occurred within the length classes of 28-28.99cm TL and 29-29.99cm TL. For males sampled during the same year, the largest percentage of fish (14.28%) was recorded in three length classes, those of 25-25.99cm TL, 28-28.99cm TL and 30-30.99cm TL. In 1998 (Fig. 11b.) the largest percentage of females (11.36%) was recorded within the length class of 28-28.99cm TL, while the largest percentage of males (20.4%) was within the length class of 26-26.99cm TL. In 1999 (Fig. 11c.) the largest percentage of female fish (13.03%) was within the length class of 29-29.99cm TL with 27.77% of males in the length class of 27-27.99cm TL.





Summary Frequencies	1997	1998	1999
Number of females captured	1164	994	2232
Number of males captured	35	49	54
Total number of fish captured	1199	1043	2286
Range in total length for females(cm)	21.2- 53.2cm	15.1-44.5cm	23.6-48.2cm
Range in total length for males (cm)	20.7- 37.5cm	16.9- 35cm	24.1-32.3cm
Mean total length and	30.98cm	30.07cm	31.22cm
standard deviation in total length for females (cm)	± 4.111cm	± 3.855cm	± 3.731cm
Mean total length and	27.96cm	26.88cm	27.70cm
standard deviation in total length for males (cm)	± 3.549cm	± 3.231cm	± 2.036cm

Table 8a.	Summary	of annual	length	frequency	<u>distributions</u>	for L	<u>, whiffiagonis</u>
for the period 1997-1999.							

Percentage length frequency distributions for female fish, and summaries for both sexes were also calculated for the same months in each of 3 consecutive years throughout the sampling period, *i.e.* January 1998, 1999 and 2000 (Figs. 12a-c, Table 8b.), February 1998, 1999 and 2001 (Figs. 13a-c, Table 8c.), April 1997, 1998 and 1999 (Figs. 14a-c, Table 8d.), October 1997, 1998 and 1999 (Figs. 15a-c, Table 8e.) and November 1997, 1998 and 1999 (Figs. 16a-c, Table 8f.).







January	1998	1999	2000
Number of females captured	126	158	97
Number of males captured	18	2	1
Range in total length for	23.5- 42.7cm	27.0-45.1cm	25.7-39.2cm
females (cm)			
Range in total length for	16.9-35.0cm	27.5-30.0cm	40.0cm
males (cm)			
Mean total length and	31.30cm	33.14cm	31.64cm
standard deviation in total	\pm 3.444cm	\pm 3.265cm	± 2.509cm
length for females (cm)			
Mean total length and	27.42cm	28.75cm	40.0cm
standard deviation in total	± 3.781cm	± 1.767cm	± 0.000 cm
length for males (cm)			
Modal percentage (%) and	16.66%	13.9%	16.49%
modal length class for females	30- 30.99cm	32-32.99cm	31-31.99cm
(cm)			32-32.99cm
			33-33.99cm

Table 8b.	Summary of	percentage	length (frequency	distributions	<u>in January</u>	
over the period 1998-2000.							

The largest percentage of females (16.66%) sampled during January 1998 (Fig. 12a.) were within the length class of 30-30.99cm TL. Males ranged from 16.9-35.0cm TL, with the largest percentage (22.22%) within the length classes of 27-27.99cm TL and 29-29.99cm TL (Table 8b.). A mean length of 31.30cm (\pm s.d. 3.44) TL was recorded for females and a mean length of 27.42cm TL for male fish (Table 8b.). Females ranged from 23.5-42.7cm TL and males from 16.9-35.0cm TL. For January 1999 (Fig. 12b.), the largest percentage of females (13.9%) were within the length class of 32-32.99cm TL. A mean length of 33.14cm (\pm s.d. 3.26) TL was recorded for female fish from this month. Female fish ranged from 27.0-45.1cm TL. For female fish sampled during January 2000 (Fig. 12c.), the largest percentage (16.49%) were recorded in the 3 modal length classes of 31-31.99cm TL, 32-32.99cm TL and 33-33.99cm TL respectively. Females ranged from 25.7-39.2cm TL and a mean length of 31.64cm (\pm s.d. 2.50) TL was obtained from fish sampled during January 2000.







February	1998	1999	2001
Number of females captured	172	154	113
Number of males captured	15	3	3
Range in total length for	21.1-41.8cm	24.5-38.9cm	23.9-39.7cm
females (cm)			
Range in total length for	22.5-29.8cm	26.2-27.5cm	25.4-27.5cm
males (cm)			
Mean total length and	27.91cm	29.59cm	28.43cm
standard deviation in total	± 2.896cm	± 2.718cm	± 3.222cm
length for females (cm)			
Mean total length and	25.07cm	26.9cm	26.56cm
standard deviation in total	± 1.802 cm	± 0.655 cm	± 1.069cm
length for males (cm)			
Modal percentage (%) and	18.6%	16.88%	21.23%
modal length class for females	26-26.99cm	28-28.99cm	27-27.99cm
(cm)	28-28.99cm		

 Table 8c.
 Summary of percentage length frequency distributions in February

 for the period 1998-2001.

The largest percentage of females (18.6%) sampled during February 1998 (Fig. 13a.) were within the length classes of 26-26.99cm TL and 28-28.99cm TL. Females ranged from 21.1-41.8cm TL and males from 22.5-29.8cm TL (Table 8c.). The largest percentage of males (26.66%) were within the length classes of 24-24.99cm TL and 25-25.99cm TL. Mean lengths of 27.91cm (\pm s.d. 2.98) TL and 25.07cm (\pm s.d. 1.80) TL were recorded for females and males respectively. For February 1999 (Fig. 13b.), the largest percentage of females (16.88%) were within the length class of 28-28.99cm TL. They ranged from 24.5-38.9cm TL and had a mean length of 29.59cm (\pm s.d. 2.71) TL. The largest percentage of females (21.23%) sampled during February 2001 (Fig. 13c.) were within the length class of 27-27.99cm TL and ranged from 23.9-39.7cm TL. A mean length of 28.43cm (\pm s.d. 3.22) TL was recorded for female fish from February 2001 (Table 8c.).







Fig. 14c. Percentage total length (TL) frequency distribution for female common megrim caught in April 1999 off the west coast of Ireland.

 20
 N= 524

 18
 16

 14
 14



April	1997	1998	1999
Number of females captured	65	144	524
Number of males captured	16	2	7
Range in total length for	24.0-45.8cm	23.0-39.1cm	23.8-48.2cm
females (cm)			
Range in total length for	24.0- 37.5cm	26.0- 30.3cm	24.1-28.8cm
males (cm)			
Mean total length and	30.72cm	28.13cm	31.62cm
standard deviation in total	± 5.324cm	± 2.880cm	± 4.488cm
length for females (cm)			
Mean total length and	28.86cm	28.15cm	27.0cm
standard deviation in total	± 3.247cm	\pm 3.040cm	± 1.840cm
length for males (cm)			
Modal percentage (%) and	15.38%	15.97%	14.09%
modal length class for females	28-28.99cm	28-28.99cm	29-29.99cm
(cm)			

Table 8d.	<u>Summary of percentage length frequency distributions in April fo</u>	or					
the period 1997-1999.							

For April 1997 (Fig. 14a.), the largest percentage of females (15.38%) were within the length class of 28-28.99cm TL. Females ranged from 24.0-45.8cm TL and males from 24.0-37.5cm TL (Table 8d.). The largest percentage of males (18.75%) were within the length class of 30-30.99cm TL. Mean lengths of 30.72cm (\pm s.d. 5.32) TL and 28.86cm (\pm s.d. 3.24) TL were recorded for female and male fish respectively for April 1997. The largest percentage of females (15.97%) from April 1998 (Fig. 14b.) were within the length class of 28-28.99cm TL. They ranged from 23.0-39.1cm TL and had a mean length of 28.13cm (\pm s.d. 2.88) TL (Table 8d.). Females from April 1999 (Fig. 14c.) ranged from 23.8-48.2cm TL and the largest percentage (14.09%) were within the length class of 29-29.99cm TL. A mean length of 31.62cm (\pm s.d. 4.48) TL was recorded for females sampled during April 1999.



Fig. 15b. Percentage total length (TL) frequency distribution for female common megrim caught in October 1998 off the west coast of Ireland.




October	1997	1998	1999
Number of females captured	230	113	84
Number of males captured	5	4	1
Range in total length for	21.2-38.8cm	25.0- 39.5cm	28.8- 42.2cm
females (cm)			
Range in total length for	23.0-28.0cm	27.0-33.2cm	31.0cm
males (cm)			
Mean total length and	27.99cm	32.59cm	33.61cm
standard deviation in total	± 2.889cm	\pm 3.048cm	± 2.634cm
length for females (cm)			
Mean total length and	26.14cm	30.22cm	31.0cm
standard deviation in total	± 2.018 cm	\pm 3.130cm	± 0.000 cm
length for males (cm)			
Modal percentage (%) and	14.78%	15.92%	19.04%
modal length class for females	28-28.99cm	33-33.99cm	32- 32.99cm
(cm)			

<u>Table 8e.</u>	Summary of	<u>percentage</u>	length	frequency	distributions	in October for
		the pe	eriod 19	997-1999 <u>.</u>		

The largest percentage of females (14.78%) sampled during October 1997 (Fig. 15a.) were within the length class of 28-28.99cm TL. They ranged from 21.2-38.8cm TL and had a mean length of 27.99cm (\pm s.d. 2.88) TL. For October 1998 (Fig. 15b.), the largest percentage of females (15.92%) were within the length class of 33-33.99cm TL. Females ranged from 25.0-39.5cm TL and had a mean length of 32.59cm (\pm s.d. 3.04) TL (Table 8e.). Females from October 1999 (Fig. 15c.) ranged from 28.8-42.2cm TL, with the largest percentage (19.04%) within the length class of 32-32.99cm TL. A mean length of 33.61cm (\pm s.d. 2.63) TL was recorded for females from October 1999 (Table 8e.).







November	1997	1998	1999
Number of females captured	89	168	86
Number of males captured	3	2	3
Range in total length for	27.7-44.8cm	15.1-40.6cm	25.0- 42.5cm
females (cm)			
Range in total length for	25.0-31.1cm	26.6-32.0cm	27.4-30.5cm
males (cm)			
Mean total length and	32.80cm	30.16cm	32.11cm
standard deviation in total	± 3.073cm	± 3.494cm	± 3.349cm
length for females (cm)			
Mean total length and	28.6cm	29.3cm	29.0cm
standard deviation in total	± 3.195cm	± 3.818cm	± 1.552cm
length for males (cm)			
Modal percentage (%) and	15.73%	14.28%	15.11%
modal length class for females	31-31.99cm	28-28.99cm	30- 30.99cm
(cm)	32-32.99cm		

<u>Table 8f.</u>	Summary o	f percentage	length free	uency	distributions	in N	ovembe	r
		for the p	eriod 1997	<u>-1999.</u>				

For females sampled during November 1997 (Fig. 16a.), the largest percentages of fish (15.73%) were within the length classes of 31-31.99cm TL and 32-32.99cm TL. They ranged from 27.7-44.8cm TL and had a mean length of 32.80cm (\pm s.d. 3.07) TL (Table 8f.). The largest percentage of females (14.28%) from November 1998 (Fig. 16b.) were within the length class of 28-28.99cm TL. Females ranged from 15.1-40.6cm TL and had a mean length of 30.16cm (\pm s.d. 3.49) TL. Finally, for November 1999 (Fig. 16c.), the largest percentage of females (15.11%) were within the length class of 30-30.99cm TL. They ranged from 25.0-42.5cm TL and had a mean length of 32.11cm (\pm s.d. 3.34) TL (Table 8f.).

3.0:3 Total length and weight regressions

The relationship between \log_e total length and \log_e body weight as presented in Fig. 17a. was highly significantly correlated (R² = 0.8686, P< 0.01). The relationship was examined for all female and male fish combined from each sample, from 1997-2001 (N= 4964). The slope of the relationship was b = 3.202. Log_ea *i.e.* the intercept of the line with the y axis was -5.781. The relationship can therefore be written as :

 $W(g) = 0.0030TL(cm)^{3.202}$

where W = weight in grams and TL = total length in centimetres. The variance (S^2) of the slope (b) is given as $S_b^2 = 0.006813$, while the 95% confidence intervals of the slope b (3.20) = ± 0.179 . As the confidence intervals for b (from 3.02 to 3.38) were greater than 3, growth was determined to be allometric for *Lepidorhombus whiffiagonis*, *i.e.* the fish becomes 'heavier for its length' as it grows larger. The relationship between log_e total length and log_e body weight for all female fish combined (Fig. 17b.) showed a highly significant correlation (R² = 0.8697, P< 0.01) and can be written as :

 $W(g) = 0.0029 TL(cm)^{3.215}$

The relationship between log_e total length and log_e body weight for all male fish combined as presented in Fig. 17c. was also highly significantly correlated ($R^2 = 0.8864$, P< 0.01). This relationship can be written as :

 $W(g) = 0.0045 TL(cm)^{3.088}$

The regression analyses for total length (TL), standard length (SL) and weight (W) are summarised in Table 9. below.



Fig. 17a. Relationship between loge total length (TL) and loge weight (W) for





Regression	No.of Females & Males	R ² value	Slope (b)	y-axis intercept
TL / SL for overall	4964	0.9865	0.8425	-0.2628
TL / SL for females	4813	0.9864	0.8418	-0.2327
TL / SL for males	151	0.9754	0.8131	0.3614
Log _e TL / log _e W overall	4964	0.8686	3.202	-5.781
Log _e TL / log _e W for females	4813	0.8697	3.215	-5.826
Log _e TL / log _e W for males	151	0.8864	3.088	-5.402

 Table 9.
 Summary of length and weight regressions for L. whiffiagonis.

3.0:4 Total length and standard length regressions

The relationship between total length (TL) and standard length (SL) shown in Fig. 18a. for females and males from all the samples combined for the entire sampling period showed a highly significant correlation ($R^2 = 0.9865$, P< 0.01). This relationship can be written as :

$$SL(cm) = 0.0026TL(cm)^{0.8425}$$

where TL and SL = total length and standard length in centimetres. The relationship between total length (TL) and standard length (SL) shown in Fig. 18b. for all female fish combined showed a highly significant correlation ($R^2 = 0.9864$, P< 0.01). The relationship can be written as :

$SL(cm) = 0.0023TL(cm)^{0.8418}$

The relationship between total length (TL) and standard length (SL) shown in Fig. 18c. for all male fish combined also showed a highly significant correlation ($R^2 = 0.9754$, P<0.01). The relationship can be written as :

$$SL(cm) = 0.0036TL(cm)^{0.8131}$$



3.0:5 Mean lengths at age

The mean total length (TL) at age was calculated for female and male fish from all samples combined (Figs. 19a. & b.), and for females and males caught during the years 1997, 1998 and 1999 (Figs. 19c-h.). A summary of mean lengths at age for *L. whiffiagonis* are shown with standard deviation and maximum and minimum lengths for each sex overall and annually, in Table 10.

Comparison of the mean lengths between female and male fish could only be carried out where an age group was common to each sex. This only ranged from 3 to 8 years of age, which was the entire recorded age range for male *L. whiffiagonis* in this investigation. Analysis of variance (ANOVA) statistical tests were carried out on the mean lengths at each age to determine if differences occur between the sexes. For female and male fish overall, and from those captured during 1997, no significant differences were observed. However, with female and male fish from 1998 and 1999, significant differences were recorded. From examination of the mean lengths in Table 10., it was observed that the mean length at each for female fish is consistently larger than that recorded for the males at the same age.

Examination of the mean lengths in Figs 19a-h. shows a steady increase in mean length as the fish grow older. However, variation occurred at the lower and upper end of the age range with mean lengths being below or above the general trend of steady increase.





Table 10.	Summary of	mean lengths at a	ge for female	e and male L.	<u>whiffiagonis</u>
			A REAL PROPERTY AND A REAL		

Age	Overall	Overall	1997	1997	1998	1998	1999	1999
Classes	Female	Male	Female	Male	Female	Male	Female	Male
(vears)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)
No. of	4609	146	1161	35	990	49	2036	50
fish								
2	25.70		24.90		*****	die bie bie bie bie	26.50	
	± 1.131		± 0.000				± 0.000	
3	26.41	22.68	25.45	23.10	26.01	24.33	27.05	
	± 2.546	± 3.466	± 2.317	± 3.394	± 2.133	± 1.814	± 1.834	
4	28.89	26.50	28.09	25.78	27.29	25.76	29.44	27.19
	± 3.608	± 2.136	± 2.725	± 2.071	± 3.002	± 2.788	± 3.049	± 1.600
5	30.61	27.58	30.37	27.92	29.48	27.35	30.98	27.50
	± 4.148	± 2.489	± 3.454	± 3.294	± 3.367	± 2.538	± 3.592	± 1,999
6	31.80	27.94	31.77	29.04	31.05	27.09	32.00	27.80
	± 4.686	± 2.270	± 4.105	± 1.954	± 3.401	±2.412	± 4.071	± 1.733
7	32.99	29.32	33.07	28.96	32.49	29.35	33.10	29.87
	± 4.714	± 3.522	± 4.258	± 4.207	± 3.932	± 3.917	± 4.078	± 2.901
8	34.54	32.25	34.28	37.50	34.42	27.00	34.81	
	± 5.064	± 7.424	± 5.060	± 0.000	± 3.721	± 0.000	± 4.768	
9	37.43		38.82		36.13		37.24	
	± 4.328		± 3.793		± 4.168		± 4.095	
10	38.20		40.60		36.67		36.61	
	± 4.919		± 6.083		± 4.005		± 2.115	
11	37.53				37.00		38.07	
	± 2.150			-	± 2.258		± 2.218	
12	43.65		42.10				45.20	
	± 2.192		± 0.000				± 0.000	
15	48.85		51.30				46.40	
	± 3.464		± 0.000				± 0.000	
16	48.30		48.30					
	± 0.000		± 0.000					
Max.	53.2	40.0	53.2	37.5	44.5	35.0	48.2	32.0
length								
Min.	15.1	16.9	21.2	20.7	15.1	16.9	23.6	24.1
length								
Anova	F-value	3.236	F-value	0.557	F-value	5.113	F-value	11.101
Tests	P-value	0.102	P-value	0.472	P-value	0.047	P-value	0.015
for	F-crit	4.964	F-crit	4.964	F-crit	4.964	F-crit	5.987
F/M	S/NS	NS	S/NS	NS	S/NS	S	S/NS	S

S= Significant.

NS= Not Significant.

3.0:6 Mean weights at age

The mean weight (W) at age was calculated for female and male fish from all samples combined (Figs. 20a. & b.), and for females and males caught during the years 1997, 1998 and 1999 (Figs. 20c-h.). A summary of mean weights at age for L. whiffiagonis are shown with standard deviation and maximum and minimum weights for each sex overall and annually, in Table 11.

As with the examination of mean lengths, comparison of the mean weights between female and male fish could only be carried out where an age group was common to each sex. Analysis of variance (ANOVA) statistical tests were carried out on the mean weights at each age to determine if differences occur between the sexes. As with the statistical analyses for mean lengths, for female and male fish overall, and from those captured during 1997, no significant differences were observed. However, with female and male fish from 1998 and 1999, significant differences were recorded. From examination of Table 11., it was observed that the mean weights at each for female fish is considerably and consistently larger than that recorded for the males at the same age.

Examination of the mean weights in Figs 20a-h. shows a steady increase in mean weight as the fish grow older. As with the mean lengths, the trend of variation occurring at the lower and upper end of the age range continued, with mean weights being below or above the general trend of steady increase. Values determined for the standard deviation around the mean weights also varied considerably.





A	0	Omenall	1007	1007	1000	1009	1000	1000
Age	Overall	Overall Mala (7)	1997 Female	1997 Mala (m)	1998 Female	1990 Mala	1999 Fomolo	1999 Mala
Class	remaie	Maie (g)	remaie	Maie (g)	remaie		remaie	(g)
(yrs.)	(g)	146	(g)	25	<u>(g)</u>	(g) 40	(g) 2036	<u>(g)</u>
NO.0I	4009	140	1101	33	990	49	2030	30
TISN	100.40		01 42				110.29	
2	100.40		ð1.43				119.30	
-	± 26.83	53.03	± 0.000	F (F)	105 35	02.00	± 0.000	
5	115.50	72.03	104.05	70.50	107.25	83.99	123.81	
	± 26.35	± 30.08	± 28.40	± 26.22	± 23.67	± 26.08	± 23.20	100.44
4	156.48	120.39	142.21	117.43	134.90	107.32	162.62	129.44
	± 48.43	± 28.91	± 44.25	± 26.54	± 46.90	± 33.38	± 43.64	± 28.43
5	190.58	130.46	186.16	142.57	171.53	119.25	196.93	133.11
	± 68.89	± 35.61	± 62.61	± 57.98	± 62.93	± 38.75	±71.81	±26.74
6	206.80	131.83	209.37	151.08	199.53	120.45	205.20	124.93
	± 81.52	± 37.93	± 78.68	± 35.31	± 70.58	± 40.69	± 86.92	± 29.77
7	233.44	156.95	243.73	160.83	232.04	156.30	226.70	152.33
	±99.66	± 66.42	± 100.73	± 77.10	± 94.87	± 78.73	± 102.36	± 45.13
8	269.51	255.37	276.07	365.88	271.25	144.87	263.84	
	±127.23	± 156.27	± 137.55	± 0.000	± 103.10	± 0.000	± 132.05	
9	351.24		402.32		332.71		321.05	
	± 135.42		± 135.40		± 130.10		± 129.78	
10	383.59		484.41		313.56		311.15	
	± 175.16		±214.62		±114.86		± 74.45	
11	324.41				301.78		347.04	
	± 102.11				± 95.29		±117.83	
12	444.97	*****	468.55				421.39	
	± 33.34		± 0.000				± 0.000	
15	708.78		1012.61				404.96	
	± 429.67		± 0.000				± 0.000	
16	598.26	and any first state state	598.26					
	+0.000		± 0.000					
Max.	1012.61	365.88	1012.61	365.88	659.82	273.70	721.14	199.07
wt.	1012.01	200100						
Min.	11.17	27.22	54.14	57.96	11.17	27.22	11.45	69.41
wt.								
Anova	F-value	2.311	F-value	0.253	F-value	5.604	F-value	18.519
Tests	P-value	0.159	P-value	0.625	P-value	0.039	P-value	0.005
for	F-crit	4.964	F-crit	4.964	F-crit	4.964	F-crit	5.987
F/M	S/NS	NS	S/NS	NS	S/NS	S	S/NS	S

Table 11.	Summary of	mean	weights at age	for fe	emale and	male <i>k</i>	. whiffiagonis

S= Significant.

NS= Not Significant.

CHAPTER THREE : PART 2. AGE AND GROWTH RESULTS

3.1 General introduction

For this investigation, 4,609 female and 146 male fish, representing 95.76% and 96.68% respectively of the entire captured population were aged. A total of 204 female ages could not be determined, the majority of these (N=187) being fish with the otoliths removed by the Marine Institute as part of their routine port sampling programme. The latter are referred to as a 'blank age' in the appropriate tables. The remaining 17 female fish without ages, had otoliths that presented difficulties in ageing and were therefore omitted from statistical analyses. Only 5 male otoliths were unreadable and omitted from analyses.

3.1:1 Age frequencies

The overall percentage age frequency distribution for all samples combined (Fig. 21.), and the annual percentage age distribution for 1997, 1998 and 1999 (Fig. 22a-c.), shows the results for males and females separately on the same graph.

For the overall percentage age frequency distribution (Fig. 21.), the largest percentage of females (27.09%) were within the age class of 5 years of age, while the largest percentage of males (30.82%) were also within the age class of 5 years of age. Females ranged in age from 2 to 16 years old, while the males had a smaller age range of 3 to 8 years old.

Percentage age frequency distributions were calculated for fish captured in years 1997, 1998 and 1999 and the results presented in Figs. 22a-c. and Table 12a. In 1997, the largest percentage (31.69%) of females occurred in the age class of 5 years. The largest percentage (31.42%) of males were within the older age class of 6 years. Female fish ranged in age from 2 to 16 years old and males from 3 to 8 years of age. A mean age of 5.57 and 5.4 years of age were recorded for female and male fish respectively during 1997. The largest percentage (24.44%) of females and males (28.57%) captured in 1998 were both recorded in age class 5. Females ranged in age from 3 to 11 years old, while males only ranged in age from 3 to 8 years old. For females, a mean age of 5.49 years old was recorded, while males had a mean age of 5.26 years. In 1999, the largest percentage (28.6%) of females were recorded in age class of 5 years of 5 years old. Mean ages of 5.36 and 5.04 years old were recorded for females and males and males respectively. Ages ranged from 2 to 15 years old for females and 4 to 7 years old for males captured during 1999.

Summary Frequencies	1997	1998	1999
Number of females aged	1161	990	2036
Number of males aged	35	49	50
Total number of fish aged	1196	1039	2086
Range in age for	2-16	3-11	2-15
females(years)			
Range in age for males	3-8	3-8	4-7
(years)			
Mean age and	5.574 years	5.490 years	5.236 years
standard deviation in age	± 1.480 years	± 1.532 years	± 1.392 years
for females (years)			
Mean age and standard	5.4 years	5.265 years	5.04 years
deviation in age for males	\pm 1.264 years	\pm 1.254 years	± 0.946 years
(years)			

Table 12a. Summary of annual age frequency distributions for L. whiffiagonisfor the period 1997-1999.

Percentage age frequency distributions and summaries were also calculated for the same months in each of 3 consecutive years throughout the sampling period, *i.e.* January 1998, 1999 and 2000 (Figs. 23a-c, Table 12b.), February 1998, 1999 and 2001 (Figs. 24a-c, Table 12c.), April 1997, 1998 and 1999 (Figs. 25a-c, Table 12d.), October 1997, 1998 and 1999 (Figs. 26a-c, Table 12e.) and November 1997, 1998 and 1999 (Figs. 27a-c, Table 12f.).















January	1998	1999	2000
Number of females aged	126	157	97
Number of males aged	18	2	No males captured
Range in age for females (years)	4-10	4-11	3-9
Range in age for males (years)	3-7	5-6	No males captured
Mean age and standard	6.087 years	6.528 years	4.587 years
deviation in age for females (years)	± 1.226 years	± 1.443 years	± 0.875 years
Mean age and standard	5.166 years	5.5 years	No males
deviation in age for males (years)	± 1.200 years	\pm 0.707 years	captured
Modal percentage (%) and	34.12%	43.31%	52.57%
modal age class for females (years)	Age class 6	Age class 6	Age class 4

Table 12b.	Summary of	<u>f percentage ag</u>	e frequency	<u>distributions i</u>	n January over
		the perio	d 1998-2000	•	

The largest percentage of females (34.12%) sampled in January 1998 (Fig. 23a.) were recorded in the age class of 6 years old and had a range in age of 4 to 10 years old. A mean age of 6.08 (\pm s.d. 1.22) years was recorded for females. For female fish captured in January 1999 (Fig. 23b.), the largest percentage (43.31%) were within the same age class as January 1998, that of age class 6. A mean age of 6.52 (\pm s.d. 1.44) years was obtained for the females and they had slightly larger range in age (4-11 years) than fish from January 1998 (Table 12b.). Finally, the largest percentage of females (52.57%) captured during January 2000 (Fig. 23c.) were within the age class of 4 years old. A mean age of 4.58 (\pm s.d. 0.87) years was obtained for fish from this month, which was considerably younger than fish from the previous two years for the same month. Females from January 2000 ranged in age from 3 to 9 years of age (Table 12b.).







February	1998	1999	2001
Number of females aged	172	153	113
Number of males aged	15	3	3
Range in age for females	3-10	3-8	3-8
(years)			
Range in age for males (years)	3-7	4-5	4-6
Mean age and standard	4.802 years	4.464 years	3.973 years
deviation in age for females	± 1.554 years	± 1.261 years	± 1.153 years
(years)			
Mean age and standard	5.133 years	4.333 years	5 years
deviation in age for males	± 1.302 years	± 0.577 years	± 1.000 years
(years)			
Modal percentage (%) and	27.90%	46.40%	42.47%
modal age class for females	Age class 4	Age class 4	Age class 3
(years)			

Table 12c.	Summary of	percentage	age frequency	distributions	in February
		over the pe	riod 1998-2001		

For February 1998 (Fig. 24a.), the largest percentage of females (27.90%) were recorded within the age class of 4 years old. They ranged in ages from 3 to 10 years and had a mean age of 4.80 (± s.d. 1.55) years old. The largest percentage of females (46.40%) captured during February 1999 (Fig. 24b.) were also recorded in the age class of 4 years old. Females from this month had a smaller range in age than those of February 1998, from 3 to 8 years old, and a slightly less mean age of 4.46 (± s.d. 1.26) years of old for February 1999 (Table 12c.). Finally, the largest percentage of females (42.47%) captured during February 2001 (Fig. 24c.) were in age class 3. This is a year less than the February's from 1998 and 1999. As with the females from February 1999, they ranged in age from 3 to 8 years and but had a younger mean age of 3.97 (± s.d. 1.15) years old (Table 12c.).







April	1997	1998	1999
Number of females aged	65	144	335
Number of males aged	16	2	5
Range in age for females	3-12	3-8	3-10
(years)			
Range in age for males (years)	4-8	4-5	5-6
Mean age and standard	5.876 years	4.562 years	6.089 years
deviation in age for females	± 1.899 years	\pm 1.1210 years	\pm 1.227 years
(years)			
Mean age and standard	5.375 years	4.5 years	5.6 years
deviation in age for males	\pm 1.147 years	\pm 0.707 years	± 0.547 years
(years)			
Modal percentage (%) and	26.15%	27.77%	34.02%
modal age class for females	Age class 5	Age class 5	Age class 6
(years)			

Table 12d.	Summary of	percentage	age frequenc	<u>y distribu</u>	<u>utions in</u>	April	over
		the perio	od 1997-1999.				

The largest percentage of females (26.15%) captured during April 1997 as shown in Fig. 25a., were recorded in the age class of 5 years old. They ranged in age from 3 to 12 years and had a mean age of 5.87 (\pm s.d. 1.89) years old. For females captured during April 1998 (Fig. 25b.), the largest percentage (27.77%) were also recorded in the age class of 5 years old. Females from this month ranged in age from 3 to 8 years old (Table 12d.). A mean age of 4.56 (\pm s.d. 1.12) years was obtained for fish from April 1998. A large number (N= 335) females were aged from fish captured during April 1999 (Fig. 25c.). The largest percentage of these females (34.02%) were in the age class of 6 years old. This is a year older than the modal percentage recorded for April 1997 and 1998. Females from April 1999 ranged in age from 3 to 10 years and had a mean age of 6.08 years old. This mean age of 6.08 (\pm s.d. 1.22) years old is considerably higher than that obtained for the previous months of April 1997 and 1998 sampled (Table 12d.).







October	1997	1998	1999
Number of females aged	230	113	84
Number of males aged	5	4	1
Range in age for females	3-9	4-11	4-9
(years)			
Range in age for males (years)	3-7	7-8	5
Mean age and standard	4.791 years	6.407 years	6.595 years
deviation in age for females	\pm 1.163 years	± 1.595 years	\pm 0.879 years
(years)			
Mean age and standard	5.4 years	7.25 years	5 years
deviation in age for males	\pm 1.816 years	± 0.500 years	± 0.000 years
(years)			
Modal percentage (%) and	36.52%	25.66%	51.19%
modal age class for females	Age class 5	Age class 6	Age class 7
(years)			

Table 12e.	Summary of percentage age frequency distributions in October over	r
	the period 1997-1999.	

For female fish captured during October 1997 (Fig. 26a.), the largest percentage (36.52%) were recorded in the age class of 5 years old. They ranged in age from 3 to 9 years old. A mean age of 4.79 (\pm s.d. 1.16) years old was obtained for females from this month (Table 12e.). The largest percentage of females (25.66%) captured during October 1998 (Fig. 26b.), were in the older age class of 6 years old. The range in age for females from this month was slightly larger than that of female fish from the previous October, from 4 to 11 years and had as expected, a slightly older mean age of 6.40 (\pm s.d. 1.59) years old. Finally, when the percentage age frequency distribution for female fish captured during October 1999 (Fig. 26c.) is compared to the two previous Octobers of 1997 and 1998, it can be seen that the largest percentage of females (51.19%) were recorded in the oldest age class of 7 years old. The modal percentage females from this month were recorded in an older age class, that of 7 years old, they only had a mean age of 6.59 (\pm s.d. 0.87) years old, which is only slightly older than that of the October 1998 (Table 12e.).







November	1997	1998	1999
Number of females aged	88	167	86
Number of males aged	3	2	3
Range in age for females	4-8	3-10	4-7
(years)			
Range in age for males (years)	4-6	6	5-6
Mean age and standard	5.217 years	5.916 years	4.941 years
deviation in age for females	± 1.180 years	± 1.432 years	± 0.872 years
(years)			
Mean age and standard	5 years	6 years	5.333 years
deviation in age for males	\pm 1.000 years	± 0.000 years	± 0.577 years
(years)			
Modal percentage (%) and	39.77%	32.93%	45.34%
modal age class for females	Age class 5	Age class 6	Age class 5
(years)			

Table 12f.	<u>Summary of</u>	percentage age	frequency	distributions	in November
		over the period	1997-199	9.	

The largest percentage of females (39.77%) captured during November 1997 as presented in Fig. 27a. were recorded in the age class of 5 years old. They ranged in age from 4 to 8 years and had a mean age of $5.21 (\pm \text{ s.d. } 1.18)$ years old. For females from November 1998 (Fig. 27b.), the largest percentage (32.93%) were in the age class of 6 years old. This a year older than the modal percentage of females from the previous November. Females from November 1998 ranged in age from 3 to 10 years old, which was a greater age range than that of the previous November. A mean age of $5.91 (\pm \text{ s.d. } 1.43)$ years old was obtained for females from November 1998 (Table 12f.). Finally, the largest percentage of females (45.34%) captured during November 1999 (Fig. 27c.) were recorded in the age class of 5 years old. They ranged in age from 4 to 7 years old which was the smallest range in age of the three November's sampled. The mean age of $4.94 (\pm \text{ s.d. } 0.87)$ years old for female fish from November 1999 was the also the smallest mean value obtained from the months of November sampled (Table 12f.).

3.1:2 Catch curves

Catch curves were plotted for male and female fish for the entire sampling period (Fig. 28.) and annually for the years 1997, 1998, 1999 (Figs. 29a-c.). Males and females were separated but presented on the same graph. From the catch curves a value of t_r or age of recruitment to the fishery was obtained. These catch curves and t_r values are summarised in Table 13.

Age of Recruitment (tr)	Overall	1997	1998	1999
Number of females aged	4609	1161	990	2036
Number of males aged	146	35	49	50
Female tr (years)	6 years	6 years	6 years	5 years
Male tr (years)	6 years	7 years	6 years	6 years

Table 13. Summary of overall and annual catch curves for L. whiffiagonis.

From Fig. 28., the catch curve of male and female fish from the entire sampling period, a t_r of 6 years of age was obtained for both male and female fish. For 1997, (Fig. 29a.) the catch curve determined a t_r of 6 years of age for female fish, and a slightly older t_r of 7 years for males. When a catch curve was calculated for male and female fish captured during 1998 (Fig. 29b.), a t_r of 6 years old was recorded for both sexes. For 1999 (Fig. 29c.), a t_r of 5 years old was recorded for female fish and a t_r of 6 years old for males. When the values obtained for t_r are compared for each sex annually, it was observed that a constant t_r of 6 years old was recorded with the exception of the t_r from 1999 which was a year less than both the previous years of 1997 and 1998. When the t_r values for male fish are compared, the t_r value decreases from 7 years in 1997 to 6 years old for both 1998 and 1999.









3.1:3 Mortality coefficients determined from catch curves

Mortality coefficients were determined from the previous calculated catch curves for male and female fish separately. These were Z (total mortality), M (natural mortality), F (fishing mortality) and S (survivorship). Percentage mortality and survival were also determined from these. Mortality coefficients were calculated for the overall sampled population (Figs. 30a. & b.) and annually for the years 1997, 1998 and 1999 (Figs. 30c-h.). These are summarised in Table 14. A total mortality coefficient (Z) of 0.91 was determined for female fish from all samples combined (Fig. 30a.), while a Z value of 1.43 was recorded for all male fish combined (Fig. 30b.). For female and male fish captured during 1997 (Figs. 30c. & 30d.), Z values of 0.81 and 1.19 were obtained respectively. When total mortality (Z) was calculated for females and 1.24 for males. Total mortality (Z) values of 0.89 and 0.75 were determined for female and male fish from 1999 (Figs. 30g. & 30h.) respectively.

A natural mortality (M) value of 0.28 was calculated for all female fish combined, while an M value of 0.57 was obtained for males. When natural mortality (M) was calculated for female fish captured during 1997, a value of 0.28 was recorded. For males sampled in 1997, 0.57 was obtained for natural mortality (M). When calculated for fish captured during 1998, an M value of 0.41 and 0.57 was recorded for female and male fish respectively. Finally, females had an M value of 0.30 and males an M value of 0.65 for fish from 1999.

Using values calculated from total mortality (Z) and natural mortality (M), fishing mortality (F) was determined for males and females overall and annually. For female fish from all samples combined, an F value of 0.62 was determined, while F was calculated to be 0.85 for all male samples combined. Fishing mortality (F) values of 0.53 and 0.61 were recorded for female and male captured during 1997 respectively. For females sampled in 1998, F was determined to be 0.40, while male fish had an F value of 0.66 for the same year. When fishing mortality (F) was calculated for fish captured during 1999, F values of 0.58 and 0.10 were determined for females and males respectively (Table 14.).

Survivorship (S) was determined to be 0.40 for all female fish combined and 0.23 for all males combined. For females captured during 1997, an S value of 0.44 was recorded, and an S value of 0.30 for male fish from the same year. Survivorship (S) values of 0.44 and 1.04 were obtained for female and male fish respectively for

fish captured during 1998. When survivorship (S) was calculated for female fish from 1999, an S value of 0.41 was recorded, while an S value of 0.47 obtained for males (Table 14.).

Once values had been determined for the previous mortality coefficients, percentage mortality and percentage survival was calculated for females and males for all samples combined and annually. For all samples combined, female fish were determined to have a percentage mortality rate of 59.74%, and males a percentage mortality rate of 76.06%. When percentage mortality was calculated for fish captured during 1997, values of 55.51% and 69.57% were recorded for females and males. A percentage mortality rate of 55.51% was also obtained for females from 1998, though the percentage mortality rate for males in 1998 increased to 71.06%. For fish captured during 1999, percentage mortality rates increased for females to 58.93%, but decreased for males to 52.76% (Table 14.).

Percentage survival rates were calculated for all fish also. This is the remaining percentage following percentage mortality determination. Females from all samples combined had a percentage survival rate of 40.25% and males from all combined samples had a rate of 23.93%. In 1997, a percentage survival rate of 44.48% was recorded for female fish, while males had a lower percentage survival rate of 30.42% for the same year. Survival rates for females in 1999 were the same as 1998 (44.48%), but decreased slightly for males in 1998 to 28.93%. Finally, percentage survival for females captured during 1999 decreased to 41.06%, but increased dramatically to 47.23% for male fish sampled in the same year.

Mortality	Overall	1997	1998	1999
Female total mortality (\mathbf{Z})	0.91 (N=1873)	0.81 (N=541)	0.81 (N=459)	0.89 (N=1307)
Male total mortality (\mathbf{Z})	1.43 (N=101)	1.19 (N=18)	1.24 (N=21)	0.75 (N=33)
Female natural mortality (M)	0.28	0.28	0.41	0.30
Male natural mortality (M)	0.57	0.57	0.57	0.65
Female fishing mortality (F)	0.62	0.53	0.40	0.58
Male fishing mortality (F)	0.85	0.61	0.66	0.10
Female survivorship (S)	0.40	0.44	0.44	0.41
Male survivorship (S)	0.23	0.30	0.28	0.47
Female % survival rate	40.25%	44.48%	44.48%	41.06%
Male % survival rate	23.93%	30.42%	28.93%	47.23%
Female % mortality rate	59.74%	55.51%	55.51%	58.93%
Male % mortality rate	76.06%	69.57%	71.06%	52.76%

Table 14.Summary of overall and annual mortality co-efficients (Z, M, F, andS) for L. whiffiagonis determined from catch curves.






3.1:4 Otolith length relationships

The relationships between mean otolith lengths, and total length (TL) and age were determined for *L. whiffiagonis* captured during February 1998, 1999 and 2001. A total of 460 pairs of otoliths were measured, while only 1 pair of otoliths were not included in the statistical analyses as they were both broken. A mean otolith length could not be obtained for this pair. Mean otolith lengths were used to calculate the following relationships. The relationship between mean otolith length and total length (TL) as presented in Fig. 31a. was correlated ($R^2 = 0.5374$, P< 0.05). This relationship can be written as :

$$OL(cm) = 0.0011TL(cm)^{0.0135}$$

where OL = mean otolith length in centimetres and TL = total length in centimetres. The relationship between mean otolith length and age as shown in Fig. 31b. showed a correlation ($R^2 = 0.3754$, P< 0.05) and can be written as :

$$OL(cm) = 0.0039 t (vrs)^{0.0247}$$

where OL = mean otolith length in centimetres and t = age in years. The relationship between the two otolith lengths (Fig. 31c.) was examined and determined to significantly correlated (R²= 0.8561, P< 0.05). This relationship can therefore be written as :

$$OL (cm) = 0.0003OL (cm)^{0.9262}$$

where OL = otolith length in centimetres. The percentage mean otolith length frequency distribution for otoliths removed from fish captured during February 1998, 1999 and 2001 was also calculated and is presented in Fig. 31d. The largest percentage (39.95%) of mean otolith lengths were recorded in the length class of 0.45- 0.49cm OL. Otoliths ranged in length from 0.4-0.7cm OL, with a mean value of 0.502cm OL (\pm 0.0560cm).

3.1:5 Otolith marginal edge examination

The outer or marginal edges of all otoliths obtained were examined and determined either to be opaque or translucent. Otoliths from male and female fish were combined and a total of 4,640 otoliths were examined in this manner. From Fig. 31e., of the monthly percentage opaque otolith edges over the entire sampling period, it was observed that the largest percentage of opaque edges from each year were recorded in October 1997 (93%), April 1998 (44%) and September 1999 (100%). These months correspond with the end and start of the summer growth period of the fish. Fig. 31f. shows the monthly percentage of translucent otolith edges over the sampling period. From this graph, it was observed that the largest percentage of translucent otolith edges were recorded in December 1997 (91%), December (97%), April 1999 (98%) and January 2000 (100%). These months correspond with the start and end of the winter period of reduced growth. Though the month of April 1998 has the largest percentage of opaque edges (44%) for the year 1998, the same month has a higher percentage of translucent edges (56%) than opaque. This corresponds with the sample from April 1999 which has a larger proportion of translucent edges than opaque. From these graphs, it was determined that opaque otolith marginal edges are laid down during the summer months and translucent otolith marginal edges during the winter months for L. whiffiagonis, giving a combined annual cycle.











3.1:6 Age at length kevs

Age at length keys were determined for the total number of male and female *L. whiffiagonis* from all samples combined. From these, the numbers of fish of each age were matched with their corresponding total lengths. For comparative purposes all age at length keys were constructed using the same length and age range. Overall keys for female and male fish are presented in Tables 15a.& b in Appendix IV. Following the calculation of the overall age at length keys, annual age at length keys were determined for females and males caught during the years 1997, 1998 and 1999 and are shown in Tables 16a-f. in Appendix IV. Age at length keys were also calculated for the annual quarters present during the sampling period. This was carried out for female fish only as there were too few male fish present to calculate age length keys for them. Quarterly age at length keys for females only are presented in Tables 17a-i. in Appendix IV.

Comparisons between female and male age at length keys were difficult due to the lack of male fish recorded in the samples. From the overall age at length keys for female and male fish as presented in Tables 15a. & b.(Appendix IV), it can be seen that female fish attain a larger size than male fish at the same age. The largest male fish aged 3 years old was within the size class of 26-26.99cm TL, compared to the largest female of the same age which was in the size class of 32-32.99cm TL. This trend continues as the age groups get older. The largest 4 year old male fish was within the size class of 30-30.99cm TL, while the largest 4 year old female was in the size class of 37-37.99cm TL. The largest 5 year female fish were recorded in the size class of 38-38.99cm TL, compared to the largest 5 year old male fish which were in the size class of 31-31.99cm TL. For 6 and 7 year old female fish, the largest individuals recorded were in the size classes of 44-44.99cm TL and 47-47.99cm TL respectively. These size classes contrasted considerably with the largest 6 and 7 year old male which were in the size classes of 32-32.99cm TL and 35-35.99cm TL respectively. Finally, the largest 8 year old male fish was within the size class of 37-37.99cm TL, while the largest female of the same age was within the size class of 38-38,99cm TL. Comparisons between female and male fish could not be carried out beyond the age group of 8 years old as no male fish were recorded older than this age.

For the annual age at length keys as presented in Tables 16a-f.(Appendix IV), comparisons between the sexes is not possible as so few males fish were present in the samples. When the female annual age at lengths keys were examined, it was

observed that the age at length keys for the years 1997 and 1998 were very similar, but that constructed for 1999 was slightly different. In the 1999 age at length key, there were a greater number of older fish present in the samples than that recorded for the previous two years. When the male annual age at length keys for the above years were compared they were observed to be very similar in their distribution of ages and lengths.

Quarterly age at length keys were constructed for females only from the years of 1997, 1998 and 1999. The number of months present in each of the quarterly periods varied slightly throughout the sampling period as there were several gaps within the sampling sequence. This meant that there were more fish present in particular quarters than others, and may possible have resulted in differences between the age at length keys. However, these quarterly age at length keys provided a useful indicator of age and length structure within the sampled years.

From examination of the three quarterly age at length keys constructed for 1997 as presented in Tables 17a., b. & c.(Appendix IV), it was observed that the keys calculated for the 2^{nd} and 3^{rd} quarter of the year were very similar in their distribution, but the key for the 4^{th} quarter of 1997 was slightly different. A greater number of 3 and 4 year old fish in the size classes of 21-21.99cm TL, 22-22.99cm TL and 23-23.99cm TL were recorded in the last quarter of 1997 than that of the previous two quarters. This indicated a larger number of younger and smaller fish present in the samples. The modal number of fish present in the 2^{nd} quarter of 1997 were in the age group of 5 years of age, while in the 3^{rd} quarter the modal number were aged 6 years old. Finally, the modal group of fish in the 4^{th} quarter were aged 5 years old.

There were only two quarters present for the year of 1998 (Tables 17d. & e., Appendix IV), these being the 1st and 4th quarters, making it difficult to compare them with those from the previous year of 1997 and the following year of 1999. The age at length keys from 1998 were very similar in their distribution to those from 1997, except for the presence of fish in the smallest size class of 21-21.99cm TL in the two 1998 quarters which were absent in those from 1997 and 1999. For the quarterly age at length keys constructed for 1998, the modal age groups in the 1st and 4th quarter were 5 and 6 years old respectively.

The quarterly age at length keys constructed for 1999 (Tables 17f-i., Appendix IV) were all similar in distribution of ages at lengths, though there were less smaller and younger fish present in the 4th quarter of the year. The youngest age group

recorded in this particular quarter was that of 4 years of age. When 1999 was compared to 1997, it was observed that a greater number of older fish were present in the quarters for 1999 than those of 1997. These older fish, however, were not in size classes which were greater than length than those from 1997, indicating a slower rate of growth, as the fish were greater in age but not necessarily greater in size. There were no fish in size classes of length less than 23cm TL in all quarters of 1999, compared to those of the previous two years where there were several fish present in size classes less than this particular total length. Finally, the modal age group for the 1st and 2nd quarters of 1999 was 4 years old, and 5 years of age for the 3rd and 4th quarters of the year.

3.1:7 Growth determination

The growth rates of *L. whiffiagonis* were calculated for overall female and male fish separately, and for the overall females and males combined. Growth rates were also determined for females from the years 1997, 1998 and 1999. There were insufficient numbers of male fish in the above years to determine growth rates separately. Growth was calculated using three different methods, those of Ford-Walford (1949), Gulland-Holt (1959) and Rafail (1973). The Von Bertalanffy (1938) growth parameters (VBGP) of L ∞ , K and t₀ were obtained using these methods. These VGBP's are summarised in Table 18. below. The growth rate of *L. whiffiagonis* using the methods of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1949) are presented in Figs. 32a-f. A comparison of female and male growth rates using the three growth determination methods are presented in Figs. 33a., b. & c.

Method	Sex	L∞	K	T ₀	R ²	Age	No.
Rafail (1973)	Female overall	50.72	0.097	-4.78	0.9616	3-9	4566
	Male overall	35.01	0.127	-6.689	0.8844	5-7	99
	Combined	47.94	0.113	-4.053	0.9531	3-9	4917
	Female & Male						
	Female 1997	53.01	0.107	-2.764	0.9402	3-10	1157
	Female 1998	76.74	0.038	-7.626	0.9958	4-8	877
	Female 1999	46.57	0.117	-4.485	0.9582	3-9	2021
Gulland-Holt (1959)	Female overall	50.74	0.072	-8.089	0.0865	3-11	4602
	Male overall	41.59	0.138	-3.062	0.048	4-8	140
	Combined	52.22	0.066	-9.292	0.0734	3-11	4742
	Female & Male						
	Female 1997	97.66	0.023	-12.71	0.098	3-8	1121
	Female 1998	58.86	0.056	-8.664	0.1435	4-10	912
	Female 1999	71.45	0.033	-13.44	0.017	3-11	2033
Ford-Walford (1946)	Female overall	45.85	0.098	-7.135	0.9466	3-11	4602
	Male overall	33.86	0.316	-0.574	0.6845	4-8	140
	Combined	46.51	0.093	-6.935	0.9456	3-11	4742
	Female & Male						
	Female 1997	61.42	0.049	-10.99	0.9481	3-8	1121
	Female 1998	55.06	0.065	-7.656	0.9813	4-10	912
	Female 1999	52.97	0.063	-9.561	0.9407	3-11	2033

Table 18.	Comparison of	VBGP for <i>L</i> .	whiffiagonis in	this investigation.

3.1:7:1 Rafail (1973) growth method

By using the method of Rafail (1973), an $L\infty$ of 50.72cm and a K value of 0.097 was obtained for all female fish combined. A t_0 of -4.78 was also recorded for these females. Though the overall age range for females recorded was 2-16 years of age, only the age range of 3-9 years was used in the calculation of the Von Bertalanffy (1938) growth equation. A total of 4,566 females were used to describe overall female growth with this method. As with the female fish, the overall age range of 3-8 years of age recorded for all male fish combined was not used in the growth calculations, that of 5-7 years being used instead. This resulted in only 99 males being used to determine a growth rate. Values of $L\infty = 35.01$ cm, K = 0.127 and $t_0 = -6.689$ years were obtained for overall male fish using the Rafail (1973) method. When the growth rate of female and male fish were combined overall, VBGP's of $L\infty =$ 47.94cm, K = 0.113 and $t_0 = -4.053$ years were recorded. The age range used for calculation of the combined total number of female and male growth rate was 3-9 years of age, and included a total of 4,917 fish. Using the method of Rafail (1973) for females captured in 1997, VBGP's of $L\infty = 53.01$ cm, K = 0.107 and $t_0 = -2.764$ years were recorded. Though female fish captured in 1997 ranged in age from 2-16 years old, only the age range of 3-10 years was used in the calculation of the VBGP's and included a total of 1,157 fish. For females captured in 1998, VBGP's of $L\infty =$ 76.74cm, K = 0.038 and t_0 = -7.626 years were obtained from an age range of 4-8 years, though the overall age range for females from 1998 was 3-11 years of age. A total of 877 fish were used in the calculation of the growth rate for female fish from 1998. Finally, using the method of Rafail (1973), the VBGP's for female fish caught during 1999 were determined. Values of $L\infty = 46.57$ cm, K = 0.117 and $t_0 = -4.485$ years were obtained. Though the overall age range for female fish from 1999 ranged from 2-15 years old, only the age range of 3-9 years was used to determine the growth rate and included a total of 2,021 fish.

3.1:7:2 Gulland-Holt (1959) growth method

Following using the method of Gulland-Holt (1959) to determine growth for megrim captured during this investigation, a second set of Von Bertalanffy (1938) growth parameters were obtained. By using the Gulland-Holt (1959) plot for all female fish combined, values for $L\infty = 50.74$ cm, K = 0.072 and $t_0 = -8.089$ years were obtained. Though the overall age range for females was captured was 2-16 years, the age range used to calculate this plot was 3-11 years of age and included a total of 4,602 fish. Following calculation of the VBGP's for all male fish combined, values for $L\infty = 41.59$ cm, K = 0.138 and t₀ = -3.062 years were determined. A total of 140 fish were included in the age range of 4-8 years that was used to construct the overall male growth rate. Only the age group 3 was not included in the calculation of the overall male growth rate as this age group was poorly represented in the samples. When the growth rate for the total number of females and males combined, VBGP's of $L\infty = 52.22$ cm, K = 0.066 and t₀ = -9.292 years were obtained from a combined total of 4,742 fish. The age range used to determine these parameters was that of 3-11 years, not the overall combined age range of 2-16 years. A total of 1,121 fish were used to obtain growth parameters for females caught during 1997. Values of $L\infty =$ 97.66cm, K = 0.023 and $t_0 = -12.716$ years were calculated for these females. The VBGP's determined for females from 1997 using the Gulland-Holt (1959) plot were obtained from fish in the age range of 3-8 years, and not that of the overall age range of 2-16 years for females from this year. Values of $L\infty = 58.86$ cm, K = 0.056 and t₀ = -8,664 years were determined for female fish caught during 1998. A total of 912 females were used to calculate these VBGP's from an age range of 4-10 years, though the overall age range of 3-11 was not used as the age groups of 3 and 11 were poorly represented throughout the sample from this year. Finally, the Gulland-Holt (1959) plot was used to determine VBGP's for female fish caught during 1999. Values of L∞ = 71.45cm, K = 0.033 and t_0 = -13.448 years were obtained. Though the overall age range for females from 1999 was 2-15 years, only the age range of 3-11 years was used to calculate the growth parameters.

3.1:7:3 Ford-Walford (1946) growth method

The third method of determining the VBGP's for L. whiffiagonis for this investigation was that of Ford-Walford (1946). Like the methods of Rafail (1973) and Gulland-Holt (1959), a complete set of VBGP's were obtained. When the method of Ford-Walford (1946) was used to calculate growth parameters for females overall, values of $L\infty = 45.85$ cm, K = 0.098 and $t_0 = -7.135$ years were recorded. The age range used to obtain these VBGP's was 3-11 years, not the overall age range for females of 2-16 years. A total of 4,602 fish were used to determine the overall female growth rate. By using the Ford-Walford (1946) method for male fish overall, VBGP's of $L\infty = 33.86$ cm, K = 0.316 and t₀ = -0.574 years were determined. These growth parameters were calculated from a total of 140 male fish, in an age range of 4-8 years. The overall male age range of 3-8 years was not used as age group 3 was poorly represented in the samples. Female and male fish were combined as with the previous two growth methods, and VBGP's of $L\infty = 46.51$ cm, K = 0.093 and $t_0 = -6.935$ years were determined. Though the overall age range for females and males combined was from 2-16 years, only the combined age range of 3-11 was used and included a total of 4,742 fish. A total of 1,121 fish were included in the calculation of growth parameters for females caught during 1997. An age range of 3-8 years was used for the calculation, not the overall age range of 2-16 years for females from this year. Values of $L\infty = 61.42$ cm, K = 0.049 and $t_0 = -10.996$ were obtained for these females. When the VBGP's for female fish caught during 1998 were calculated, values of Loo = 55.06cm, K = 0.065 and $t_0 = -7.656$ years were obtained. Though females from 1998 had an overall age range of 3-11 years, only the age range of 4-10 years was used to determine the growth rate and included a total of 912 fish. The final Ford-Walford (1946) plot was to determine VBGP's for female fish caught during 1999.

Following calculation of these VBGP's, values of $L\infty = 52.97$ cm, K = 0.063 and $t_0 = -9.561$ years were determined. A total of 2,033 fish were used to fit the growth models for females from 1999, from an age range of 3-11 years, though the overall age range for these females was 2-15 years. Age groups below and above the age range of 3-11 years were poorly represented, and the model failed to converge with their inclusion.

3.1:7:4 Von Bertalanffy (1938) growth curves

Von Bertalanffy (1938) growth curves were used to examine the differences in growth rates of the fish. These were determined by use of the VGBP calculated by using the growth methods of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946). By plotting all three growth curves on each graph, it was possible to determine the best fitting growth model for each set of data examined.

From examination of the Von Bertalanffy (1938) growth curves for overall female fish (Fig. 32a.), it was observed that all three growth curves were similar in their distribution over the total length and age relationship. The method of Rafail (1973) recorded the lowest theoretical length at age group 1 whilst also recording the highest theoretical length at age group 20. The growth curves for the other two methods, those of Gulland-Holt (1959) and Ford-Walford (1946) were almost identical in their distribution over the examined data.

The Von Bertalanffy (1938) growth curves for overall male fish (Fig. 32b.) displayed a similar distribution over the data. The plot for Gulland-Holt (1959) attained the greatest theoretical length, whilst those of Rafail (1973) and Ford-Walford (1946) were the same. However, the growth curve of Ford-Walford (1946) recorded an extremely low theoretical length for age group 1 (13.24cm TL) which was considerably lower than that of the two other growth methods.

Female and male data was combined and a growth rate determined (Fig. 32c.). The Von Bertalanffy (1938) growth curves were all very similar in distribution over the combined data. The method of Rafail (1973) recorded a lower theoretical length than the other two growth curves, but attained the highest overall theoretical length.

The Von Bertalanffy (1938) growth curves for female fish caught during 1997 (Fig. 32d.) were closely matched at the upper end of the curve, however there was considerable variation at the younger ages. The theoretical length at age group 1 for the method of Rafail (1973) had the lowest value, that of 17.55cm TL. This was in comparison to the 26.41cm TL and 27.28cm TL recorded at the same age for the methods of Gulland-Holt (1959) and Ford-Walford (1946) respectively.

For female fish caught during 1998 (Fig. 32e.), the Von Bertalanffy (1938) growth curves were similar in their entire range of distribution, with the growth curve of Rafail (1973) attaining the greatest theoretical length.

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The Von Bertalanffy (1938) growth curves for the female fish from 1999 (Fig. 32f.), were again similarly distributed over the theoretical lengths but with the growth curve of Rafail (1973) recording a lower theoretical length at age group 1.

The female and male Von Bertalanffy (1938) growth curves were plotted separately on the same graph for each growth method to compare growth rates between the sexes. From examination of female and male growth rates using the growth method of Rafail (1973) (Fig. 33a.), it was clearly observed that female fish attain a higher growth rate than males, however, their theoretical length at age group 1 was the same. Female and male growth was similar using the method of Gulland-Holt (1959) (Fig. 33b.) with female fish again attaining a higher theoretical length. Males demonstrated a faster rate of growth from age group 1 to age group 7, but females had overall higher theoretical lengths within this age range. From age group 7 onwards, the female and male growth rate was similar, but with females having higher theoretical lengths. Lastly, for female and male growth rates using the method of Ford-Walford (1946) (Fig. 33c.), females had higher theoretical lengths than male fish. At age group 1, male theoretical length was considerably less than that of female fish, but rapidly increased and levelled out at age group 7.







Plot of Von Bertalanffy growth curves using the method of Rafail (1973)

Fig. 33b. Plot of Von Bertalanffy growth curves using the method of Gulland-Holt (1959) for female and male common megrim from off the west coast of Ireland.







Analysis of variance (ANOVA) statistical tests were carried out on the theoretical lengths at each age to determine if differences occur between the three growth determination methods for the same data, as well as differences between the various population groups. The results of these ANOVA tests are presented in Tables 19a. & b. below.

Table 19a.	ANOVA comparison between growth methods for each populatio	n
	group of L. whiffiagonis.	

Rafail (1973) Gulland-Holt (1959)	Overall Females	Overall Males	Combined Females	Females 1997	Females 1998	Females 1999
Ford-Walford (1946)			& Males			
F-value	0.1720	1.9672	0.1521	0.4311	0.0475	0.4907
P-value	0.8423	0.1492	0.8592	0.6518	0.9535	0.6147
F-crit	3.1588	3.1588	3.1588	3.1588	3.1588	3.1588
S / NS	NS	NS	NS	NS	NS	NS

S= Significant.

NS= *Not Significant.*

No significant differences were recorded between the growth methods of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946) for overall females, overall males, combined female and male fish, and females caught during 1997, 1998 and 1999.

Table 19b. ANOVA comparison between population groups of growth methods for L. whiffiagonis.

Parameters	Overall	Females	Females	Females
	Females/Males	1997 / 1998	1997 / 1999	1998 / 1999
F-value	6.1970	0.6408	0.4471	0.1832
P-value	4.05E-05	0.6689	0.8145	0.9684
F-crit	2.2939	2.2939	2.2939	2.2939
S/NS	S	NS	NS	NS

S= Significant. **NS**= *Not Significant.*

When ANOVA tests were carried out between the various population groups that were examined for growth, it was observed that no significant differences occurred between female fish from 1997 and 1998, 1997 and 1999, and 1998 and 1999. However, a significant difference was recorded between female and male fish.

3.1:8 Yield per recruit

Yield per recruit was determined for *L. whiffiagonis* using the model of Beverton-Holt (1957). As with the determination of growth rates, the same groups of fish were used for yield per recruit calculations, *i.e.* females overall, males overall, combined females and males overall, females caught during the years 1997, 1998 and 1999. The total yield per recruit was examined at different levels of exploitation or fishing mortality (F= 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2 and 1.4) and the results of these are presented in the Table 20. below.

F / Yield (g)	0.1	0.2	0.4	0.6	0.8	1.0	1.2	1.4
Combined	52.41	85.59	123.81	144.00	155.41	161.75	164.83	165.66
Females &								
Males								
Females	81.18	123.12	161.43	177.15	184.27	187.10	187.36	185.91
(overall)								
Males	24.02	42.91	69.59	86.28	96.65	102.92	106.41	107.96
(overall)								
Females	86.01	128.80	165.75	179.70	185.42	187.20	186.70	184.69
1997								
Females	54.44	90.57	132.46	153.78	165.22	171.25	173.94	174.36
1998								
Females	68.65	105.47	140.99	156.71	164.43	167.98	168.97	168.22
1999								

Table 20. Total yield per recruit at varying levels of F for L. whiffiagonis.

When the total yield per recruit was determined for each group of L. *whiffiagonis* individually, at varying levels of fishing mortality, they were plotted separately on the same graphs to demonstrate and compare the optimum levels of exploitation or fishing effort, and these are presented in Figs. 34a. & b.

From examination of the yield per recruit calculations for the combined female and male fish (Fig. 34a.), it was observed that with the increasing fishing mortality (F), the yield per recruit began at 52.41g at F=0.1 and reached a maximum yield of 165.66g at F=1.4. At F=0.1 for females overall (Fig. 34a.), yield per recruit was 81.18g, reaching a maximum yield of 187.36g at F=1.2, then decreased slightly to 185.91g at F=1.4. For males overall (Fig. 34a.), a yield of 24.02g was recorded at F=0.1 and reached maximum yield per recruit of 107.96g at F=1.4.

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The yield per recruit determination for females sampled during 1997 (Fig. 34b.) was recorded as 86.01g at F=0.1. It reached a maximum yield of 186.70g at F=1.2, then decreased slightly to 184.69g at F=1.4, indicating that maximum yield per recruit for female fish from 1997 was attained at F=1.2. For female fish from 1998 (Fig. 34b.), yield at F=0.1 was recorded at 54.44g, and reached maximum yield of 174.36g at F=1.4. Finally, for female fish sampled during 1999 (Fig. 34b.), a yield per recruit of 68.65g was recorded at F=0.1 and reached a maximum yield of 168.97g at F=1.2, then decreased very slightly to 168.22g at F=1.4. This indicated that maximum yield per recruit for female fish from 1999 was at a fishing mortality or effort of 1.2.





Analysis of variance (ANOVA) statistical tests were carried out on the calculated yield per recruit values to examine if differences occurred between the population groupings. The results of these ANOVA tests are presented in Table 21. below.

Parameters	Overall Females/Males	Females 1997 / 1998	Females 1997 / 1999	Females 1998 / 1999
F-value	21.1254	1.3216	1.2195	0.02404
P-value	0.0004	0.2695	0.2880	0.8789
F-crit	4.6001	4.6001	4.6001	4.6001
S/NS	S	NS	NS	NS

Table 21.	ANOVA comparison between population groups of yield per recruit
	values for L. whiffiagonis.

S= Significant. **NS**= Not Significant.

From examination of the ANOVA statistical tests, it was observed that no significant differences occurred between female fish in 1997 and 1998, 1997 and 1999, and 1998 and 1999. However, a significant difference was recorded between female and male fish for total yield per recruit values.

3.1:9 Student's T-test for distribution

Following statistical testing using Student's *T*-test for distribution, it was observed that significant differences occurred between the total numbers of female and male fish regarding total length. Differences were also recorded between females from 1997 and 1998. However, no significant differences were observed between female fish from 1997 and 1999, and 1998 and 1999. When the parameter of age was examined, it was observed there was no significant difference between overall females and males, and between female fish from 1997 and 1998. However, differences were recorded between females from 1997 and 1998. The results of the *T*-tests are also presented in Table 22.

Pop.	Overall	1997 &	1997 &	1998	Overall	1997	1997	1998
Group	Females	1998	1999	&	Females	&	&	&
Examined	& Males			1999	& Males	1998	1999	1999
Tested	TL	TL	TL	TL	Age	Age	Age	Age
F-Test Two-Sample for Variances								
F-value	1.6616	1.1369	1.2135	1.0674	1.6427	0.9343	1.1303	1.2098
P-value	3.57E-05	0.0181	6.5E-05	0.1110	6.6E-05	0.1329	0.0088	0.0002
F-crit	1.2257	1.1060	1.0871	1.0918	1.2303	0.9044	1.0887	1.0934
S/NS	S	S	S	NS	S	S	S	S
		T-Test Two	-Sample Ass	uming Eq	jual Varianc	es		
tStat	10.5398	5.2349	-1.746	-7.980	1.1263	1.2922	6.4460	4.551
t Crit	1.9604	1.9610	1.9606	1.9606	1.9604	1.9610	1.9607	1.9607
S/NS	S	S	NS	NS	NS	NS	S	S
Q Q;	10	TO 37 . OF	10					

Table 22. F-tests and T-tests carried out on total length and age between population groups for L. whiffiagonis.

S= Significant. NS= Not Significant.

CHAPTER THREE : PART 3. REPRODUCTIVE RESULTS

3.2 General introduction

Presented in this section are the reproductive results recorded for L. whiffiagonis from off the west coast of Ireland.

3.2:1 Sex ratios

Females comprised 96.95% (N= 4813) and males 3.04% (N= 151) of the sampled population (Fig. 35a.), resulting in a male to female sex ratio of 0.031:1. This was significantly different from the expected male to female ratio of 1:1 ($\chi^2 = 4378.3$, P< 0.05). However, when the sex ratio was examined according to fish length, differences occurred as the fish got larger. Females comprised 84.70% and males 15.30% of fish in the size category less than 24.99cm ($\chi^2 = 73$, P< 0.05) (Fig. 35b.). The latter size category indicated a considerably higher percentage of male fish than that of the overall 3.14% of males recorded from the entire combined samples. When the sex ratio was examined for fish of lengths between 25 and 34.99cm (Fig. 35c.), a sex ratio similar to that for the overall population was recorded *i.e.* females comprised 97% of the fish present, while males comprised the remaining 3% ($\chi^2 = 3654.8$, P< 0.01). For fish between lengths of 35 and 44.99cm (Fig. 35d.), females comprised almost all of the fish in the length range (99.30%), with males comprising a mere 0.70% ($\chi^2 = 637.08$, P< 0.01). Finally, all fish larger than 45cm were female, with no males present. (Fig. 35e.).

Fig. 35a. Percentage sex ratio of the total number of females to males for common megrim captured from off the west coast of Ireland 1997-2001.





3.2:2 Macroscopic maturity assessments

During the dissection of *L. whiffiagonis*, a macroscopic examination of the maturity stages of the fish was made and were assigned maturity stages of I-V. Following macroscopic examination, an annual percentage maturity assessment was determined for female and male megrim and the results presented in Figs. 36a. & b.

<u>Females</u>

For female fish (Fig. 36a.), immature (Stage I) individuals were recorded in each month from January to December. The numbers of immature fish began to increase from June (26.3%) and reached maximum occurrence in the months of July (39.4%) and August (42.1%). Thereafter they decreased in numbers in September (20.1%) but increased again in October (31.6%). Maturing or resting (Stage II) females were recorded in each month from January to December. The numbers of maturing or resting fish began to increase in April (25.6%), reached maximum occurrence in May (53.8%), thereafter decreasing to 20.5% in June. During the subsequent months following June, there was little variation in the numbers of Stage II fish recorded; July (28.6%), August (20.9%), September (29.1%) and October (16.3%). Only small numbers of maturing or resting fish (Stage II) were observed in the remaining months of the year, ranging from November (0.29%) to February (16.4%) in percentage occurrence. Mature (Stage III) female fish were recorded in all months of the year with the exception of May. The numbers of mature fish began to increase in June (53%), and slowly increased July (29.5%), August (35.9%), September (49.6%) and October (48.7%) and reached a maximum occurrence in November (70.9%). Following this maximum occurrence of mature fish, the numbers decreased rapidly to 37.2% in December. Small numbers of Stage III fish were noted in the remaining months, ranging from March (1%) to January (15.4%). Pre-spawning and spawning (Stage IV) fish were recorded in September (1.1%) and increased steadily in the subsequent months; October (3.2%), November (13.1%) and December (22.6%). Stage IV fish reached a maximum occurrence in January (69%). This is consistent with just prior to the spawning period for the species. Thereafter, subsequent to spawning, the numbers decreased rapidly in February (34.1%) and March (1.9%). There were examples of pre-spawning and spawning fish recorded from April to August. Post-spawning (Stage V) fish were recorded throughout most of the months of the year for female fish, which is contrary to the percentage occurrence of Stage V as determined from histological examination of the ovaries. Therefore the

macroscopic assessment of maturity stages for Stage V fish may be subject to some misidentification of the stage. The numbers of post-spawning fish started to increase in January (8.6%) and rose rapidly in February (25.5%) to a maximum occurrence in March (88.1%). Subsequent months resulted in a dramatic drop, April (0.4%) and May (41.9%). A small percentage of Stage V fish were noted in November (12.3%) and December (15.4%). No examples of this stage were observed in the months of June, September and October.

<u>Males</u>

For males (Fig. 36b.), immature (Stage I) fish were recorded in less than half of the 12 months of the year. In April and May, percentages of 25% and 12.5% were obtained for immature fish respectively. However, the majority of Stage I fish were recorded in August (57.1%) and October (50%). There were no examples of this stage present in the remaining months of the year. Maturing or resting (Stage II) male fish were noted in the majority of months with the exception of January, October and November. The numbers of Stage II males began to increase in February (19%) and gradually increased in the subsequent months; March (30.7%), April (50%) and May (62.5%). There was a drop in the number of maturing or resting fish in June (25%), but increased dramatically to a maximum occurrence in July (100%). Thereafter, a decrease in numbers was noted, August (7.1%) and September (64.2%) and finally in December (12.5%). Numbers of mature (Stage III) male fish were present in all months of the year with the exception of January and July. Stage III fish were first recorded in the month of February (4.7%), and increased in March to 69.2%. There was a drop in the number of the stage present in April and May, (25%) in each month, but reached a maximum occurrence in June (75%). Following this, numbers were relatively consistent in the months of August (35.7%), September (21.4%), October (30%), November (25%) and December (25%). Pre-spawning and spawning (Stage IV) males were recorded in September (7.1%), and increased in October (20%) and peaked in numbers in November (75%). There was a drop in the occurrence of the stage following this peak, though numbers were consistent in the following months; December (62.5%), January (50%) and February (66.6%). No examples of Stage IV male fish were recorded from March to August. The numbers of post-spawning (Stage V) males were only recorded in the months of January and February, 50% and 9.5% respectively. Following these occurrences of Stage V, no examples were noted for male fish in any of the remaining months of the year.

Annual percentage occurrences of each macroscopic maturity stage (I-V) for female and male fish are presented in Figs. 37a-e.








3.2:3 Histological maturity assessments

Following histological examination, an annual percentage maturity assessment was determined for female and male megrim in a similar manner as was carried out macroscopically. The results are presented in Figs. 38a. & b. Maturity stages of I–V were present throughout a year.

<u>Females</u>

For females (Fig. 38a.), immature (Stage I) fish were recorded from February to November with the exception of June. Numbers however, were low in each case with maximum occurrence in July (10%). Maturing or resting (Stage II) female fish were recorded in each month throughout the year with the exception of March. Numbers of maturing (Stage II) fish increased rapidly in April, reached maximum occurrence from May (96.6%) to August (95%), thereafter decreasing in abundance. Mature (Stage III) fish were recorded from August (1.6%) onwards. The majority however, were recorded from September (30%) to December (80%) with maximum occurrence in November (85.5%). Small numbers were also noted in January (3.3%) and February (1.1%). Pre-spawning and spawning (Stage IV) females were recorded from December (1.6%), and reached a maximum occurrence in January (83.3%). Thereafter the numbers decreased in February (46.6%), as a subsequence of the majority of fish spawning. Post-spawning or spent (Stage V) females were recorded from November (1.1%) and increased slightly through December (1.6%) and January (6.6%). They increased rapidly in February (46.6%) and reached a maximum occurrence in March (95%). A small number of post-spawning (Stage V) fish were noted in April (12.2%) and none thereafter.

<u>Males</u>

For males (Fig. 38b.), immature (Stage I) fish were recorded in May (12.5%), September (2.6%) and December (12.5%). There no immature males recorded in any of the remaining months throughout the year. Maturing or resting (Stage II) males were recorded from March (30.7%) and increased rapidly, *i.e.* April (71.4%), May (87.5%) and reached a maximum occurrence in June (100%), July (100%) and August (100%). Thereafter the numbers of maturing (Stage II) fish decreased in September (36.8%). Mature (Stage III) male fish were recorded from September (60.5%) and reached a maximum occurrence in October (100%). The number of mature (Stage III) fish decreased in November (50%) and December (50%). Pre-spawning and spawning (Stage IV) fish were recorded in November (50%) and December (37.5%) and reached a maximum occurrence in January (100%) and February (100%). Stage IV (pre-spawning and spawning) males decreased in abundance in March (23%) and were not recorded in the remaining months of the year. Post-spawning (Stage V) male fish were recorded in March (46.1%) and April (28.5%), however, none were recorded in any other months.

Annual percentage occurrences of each histological maturity stage (I-V) for female and male fish are presented in Figs. 39a-e.









3.2:4 Comparison between macroscopic and histological maturity assessments

A comparison between the macroscopic and histological maturity assessments was made to establish the validity of carrying out visual or macroscopic assessments. This was carried out for both female and male *L. whiffiagonis*. The results of these comparisons are given below.

Females

Ovaries which were assessed using histological analysis, were compared with the macroscopic assessment had been made for them at the time of dissection. A total of 870 ovaries were examined using the macroscopic and histological maturity assessments. This allowed a concise comparison to be made for the species in this manner. The results of these comparisons are presented in Table 23. below.

 Table 23. Comparison between histological and macroscopic assessed maturity

 stages for female L. whiffiagonis.

Females	Histological maturity stages										
maturity s	Maturity Stage	Stage I	Stage II	Stage III	Stage IV	Stage V	Total				
	Stage I	18	104			12	134				
	Stage II	2	132	15	4	15	168				
pic	Stage III	2	144	136	14	6	302				
st st	Stage IV		1	35	100	3	139				
ros	Stage V	3	35	3		82	123				
fac	Unidentified		4				4				
Ň	Total	25	420	189	118	118	870				

From the above table, it is possible to see that there was a relatively good match between the macroscopic and histological maturity assessments. The maturity stage which compared most favourably was that of Stage IV (pre-spawning and spawning), with 84.7% of the ovaries having the same maturity assessment following use of both assessment methods. Stage I (immature) had the second highest most favourable comparison of assessment methods, with 72% of ovaries having the same maturity stage. An almost identical percentage (71.9%) of Stage III (mature) ovaries, had the same maturity assessment, while Stage V (post-spawning or spent) ovaries had a 69.4% match between the two assessment methods. The maturity stage with the least favourable comparison between macroscopic and histological assessments was that of Stage II (in maturation or resting). Only 31.4% of Stage II ovaries which were identified histologically, were assessed as Stage II's using macroscopic maturity

assessment. The overall percentage of maturity stages which compared favourably between the two assessment methods was 53.79%, which is a larger percentage than that recorded by other similar studies.

<u>Males</u>

A comparison was also made between the macroscopic and histological maturity assessments for the male testis maturity stages. A total of 118 testis were used for comparative purposes, this being the total number of male gonads available for histological examination. The results of these comparisons are presented in Table 24. below.

Males	Histological maturity stages										
pic ages	Maturity Stage	Stage I	Stage II	Stage III	Stage IV	Stage V	Total				
	Stage I	1	13	1			15				
sco.	Stage II	1	24	1	5	4	35				
rity	Stage III	1	13	9	3	6	32				
Aac atu	Stage IV		1	6	24		31				
M	Stage V				5	0	5				
	Total	3	51	17	37	10	118				

 Table 24. Comparison between histological and macroscopic assessed maturity

 stages for male L. whiffiagonis.

From the above table, it is possible to see that there was a relatively good match between the macroscopic and histological maturity assessments for male megrim. Though only a small number of male gonads were available for comparative purposes, it is still useful validation of macroscopic maturity assessment for the species as this has not been carried out before in Ireland. The maturity stage which compared most favourably using both assessment methods, was that of Stage IV (pre-spawning and spawning), with 64.8% of the testis having the same assessed maturity stage. This corresponds to the most favourable maturity stage of the female fish which was also Stage IV. This maturity stage for male fish is quite different from the other male maturity stages and macroscopic maturity assessment is easily made. Stage III (mature) had the second highest most favourable comparison of assessment methods, with 52.9% of testis having the same maturity stage. For Stage II (in maturation or resting) testis, 47.05% had the same maturity assessment following examination using both methods. Only 3 males were assessed as Stage I (immature) macroscopically, while 1 of these was actually a Stage I, following histological determination. No

Stage V (post-spawning or spent) were found to be correctly assessed using macroscopic maturity assessment, though 10 Stage V males were identified using histological examination. The maturity stage in which the greatest error occurred using macroscopic assessment, was that of Stage II, where 13 gonads were macroscopically assessed to be Stage I and 13 gonads assessed as Stage III, but were actually Stage II, identified as such following histological assessment. The overall percentage of maturity stages for males which compared favourably between the two assessment methods was 49.15%, which was slightly less than the overall percentage for females (53.79%).

3.2:5 Maturity at length keys

Macroscopic and histological maturity at length was determined for female and male fish. For these, the numbers of fish of each maturity stage (I-V) were matched with their corresponding total lengths, giving an indication of at what length a fish should be at a certain maturity stage. For comparative purposes all maturity at length keys were constructed using the same length and age range. Maturity at length, from both macroscopic and histological examinations are presented in Tables 25a-d.

From examination of the macroscopic maturity key for female fish (Table 25a.), it was possible to see in which length classes each maturity stage occurred. The smallest Stage I female was within the length class of 15-15.99cm TL, while the largest female of this maturity stage was within the length class of 39-39.99cm TL. The greatest number (N= 133) of Stage I females were in the length class of 26-26.99cm TL. For female Stage II fish, the smallest were in the length class of 23-23.99cm TL, while the largest Stage II female was in the length class of 44-44.99cm TL. The greatest number (N=113) of Stage II females were in the length class of 30-30.99cm TL. For Stage III females assessed macroscopically, the smallest and largest fish were in the length classes of 22-22.99cm TL and 53-53.99cm TL respectively. The greatest number (N= 177) of Stage III females were in the length class of 31-31.99cm TL. For Stage IV females, the smallest fish was in the length class of 23-23.99cm TL and the largest in the length class of 45-45.99cm TL. The greatest number (N= 63) of Stage IV females were in the length class of 32-32.99 cm TL. Finally, for Stage V macroscopically assessed females, the smallest and largest fish were in the length classes of 23-23.99cm TL and 48-48.99cm TL respectively. The greatest number (N= 159) of Stage V females were in the length class of 28-28.99cm TL.

The macroscopic maturity assessment for male fish (Table 25b.), revealed that the smallest Stage I fish was in the length class of 20-20.99cm TL, while the largest male of this maturity stage was in the length class of 28-28.99cm TL. The greatest number of Stage I males occurred in two length classes, those of 24-24.99cm TL and 26-26.99cm TL, with 5 individuals present in each length class. The smallest and largest Stage II male fish occurred in the length classes of 22-22.99cm TL and 32-32.99cm TL respectively. As with the Stage I male fish, the greatest number of Stage II fish were within two length classes, those of 27-27.99cm TL and 28.28.99cm TL, with 7 males present in each length class. For Stage III male fish, the smallest were in the length class of 23-23.99cm TL, while the largest Stage III male was in the length class of 35-35.99cm TL. The greatest number (N= 9) of Stage III male fish were in the length class of 28-28.99cm TL. The smallest and largest Stage IV macroscopically assessed male fish were in the length class of 22-22.99cm TL and 40-40.99cm TL respectively. For Stage IV male fish, the greatest number (N= 8) were in the length class of 26-26.99cm TL. Finally, for Stage V males, only 5 fish were identified for this maturity stage. The smallest Stage V male was within the length class of 24-24.99cm TL, while the largest was in the length class of 30-30.99cm TL. The greatest number (N= 3) of Stage V male fish were in the length class of 27-27.99cm TL.

Female histological maturity at length as presented in Table 25c., revealed that the smallest Stage I fish were in the length class of 23-23.99cm TL, while the largest Stage I female was in the length class of 33-33.99cm TL. The greatest number (N= 6) of Stage I female fish were in the length class of 26-26.99cm TL. For Stage II females, the smallest and largest fish were in the length classes of 24-24.99cm TL and 45-45.99cm TL respectively. The greatest number (N= 58) of Stage II females were in the length class of 31-31.99cm TL. The smallest Stage III histologically assessed female fish was in the length class of 25-25.99cm TL, while the largest fish was in the length class of 39-39.99cm TL. For Stage III females, the greatest number (N= 29) were in the length class of 32-32.99cm TL. Stage IV female fish ranged in length classes from 24-24.99cm TL to 42-42.99cm TL, with the greatest number (N= 17) in the length class of 27-27.99cm TL. Finally, the smallest and largest Stage V female fish were in the length classes of 25-25.99cm TL and 45-45.99cm TL respectively. The greatest number (N= 17) of Stage V female histologically assessed were in the length class of 28-28.99cm TL.

Only 3 males (Table 25d.) were histologically assessed to be Stage I fish, these being in the length classes of 25-25.99cm TL, 26-26.99cm TL and 28-28.99cm TL. The maturity stage with the most fish was Stage II (N= 51), and ranged in length classes of 20-20.99cm TL to 35-35.99cm TL. The greatest number (N= 10) of Stage II males were in the length class of 27-27.99cm TL. The smallest and largest Stage III male fish were in the length classes of 22-22.99cm TL and 33-33.99cm TL, with the greatest number (N= 3) being in the length class of 27-27.99cm TL. Stage IV males ranged in length from 22-22.99cm TL to 40-40.99cm TL, the greatest number (N= 9) being in the length class of 26-26.99cm TL and 31-31.99cm TL respectively.

Length Class	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
(cm)						
15-15.99	1					1
16-16.99						0
17-17.99						0
18-18.99						0
19-19.99						0
20-20.99						0
21-21.99	3					3
22-22.99	9		1			10
23-23.99	20	2	2	1	1	26
24-24.99	74	4	3	6	3	90
25-25.99	105	28	16	14	19	182
26-26.99	133	33	43	21	61	291
27-27.99	108	54	66	30	144	402
28-28.99	123	108	118	42	159	550
29-29.99	108	111	165	30	146	560
30-30.99	81	113	152	46	105	497
31-31.99	44	104	177	51	96	472
32-32.99	30	106	172	63	65	436
33-33.99	15	74	155	53	35	332
34-34,99	14	56	100	48	34	252
35-35,99	7	50	75	45	25	202
36-36.99	2	24	46	32	14	118
37-37.99	4	18	42	18	13	95
38-38.99	1	13	26	23	11	74
39-39.99	1	8	23	16	5	53
40-40.99		7	9	7	1	24
41-41.99		7	11	9	2	29
42-42.99		3	12	6	2	23
43-43.99		2	3	1	1	7
44-44.99		1	9	2	2	14
45-45.99			9	1	1	11
46-46.99			3		1	4
47-47.99			2			2
48-48.99			2		1	3
49-49.99						0
50-50.99						0
51-51.99			1			1
52-52.99			1			0
53-53.99			1			1
Total	883	926	1444	565	947	4765

Table 25a.Macroscopic maturity at length for female L. whiffiagonis sampledfrom 1997-2001.

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Length	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
Class						
(cm)			_			0
15-15.99			_			0
16-16.99						0
17-17.99						0
18-18.99						0
19-19.99		_				0
20-20.99	1		-			1
21-21.99						0
22-22.99		1		2		3
23-23.99	1		2	1		4
24-24.99	5	5	1.	1	1	12
25-25.99	1	6	4	4		15
26-26.99	5	4	4	8		21
27-27.99	4	7	4	3	3	21
28-28.99	3	7	9	1		20
29-29.99			4	6		10
30-30.99		3	6		1	10
31-31.99		2	1	2		5
32-32.99		1	4	1		6
33-33.99				1		1
34-34.99						0
35-35.99			1			1
36-36.99						0
37-37.99						0
38-38.99						0
39-39.99						0
40-40.99				1		1
41-41.99						0
42-42.99						0
43-43.99						0
44-44.99						0
45-45.99						0
46-46.99						0
47-47.99						0
48-48.99						0
49-49.99						0
50-50.99						0
51-51.99						0
52-52.99						0
53-53.99				-		0
Total	20	36	39	31	5	131
T. O. 1991						

Table 25b.Macroscopic maturity at length for male L. whiffiagonis sampled1997-2001.

Length Class (cm)	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
15-15.99	†					0
16-16.99						0
17-17.99			1			0
18-18.99						0
19-19.99	1					0
20-20.99						0
21-21.99						0
22-22.99						0
23-23.99	2					2
24-24.99	2	2		1		5
25-25.99	3	12	5	1	2	23
26-26.99	6	22	7	10	6	51
27-27.99	1	30	12	17	14	74
28-28.99	5	48	5	14	17	89
29-29.99	3	37	18	9	11	78
30-30.99	1	52	14	7	14	88
31-31.99		58	24	12	10	104
32-32.99		45	29	15	13	102
33-33.99	2	28	27	10	6	73
34-34.99		22	12	6	7	47
35-35.99		22	15	7	6	50
36-36.99		11	9	1	3	24
37-37.99		5	6	1	2	14
38-38.99		5	5	4	4	18
39-39.99		6	1	1		8
40-40.99		2		1		3
41-41.99		2				2
42-42.99		6		1	1	8
43-43.99			1			0
44-44.99		4	1		1	5
45-45.99		1			1	2
46-46.99						0
47-47.99						0
48-48.99						0
49-49.99			1			0
50-50.99						0
51-51.99						0
52-52.99						0
53-53.99			1			0
Total	25	420	189	118	118	870

Table 25c.Histological maturity at length for female L. whiffiagonis sampledfrom 1997-2001.

Length	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
Class						
(CM)						0
15-15.99						
16-16.99						
17-17.99						0
18-18.99		_				0
19-19.99						0
20-20.99		1				
21-21.99						0
22-22.99			1	2		3
23-23.99		I		1		2
24-24.99		5	1	5		11
25-25.99	1	6	2	5	1	15
26-26.99	1	7	2	9	1	20
27-27.99		10	3	6	1	20
28-28.99	1	9	1	2	4	17
29-29.99		3	1	4	1	9
30-30.99		4	2	1	1	8
31-31.99		1	2		1	4
32-32.99		3	1	1		5
33-33,99			1			1
34-34.99						0
35-35.99		1				1
36-36.99	1					0
37-37.99						0
38-38.99					1	0
39-39.99						0
40-40.99				1		1
41-41.99					1	0
42-42.99						0
43-43.99			1			0
44-44 99						0
45_45 00						0
46_46 99						0
47_47 00						0
18_18 00						0
10 10 00						0
47-47.77 50 50 00						0
50-50.99						0
51-51.99						0
52-52.99						0
33-33.99			1.0	28	10	110
Total	3	51	17	37	10	118

Table 25d.Histological maturity at length for male L. whifflagonis sampledfrom 1997-2001.

3.2:6 Maturity at age keys

Macroscopic and histological maturity at age was determined for female and male fish. For these, the numbers of fish of each maturity stage (I-V) were matched with their corresponding age. This was an indicator of at what age a fish should be at a certain maturity stage. For comparative purposes all maturity at age keys were constructed using the same length and age range. Maturity at age, both macroscopic and histological are presented in Tables 26a-d.

Following macroscopic maturity at age for females (Table 26a.), it was observed that the age range of Stage I fish was from 2 to 9 years old. The greatest number (N= 278) of Stage I females were aged 4 years old. For Stage II female fish, the age range was 3 to 10 years old, with age group 5 having the greatest number (N= 260) of Stage II fish. Stage III females ranged in age from 3 to 16 years old, the greatest number (N= 399) being in age group 5. For female macroscopic maturity at age, Stage IV fish ranged in age from 3 to 11 years old, with age group 5 having the greatest number (N= 144) of Stage IV individuals. Finally, for females, Stage V fish ranged in age from 2 to 15 years old. The greatest number (N= 397) of Stage V female fish were in age group 4.

The age range of Stage I macroscopic maturity at age for males (Table 26b.) was from 3 to 7 years old. The greatest number of Stage I males occurred in two age classes, those of 4 and 7 years old with 4 individuals present in each age class. For Stage II male fish, the youngest and oldest fish were in age groups 4 and 7 respectively. Age group 5 had the greatest number (N= 13) of Stage II male fish. The age range for Stage III male fish was from 4 to 8 years old, with the greatest number (N= 14) of this maturity stage being in age group 4. For Stage IV males, the youngest age was 4 years old, while the oldest age was 7 years. The greatest number (N= 10) of Stage IV males were in the age group of 5 years old. Finally, for macroscopic maturity at age for males, there were only 5 individuals that were Stage V. The age range was from 4 to 6 years old, with the greatest number (N= 3) of Stage V males being in the age group of 5 years old.

Histological maturity at age for female fish (Table 26c.) revealed an age range of 1 to 6 years old for Stage I fish. The greatest number (N=11) of Stage I females were in the age group of 4 years old. For Stage II female fish, the youngest and oldest individuals were in the age groups of 3 and 12 years respectively. Age group 5 with 112 fish present was the most frequently recorded age group for Stage II females. Stage III females had an age range of 3 to 8 years old, with the greatest number (N= 73) of Stage III fish being in the age group of 5 years old. An age range of 3 to 10 years old was recorded for histologically assessed female fish of maturity Stage IV. The greatest number (N= 35) of Stage IV females were aged 4 years old. Finally for Stage V female fish, an age range of 3 to 9 years old was observed, with the age group of 4 years being the most frequently recorded, having 46 individuals present.

For histological maturity at age for male fish (Table 26d.), there were only 3 Stage I fish, these being in the age classes of 4 and 7 years old. Stage II males ranged in age from 3 to 7 years old, with the greatest number (N= 15) being in the age group of 5 years old. For Stage III male fish, an age range of 3 to 8 years old was recorded, with the greatest number (N= 5) of Stage III being in the age group of 4 years old. The youngest and oldest Stage IV males had an age range of 3 to 7 years old, while the greatest number (N=15) of Stage IV fish were in the age group of 5 years old. Finally, for Stage V male fish, an age range of 4 to 7 years old was observed, with the age group of 5 being the most frequently recorded, having 4 individuals present.

Age Class (years)	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
2	1				1	2
3	180	30	24	27	50	311
4	278	184	194	107	397	1160
5	202	260	399	144	241	1246
6	101	246	362	137	127	973
7	45	114	228	89	80	556
8	24	41	76	32	31	204
9	2	11	33	16	10	72
10		5	11	9	3	28
11			4	3	1	8
12			2			2
15			1		1	2
16			1			1
Blank Age	50	35	109	1	5	200
Total	883	926	1444	565	947	4765

Table 26a.Macroscopic maturity at age for female L. whiffiagonis sampledfrom 1997-2001.

Table 26b.Macroscopic maturity at age for male L. whiffiagonis sampled from1997-2001.

Age Class	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
(years)						
2						0
3	2			1		3
4	4	12	14	7	1	38
5	3	13	9	10	3	38
6	5	8	6	9	1	29
7	4	2	8	3		17
8			1			1
9						0
10						0
11						0
12						0
15						0
16						0
Blank Age	2	1	1	1		5
Total	20	36	39	31	5	131

Age Class (years)	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
2	1					1
3	9	15	2	12	12	50
4	11	96	31	35	46	219
5	3	112	73	26	19	233
6	1	93	43	23	17	177
7		62	31	15	13	121
8		29	9	5	6	49
9		9			5	14
10		3		1		4
11						0
12		1				1
15						0
16						0
Blank Age				1		1
Total	25	420	189	118	118	870

Table 26c.Histological maturity at age for female L. whiffiagonis sampled from1997-2001.

Table 26d.Histological maturity at age for male L. whiffiagonis sampled from1997-2001.

Age Class (years)	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
2						0
3		1	1	1		3
4	2	14	5	10	3	34
5		15	3	15	4	37
6		12	4	7	2	25
7	1	5	3	3	1	13
8			1			1
9						0
10						0
11						0
12						0
15						0
16						0
Blank Age		4		1		5
Total	3	51	17	37	10	118

3.2:7 Maturity ogives

Maturity ogives were constructed for the total number of female and male fish sampled. From these, macroscopic and histological estimates of first maturity at length and age were determined. The estimates from the maturity ogive determinations are presented in Table 27., and in Figs. 40a-h.

Table 27.	Maturity	ogive	estimates	for	female	<u>& 1</u>	nale <i>l</i>	. H	hiffiagor	<u>uis</u>	sampled
			during	<u>g 19</u>	97-2001	÷					

Parameter		Female		Male				
Length (cm)	L25%	L 50%	L75%	L25%	L50%	L75%		
Macroscopic	24.0cm	25.0cm	27.0cm	21.0cm	22.0cm	24.0cm		
Histological	23.0cm 24.0cm		25.0cm	25.0cm	25.0cm	26.0cm		
		Female		Male				
Age (years)	A 25%	A 50%	A 75%	A 25%	A 50%	A 75%		
Macroscopic	lyr	2yrs	4yrs	2yrs	3yrs	4yrs		
Histological	1.75yrs	2yrs	3yrs	2yrs	2.5yrs	3yrs		

The macroscopic maturity at length ogive for female fish (Table 27.), provided an estimate for $L_{25\%}$ of 24.0cm, which was closely followed by 25.0cm for $L_{50\%}$ (Fig. 40a.). The estimate for $L_{75\%}$ recorded a larger value of 27.0cm. When a histological maturity at length ogive for the same fish was examined (Table 27.), estimates of 23.0cm, 24.0cm (Fig. 40b.), and 25.0cm were obtained for $L_{25\%}$, $L_{50\%}$ and $L_{75\%}$ respectively. For the male macroscopic maturity at length ogive (Table 27.), an estimate of 21.0cm was determined for $L_{25\%}$, closely followed by 22.0cm for $L_{50\%}$ (Fig. 40c.). A larger estimate was recorded for $L_{75\%}$, that of 24.0cm. When the males were examined histologically (Table 27.), an estimate of 25.0cm was determined for $L_{25\%}$ and $L_{50\%}$ (Fig. 40d.), while a value of 26.0cm was obtained for $L_{75\%}$.

For macroscopic maturity at age for female fish (Table 27.), an estimate of 1 year was determined for $A_{25\%}$, closely followed by 2 years for $A_{50\%}$ (Fig. 40e.). For A-75%, an estimate of 4 years of age was obtained. When a histological maturity at age ogive for the same fish (Table 27.), was constructed, an estimate of 1.75 years was determined for $A_{25\%}$. This value was only just behind that obtained for $A_{50\%}$, (Fig. 40f.) which was 2 years of age, while an estimate of 3 years of age was recorded for $A_{75\%}$. For the male macroscopic maturity at age ogive, (Table 27.), estimates of 2, 3 and 4 years of age were recorded for $A_{25\%}$, $A_{50\%}$ (Fig. 40g.) and $A_{75\%}$ respectively. Estimates of maturity differed slightly for males examined histologically, (Table 27.), where maturity at age was determined to be 2 years for $A_{25\%}$, 2.5 years for $A_{50\%}$ (Fig. 40h.) and 3 years of age for $A_{75\%}$.

Following examination of the estimates for first maturity calculated by use of the maturity ogives for the female and male *L. whiffiagonis*, differences between the sexes became apparent. Differences between macroscopic and histological maturity for female and male fish were also recorded. These differences are examined in greater detail in Chapter 4.







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3.2:8 Histological image analysis

Image analysis was carried out on the histologically prepared slides of the female and male reproductive tissues. Percentage oocyte length frequency distributions were then constructed for the female maturity stages. The prevalence of atresia (Pa) and the relative intensity of atresia (Ia) in female gonads was also estimated. Histological developmental structures observed on the prepared slides of the ovaries and testes of the fish were identified and presented in annotated images in *Plates 31-36.* and *37-42.* respectively.

3.2:8:1 Oocyte length frequencies

Percentage oocyte length frequency distributions are presented in Figs. 41a-e. Five hundred oocytes were measured for each of the female maturity stages I-V, making a total of 2,500 oocyte diameters recorded. For Stage I female fish, an oocyte diameter range of 27-123 μ m and a mean diameter of 57.86 μ m (± s.d. 12.00) were obtained (Fig. 41a.). The largest percentage (57%) of Stage I oocytes were recorded in the diameter class of 45-64µm. Only 5 diameter classes were constructed for the Stage I oocytes, indicating the similarity in oocyte size throughout Stage I ovaries. Stage II oocytes (Fig. 41b.) ranged in diameter from 45-246µm with a mean oocyte diameter of 136.85µm (± s.d. 27.60). The largest percentage (20.6%) of Stage II oocytes were found in the diameter class of 125-144µm. For Stage III females (Fig. 41c.), an oocyte diameter range of 126-451µm and a mean diameter of 272.52µm (± 48.78) were recorded. The largest percentage (15.6%) of Stage III oocytes were recorded in the diameter class of 285-304µm. An oocyte diameter range of 136-686µm was obtained for oocytes measured in Stage IV ovaries. The largest percentage (10.8%) of Stage IV oocytes (Fig. 41d.) were in the diameter class of 345-364µm and had a mean oocyte diameter of 346.64µm (± 78.19). Lastly, for Stage V female fish (Fig. 41e.), an oocyte diameter range of 61-616 μ m and a mean diameter of 233.53 μ m (± 57.14). The largest percentage (16.8%) of Stage V oocytes were in the diameter class of 105-124µm.

Maturity Stage	Oocyte Diameter Range (µm)	Mean Oocyte Diameter (µm)	Standard Deviation	
Stage I	27-123	57.86	± 12.0051	
Stage II	45-246	136.85	± 27.6081	
Stage III	126-451	272.52	± 48.7843	
Stage IV	136-686	346.64	± 78.1949	
Stage V	61-616	233.53	± 57.1404	

Table 28.	Oocyte	length	parameters 1	for f	emale	maturity	/ stages I-	<u>V.</u>
			_					



3.2:8:2 Estimation of atresia

The prevalence of atresia (Pa) was determined by examining all Stage V (postspawning or spent) ovaries. A total of 10 monthly samples were observed to have Stage V fish present. The presence or absence of atretic oocytes were then noted in all of the Stage V ovaries. From these 10 monthly samples, atretic oocytes were observed in 9 of the samples. A total of 75 fish were observed with atretic oocytes out of 118 overall Stage V females. This represented an overall percentage of 63.5% atretic oocytes. The atretic oocytes were identified as either alpha (α) or beta (β) phase, with 88.05% being alpha (α) phase and remaining 11.94% recorded as beta (β) phase atresia. For the 10 monthly samples examined, the prevalence of atresia is presented in Fig. 42. From examination of Fig. 42., it was observed that the presence of atresia varied considerably. No atretic oocytes were recorded in the Stage V fish from November 1998, while for the months of December 1997 and April 1999, 100% of Stage V ovaries contained atretic oocytes. The remaining 7 monthly samples with Stage V females ranged in prevalence of atresia from 55.5% to 70%.



The relative intensity of atresia (Ia) was calculated by examining a total of 31 Stage V (post-spawning or spent) female ovaries from the 9 monthly samples which had atretic oocytes present. It was only possible to determine the relative intensity of atresia from 7 of the monthly samples with atretic oocytes, as 2 of the samples (December 1997 & April 1999), had only 1 Stage V ovary with atresia present. These were deemed insufficient to get an accurate estimation of atresia. For 5 of the remaining 7 samples, 5 ovaries were examined, 4 ovaries from January 1999, and 2

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from February 2001. An overall mean percentage relative intensity of atresia of 24.29% was calculated for the Stage V ovaries, and ranged from 13.69% to 39.60%.



As observed in Fig. 43. above, there was considerable variation in the percentages of atresia. For the 5 Stage V ovaries examined from April 1997, percentages of atresia ranged from 13.69% to 22.46%, with a mean percentage of 19.42%. This mean value was the lowest average percentage recorded from all examined samples. A range of 20.72% to 36.76% was recorded for February 1998, with a mean percentage atresia rate of 25.63% which was similar to the overall mean percentage determined. When January 1999 was examined, a percentage range of 21.5% to 39.60% was recorded. The value of 39.60% was the highest percentage observed for the relative of intensity of atresia (Ia). A mean percentage of 27.17% was obtained for January 1999. For February 1999, a range of 21.66% to 30.86%, and a mean percentage of 24.69% was determined. A range of 22.52% to 37.33% was recorded for March 1999 which was the second highest percentage value obtained for the examined samples. A mean percentage of 27.25% was also determined for the sample from March 1999. When ovaries from March 2000 were examined, a range of 16.75% to 30.16% and a mean percentage of 24.78% was recorded. The minimum percentage (16.75%) obtained for this sample was the second lowest value determined during the estimation of the relative intensity of atresia. The last sample examined for atresia was that from February 2001 which had only 2 Stage V ovaries with atretic oocytes present. These 2 ovaries returned percentages of atresia of 18.42% and

23.84%, with a mean percentage of 21.13%. Along with an Stage V ovary from the April 1997 sample which had the same percentage (18.42%) as February 2001, these were the third lowest values recorded during the determination of the relative intensity of atresia. The descriptive statistics recorded for the relative intensity of atresia are presented in Table 29. below.

Parameter	r Month							
	April 1997	February 1998	January 1999	February 1999	March 1999	March 2000	February 2001	Overall
Min. %	13.69	20.72	21.50	21.66	22.52	16.75	18.42	13.69
Max. %	22.46	36.76	39.60	30.86	37.33	30.15	23.84	39.60
Mean %	19.42	25.63	27.17	24.69	27.25	24.78	21.13	24.29
Std. Dev.	±3.609	±6.411	±8.354	±3.752	± 5.835	±5.455	±3.832	±2.971
Variance	13.027	41.112	69.792	14.084	34.053	29.767	14.688	8.831

Table 29. Summary of relative intensity of atresia (Ia) for L. whiffiagonis.

3.2:8:3 Female histological structures

The developmental structures recorded within oogensis for histologically examined female *L. whiffiagonis* in maturity stages I-V were identified and annotated on *Plates 31-36.* as presented below.

For Stage I (immature or virgin) female fish (*Plate 31.*), most of the gonad was composed of oogonia or immature oocytes. The oogonia were extremely small in size, approximately 6-10 μ m in diameter and were normally located within the gonad in clusters with lumen (*L*) in between. The remaining principal developmental structure present in this maturity stage was the chromatin nucleolus stage which consisted of larger oocytes ranging in diameter from 30-70 μ m. The chromatin nucleolus stage was characterised by a large circular nucleus which stained a lighter colour than the surrounding tissue which was darker in appearance. The ovarian walls (*OW*) of Stage I female fish were thin, reflecting the immature reproductive status of the gonads.

The histological characteristics of Stage II (in maturation or resting) female fish (*Plate 32.*) contained more developmental phases than those of Stage I ovaries. As with Stage I ovaries, oogonia were present in large numbers, though not quite as densely packed as the previous maturity stage. Chromatin nucleolus oocytes were also present but not as frequently as in Stage I fish. The most distinctive developmental characteristic present in Stage II females was that of perinucleolar stage oocytes (PN). Perinucleolar oocytes were characterized by a large circular nucleus and peripheral nucleoli and ranged in diameter from 300-500 μ m. The Stage II developmental characteristics were interspersed with lumen.

When Stage III (mature) females (*Plate 33.*) were examined, it was observed that the oocyte composition of the ovaries changed dramatically in appearance when compared to the previous two reproductive maturity stages. Almost the entirety of the ovaries consisted of vitellogenic oocytes which ranged in diameter from 600-800 μ m. Within the vitellogenic oocytes were the cortical alveoli (*CA*) which appeared as large circular clear vacuoles around the periphery of the oocytes. Also present in the Stage III ovaries were oocytes at the perinucleolar stage. For Stage III females, the thickness of the ovarian wall began to become reduced as the ovary ripened towards the prespawning and spawning maturity stage. Scattered within the ovaries between the vitellogenic oocytes were small clusters of oogonia and lumen.

For Stage IV (pre-spawning & spawning) fish (Plate 34.), several developmental characteristics were recorded. The maturity stage was primarily composed of vitellogenic oocytes at a later phase of development than that of the previous maturity stage. Within these vitellogenic oocytes were the Stage V characteristics of the migratory nucleus (MN) and yolk vesicles (YV). Migratory nuclei were observed in the vitellogenic oocytes beside a yolk vesicle which increased in size and moved the nucleus through the oocyte cytoplasm toward the periphery of the oocyte. This can be observed in Plate 34., along with vitellogenic oocytes that have a central nucleus which have not undergone the migratory nucleus phase of oogensis. The yolk vesicles were a later development of the cortical alveoli which were present in some slightly smaller and not as developed oocytes. Also present were several hydrated oocytes which were the final stage of vitellogenesis before ovulation. Hydration results in the enlargement of the oocyte due to a intake of water. As with earlier maturity stages, oogonia and lumen were observed throughout the Stage IV ovaries. The ovarian walls of the Stage IV female fish were very thin indicating the onset of the spawning event and the imminent release of ova.

When recording the developmental structures of Stage V (post-spawning or spent) female fish, it was decided to divide this maturity stage into early and advanced phases, (*Plates 35. & 36.*) respectively. This was necessary in order to examine early and advanced phases of atresia. Present within the early Stage V ovaries were the

developmental characteristics observed earlier such as oogonia, chromatin nucleolus and perinucleolar stage oocytes. Early atretic oocytes were recorded and identified by the presence of the zona radiata (ZR). These were oocytes in the alpha (α) phase of the atretic process. The zona radiata begins to separate from the cytoplasm of an atretic oocyte and breaks down as atresia progresses. This can be clearly observed with atretic oocytes in *Plate 35*. The early atretic oocytes ranged in diameter from 150-400 μ m.

Advanced post-spawning Stage V ovaries (*Plate 36.*) were characterised by large advanced atretic oocytes, ranging in diameter from $300\mu m$ to >500 μm . Contained within these large advanced atretic oocytes were yolk vesicles which measured approximately 65 μm in diameter. The advanced atretic oocytes which were in the beta (β) phase of atresia, were identified by the separation of the zona radiata from the oocyte cytoplasm as with the early atretic oocytes. This separation was more evident in the advanced atretic oocytes than the early atretic oocytes. Along with some oogonia and lumen, there were several hydrated oocytes observed in the Stage V ovaries. The principal developmental characteristic recorded in the Stage V ovaries other than advanced atretic oocytes, were the presence of numerous post-ovulatory follicles (*POF*). These were identified by the large empty spaces present within the gonad. Post-ovulatory follicles were also used as an indication of a recent spawning event, as the empty follicle represented an ovulated vitellogenic oocyte. The ovary walls of Stage V fish were very thick following spawning and the recovery process.



Plates 31-36. Histological structures of female maturity Stages I-V.

Plate 31. Stage I (immature or virgin) ovary. 1-Chromatin nucleolus stage, 2-Oogonia, L-Lumen. (Magnification-100x)



Plate 32. Stage II (in maturation or resting) ovary. 1-Chromatin nucleolus stage, 2-Oogonia, L-Lumen, PN-Perinucleolar stage oocyte, OW-Ovarian wall. (Magnification-40x)



Plate 33. Stage III (mature) ovary. 2-Oogonia, 3-Vitellogenic oocyte, L-Lumen, CA-Cortical alveoli, PN-Perinucleolar stage oocyte. (Magnification-40x)



Plate 34. Stage IV (pre-spawning & spawning) ovary. 2-Oogonia, 3-Vitellogenic oocyte, 4-Hydrated oocyte, L-Lumen, N-Nucleus, CA-Cortical alveoli, YV-Yolk vesicle, MN-Migratory nucleus. (Magnification-100x)



Plate 35. Stage V (early post-spawning or spent) ovary. 1-Chromatin nucleolus stage, 2-Oogonia, 5-Early atretic oocyte, L-Lumen, ZR-Zona radiata, PN-Perinucleolar stage oocyte. (Magnification-100x)



Plate 36. Stage V (advanced post-spawning or spent) ovary. 2-Oogonia, 4-Hydrated oocyte, 6-Advanced atretic oocyte, L-Lumen, ZR-Zona radiata, YV-Yolk vesicle, POF-Post ovulatory follicle. (Magnification-100x)

3.2:8:4 Male histological structures

The developmental structures recorded within spermatogensis for histological examined male *L. whiffiagonis* maturity stages I-V were identified and annotated on *Plates 37-42.* as presented below.

For Stage I (immature or virgin) (*Plate 37.*) male fish, the principal developmental characteristic was the presence of spermatogonia (SG) within the testis. These were extremely small and closely packed together, and were distinguished by a central nucleus and nucleolus. Located also within the testis, were spermatocytes (SC) which were formed from the meiotic division of the spermatogonia. These spermatocytes were a later developmental phase of the male reproductive process. Seminiferous tubules were clearly observed in the testis, the sperm (SP) later using these to travel directly to the exterior of the fish during the spawning event. Gonadal tissue such as connective membranes and blood vessels as well as lumen (L) were also recorded within the Stage I male fish.

When the testes of the fish reached Stage II (in maturation or resting) (*Plate* 38.), considerable changes were observed. Apart from the developmental structures recorded for the previous maturity stage such as seminiferous tubules and lumen, several more advanced phases of spermatogensis were observed. There were a lot less spermatogonia present in the testis than for Stage I fish, but more spermatocytes were noted. The spermatocytes were larger and were observed to be more developed than the previous maturity stage at the same magnification. Recorded for the first time in the Stage II testes were the presence of a few spermatozoids (*SZ*), which were located in the proximal tubules, but in an early phase of development.

When Stage III (mature) male fish (*Plate 39.*) were examined, several different developmental characteristics were recorded. Spermatogonia and spermatocytes were observed but only in the testis cortex (*see Plate 42.*). Spermatozoids were predominant, but a new developmental structure, that of spermatids (*ST*) was recorded. The spermatids were formed following the division of some of the spermatocytes and could be recognized by nuclear condensation which began around one side of the nucleus and the formation of a flagella. As in the previous maturity stages, seminiferous tubules and lumen were observed. For the Stage III testes, it was noted that the gonads were tightly packed with developmental structures, leaving very little intercellular space other than the proximal tubules containing the spermatozoids, the seminiferous tubules and a little lumen.
The Stage IV (pre-spawning & spawning) testes (*Plate 40.*) were very similar to those for the Stage III males, except that developmental characteristics were more advanced. Spermatozoids were again predominant and within the proximal tubules as spawning time approached. These were longitudinal in appearance and located at the distal edge of the testis. An occasional spermatogonia was observed as were spermatocytes which appeared circular and were located close to the spermatozoids. This maturity stage was the most easily recognisable phase of spermatogensis.

Finally, Stage V (post-spawning or spent) testes (*Plate 41.*) were characterised by empty seminiferal ducts which were clearly observed. These were empty due to spawning and the release of the sperm from the testis. Within some of these ducts were residual spermatozoids and sperm which had not been released. A few spermatogonia were recorded, these giving rise to the future development of new spermatozoids. As in previous maturity stages, small amounts of lumen was observed within the testes, though this was difficult to detect as Stage V male gonads contained many intercellular spaces such as the empty seminiferal ducts and proximal tubules.



Plates 37-42. Histological structures of male maturity Stages I-V.

Plate 37. Stage I (immature or virgin) testis. 1-Seminiferous tubules, 3-Gonadal tissue, L-Lumen, SG-Spermatogonia, SC-Spermatocytes. (Magnification-400x)



Plate 38. Stage II (in maturation or resting) testis. 1-Seminiferous tubules, L-Lumen, SG-Spermatogonia, SC-Spermatocytes, SZ-Spermatozoids. (Magnification-400x)



Plate 39. Stage III (mature) testis. 1-Seminiferous tubules, L-Lumen, SG-Spermatogonia, SC-Spermatocytes, ST-Spermatids, SZ-Spermatozoids. (Magnification-400x)



Plate 40. Stage IV (pre-spawning & spawning) testis. 1-Seminiferous tubules, L-Lumen, SG-Spermatogonia, SC-Spermatocytes, SZ-Spermatozoids. (Magnification-100x)



Plate 41. Stage V (post-spawning or spent) testis. 2-Seminiferal ducts, L-Lumen, SG-Spermatogonia, SZ-Spermatozoids, SP-Sperm. (Magnification-100x)



Plate 42. Overview of a Stage II (in maturation or resting) testis. 1-Seminiferous tubules, L-Lumen, SG-Spermatogonia, SC-Spermatocytes, TC-Testis cortex. Presence of later developmental stages further from testis cortex visible. (Magnification-100x)

3.2:9 Gonadosomatic index

The gonadosomatic index (GSI) was calculated for the combined sexes of L. whiffiagonis over the entire 36 month sampling period and the results presented in Fig. 44., along with the plot for condition factor. Sexes were combined as there were several months of samples where no male fish were recorded. The ascent to the peak spawning times varied throughout the sampling period. During 1997, the GSI value started to increase during November 1997 and thereafter followed an average gradual increase in the GSI value, with a maximum GSI attained in during January 1998. The increase in GSI value for the following spawning season began in October 1998 with a dramatic increase from December 1998 to a peak in January 1999. A similar dramatic increase in GSI value occurred towards the latter end of 1999, with the increase starting in November 1999 and reaching a peak in January 2000. These peak spawning times correspond with the majority of fish being at maturity Stage IV (prespawning & spawning). Peak spawning times for L. whiffiagonis were clearly observed for each year sampled. Three peak spawning times were recorded over the duration of the investigation. These were the February 1998, January 1999 and January 2000. Immediately following these months, there was a dramatic drop in the mean GSI value which indicated that the fish had spawned, and had a resulting lower percentage of gonad comprising total body weight. From the GSI, it was determined that L. whiffiagonis had spawned twice within a single year, i.e. February 1998 and January 1999, and subsequently again within the following 12 month period, in January 2000. On the graph (Fig. 44.), any months when no sample was obtained has been omitted in order to present a continuous and representative estimation of GSI.

3.2:10 Condition factor

The condition factor (CF) was calculated from the monthly samples with female and male fish being combined, and is presented on Fig. 44. along with gonadosomatic index (GSI). Highest values for condition factor were observed in the months just prior to spawning, *i.e.* January 1998 and 1999, as well as November 1999. The latter occurred 2 months before the spawning time of January 2000. Following these highest condition factor values, there were also relatively high peaks recorded during July and September 1999. The value determined for September 1999 was very close to that recorded for November 1999 which was the highest value for that year. The lowest values recorded for condition factor in descending order were in April 1999, March 2000, April 1998 and April 1997. The ascending part of the condition

Chapter Three: Results.

factor peaks were not as direct as those for the gonadosomatic index, with the peaks being less prominent. As with the plot for gonadosomatic index (Fig. 44.), the plot for condition factor has months when no sample was obtained omitted. The condition factor determined for *L. whiffiagonis* is summarised in Table 30. below.

Months	Year	Month	No. of Mean CF		Standard
			Fish	Value	Deviation
1	1997	April	81	0.005896	± 0.000643
2	1997	May	170	0.006108	± 0.001013
3	1997	June	50	0.006145	± 0.000790
4	1997	July	139	0.006437	± 0.000591
5	1997	August	192	0.006015	± 0.000681
6	1997	September	163	0.006163	± 0.000623
7	1997	October	235	0.006272	± 0.000907
8	1997	November	92	0.007419	± 0.000682
9	1997	December	78	0.007611	± 0.000878
10	1998	January	144	0.006331	± 0.000805
11	1998	February	187	0.006022	± 0.000732
12	1998	April	146	0.005853	± 0.000608
13	1998	October	117	0.006681	± 0.000886
14	1998	November	170	0.006418	± 0.000823
15	1998	December	279	0.006720	± 0.001199
16	1999	January	160	0.006590	± 0.000787
17	1999	February	157	0.006146	± 0.001521
18	1999	March	369	0.005795	± 0.000558
19	1999	April	531	0.005414	± 0.000481
20	1999	May	284	0.005879	± 0.000504
21	1999	June	202	0.006204	± 0.000747
22	1999	July	129	0.007133	± 0.000954
23	1999	August	161	0.006164	± 0.000875
24	1999	September	119	0.007369	± 0.000689
25	1999	October	85	0.006368	± 0.00070
26	1999	November	89	0.007420	± 0.001132
27	2000	January	98	0.007343	± 0.000869
28	2000	March	221	0.005738	± 0.000582

Table 30. Summary of condition factor for L. whiffiagonis during 1997-2000.



3.2:11 Fecundity

The fecundity of *L. whiffiagonis* was determined from 3 samples of Stage IV (pre-spawning) ovaries from the months of January 1998, January 1999 and February 2001. No fecundity samples were obtained for examination during 2000 due to adverse weather conditions. The counted oocytes were back calculated to numbers of oocytes at ovary weight to obtain absolute and relative fecundity. Values of mean, maximum and minimum number of oocytes between ovaries and samples were determined, as well as mean oocyte length and the oocyte length range for each sample. Regression analyses were carried out between fecundity or number of eggs and total length, total weight, age and gonad weight (Figs. 45a-d.). Percentage oocyte length frequency distribution and mean fecundity for the months examined were determined (Figs. 45e. & f.). All fecundity calculations were determined using all samples combined and based upon estimates of absolute fecundity.

The relationship between fecundity and total length (TL) was examined (Fig. 45a.) and showed a significant correlation ($R^2 = 0.6002$, P< 0.05). This relationship can be written as :

$$F=0.0058TL(cm)^{24455}$$

where F = fecundity in number of eggs and TL = total length in centimetres. The relationship between fecundity and total weight (W) (Fig. 45b.) also showed a significant correlation ($R^2 = 0.7014$, P<0.01). The relationship can be written as:

$$F=0.0063W(g)^{1082.1}$$

where F = fecundity in number of eggs and W = weight in grams. There was a correlation ($R^2 = 0.2394$, P< 0.05) for the relationship between fecundity and age (Fig. 45c.). The relationship can be written as:

$$F = 0.0056 A(yrs)^{44294}$$

where F = fecundity in number of eggs and A = age in years. The relationship between fecundity and gonad weight (Fig. 45d.) was highly significantly correlated ($R^2 = 0.7073$, P< 0. 05). The relationship can be written as:

$$F = 0.0021 GW(g)^{9299}$$

where F= fecundity in number of eggs and GW = gonad weight in grams.





The percentage oocyte length frequency distribution (Fig. 45e.) recorded an oocyte size range of $325-725\mu$ m. When the oocyte lengths were compared between the monthly samples, it was observed that January 1998 had the smallest size range, that of $325-525\mu$ m, followed by January 1999 ($325-600\mu$ m), while February 2001 had the largest, that of $325-725\mu$ m. The largest percentage (29.7%) of oocyte lengths for January 1998 were in the size range of $425-449\mu$ m and had a mean length of 433.75μ m. For the sample from January 1999, the largest percentage (20%) of oocyte lengths were in the size range of $500-524\mu$ m with a mean length of 500.75μ m. Finally, the largest percentage (20.8%) of oocyte lengths for February 2001 were in the size range of $575-599\mu$ m. Oocytes from February 2001 had a mean length of 553.75μ m.

When mean fecundity for the 3 months was examined (Fig. 45f.), it was observed that the highest number of oocytes were recorded during January 1999, followed by January 1998 and February 2001, the latter being considerably lower in fecundity than the previous two monthly samples. This was an interesting result as many more ovaries (N= 68) were examined for fecundity for February 2001 than for January 1998 and 1999, N= 35 and N= 13 respectively. Fecundity determination for *L. whiffiagonis* is summarised in Table 31. below.

Monthly No. of A		Absolute	Absolute Relative		num	Maximum	Standard	
Sample	Ovaries	Fecunality	recunalty	Fecun	aity	recunally	Deviation	
January 1998	35	200860.5	696000	35817		607493	139673.3	
January 1999	13	237699.9	869000	42318		640523	181430.5	
February 2001	68	123999.2	818000	26522		451730	92344.86	
Monthly S	ample	Mean Oo	Mean Oocyte Length (µm)			Oocyte Length Range (µm)		
January 1998			433.75			325-525		
January 1999			500.75			325-600		
February 2001			553.75			325-725		

Table 51. Summary of fecunity parameters determined for L. with finger	rameters determined for L. whiffiagon	ters dete	param (ecundity	y of	Summary	Table 31.
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Chapter Four

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CHAPTER FOUR : PART 1. SAMPLING DISCUSSION

4.0 General introduction

The sampling procedures, length frequencies, length-weight regressions and mean lengths and weights at age determined for *L. whiffiagonis* off the west coast of Ireland were compared with similar works and assessments elsewhere in Ireland and Europe for the species.

4.0:1 Samples

Over the duration of the present investigation, a total of 4,964 *L. whiffiagonis* were examined from 29 monthly samples. This extensive sampling period was relatively sequential, though gaps were present in certain parts of the sampling programme, namely the summer months of 1998, *i.e.* May to September, when samples stored at Rossaveal port were inadvertently used as bait by the Galway and Aran Fishermen's Co-operative. Occasional other months were also missing from the sequence due to adverse weather conditions.

Though it was considered that the commercial samples were relatively representative of the population present, it would have been preferential to use fish that were caught using on board research vessels. This was not possible due to the restricted and limited access to research vessels and surveys during the investigation. Standard commercial codends normally use approximately an 80mm mesh, while research vessels use a stretched mesh size 40mm, enabling the smaller male fish to be retained in the cod-end. The 80mm mesh used during the present study probably allowed the majority of males to escape from the catches. From this, a more accurate estimation of sex ratio could have been determined for the species, as a larger percentage of male fish were present in the smaller length classes. Commercial samples of megrim were already purchased and stored in the laboratory prior to the start of the study. Sampling from research survey sources thereafter, would have led to incompatibility in the determination of the various biological parameters.

A problem identified with regard to the sampling process, was that of size selection. The fish were obtained at a point of sale, following a series of steps where size selection was likely to have occurred. The first of these steps, was that of net selectivity, followed by discard selectivity, then on board selectivity and finally, selection at the point of purchase.

Net selectivity, as discussed above, meant that smaller male fish had a greater probability of escape during fishing. For mobile organisms like fish, no sampling gear is completely non selective with respect to body size. Nets are obviously selective in terms of mesh size and non retention of smaller fish (Hilborn & Walters, 1992).

Discard selectivity involves fishermen discarding any megrim smaller than marketable size (20cm TL), a process of selection that is carried out by eye. This practise depends on catch rates and TAC constraints, but often results in large numbers of small fish (predominantly male) being thrown overboard.

On board selectivity occurs when the fishermen, with limited space available, often discard marketable fish in favour of more valuable species such as *Nephrops*. The practise of on board sorting may have significant effects on the outcome of any study. It is an unquantifiable process with very little known about its effects and requires further investigation. Following discarding of non commercial sized fish, the sorting/grading of marketable fish begins, usually on board the fishing vessel.

Though grading may have occurred, a full and considerable size range was recorded for all samples examined during the present investigation. This confirmed by the percentage length frequency distributions as presented in (Figs. 11a-c). Megrim have in the past, been segregated into five grades determined by weight as follows; >700g, 500-699g, 300-499g, 250-299g and <250g (Fahy & Fannon, 1991). Grading is carried out to ensure that fish of similar sizes are sold together. This is especially relevant for larger fish, where a better commercial sale is attained. Possible grading undertaken during the present study may be evidenced by the lack of male fish in the samples. Male megrim are invariably smaller than females and attain smaller asymptotic lengths (Fahy & Fannon, 1991; Sanchez *et al.* 1998).

As most of the samples of megrim were purchased from the Rossaveal Cooperative, boxes of fish were provided that would have normally been sold during the weekly fish auction at the port. These randomly selected boxes of fish contained individuals of varying lengths and ages. The sex ratio however, was biased which may have been due in part to grading prior to sale.

4.0:2 Length frequencies

The length frequencies determined during the present investigation were compared to those recorded elsewhere for the species. Length ranges of 15.1-53.2cm TL and 16.9-40.0cm TL were determined for female and male fish respectively. The modal group for females was in the length class of 29-30cm TL, while the modal

group for males was in the of length class of 27-28cm TL. The lower end of the length ranges recorded during the present study, were similar to those recorded by Anon. (2001a), who observed length ranges of 15-63cm TL and 14-56cm TL for female and males respectively for fish from Sub Area VI. However, it was observed that the upper length ranges of the latter study were considerably larger than those recorded off the west coast of Ireland. The largest female fish recorded by Anon. (2001a) was almost 10cm longer than the equivalent during the present study, while the largest male megrim was 16cm longer. Wheeler (1969) recorded a maximum length of 61cm TL for L. whiffiagonis in the northeast Atlantic, which is only slightly smaller than the largest female (63cm TL) recorded by Anon. (2001a). The differences observed between the maximum sizes of these studies may be explained by the numbers of fish examined. A much larger number of fish were measured by Anon. (2001a) i.e. 18,214 females and 2,626 males, compared to 4,812 females and 151 males during the present study. By measuring such a large number of individuals, a greater probability of encountering particularly large fish was increased significantly. The number of individuals studied by Wheeler (1969) is not known.

The percentage length frequency distributions for the total number of female and male fish measured during the present study (Fig. 10.) indicated that males predominated the smaller length classes, and females the larger. Both distributions were unimodal, with a single length frequency class composing the largest percentage of fish present. This was not to be expected, as length frequencies containing large numbers of individuals, *i.e.* almost 5,000 fish, would normally have several modal groupings, representing cohorts of fish within the distribution. From the length frequency distributions determined during the present investigation, it was clearly observed that female *L. whiffiagonis* reached longer total lengths, indicating a greater rate of growth than for male fish.

4.0:3 Regression analyses

The length-weight relationship obtained during the present investigation for female and male fish combined resulted in values of a = -5.781 and b = 3.202. From the regression analysis of the relationship between total length and weight, it was concluded that the growth of *L. whiffiagonis* was allometric, meaning that the fish become "heavier for their length". When the regression analysis for total length and weight were compared with a study of *L. whiffiagonis*, by Santurtun *et al.* (1998a) similar results were observed. A significant correlation was recorded between total

length and standard length for the species during the present study. It can thus be stated with some certainty, that the standard length equation of $SL=a.TL^b$ may be used to determine an accurate estimation of length in the absence of a caudal fin, and resulting lack of a total length measurement.

4.0:4 Mean lengths and weights at age

The mean lengths at age recorded during the present investigation were compared to those obtained for L. whiffiagonis by Landa et al. (1996), Santurtun et al. (1998a) and Anon. (2001a). For mean length at age, it was observed that male fish were smaller in length than females of the same age. Santurtun et al. (1998a) determined that younger fish were similar in length but from age 2 onwards, females were larger. This result is similar to that recorded during the present study, were the mean lengths of both sexes were also within the ranges obtained by Landa et al. (1996) for L. whiffiagonis from the northeast Atlantic. As was found by Landa et al. (1996) and Santurtun et al. (1998a), during the present study, it was observed that differences in mean length between female and male fish began from age 2. This age corresponds to the onset of sexual maturity for L. whiffiagonis off the west coast of Ireland, which may be the trigger which initiates the differential growth rate. The marked dimorphism in the growth of L. whiffiagonis off the west coast of Ireland, is discussed in greater detail later in the chapter, and is a recognised feature of pleuronectiform fish (Landa et al. 1996). Anon. (2001a) also recorded significant differences in mean length between the sexes, with females being larger at age than male fish. The mean weights at age recorded during the present study could not be compared with similar works elsewhere, as no published information was available. However, a similar trend to the mean lengths at age was observed, with female fish weighing more than males of corresponding age. This is to be expected, if female fish were greater in length at the same age, then they would by implication, be heavier also.

CHAPTER FOUR : PART 2. AGE AND GROWTH DISCUSSION

4.1 General introduction

The mortality co-efficients, recruitment, age, growth and yield per recruit results determined for *Lepidorhombus whiffiagonis* off the west coast of Ireland were compared with similar works and assessments elsewhere in Ireland and Europe for the species.

4.1:1 Age frequencies

The age frequencies determined during the present study revealed that the age structure of the sexes at time of capture varied considerably. A modal age group of 5 years was determined for both female and male fish, though considerable differences were observed for the age ranges, with females having a much greater age range (2-16 years of age) than males (3-8 years of age). Pineiro *et al.* (1993) recorded a similar age range for male *L. whiffiagonis* (2-8 years of age), but a lesser age range of 2-9 years for females from the northeast Atlantic.

An age range of 1-16 years of age was recorded for females and 1-12 years for male fish in Sub Area VI by Anon. (2001a). The age range for male fish observed by Anon. (2001a) was considerably larger than that recorded during the present study, where no males younger than 3 years of age were recorded and the oldest male fish were only 8 years of age. This difference in the male age ranges may be explained by the larger amount of males aged during the study of Anon. (2001a), where 553 male megrim were examined. Only 146 males (from a total of 151) were aged successfully during the present investigation. Very few otoliths were rejected from age determination during both studies, indicating that most otoliths were easily readable. The percentages of successfully read otoliths during the present study were 95.76% and 96.68% for female and male fish respectively, compared similarly with 99.58% and 98.74% for females and males aged by Anon. (2001a). The ages were validated by technicians of the Marine Institute FSS, and although high levels of accuracy was achieved, precision at age for each of the age groups was not examined during the present investigation.

4.1:2 Otolith marginal edges

The otolith marginal edges recorded during the present study were compared to results recorded by Landa & Pineiro (2000) and Anon. (2001a) for *L. whiffiagonis* from the northeast Atlantic and west of Scotland respectively. During the present study, it was observed that opaque otolith marginal edges were laid down during the summer months, and translucent or hyaline edges in the months of winter. This observation corresponds to that recorded by the above studies. The period of opaque marginal edge development *i.e.* summer months, was considered to be the time when the growth rate of megrim was optimal, with annual maximum growth achieved. From this, it can be concluded that for *L. whiffiagonis* best growth was during the summer.

In most recent megrim studies (Landa *et al.* 1996; Landa & Pineiro, 2000; Anon., 2001a), whole sagittal otoliths have been examined chiefly using water as a medium. Various other mediums other than water were considered to immerse the otoliths in for the purpose of ageing during the present investigation. Glycerin was the main other medium considered, but this rendered the otolith unreadable after the first ageing. When using glycerin, the concentric rings became extremely blurred and age could not be determined. As the otoliths in this project needed to be aged on several occasions for validation reasons, it was decided not to use glycerin as the main medium during age determination. Back-calculation of lengths at age using otoliths annuli was not carried out during the present study.

4.1:3 Mortality

Estimates of total instantaneous mortality (Z), natural mortality (M), and fishing mortality (F) were determined for female and male *L. whiffiagonis* during the present investigation. The results obtained were compared with those recorded by Fahy & Fannon (1991) and Fahy & Glesson (1992), as well as from the Marine Institute 2003 Stockbook assessment for megrim in Irish waters (Anon., 2003). No values for mortality were available from elsewhere in Europe, for the species.

The early life stages of a fish species are characterised by high natural mortality (M). Each year a proportion of the fish alive at the beginning of the year will die from predation, disease or other natural causes. Once the fish reach a size where they can be taken by the fisheries, fishing mortality (F) becomes the major cause of death. The combined levels of natural and fishing mortality together lead to total mortality (Z) (Anon., 1999).

The values for Z or the instantaneous mortality coefficient, during the present investigation were determined from the construction of catch curves as described earlier in Chapter 2. The only available mortality rates for *L. whiffiagonis* in Irish waters, was that of Fahy & Fannon (1991) who determined a female value for Z of 0.45. A separate estimation of Z was not calculated for male fish, although a combined female and male value of 0.49 was recorded. A second assessment of megrim mortality in Irish waters by Fahy & Gleeson (1992) obtained a combined female and male total mortality (Z) of 0.45. When compared to the total mortality (Z) determined during the present study (0.91 and 1.43 for overall female and male fish respectively), the values recorded by Fahy & Fannon (1991) are considerably lower. The most likely reason for the large difference in mortality estimates between the studies may be a recent increase in fishing effort with resulting higher mortality rates subsequent to those attained approximately 10 years earlier.

Fahy & Fannon (1991) did not determine any estimates for natural mortality (M), although a value of 0.2 was adopted. This arbitrary value of 0.2 is assumed for natural mortality in most demersal fish stock assessments in ICES areas (Anon., 2003). Estimates for natural mortality (M) of 0.28 and 0.57 were determined during the present investigation for female and male megrim respectively. Although fishing mortality (F) may decrease or increase depending on exploitation levels of the species, natural mortality (M) rates are likely to remain relatively similar over time. It is very difficult to get an accurate estimate of natural mortality (M). There are several different methods used, which vary considerably. These include regression analyses, and Pauly's (1980) environmental parameters method, which predicts the M is positively correlated with K and L ∞ , from the Von Bertalanffy (1938) growth model, but is negatively correlated with temperature.

Natural mortality (M) may also be calculated using the Rikhter & Efanov (1976) method. This is based on the age at which 50% of the population are mature. The method predicts that M is negatively correlated with age at maturity and suggests that it is greater than 0.2 for fish that mature before age 7, contradicting the assumption that M=0.2 in traditional demersal assessments. This technique was examined during the present study, however, no viable estimates of M were obtained following its use. An estimate of Z from an unexploited stock provides the best estimate of M available. This approach has been taken for new fisheries for deepwater species on the Hatton Bank and the Mid-Atlantic Ridge. It illustrates the importance of gathering age data from newly developing fisheries (Anon., 2003).

Fishing mortality (F) is a measure of the proportion of the stock that is taken by fishing, and can be expressed as a percentage or as a fishing mortality rate. These rates are an expression of the likelihood that a fish will die at any instant in time. High levels of fishing mortality combined with poor recruitment of young fish to the population, can seriously decrease stock size (Anon., 1999). Fahy & Fannon (1991) determined a fishing mortality (F) of 0.25 for female megrim, and a combined female and male estimate of 0.29. No separate male fishing mortality estimation was made. These values for F are considerably lower than those recorded during the present study, which obtained values of 0.62 and 0.85 for female and male fish respectively. As discussed above with estimates of total mortality (Z), this may be a reflection of

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increased fishing effort since the early 1990's. This theory is confirmed when the estimates of F recorded by Fahy & Fannon (1991) are compared to current Marine Institute FSS assessments. A fishing mortality of 0.39 was determined for megrim in 2002 in Sub Area VII, compared to a proposed F_{pa} (precautionary reference point designed to ensure that F_{lim} is avoided) of 0.3. F_{lim} is the limit fishing mortality, to be avoided as it is associated with unknown stock dynamics and the probability of stock collapse (Anon., 2003). Currently, the Marine Institute FSS estimates that F_{lim} for *L. whiffiagonis* in Sub Area VII is 0.44. Fishing mortality for megrim in this area has been around F_{pa} since the mid 1990's (Anon., 2003). Recently, there has been a downward revision of *F* for megrim in Sub Area VII, however, the FSS has still made recommendations that fishing mortality (*F*) rates for *L. whiffiagonis*, need to be reduced to below F_{pa} , to safe biological limits (Anon., 2003).

When the percentage survival and mortality rates recorded for *L. whiffiagonis* during the present study were compared to similar information available, considerable differences were observed. Percentage mortality rates of 59.74% and 76.06% were recorded for female and male fish caught off the west coast of Ireland, compared to 30% for megrim captured in the Celtic Sea (Anon., 1999). However, the fishery for megrim in the Celtic Sea is a much smaller fishery, and may explain the differing percentage mortality determined for the west coast.

Considerable differences were observed in mortality rates between the sexes during the present study. Male total (Z), natural (M) and fishing mortality (F) were all observed to be much higher than that determined for female fish. Higher natural mortality (M) and a lower life expectancy (Fahy & Fannon, 1991) in male fish may have contributed to the heavily female biased sex ratio recorded. Male fish seem to be more susceptible to the fishing gear, as evidenced by the higher fishing mortality (F) rates recorded.

Very little is known regarding juvenile megrim mortality, and this is an area that requires further detailed examination. Juveniles have a different distribution pattern to the adult fish and are not usually taken in the same fishery. Fishing mortality (F) on juvenile megrim depends considerably on whether they are abundant on the fishing areas at sizes large enough to be caught and discarded (Anon., 1999).

The mortality co-efficients determined during the present investigation are considerably high when compared to those calculated by the FSS for the species in Irish waters. However, this may be a reflection of the extensive assessments (Sub Areas VI and VII, and Divisions VIII_{a,b,d+e}) made by the FSS, compared to the relatively small area fished off the west coast of Ireland (Sub Areas VII_{b+c}) during the present study. The mortality co-efficients determined for the present population especially with regard to fishing mortality is an indication of fishing effort, and reflects the pressure on the stock in this directed fishery (Anon., 2002; 2003). The methods used to determine the mortality co-efficients during the present study have limitations as they were based on catch curves with their own associated assumptions.

4.1:4 Recruitment

Recruitment can be defined as the process whereby young fish, previously inaccessible to the fishing gear, become as a result of growth, or movement on to the fishing grounds, potentially vulnerable to fishing effort. The term is also used to refer to the number of fish recruiting to the stock in a particular year, reaching a certain age or entering the spawning population (Anon., 1999). The number of young fish produced each year varies widely and can have a pronounced effect on the abundance of spawning fish and on commercial catches in subsequent years. Variations in recruitment are caused partly by changes in egg production, particularly when the spawning biomass has fluctuated widely, but also by egg and larval survival, and environmental conditions (Anon., 1999). Recruitment often requires modelling to better understand the population dynamics, with forecasting of recruitment being an essential element of proper fisheries management (Anon., 2003).

Catch curves were used to provide an estimation of the age at recruitment (t_r) of the fish into the fishery. An estimate of 6 years of age was determined for t_r , for both female and male fish during the present study. A t_r of 6 years corresponded with a female mean length of 31.80cm TL and a mean weight of 206.80g, while a mean length of 27.94cm TL and a mean weight of 131.83g was recorded for male fish of 6 years of age. This demonstrates that male *L. whiffiagonis* are smaller and lighter when fully recruited to the fishery.

The values recorded for recruitment during the present study seem quite high when compared to the t_r of 3.5 years of age, recorded by Fahy & Fahy (1991) for the species. This age also is considerably higher than the estimates of first maturity recorded for *L. whiffiagonis* off the west coast during the present study. Depending on the shape of the catch curve, an indication of the susceptibility of the fish to the fishing technology may be determined. This ranges from an indication of decreasing vulnerability to the fishing gear, to an increasing vulnerability of larger fish (Anon.,

1999). The catch curve was determined as no error type in the present investigation, therefore it was not possible to determine an accurate indication of susceptibility from the catch curves calculated. A possible trend of an increasing vulnerability of larger fish to the fishing gear off the west coast of Ireland was however indicated. However, the limitations of catch curves used during the present investigation must be acknowledged, as they can be primitive and biased, according to the type of data analysed.

4.1:5 Growth

A detailed comparison of the Von Bertalanffy (1938) growth parameters recorded by other megrim growth studies, including the present investigation, is presented in Table 32. below. A total of three different growth determination methods were used in the present study, in an attempt to describe the most concise and accurate rates of growth for the species off the west coast of Ireland. The three growth methods used were Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946) and have been included in the megrim growth comparison table below.

Author	Year	Div.	Fem	Fem	Fem	Fem	Male	Male	Male	Male
			N	Lao	K	to	N	L∞	K	to
Conan et al.	1981	VII	210	67.65	0.12	-0.51	6	29.74	0.25	-1.59
Rodriquez&Iglesias	1985	VII	444	63.13	0.11	-0.07	181	39.36	0.29	0.14
Aubin-Ottenheimer	1985	VIIg	190	59.63	0.14	-0.05	72	38.45	0.34	-0.06
Moguedet & Perez	1988	VII	342	65.20	0.09	-1.87	184	43.67	0.14	-1.76
Peronnet&Rivoalen	1989	VII	888	66.80	0.11	-0.33	230	44.80	0.14	-1.76
Peronnet	1990	VII	726	66.80	0.11	-0.33	204	50.31	0.10	-1.88
Alperi	1990	VIIIc	124	52.25	0.17	-1.58	81	32.27	0.38	-0.77
Dawson	1991	VII	192	64.90	0.08	-2.40	74	34.40	0.16	-1.65
Fahy & Fannon	1991	All	913	50.95	0.18	-0.73	492	32.50	0.20	-2.92
Fahy & Glesson	1992	VII _{bk}	1111	51.26	0.17	-0.97	Fema	les & Ma	les Con	ıbined
Pinerio et al.	1993	VII	788	66.00	0.10	-1.08	414	46.00	0.06	-7.95
Landa et al.	1996	VII _{ab}	54	59.00	0.12	-1.34	54	45.00	0.14	-1.85
Perez	1998	VII	537	65.00	0.08	-2.47	101	55.00	0.10	-2.20
Santurtun et al.	1998a	VIII	1608	60.00	0.09	-2.82	1337	41.00	0.19	-2.01
Landa & Pineiro	2000	VII	135	62.70	0.14	0.40	79	43.70	0.16	-0.15
Anon. (2001a)	2001a	VI _{ab}	2339	56.17	0.14	-1.23	553	44.69	0.17	-0.67
Megrim growth	rates off t	he west	coast o	f Ireland	recorded	during	the pre	esent inve	estigatio	n.
Rafail plot	2004	VII _{bc}	4566	50.72	0.097	-4.78	99	35.01	0.12	-6.68
Gulland-Holt plot	2004	VII _{bc}	4602	50.74	0.072	-8.08	140	41.59	0.13	-3.06
Ford-Walford plot	2004	VII _{be}	4602	45.85	0.098	-7.13	140	33.86	0.31	-0.57

 Table 32. Comparison of VBGP for L. whiffagonis recorded during the present study with those given by other studies in European waters.

4.1:5:1 Female growth

The Von Bertalanffy (1938) growth parameters of L ∞ , K and t₀ obtained during this study by use of three different growth models, those of Rafail (1973), Gulland-Holt (1959) and Ford-Walford (1946) were relatively close to one another, indicating a level of precision in growth estimation. The values for L ∞ for all female fish combined, attained using the Rafail (1973) and Gulland-Holt (1959) growth models were remarkably similar, 50.72cm and 50.74cm respectively. The Ford-Walford (1948) growth plot for the same fish resulted in a considerably lower L ∞ value of 45.85cm. This value was undoubtedly inaccurate as the largest female fish recorded during this study (in 1997) measured 53.2cm TL.

The values for $L\infty$ for all female fish combined were very similar to the two only other published studies of megrim growth in Ireland, those of Fahy & Fannon (1991) and Fahy & Glesson (1992), which recorded overall female megrim $L\infty$ values of 50.05cm and 51.26cm respectively. The values of Loo recorded in the present investigation for the total number of female fish were similar to those recorded by other studies elsewhere in Europe. From examination of the above table, a noticeable trend of decreasing Loo values was observed for female megrim over time. The largest value, that of 67.65cm recorded by Conan et al. (1981) was considerably greater than those observed during the present study. The Conan et al. (1981) study was undertaken over twenty years ago. The lowering of the $L\infty$ value possibly indicates changes in the stock dynamics due to an increase in exploitation rate on the stock of megrim in Sub Area VII over time. The rate of growth K, appeared to be relatively constant throughout the above comparative table, (Table 32.) although when compared to the three K values recorded in the present study, differences were observed. K values for megrim from off the west coast of Ireland determined by the different growth models appeared to be slightly lower than those recorded elsewhere in Europe. This slower rate of growth corresponds to a lower L^{∞} value, with the megrim thus attaining a much smaller overall theoretical size.

It is interesting to note that the numbers of fish examined by other authors in previous studies varies considerably, with many examining far less individuals than the present investigation. Numbers ranged from 6 males (Conan *et al.* 1981) to 2,339 female fish (Anon., 2001a). Use of such low numbers of fish, makes it more difficult to obtain accurate growth rates or draw precise conclusions.

When the annual growth rates for the years of 1997 and 1999 were examined, the values of $L\infty$ obtained for female fish seemed to be unrealistic. The values of $L\infty$ = 97.66cm and 71.45cm recorded by using the Gulland-Holt (1959) method, for female fish from 1997 and 1999 respectively was quite large when compared to other values of $L\infty$ obtained for the same fish using different growth models, and were obviously inaccurate, but were the closest fits of the model to converge. The VBGP for females captured during 1998 were similar to those recorded for the same fish by other growth determination methods.

All values of t_0 determined during the present investigation were considerably higher than any presented in previous similar studies. However, the most similar value of t_0 (-4.78 from Rafail method) in the present study was that recorded by Santurtun *et al.* (1998), where a value of t_0 =-2.82 was presented.

4.1:5:2 Male growth

When the values for $L\infty$ for all male fish combined, determined by using the three growth models were examined, considerable variation was noticeable. The lowest value recorded for $L\infty$ for this group of fish, that of 33.86cm determined using the Ford-Walford (1946) growth model, was considerably lower than the largest estimate of $L\infty$ which was 41.59cm, calculated by using the Gulland-Holt (1959) growth model. An $L\infty$ of 33.86cm was probably inaccurate, as the largest male fish recorded in this study measured 40.0cm TL, which was considerably larger than the calculated $L\infty$ value. The estimate of $L\infty$ determined using the Gulland-Holt growth (1959) model was considered to be the most accurate estimate of growth obtained for the total number of male fish examined during the present investigation.

Growth in terms of asymptotic length $(L\infty)$ for male *L. whiffiagonis* from off the west coast of Ireland was considerably less than that recorded for female fish. However, the K (rate of growth) values for males determined during the present study, from all three methods, were higher than the K values recorded for females. This agrees with the findings of Landa *et al.* (1996) and Santurtun *et al.* (1998a), who observed that though females attained greater maximum lengths, male fish had higher instantaneous growth rates (K).

Male values of L^{∞} obtained during the present study (Table 32.), were closest to those recorded by Dawson (1991) and Fahy & Fannon (1991), while the rates of growth (K), were most similar to those determined by Moguedet & Perez (1988) and Peronnet & Rivoalen (1989) for megrim from Sub Area VII. The values of t_0 determined during the present study were similar to almost all of those recorded for male fish elsewhere, but particularly to Anon. (2001a), Fahy & Fannon (1991) and Pineiro *et al.* (1993).

The results of the VBGP for *L. whiffiagonis* recorded during the present investigation from off the west coast of Ireland, concur with other studies elsewhere in which faster and greater growth has been shown to occur in female flatfish than in male (Conan *et al.* 1981; Moguedet & Perez, 1988; Alperi, 1990 and Landa *et al.* 1996). The slower growth rates, and smaller asymptotic lengths recorded during the present study, may be due to variations in metabolic rates with regard to temperature. With the exception of Anon. (2001a), megrim from the present study were captured at a more northerly latitude than those recorded by other authors (Table 32.), Oceanographic temperatures tend to be colder at more northerly latitudes, and as growth is positively correlated with increased water temperature, this may result in a slower growth process for megrim from Irish waters. In addition to this factor, variations in diet and other oceanographic factors may also influence growth (Pauly, 1994b). For the determination of the growth rates during the present study, various assumptions were made with regard to the models used, the principal one being the fitting of growth curves across several cohorts.

4.1:6 Yield per recruit

The yield per recruit values determined during the present investigation are the first time attempts to model the growth for *L. whiffiagonis* from off the west coast of Ireland.

Yield per recruit models examine the trade-off between capturing large numbers of fish early in their life span, and capturing a smaller number of larger fish later in their life span (King, 1995). During the present study, yield per recruit curves for *L. whiffiagonis* determined that optimum yield was reached at a fishing mortality (F) of 1.2 and 1.4 for overall female and male fish respectively. This equated to 187.36g for female fish, and 107.96g for males. A considerable difference was observed between the sexes in terms of the weights at optimum yield, reflecting greater growth of female fish off the west coast. These results were compared to those of Fahy & Fannon (1991) who recorded optimum yield to be at a fishing mortality (F) of 0.3 for female megrim, while no values were presented for male fish. This level of F is considerably less than that determined from off the west coast of Ireland for optimum yield for the species. Fahy & Fannon, (1991) concluded that the yield per recruit curves shown indicated that exploitation was close to F_{max} for female fish and on the negative slope for the sexes combined.

Several problems with the Beverton-Holt (1957) model were identified during the present study. Foremost of these was that the model assumes a steady-state stock structure, which is the assumption that total yield in any one year from all age classes is the same as that from a single cohort over its whole lifespan. Other assumptions that are made for this particular yield per recruit model is that the fish stock being examined is assumed to be a constant entity, and not part of a changing ecosystem. A constant exploitation pattern as well as constant natural mortality (M) are assumed and growth rates, discarding and discarding survival rates are all also assumed to be constant. An assumption of constant recruitment to the fishery is also made, but is not included in the equation.

The exclusion of recruitment from the model provides no guide to the fishing levels at which recruitment overfishing occurs. Recruitment overfishing takes place when heavy fishing reduces the spawning stock to a level at which adequate production of young fish, the future recruits to the fishery, is reduced (Anon., 1999). However, the number of recruits entering the fishery from spawning in a given year is highly variable, as discussed earlier. It is very difficult to distinguish whether a run of poor year-classes is due to low spawning stocks, or unfavourable environmental conditions, or a combination of both. Recruitment overfishing is less common than growth overfishing, (where young fish are caught before they can reach their full growth potential), but if it does occur, the consequences may be serious to the fishery (Anon., 1999). Assumptions extend to gear selectivity, where it is assumed that after mean age at first capture, t_c , all fish coming into contact with the fishing gear have equal probability of capture (King, 1995). Also biological and environmental factors such as migration, feeding and spawning conditions are assumed to remain constant (King, 1995).

The model of Beverton-Holt (1957) works best when applied to species with low mortality rates, ideally less than 0.5 for natural mortality (M) (King, 1995). If mortality rates are high, as determined for *L. whiffiagonis* during the present study, the yield per recruit curve may not reach a maximum within a reasonable range of fishing mortality (F) values. This was observed during the present study, where optimum levels of yield were recorded at a fishing mortality (F) of 1.4, for combined

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females and males, overall males, and female fish captured during 1998 (Table 20.), however, the value of F was the last fishing mortality at which yield was examined. If yield was examined for these fish at increasing higher levels of fishing mortality (F) until an optimum was reached, inaccurate estimates of safe exploitation rates would have been obtained. This may be misleading, suggesting that an extremely high, or sometimes infinite fishing mortality (F) was required to secure the maximum yield.

Where a yield per recruit curve continues to increase, or approaches a broad, flat-topped maximum, the optimum fishing mortality is taken to be the value at which an increase in one unit of F increases the catch by one-tenth (0.1) of the amount caught by the first unit of F (Gulland, 1985). This means that the optimum level of F occurs at a point where the slope of the yield curve is 0.1 of the value of the slope at low levels of fishing mortality. The calculation of this value is known as $F_{0.1}$ (King, 1995). The Marine Institute FSS assessment for *L. whiffiagonis* in Sub Area VII and Divisions VIII_{a,b,d+e} determined a $F_{0.1}$ of 0.061 at a fishing mortality (F) of 0.12 during 2003 (Anon., 2003).

From an examination of the shape of the yield per recruit curves constructed during the present study, an indication of the type of life history strategy of L. *whiffiagonis* was obtained. This may be either an r or k based strategy, and varies between species of fish (Bone, 1997). A k strategy was recorded for L. *whiffiagonis* off the west coast of Ireland during the present study. This theory was validated after fecundity determination, as discussed later in this chapter.

The yield per recruit estimates recorded during the present investigation are important in that they provide initial assessments of optimum yield, and the level of fishing mortality (F) at which optimum yield may be achieved, for both sexes of L. whiffiagonis off the west coast of Ireland.

CHAPTER FOUR : PART 3. REPRODUCTIVE DISCUSSION

4.2 General introduction

The reproductive results determined for *L. whiffiagonis* off the west coast of Ireland were compared with similar works elsewhere in Europe for the species. Where no published information was available on megrim reproductive biology, that of other flatfish was used for comparative purposes.

4.2:1 Sex ratio

The sex ratio determined for *L. whiffiagonis* during this investigation was heavily biased in favour of female fish. The actual overall sex ratio percentage as presented in the results chapter, was approximately 97% female to 3% males.

Although female biased sex ratios are a commonly observed phenomenon in flatfish biology (Walsh, 1994; Swain, 1997), and also in other megrim studies (Anon., 2001a), no results show such a skewed sex ratio as those determined in the present work. Possible reasons for such a skewed sex ratio range from differences in the distribution of the sexes according to depth, temperature, and size, to selectivity of the fishing gear and also sampling timing and location.

Sex ratios related to distribution at varying depths were not examined as part of this investigation, however, it has been observed elsewhere that smaller and younger fish are more commonly recorded at greater depths, and are invariably male (Boon, 1984). Poulard *et al.* (1993) in the Bay of Biscay and Celtic Sea observed sex segregation, with more females down to 150m in depth, and slightly more males deeper than 150m. Between depths of 211-240m, males were more frequently recorded. These results are further confirmed by Boon (1984) who observed larger (>30cm TL) fish, which were predominantly female, in shallower waters (<115m) of the Celtic Sea. As depths increased, smaller fish (<30cm TL) were recorded and were mostly male. However, a joint Irish and Scottish study on megrim and anglerfish in 2001 (Anon., 2001a) observed no apparent depth related trends in sex ratio for fish sampled from Division VI_a. It is not stated how detailed the study was in terms of depth related distribution of the sexes, but it was concluded that the possibility of using separate sex assessments for the species may be worth investigating for the area in the future (Anon., 2001a).

Sex specific temperature distribution has been recorded in long rough dab (*Hippoglossoides platessoides*) by Swain (1997) in the Gulf of St. Lawrence, who observed that females occupied warmer waters than male fish. After accounting for annual variation in temperatures, it was observed that female distribution in relation to temperature, was density dependent but males tended to occupy colder water at higher levels of abundance.

The difference in distribution between male and female long rough dab in relation to temperature (Swain, 1997), is consistent with an explanation involving sex specific foraging strategies. The higher growth rate of female megrim as recorded in this investigation and other megrim studies, suggests that benefits of growth are greater for females than males, perhaps because increases in fertility with body size are greater for female fish than male. If so, females would be expected to risk a higher foraging rate than males and consequently obtain a higher food ration. Because the optimal temperature for growth increases with ration size (Swain, 1997), females would be expected to occupy warmer temperatures than males, therefore resulting in sex specific temperature distribution, and invariably a biased sex ratio during sampling.

A clearly observed aspect of differing sex ratio is that related to the size of the fish. In the present investigation, it was observed that a slightly higher number of male fish were recorded in the smaller size classes, (Figs. 35b-e). The greatest percentage (15.3%) of males in proportion to females were less than 25cm TL, while this percentage decreased dramatically as the fish became larger, until no male fish were recorded >45cm TL. This trend was also recorded by Tyndall (1980) for Galway Bay megrim, where a heavily female biased sex ratio was observed, with approximately 1% of fish sampled being male, and all those being <32cm TL. Santurtun et al. (1998a) recorded a sex ratio for megrim in the Bay of Biscay with only a slight departure from a sex ratio of 1:1 for small length classes of fish, (<34cm), but changed significantly towards greater length classes. Males were found to be slightly more abundant in smaller length classes while females dominated the larger length classes. It was concluded by Santurtun et al. (1998a) that the departures in sex ratio were due to differences in growth patterns or in the catchability of the sexes. The joint Irish and Scottish study on megrim and anglerfish also recorded varying sex ratio according to size. Male megrim were more common than females less than 20cm TL, while female fish dominated the larger length classes (Anon., 2001a).

Sex ratio, as well as being related to size or length, has also been shown to vary with age and mortality. A study by Sanchez *et al.* (1998) on the northern Spanish shelf, observed that in general after 4 years, the ratio of males to females decreased considerably, primarily because of differing rates of mortality. This leads to speculation that male mortality rates differ from those of females, with male fish reaching their level of natural mortality before that of female fish. Male megrim total mortality (Z) was considerably higher than that for females during the present study *i.e.* 1.43:0.91 respectively, as was natural mortality (M), 0.28:0.57 for female and

male fish. Fahy & Fannon (1991) recorded a female biased sex ratio for L. whiffiagonis in Irish waters and concluded that it was caused by a lower male growth asymptote and lower life expectancy for male fish. Although females were predominant throughout the commercial catches, Fahy & Fannon (1991) found that male fish composed the majority of discards landed, with a ratio of approximately 134:223 females to males being recorded respectively. Mortality rates for L. whiffiagonis were examined in greater detail earlier in the chapter.

The most likely cause of the female biased sex ratio off the west coast of Ireland is that of net selectivity. As mentioned earlier in Chapter 2, the samples for this study were commercially obtained. This meant that the fish were caught using an otter board trawl, with an 80mm cod-end. This mesh size is considerably larger than that used by research survey vessels, which usually have approximately 40mm mesh. By having a larger mesh size, small fish would have escaped during the duration of the fishing tows, through the larger mesh panels. As shown in this investigation, (Figs. 35b-e), larger numbers and percentages of male fish than females occurred at the smaller size classes. However, selectivity studies by Robles et al. (1980; 1985) and Trujillo et al. (1993) who examined mesh selectivity of megrim (as well as other demersal species) in Spanish waters did not provide any relevant information regarding differing selectivity of the fishing gear for the separate sexes. Female biased sex ratios have been observed for the four spot megrim Lepidorhombus boscii (Risso, 1810) which is a close relative of L. whiffiagonis. A study on the age and growth of L. boscii off the west coast of Ireland (Robson et al. 2000), recorded a male to female sex ratio of 0.293:1. It was concluded that the primary reason for this female biased sex ratio was net selectivity.

Heavily female biased sex ratios recorded during this study may also have been due to seasonality and geographical distribution. It is widely accepted that female and male fish have different geographical distributions according to the time of year (Pitcher, 1996). Both sexes accumulate on suitable spawning grounds as spawning time approaches, but often migrate to different areas once fertilisation is complete (Pitcher, 1996). Therefore, depending on the time and site of sampling, different sex ratios may be recorded for each of the catches. During the present study, greater numbers of males were recorded in the monthly samples prior to spawning, than at other times of the year. However this theory was deemed unsubstantiated as so few males overall were obtained for the investigation. Geographical distribution of the

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sexes was not within the scope of the present study. However, no geographical trends in sex ratio for *L. whiffiagonis* were apparent in the study undertaken by the joint Irish and Scottish investigation on anglerfish and megrim from 2001 (Anon., 2001a).

Such a heavily female biased population would surely start to endure the possibility of failing to reproduce and sustain sufficient numbers over time if so few numbers of males were present to facilitate successful spawning. But, megrim recruitment has been steady over previous years (Anon., 2003) indicating a stable spawning stock within safe biological limits. In conclusion, it is impossible that one factor is directly responsible for recording such a skewed sex ratio. It is more likely that a combination of the above factors, more especially net selectivity and differing distributions at the time of capture of the sexes, are responsible.

4.2:2 Macroscopic and histological maturity assessments

The use of macroscopic and histological assessments to determine the spawning time of marine teleost fish has been widely used (Htun-Han, 1978; Van Eenennaam & Doroshov, 1998; Rideout *et al.* 1999; Tomkiewicz *et al.* 2003).

The reproductive status of fishes is often determined from the gross anatomy of the gonads and subsequently, a large number of macroscopic maturity scales exist (Tomkiewicz *et al.* 2003). Macroscopic assessment is a rapid and inexpensive method of determining maturity status, and allows for a large number of specimens to be processed on board research/commercial vessels, and is especially useful where facilities to carry out extensive histological examinations are absent. Although macroscopic staging can enable detailed recording of the seasonal occurrence of differing reproductive stages, histological analyses of the gonads provide a more precise determination. Cellular substructures can be recognised in the developing follicles and ovarian tissue, which allow for interpretation of reproductive status. While both have their advantages and disadvantages, a combination of both methods of analysis is suggested.

Following both macroscopic and histological examination of the ovaries and testes of *L. whiffiagonis*, five maturity stages were identified as described earlier in Chapters 2 and 3. The overall percentage of maturity stages, which compared favourably for females between the two assessment methods, was 53.79%. This value is considerably higher than the 39.28% recorded by Anon. (2001a) for *L. whiffiagonis* in VI_a+_b . The overall percentage of maturity stages for males during the present study, which compared favourably was 49.15%, though this cannot be compared with Anon.

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(2001a) as only females were examined in that investigation. The most likely reason for the higher percentage attained during the present study in comparison of the two assessment methods, is that only 5 maturity stages were identified both macroscopically and histologically for the fish off the west coast, while for the Anon. (2001a) study, 7 and 5 maturity stages were observed, macroscopically and histologically respectively. By determining an extra 2 maturity stages macroscopically during that investigation, meant that some of these subjective maturity stages would therefore not match up with those histologically assessed.

When the comparison between macroscopic and histological maturity assessments for female megrim during the present study was made, several discrepancies were noted. It was clear that the majority of difficulties in macroscopic assessment occurred when subjectively identifying Stage II ovaries as Stage I and Stage III ovaries. This can easily happen when making a macroscopic maturity assessment as all three maturity stages are quite similar, unlike Stage IV and Stage V, which are very distinctive. This is in contrast to identifying Stage II ovaries using histological maturity assessment, where this particular maturity stage is unmistakable and not possible to confuse with a different maturity stage.

Santurtun *et al.* (1998a) recorded only four macroscopic maturation stages for megrim from the Bay of Biscay. The stages were determined in relation to the relative size and weight, as well as the external appearance and colour of the gonads. Also four histological maturity stages were established, which were comparable to those identified macroscopically (Santurtun *et al.* 1998a). When this result is compared to the present study, where 5 maturity stages were observed, it appears that Santurtun *et al.* (1998a), differed with regard to Stage III, which was recorded as "spawning" by that study, but as "mature" during the present one. Presented below is a reproductive cycle for *L. whiffiagonis*, showing all maturity stages recorded during the present investigation.



Figure 46. Maturity stages of *L. whiffiagonis* combined into a reproductive cycle based on histological features.

In the present study, oogensis was described in five stages with the descriptions based on easily recognisable anatomical and size differences. Based on the features determined from histological examination, the maturity stages were aggregated into phases of the reproductive cycle as follows; immature, in maturation or resting, mature, pre-spawning and spawning, and post-spawning or spent.

Stage II ovaries were classified as maturing or in a resting state. This meant that the Stage II ovaries may have been maturing for the first time following Stage I (immature) development, or may have been in resting or recovering following spawning (*see* Fig. 46.). This latter process of recovery occurred for older fish that had undergone gonadal development during previous seasons prior to spawning. No

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distinction was made between maturing and resting Stage II ovaries, as it was difficult to distinguish between them, even when identifying developmental structures such as late phases of atresia within the gonad. It would have been interesting to record what proportion of Stage II ovaries had previously spawned or were developing for the first time. This was not possible due to the poor condition of some of the Stage II ovaries, following sectioning. The age of each Stage II female would have given an indication of prior spawning, but could not be regarded as accurate as some females did not develop until later in their lives.

By successfully comparing the macroscopic and histological maturity assessments for *L. whiffiagonis*, and in conjunction with the determination of the GSI, a concrete estimation of spawning periodicity was formulated for the species off the west coast of Ireland during the present study. The five maturity stages were identified and characterised. Also it was demonstrated that histological assessment provides a successful and useful method of validation for the macroscopic examination of megrim gonads.

4.2:3 Maturity

Precise estimates of maturity at length and age are essential in order to measure the effect of fishing pressure on the spawning stock biomass and yield per recruit, and to advise fisheries managers on minimum landing sizes necessary to protect juvenile fish. Maturity at length and age for *L. whiffiagonis* was examined during the present study using maturity keys and ogives. The estimates of first maturity presented from other reproductive studies by other authors for *L. whiffiagonis* elsewhere in Europe, were all histologically determined, therefore results from histological examination from the present study only, were compared. Histological examinations therefore, were used to estimate maturity during the present study and may have contributed to any differences. These comparisons are presented in Table 33. below.

Author	Year	ICES Division	Spawning	Female	Male	Female	Male
		or Area	Period	L _{50%}	L.5(1%	A50%	A50%
Furnestin	1935	X, XII, IV _{a-c}	April	15-20cm	19-23cm	3yrs	4yrs
Dwivedi	1964	IV_{a-c} , $VIII_{a-c}$	Jan Apr.	27cm	24cm	*******	
Dawson	1991	VIII _{a-d}	March	21cm	15cm	3 yrs	2yrs
Perez	1998	VII	MarApr.	19.9cm	17.4cm	2.5yrs	1.7yrs
Perez	1998	VIII _c , IX _a	MarApr.	17.0cm	17.4cm	1.5yrs	1.1yrs
Santurtun et al.	1998a	VIII _{a-d}	Jan Mar.	24.9cm	20.6cm	3yrs	2yrs
Anonymous	2001a	VI _{ab} (1999)	Jan Apr.	32.5cm	20.6cm	2.8yrs	2yrs
Anonymous	2001a	VI _{ab} (2000)	Jan Apr.	26.5cm	17.1cm		
	Macroscopic estimates of first maturity						
Present work	2004	VΠ _b	Jan Feb.	25.0cm	22.0cm	2yrs	3yrs
		Histolog	ical estimates	s of first ma	<i>turity</i>		
Present work	2004	VII _b	Jan Feb.	24.0cm	25.0cm	2yrs	2.5yrs

Table 33.	<u>L. whilfagonis first maturity estimates recorded by other studies in</u>
Europe	ean waters, compared with results determined during the present
	investigation.

The estimates of first maturity at age and length determined during the present investigation are well within the ranges of those observed elsewhere for the species. Although they are very similar to many of the results recorded by others elsewhere, estimates of maturity for the west coast of Ireland are overall closest in numerical terms, to those determined by Santurtun *et al.* (1998a) for *L. whiffiagonis* from the Bay of Biscay.

When the present maturity at length estimates are compared to those carried out for megrim in Irish waters previously by Anon. (2001a), it was observed that both macroscopic and histological maturity at length for females occurred at a smaller length. However, the opposite was apparent for male fish, with those examined by Anon. (2001a) reaching $L_{50\%}$ before that of males from the west coast of Ireland. For $A_{50\%}$, maturity at age occurred at similar age classes. It is interesting to note that for (Anon., 2001a), estimates of maturity varied considerably between 1999 and 2000, with the maturity occurring at a smaller length in the latter year. It was subsequently concluded that the length at which first maturity occurs varies between years (Anon., 2001a). The estimates of first maturity at length and age, determined by Perez (1998) for Sub Area VII and Divisions VIII_c and IX_a, were the lowest presented by the authors elsewhere for the species, and were considerably lower than those determined during the present investigation.
Once estimates of first maturity for both sexes had been recorded, differences between them were calculated. When macroscopic determined estimates for $L_{50\%}$ were compared between the sexes, it was observed that male fish reached a length at which 50% of fish were sexually mature before that of females, *i.e.* 22.0cm and 25.0cm, for males and females, respectively. When maturity at length between the sexes was estimated histologically, the opposite was observed, with 50% of female fish becoming mature before males, at a length of 24.0cm, in comparison to the 25.0cm recorded for male fish. However, very fish male fish were available for assessment in the present study.

A comparison of first maturity at age ($A_{50\%}$) between female and male fish examined both macroscopically and histologically, revealed that 50% of females were mature at an age earlier than that reached by male fish. Macroscopic maturity at age for females was observed to occur a year earlier than for male fish *i.e.* at ages 2 and 3 respectively, while histological maturity at age was only marginally earlier, 2 and 2.5 years, for females and males respectively.

Differences were observed in maturity for the female and male fish, between the two ogive determination methods. When a comparison was made between macroscopic and histological maturity at length for female fish, it was observed that the estimates for $L_{25\%}$ and $L_{50\%}$ were very similar, approximately a centimetre in the difference. However, the difference in the estimates for $L_{75\%}$ was greater, the histological determined estimate being 2cm less than the macroscopic. For male *L. whiffiagonis*, considerable differences were recorded between the macroscopic and histological maturity at length estimates. For $L_{25\%}$, the macroscopic maturity ogive demonstrated that maturity was reached at a length of 4cm before that determined histologically. For $L_{50\%}$ and $L_{75\%}$, macroscopic maturity at length was determined to occur at a length before that recorded histologically.

The results of the maturity ogives at length and age for *L. whiffiagonis* determined during the present investigation have an impact on the fishery for the species off the west coast. The minimum landing size was 25cm TL for megrim when the majority of the samples used for maturity ogive calculation were obtained, however this was reduced to a minimum landing size of 20cm TL in January 2000. The estimates of maturity at length recorded during the present study were all close to the minimum landing size prior to 2000, indicating that fish were generally sexually mature at the time of capture. However, as the minimum landing size was reduced,

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this results in megrim being landed that have not reached lengths at which they become mature. This leads to a situation, where young fish are captured before reaching maturity, reducing the future potential spawning stock biomass. From these maturity ogives, therefore it can be concluded that the minimum landing size of 20cm TL is too small and should be increased to the previous level of 25cm TL.

Though comparisons could not be made between macroscopic and histological maturity for other studies as no macroscopic maturity estimates were available, comparisons in first maturity between the sexes were carried out for the present study. For almost all of the studies presented in Table 33. above, with the exception of that of Furnestin (1935), male L. whiffiagonis reached L_{50%} and A_{50%}, at lengths and ages before those of the female fish. In the study of Furnestin (1935) from the Atlantic and North Sea, females were mature at a length of one centimetre or two before that of males, and a year earlier. It is logical that female fish reach maturity at lengths and ages before those of males, as female L. whiffiagonis have been shown to have greater rates of growth, demonstrated both by the present study and by those carried out elsewhere for the species (Rodriguez & Iglessias, 1985; Moguedet & Perez, 1988; Dawson, 1991). It has been recorded that temporal and geographic variation in maturity at length and age can occur in flatfish. A study by Morgan & Bowering (1997), observed that Greenland halibut (Reinhardtius hippoglossoides) showed a high degree of temporal and geographic variability of maturity, primarily as a result of migration between areas. Other external factors such as environmental conditions, fishing pressure and mortality rates may also result in one sex reaching maturity before that of the other (Morgan & Bowering, 1997). Females reaching length and age at first maturity before that of males coincides with the mean lengths at age (Table 10.), where female fish were consistently larger than males observed at the same age.

The maturity at length and age keys (Tables 25a-d. & 26a-d.) constructed, provide an initial profile of at which age and length, megrim reach sexual maturity off the west coast of Ireland. By using the keys to determine the percentage of mature individuals present in a particular age or length class, the maturity ogives were constructed. These allowed estimates of first maturity to be made. The keys are therefore, an important and useful tool in fisheries management.

Maturity ogives were not calculated for each of the sampled years as there were not sufficient numbers of male fish present for accurate maturity estimations or comparisons. As there was no annual maturity estimates for males, it was deemed

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unnecessary to calculate ogives for female fish on a yearly basis. While 30 randomly selected ovaries, from each monthly sample were sufficient to calculate maturity ogives for the overall population, it was deemed insufficient to determine maturity ogives on a yearly basis. The lack of male fish in the samples also prevented the use and fitting of specific logistic curve models to the maturity ogives. This would have resulted in more accurate estimations of maturity and will be done in future.

There is the possibility that megrim, larger and older than the first length and age at maturity estimates for the species, may not necessarily be mature. During the present investigation, a detailed examination of the length and age at maturity keys (Tables 25a-d. & 26a-d.) confirmed this theory. The latter was also recorded by Anon. (2001a) for Sub Area VI. A Stage I (immature) female in the length class of 39-39.99cm TL for the macroscopically assessed fish, was much larger than the estimate for $L_{50\%}$ of 25.0cm. Similarly, there were two females aged 9 years which were macroscopically staged as immature. This age was considerably older than the estimate for $A_{50\%}$ of 2 years of age. As with any population of fish, a proportion of megrim reach maturity later in life than the normal age at maturity.

Estimates of first maturity have been presented for *L. whiffiagonis* in Ireland previously (Anon., 2001a). However, those determined during the present investigation provide the first specific maturity estimation for the population of megrim inhabiting the waters off the west coast in Sub Areas VII_{b+c}. It can be concluded from these maturity ogives, that females mature at lengths and ages earlier than those of males. Further studies on first maturity for *L. whiffiagonis*, especially for male fish, may show significant changes over time, as demonstrated by the study of Anon. (2001a).

4.2:4 Spawning period

The results obtained during the present study are closely related to reproductive studies carried out in Irish, Spanish and U.K. waters. There are however, differences from area to area, with each region having its own distinctive spawning period. Spawning time for megrim in Sub Areas VII_{b+e} occurs from January and is most likely entirely complete by the end of February. As observed in other reproductive investigations of *L. whiffiagonis* elsewhere (Dawson, 1991c; Santurtun *et al.* 1998), male fish have a longer spawning period than females, maturing earlier in the season and spawning later.

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The singular investigation of megrim reproductive biology in Irish waters (Sub Areas VI_{a+b}), that of Anon. (2001a), which examined only female fish, determined that megrim spawned between January and April. Spawning was spatially and bathymetrically widespread throughout the areas of spawning fish present at depths ranging from 80-900m (Anon., 2001a). Peak GSI was recorded in April, which was 3 months later than that recorded during the present study. However, Sub Areas VI_{a+b} are at considerably more northern latitudes than Division VII_{b+c} of the present study. There are indications from the fishery that there is a migration towards the continental shelf edge to spawn (Url. 2.). It has been shown by Dawson (1991c) that megrim from southern latitudes spawn earlier than those from northern latitudes. When warmer water progressed northwards, so too did the spawning frequency of more northern populations of fish (Dawson, 1991c). Dawson (1991c) studied the maturity and spawning distribution of L. whiffiagonis from the Celtic Sea, western Channel and the northern Bay of Biscay. Spawning fish were most frequently recorded between 140-164m, from a total depth range of 90-250m. Interestingly, a very small (~24m) depth spawning window was observed, with the majority of spawning fish caught within that depth. It was also observed that male fish for any given area were always more further advanced in their state of maturity than females and it was concluded that spawning occurred in the more southern areas in March (Dawson, 1991c).

Perez (1998) observed a spawning period of March to April for ICES Sub Area VII & Div VIII_c and IX_a male megrim, whilst the female spawning period was restricted to March only. Similar spawning times were recorded for all areas examined, however, Perez (1998) noted that whereas the female spawning period was relatively specific, that of the males ranged over a considerably longer period, possibly suggesting multiple male spawning events. Santurtun *et al.* (1998a) recorded a spawning period of January to March, with maximum peak in February, for *L. whiffiagonis* from the Bay of Biscay. It was observed that males matured more rapidly in January than females, but had a longer spawning season, with fish spawning in March and April in the more northern areas of the Bay of Biscay (Santurtun *et al.* 1998a). A second histologically based study by Santurtun *et al.* (1998b) also on megrim sampled from the Bay of Biscay, revealed a spawning period ranging from January to March, with a slightly later maximum peak in February-March.

By examining the gonads macroscopically and also microscopically, precise spawning times can be identified. Hydrated oocytes present in the ovary under macroscopic examination, appear opaque and indicate the onset of spawning females. For male fish, the easy extrusion of sperm from the testis reflects the an imminent spawning event. Microscopic examination, while time consuming and labour intensive, provides the most concise estimate of the onset of spawning in fish reproductive biology.

4.2:5 Oocvte dynamics

The results of the oocyte length measurements on pre-spawning female L. *whiffiagonis* were compared with similar previous work for megrim, principally those of Anon. (2001a) and Santurtun *et al.* (1998a). As there is no available published information on atresia for megrim, comparisons have been made with that of other species.

The oocyte diameter frequency distribution determined for L. whiffiagonis during the present investigation was similar to that presented in the study of Anon. (2001a). However, minimum values for oocyte diameter ranges for each maturity stage for the Anon. (2001a) study were considerably smaller than any of those recorded during the present study. This may be due to the difficulty in measuring oogonia for fish from the west coast of Ireland. The maximum oocyte diameters determined for each maturity stage during the present study were much larger than those of the Anon. (2001a) work. Oocytes from the oogonia phase up to that of nonhydrated oocytes were examined in the latter investigation, while all oocytes with an identifiable nuclei were measured during the present study. Another possible reason for any differences observed may be due to the fixation processes used. The samples from the study of Anon. (2001a) were fixated from fresh samples on board fishing vessels, whereas the samples during the present study were fixated following freezing. This may have altered the oocyte diameters in the present study, as shrinkage is known to occur following freezing. Different fixatives were used between the two studies also, formalin by Anon. (2001a) and Bouin's Fluid during the present investigation, with possible differing results. Though the ranges between the studies may differ in terms of actual diameter sizes, the distribution of oocyte diameter frequencies were very similar. A full comparison of the oocyte diameter ranges is presented in Table 34. below.

Maturity Stage	Present Study (2004) Oocyte Diameter Range (µm)	Anon. (2001a) Oocyte Diameter Range (µm)
Stage I	27-123	15-50
Stage II	45-246	5-120
Stage III	126-451	15-210
Stage IV	136-686	15-225
Stage V	61-616	15-210

Table 34. Comparison of oocyte diameter ranges for L. whiffiagonis.

The annual evolution of oocyte diameter was studied by Santurtun *et al.* (1998a) for *L. whiffiagonis* from the Bay of Biscay. It was observed that the oocyte diameters increased toward spawning time. The ranges of oocyte diameters were not identified for each individual maturity stage, but ranged overall from 20-700 μ m. This value is very close to the overall range of 27-686 μ m recorded during the present study for oocyte diameter frequencies. Because the mean oocyte diameters increased for each maturity stage toward spawning time, an indication of spawner type for megrim was determined.

Atretic oocytes have been identified in most teleost species and is recognised as a significant regulatory process of potential fecundity (Witthames, 2000). There is no available published information on rates of atresia for L. whiffiagonis or for any species of flatfish, other than a rate of 2.7% for plaice (Pleuronectes platessa L.) in the Irish Sea (Ellis & Nash, 1997). Hardardottir et al. (2001) determined a prevalence of atresia (Pa) of 24.5% for Icelandic cod (Gadus morhua L.), while the relative intensity of atresia (Ia) varied from 1% to 29%. It was observed that 42% of prespawning females had atresia, and 16% of spawning fish (Hardardottir et al. 2001). During the present investigation, an overall Pa of 63.5% was observed for megrim, which is a considerably high value, compared to the Icelandic cod above. This high value may be in part due to the breakdown of oocytes during the freezing process which were later mis-identified as atresia. No atresia was observed in pre-spawning females. When it is compared to that recorded for northern anchovy (Engraulis mordax) by Hunter & Macewicz (1985), it does not seem excessively high. A Pa of >50% was determined for northern anchovy. Hunter & Macewicz (1985), observed that the rate of atresia increased from only a few percent in the peak spawning months to much higher rates near the end of the spawning season. The atresia rates determined for L. whiffiagonis during the present study showed that the months prior to, and subsequent to spawning, *i.e.* December and April had the highest percentages of atresia observed.

For the relative intensity of atresia (Ia), an overall mean percentage of 24.29% (± 2.971) was determined, which is within the range of that recorded for Icelandic cod by Hardardottir *et al.* (2001). The relative intensity of atresia (Ia) is a measure of the amount of atresia occurring within an individual ovary (Hardardottir *et al.* 2001). This is normally quite a low percentage, although values as high as 87%, have been recorded in Atlantic herring (*Clupea harengus*) by Kurita *et al.* (2003), where the mean Ia was 4%, with almost all fish recording atretic oocytes.

Rates of atresia seem to be mainly initiated by unfavourable environmental conditions, more specifically low nutritional status prior to spawning (Hardardottir *et al.* 2001). Fish in poor condition undergo extensive follicular atresia of vitellogenic oocytes, and consequently have a much reduced potential fecundity (Abdel-Aziz, 1994). Therefore, the presence of high atresia rates, particularly (Ia), is most likely due to a lack of food availability or difficulty in finding prey items. Variation in female nutritional state, food ration, water temperature and day length may affect rates of atresia (Hunter & Macewicz, 1985).

A prevalence of atresia (Pa) of 63.5% determined for the population of *L*. *whiffiagonis* off the west coast of Ireland indicates that atresia is a rather common and natural phenomenon. It also implies the necessity and ultimate importance of including atresia in egg production estimates as a correction factor, in order to reduce bias occurring between potential fecundity and realised fecundity. This would allow for more accurate modelling of the reproductive potential for the species.

4.2:6 Histological structures

The developmental structures identified and recorded for both sexes were consistent with the developmental phases observed for megrim, (Santurtun *et al.* 1998b) and in other flatfish reproductive studies, such as that described by Abdel-Aziz (1994) for Egyptian sole (*Solea aegyptiaca*, Maddock & Burton (1999) for long rough dab (*Hippoglossoides platessoides*), and Rideout *et al.* (1999) for Greenland halibut (*Reinhardtius hippoglossoides*).

Due to the rather long period of time elapsed between the death of the fish and fixation, necrotic oocytes were found throughout all maturity stages. The images of post-ovulatory follicles obtained were only sufficient for their identification but not exposition. The presence of post-ovulatory follicles were direct evidence of recent

ovulation as the follicle which supported the developing oocyte was broken down. Residual eggs in the lumen of the ovary were also an indication of recent spawning. These post-spawning features were accompanied by many immature oogonia, a characteristic of single episode spawners (Maddock & Burton, 1999). As the majority of oocytes within pre-spawning ovaries were similar in size, this reflected the fact that development within the ovaries was heterogeneous, and did not have many differing developmental phases present. This demonstrated that the species are total spawners, *i.e.* releasing all oocytes in a single spawning event once annually. The latter was also recorded by Anon. (2001a). However, it was stated by Anon. (2001a) that megrim were asynchronous batch spawners for Sub Areas VI_{a+b} .

Several problems were encountered during the study, which affected the interpretation of the developmental structures. It was observed that many oocytes were ruptured or not intact following the histological process. This occurred as a result of freezing of the samples prior to histological preparation. It would have been preferable to prepare the gonadal tissue for histology as soon as the samples were collected, *i.e.* place in Bouin's Fluid fixative or formal saline, but this was not possible as a large number of samples were frozen prior to the start of the investigation and later whole samples were frozen at the auction hall prior to collection.

Almost no hydrated oocytes were recorded in the Stage IV pre-spawning and spawning ovaries of *L. whiffiagonis*. Hydrated oocytes are only present within pre-spawning ovaries for a very limited amount of time prior to ovulation. By sampling only once a month, the likelihood of missing this critical phase of vitellogenesis was greatly increased. More frequent sampling however, was not possible during the present study due to limited samples being made available.

During the histological process there was in some cases, failure to get complete wax impregnation for some of the ovarian tissues. The cells of the middle or inner areas of larger sized gonads, usually Stage IV ovaries, frequently did not become fully embedded with paraffin wax, resulting in the tissue collapsing and breaking during sectioning. Developmental structures could not therefore, always be successfully identified. Cutting the larger ovaries into several pieces to allow full wax impregnation was implemented. The latter technique however, meant that image analysis could not be carried out as a complete transverse section was not present (Tomkiewicz *et al.* 2003).

The examination of atresia within the ovaries provided some difficulty in deciding which phases of atresia to use in the estimation process. As mentioned earlier in Chapter 2., atresia goes through two main phases, *i.e.* alpha (α) and beta (β), the occurrence of which were used for atresia estimation. However, there are further later phases of atresia such as gamma (γ) and delta (δ), but these were deemed too difficult and time-consuming to identify and use in the estimation of atresia in *L. whiffiagonis.* The timing of the latter phases have been used by other authors in calculating energetics for other fish species, correlating atresia with levels of poor condition factor.

4.2:7 Gonadosomatic index

When the GSI recorded for this study is compared to that of previous megrim works, the results are very similar. Santurtun et al. (1998a) for megrim from the Bay of Biscay, observed that the GSI for small fish (<25cm TL) followed a rather constant pattern throughout the year, most probably due to the smaller fish not having reached sexual maturity and undergone gonadal development. As an overall GSI was calculated for the present study, and not one relating to fish lengths, this result cannot be confirmed. For female and male megrim >25cm TL, Santurtun et al. (1998a), recorded maximum GSI values in the winter months and minimum values in spring and summer. The GSI values for males decreased from January to April, and for females from February to April, suggesting that the male fish reached peak spawning slightly before females in the Bay of Biscay. For the remaining months of the year, the GSI values for both sexes were observed at very low levels, and there were no increments in the general trend until December, when it appeared that the larger fish started to prepare for the next spawning season (Santurtun et al. 1998a). Peak GSI was observed to be during the month of March for L. whiffiagonis caught in the Celtic Sea (Aubin-Ottenheimer, 1985). During the present investigation, it was observed that a general trend of increasing GSI values for megrim was recorded throughout the last quarter of each year, reaching a peak in the months of January and February, depending on the respective year, followed by a dramatic decrease. Values were at very low levels through the remaining spring and subsequent summer months until the start of the next spawning season, when GSI values began to increase once again.

Although GSI is a useful indicator of estimating the spawning time of a species, it does have associated problems. It works on the principal of proportion of gonad weight in relation to the bodyweight of the fish. The proportion increases

approaching spawning time, then decreases dramatically indicating the release of eggs and sperm. It is more accurate for females than males, as female gonad weights attain much larger proportions than that for male fish. The use of GSI has also been shown to greatly underestimate the reproductive effort in serial spawners (Kamler, 1995). Moreover, decreases in bodyweight due to lack of available prey items during the approach to the spawning period can negatively affect the GSI, and result in inaccurate estimates of spawning time.

4.2:8 Condition factor

The condition factor was used during the present study as an index of "wellbeing" or "fatness" (Bagenal, 1978). The more a fish weighs for a given length, the greater will be its condition factor. Condition factors calculated from monthly samples, for example, may be used to detect seasonal variations in the condition of the fish, which may vary with food abundance and the average reproductive stage of the stock (King, 1995).

Though there are several different methods to determine condition factor, that of Fulton's condition factor (Fulton, 1911) was used during the present study. Fulton's condition factor is suitable for comparing different individual fish of the same species, and it can also indicate differences related to sex, season or place of capture (Ricker, 1975). It can be used even when a species shows allometric growth, as was determined for *L. whiffiagonis* in the present study, as long as the fish are approximately the same length (Bagenal, 1978).

Santurtun *et al.* (1998a) observed that for small megrim (males <20cm and females <25cm), the monthly pattern of the condition factor showed maximum values during January and February for both sexes, decreasing to a minimum value in April for females, and May for male fish. For the remainder of the year, the condition factor for small females increased, reaching the same level as at the beginning of the year, but with a decrease in September (Santurtun *et al.* 1998a). For larger fish (males >20cm and females >25cm), the same general pattern was observed for males and females (Santurtun *et al.* 1998a). Maximum values were recorded in January and February, and minimum values in April, increasing again to higher values in October. As with the smaller fish, a sharp decrease in September was observed. For females and males, it was concluded that optimal condition of the fish occurred in January in the Bay of Biscay. These optimum conditions decreased in both sexes to their lowest

values in April, and indicated when the expected spawning time of the species occurred (Santurtun et al. 1998a).

Condition factor was used by Perez (1998) in ICES Areas VII, VIII and IX, to estimate the spawning period of the species. It was observed that the maximum values for males occurred in March as well as July, while for female fish, maximum values were recorded during February and March, and also in July. For both female and male megrim, condition factor values were relatively low throughout the remainder of the year (Perez, 1998).

When the condition factor results from previous studies are compared with those determined during the present investigation, it can be seen that those of Perez (1998) are closest in similarity. The maximum values recorded for condition factor during the present study, were observed in January and November, with a peak recorded in July. Unlike the study of Santurtun *et al.* (1998a), a peak in condition factor was recorded in September also. The lowest or minimum values were observed mainly in April, as well as in March for one of the examined years, that of 2000. *Lepidorhombus whiffiagonis* from the waters off the west coast of Ireland attain maximum condition slightly earlier than fish from the Bay of Biscay.

When condition factor was compared with gonadosomatic index (GSI) values for megrim recorded during the present investigation, a distinct pattern emerged, (Fig. 44.) in Chapter 3. It was noted that the peak or maximum values for condition factor occurred just before those of the GSI, indicating that megrim were in their "best" condition immediately prior to spawning. Subsequent to spawning, the condition of the fish deteriorated, as did the GSI, but then started to recover over the following months. Condition factor is closely related to feeding, as condition improves or decreases dependent on feeding intensity and prey availability (Morte et al. 1999; Steinarsson, 1979). The intensity of feeding of megrim varies throughout the year (Du Buit, 1984; 1992). In younger fish, feeding increases in the first three months of the year, and declines a little in April, and then increases again to a maximum level in September. Larger fish reach the highest level of feeding in March and, following a period of relatively light feeding in April and May, again from July to September (Rae, 1949;1963). These rates of feeding intensity compare favourably to the values of condition factor recorded during the present investigation. The hepatosomatic index (HSI) was not examined during this study as a measure of condition, as the liver

from the fish had deteriorated too much during freezing to allow further detailed examination.

4.2:9 Fecundity

There is no published information on the fecundity for *L. whiffiagonis*. Any results therefore determined in the present study cannot be compared with works elsewhere. However, these first results are important to future sustainable management of the Irish megrim fishery. Because of the lack of available relevant fecundity literature for megrim, comparisons have been made with information on fecundity from other species of flatfish such as witch (*Glyptocephalus cynoglossus* L.), plaice (*Pleuronectes platessa* L.), arrowtooth flounder (*Atheresthes stomias*) and Egyptian sole (*Solea aegyptiaca*).

Total fecundities for different species of teleost fish may range from tens of thousands to millions of eggs (Bone *et al.* 1997). This range of total fecundities depends of the reproductive strategy of a particular species, whether it spawns once a year or several times annually. Species such as cod (*Gadus morhua* L.) spawn several times a year and release high numbers of eggs into the marine environment. Eggs from these species are small in size and have low percentages of survival. The high fecundity levels are therefore to ensure increased survival rates. Megrim have relatively low fecundity compared to other species and have larger egg sizes. Large eggs take longer to develop than small eggs and produce larger larvae at hatching with a longer period of feeding on yolk reserves (Bone *et al.* 1997). This particular reproductive strategy is referred to as a k-strategy and is preferred by species that inhabit stable crowded environments where a low fecundity, larger egg and long developmental period are favoured (Bone *et al.* 1997).

The minimum fecundity recorded for L. whiffiagonis during this study, that of approximately 26,500 eggs from the sample of February 2001, was from a 3 year old female measuring 25.1cm TL. This compares similarly with the minimum fecundity determined for witch (G. cynoglossus) from the Georges Bank region of the NW Atlantic where 48,800 eggs were observed for a 31cm TL fish (Burnett *et al.* 1992). Maximum fecundity for megrim sampled during the present study was that of approximately 640,500 eggs from the sample in January 1999, and was from a 9 year old female measuring 45.1cm TL. When compared with the fecundity of a 60cm TL witch which had 508,300 eggs, it can be seen that the maximum recorded fecundity from the present study was considerably higher for a megrim that was almost 15cm

smaller. Burnett *et al.* (1992) found that fecundity was most highly correlated with weight, followed by length, and then age. This was also observed by Bowering (1978) for witch (*G. cynoglossus*) from the Grand Banks area of Newfoundland. This result is similar to that recorded during the present study for megrim fecundity.

Plaice (*Pleuronectes platessa*) fecundity from the Irish and North Sea has been examined by Simpson (1959a & b) and Ellis & Nash (1997). Mean numbers of eggs ranged from 42,000 for a 2 year fish, to 239,000 for a 9 year female, and averaged approximately 86,000 eggs for 5 year old fish. Though these fecundities were in relation to age and not length, it can be seen that plaice are in general more fecund than megrim, this being probably due to the fact that female plaice attain greater maximum lengths than *L. whiffiagonis*.

The fecundity of arrowtooth flounder (*Atheresthes stomias*), a large flatfish from the Gulf of Alaska, was determined by Zimmermann (1997), who recorded 246,000 eggs for a female measuring 48cm TL. This number of oocytes is considerably lower in proportion to that obtained for a *L. whiffiagonis* of similar length during the present study. However, the above fecundity estimate for the arrowtooth flounder was for a relatively small specimen of the species. This species of flatfish can reach lengths of >90cm TL, and have very large numbers of eggs, for example 2,224,000 oocytes were recorded for an 83cm TL female (Zimmermann, 1997).

The fecundity of Egyptian sole (*Solea aegyptiaca*) from the Mediterranean Sea, off the Egyptian coast was studied by Abdel-Aziz (1994), who recorded a low potential fecundity for the species. An average of 10,240 eggs were determined for fish of 20cm TL, while for larger fish (>30cm), an average of 89,860 eggs were noted (Abdel-Aziz, 1994). These fecundity values recorded for Egyptian sole are considerably lower than those calculated for *L. whiffiagonis* of similar lengths during the present study, and demonstrate that even though megrim have relatively low fecundities compared to some species of flatfish such as arrowtooth flounder or plaice, they are by no means the lowest fecundity recorded for flatfish.

Various egg size ranges have been recorded for megrim by different authors. Wheeler (1969) gave an egg size range of 1.07-1.22mm for the species, while Hempel (1979) recorded a size range of 1.0-1.20mm. Russell (1976), Ahlstrom *et al.* (1984) and Miller & Loates (1997) all determined egg size ranges of 1.02-1.22mm for megrim. A total egg size range of $325-725\mu m$ was observed during the present

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investigation, which is considerably smaller than the previously mentioned size ranges. The largest egg measured during the present study (725 μ m) was much smaller than even the minimum end of other egg size ranges determined for megrim. The most likely explanation for this phenomenon is that of shrinkage of the eggs during storage. Although it may have occurred during freezing when the fish were stored at - 18°C, it is most likely that shrinkage occurred whilst the eggs were in Gilson's Fluid. It has been shown by Witthames & Greer Walker (1987) that up to 20% shrinkage can occur in plaice and sole (*Solea solea* L.) eggs stored in Gilson's Fluid for any amount of time.

Considerable variation can occur in egg size as the spawning season progresses. In marine species of fish, it is well recognised that there is a seasonal decline in egg size and volume (Bagenal, 1971). In fish that spawn only once per season such as megrim, the decrease in egg size towards the end of the spawning season can be partly explained by a change in age composition of spawners. Fish spawning for the first time have been shown to produce smaller eggs than those spawning for the second time. The availability of food for adults can also lead to decreases in egg size through the spawning season (Kamler, 1995). The egg size of sole (Solea solea L.) from the North Sea was studied by Rijnsdorp & Vingerhoed (1994), who reported a decrease in egg size from 1.37mm to 1.13mm, representing a decrease in volume of 44%, from differing geographical areas, with the decrease strongly influenced by temperature and photoperiod. When the egg size for L. whiffiagonis is examined for each of the fecundity months sampled, it can be seen that the two samples taken in January (1998 & 1999) had smaller size ranges than the sample caught in February (2001), suggesting a increase in egg size as the spawning season occurs. This theory is supported by the fact that as spawning for megrim takes place during these months, fish which have not spawned in January have additional time for egg development, until they spawn in February. These observations lead to questions such as whether larger eggs are produced in different years, and how does this affect fecundity and recruitment in subsequent years.

It was established by Horwood *et al.* (1986) for plaice, that fecundity can vary from year to year. It was shown that fecundity for plaice was 1.44 times greater in 1980 than 1979, for the same location. This variation, it was concluded, was caused by environmental factors, more specifically probably that of food availability. Walsh (1994) observed that long rough dab (*Hippoglossoides platessoides*) were more fecund from the western North Atlantic (Grand Bank area) than in the eastern side. When the mean fecundity is compared between each of the yearly samples for the present study, considerable variation can be seen. The mean fecundity recorded for January 1999 is 1.59 times greater than that for February 2001, while it was only 1.18 times greater than that recorded for January 1998. No pattern can be discerned with regard to fecundity variation in the present study. It may be due to several factors such as sample size, month examined and annual environmental conditions for the area.

The eggs examined for the purpose of fecundity estimation during the present investigation were all taken from the dorsal lobe of the female ovary. It has been shown that different numbers of eggs develop in the dorsal and ventral lobes of ovaries (Zimmermann, 1997). In general more oocytes are present in the dorsal lobe of the ovary than the ventral lobe which is located underneath the dorsal lobe. This occurs for the obvious reason, that there is more space available to the dorsal lobe to develop and fill with eggs, while the lower ventral lobe is limited by its position beneath the fish. Future work could determine if a considerable difference in the number of eggs occurred between the dorsal and ventral ovary lobes for L. whiffiagonis. No work of this sort has been carried out for the species anywhere.

As described in Chapter 2., a variant subsampling method was used to estimate fecundity. This was carried out to reduce the amount of time and tedium spent counting eggs. However, this method though effective, was still timeconsuming and not as accurate as total counts which would have been better in determining the exact number of oocytes within an original 0.5g subsample from a ripe ovary. It would have been preferable to have had more fecundity samples to examine for this investigation in order to obtain an even more accurate estimation of the fecundity for the species. However, this was not possible as only one sample per month was obtained for the study, and this meant that only one sample per year could be used for fecundity determination as the spawning window for the species is restricted to a very short period of time. The use of a counting device such as a coulter counter would have reduced the amount of time and error significantly for fecundity determination. It would also have facilitated the removal of debris and nonreproductive material from the fecundity samples, which was not possible during the study.

From the study of fecundity for *L. whiffiagonis* during the present investigation, it can be concluded that the species are total spawners which spawn

once annually and have relatively low rates of fecundity, producing large eggs, when compared to other species of flatfish.

CHAPTER FOUR : PART 4. FUTURE STUDIES

4.3 Future studies

Results of this investigation of the common megrim *Lepidorhombus* whiffiagonis from off the west coast of Ireland, represent an accurate and detailed account of the biology of the species, in particular age, growth and reproductive cycle as well as population dynamics.

Considerable new information is presented on the reproductive biology of megrim off the west coast which makes an important addition to the contribution of the Working Group. A female biased sex ratio was determined, as well as estimates of the age and length at first maturity for female and male fish. The first ever fecundity values for megrim in Irish waters were obtained, revealing that megrim are total spawners and produce relatively small numbers of large eggs.

- While an account of the biology of the adult population is given here, much more quality information is required on the biology and population dynamics of juvenile *L. whiffiagonis*, in order to enable an estimation of the impact of the effects of discarding of small fish on the future of the fishery. Data is available on discarding rates for adult megrim in Irish waters but this does also requires considerable further study for the west off Ireland population of *L. whiffiagonis*.
- Though some work is currently being carried, very little is known about the spawning grounds, nursery areas and larval stages of the life of megrim, both in Ireland, but also in European waters, and requires further attention.
- The importance and relevance of atresia needs to be taken into account during estimations of potential spawning stock assessments. This can be done by increasing the amount of information known on the phenomenon.
- The distribution and abundance of female and male megrim with regard to depth and seasonality, needs to be further investigated off the west coast off Ireland.

- The amount of available information on male *L. whiffiagonis* is very limited and this requires much more detailed study in terms of both their growth and reproductive biology.
- Further work is needed with regard to selectivity, mesh sizes and accurate minimum landings sizes. Some of this work may be done in conjunction with research vessels on their annual groundfish surveys of Irish waters.
- Conservation measures need to be put in place in the event of the species becoming exploited beyond safe biological limits. Spawning areas need to be identified throughout the distribution range for megrim.
- While the Working Group contributes to the overall assessment of the stock, further detailed examination of the fishing mortality and yield per recruit dynamics of the species is needed, to ensure the sustainable exploitation of the fishery.

It is suggested that the work produced will aid fisheries managers in the introduction of management measures for the Irish megrim fishery, and contribute to the sustainable utilisation of this valuable resource. **Bibliography**

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WEBSITE CITATION

Url. 1. Http://www.fao.org/fi/default_all.asp. (Food & Agriculture Organisation) Url. 2. Http://www.marine.ie/industry+services/fisheries/index.htm. (Marine Institute)

Appendix I

Publications associated with this Ph.D. work.

- Robson, S. M., King, P. A., Hannan, J. and McGrath, D. 2000 Age and growth of a sample of four-spot megrim, *Lepidorhombus boscii*, from off the west coast of Ireland. *Biology and Environment : Proceedings of the Royal Irish Academy*, Vol. 100B, No.3, 143-148. (Appendix III)
- Robson, S. M., O'Dwyer, F. and King, P. A. 2003 The meristic characteristics of witch, *Glyptocephalus cynoglossus* L. (Pisces: Pleuronectidae), sampled off the west coast of Ireland. *Irish Naturalists' Journal.* 27, No.8, 289-294.
- Robson, S. M., King, P. A. and McGrath, D. (*in review*) The morphometric and meristic characteristics of the common megrim *Lepidorhombus whiffiagonis* and the four spot megrim *Lepidorhombus boscii* sampled from off the west coast of Ireland. *Aquatic Living Resources.* 2004. (Appendix II)

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Reproduction and growth of a population of the common megrim. The Irish Scientist MilleniumYearbook 2000, Page 42.

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King, P. A. and **Robson, S. M.** Fishing for witch in Irish waters. *The Irish Scientist Yearbook* 2001, Page 119.

Robson, S. M. and King, P. A.

Age determination of the common megrim *Lepidorhombus whiffiagonis* using otoliths.

The Irish Scientist Yearbook 2002, Page 115.

Appendix II

THE MORPHOMETRIC AND MERISTIC CHARACTERISTICS OF THE COMMON MEGRIM *LEPIDORHOMBUS WHIFFIAGONIS* AND THE FOUR SPOT MEGRIM *LEPIDORHOMBUS BOSCII* SAMPLED FROM OFF THE WEST COAST OF IRELAND

Stephen M. Robson, Pauline A. King and David McGrath

Stephen M. Robson (corresponding author), Pauline A. King and David McGrath, Commercial Fisheries Research Group, Department of Life Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland.

Telephone(091)753161Fax(091)758412

ABSTRACT

One hundred common megrim Lepidorhombus whiffiagonis (Walbaum 1792) and 100 four spot megrim Lepidorhombus boscii (Risso 1810) were sampled from the west coast of Ireland between November 1998 and July 1999. The purpose of the present work was to conduct a baseline study on the morphometrics and meristics for the two species as no published work to date has been carried out in Irish waters. The fish were examined morphometrically and meristically. A range of 80-96 and 79-89 dorsal fin rays were recorded for L. whiffiagonis and L. boscii respectively. Anal fin ray counts ranged in number from 60-74 rays for L. whiffiagonis, and 63-71 rays for L. boscii. For vertebral counts, ranges of 40-43 and 39-43 were recorded for L. whiffiagonis and L. boscii respectively. Results were compared with works by other authors elsewhere in Europe, and it was found that they were most similar to those of Furnestin (1935) and Wheeler (1969). It was concluded that the morphometric and meristic characteristics recorded in the study were specific to the populations of L. whiffiagonis and L. boscii inhabiting the waters off the west coast of Ireland.

Keywords : Morphometric, meristic, megrim, Lepidorhombus whiffiagonis, L. boscii.

INTRODUCTION

Two species of megrim, the common megrim, Lepidorhombus whiffiagonis (Walbaum 1792), and the four spot megrim, Lepidorhombus boscii (Risso 1810), are common in the waters around Ireland. They are demersal flatfish of the family Scophthalmidae and are commercially exploited by the Irish demersal fishing fleet (Fahy and Gleeson, 1992). Megrim are caught as a by-catch of gadoid fisheries and are particularly associated with fisheries for prawns (Nephrops norvegicus L.), angler fish (Lophius species) and ray (Raja species) (Fahy and Fannon, 1991). Though there is no distinction made between L. whiffiagonis and L. boscii in the Irish catches, L. whiffiagonis constitutes the bulk of all landings in Irish waters (Robson *et al.* 2000) with a combined total of 3669 tonnes being landed in 2001, at a value of \in 11.0m (Anon. 2002).

The common megrim, *Lepidorhombus whiffiagonis*, has the mouth to the left of the eyes. The lower jaw is strongly projecting with a stout point at its tip. The eyes are large and the lower eye is distinctly in advance of the upper eye while the space between them is very narrow. The snout is longer than the diameter of the eye (Furnestin, 1935; Wheeler, 1969). The body is long and narrow. The head is also long and its length equals the body width at the origin of the anal fin. The pectoral fins are unequal in length, that on the eyed side being well developed, while the pelvic fins are long based and equal in length. The dorsal fin is long and the last rays of both dorsal and anal fins are just on the underside of the tail (Wheeler, 1969). The common megrim is a yellowish brown colour with ill defined spots while the dorsal and anal fins have obscure dark marks towards their ends (Dwivedi, 1964; Wheeler, 1969).

Lepidorhombus whiffiagonis tends to inhabit shallower waters than L. boscii (Sanchez et al. 1998) and can be found from depths of 51m to 512m (Poulard et al. 1993), though its greatest abundance occurs at depths of more than 200m (Silva and Azevedo, 1994). L. whiffiagonis is mainly distributed on the oceanic coasts of northern Europe (Wheeler, 1969) and has been recorded as far south as the Mediterranean (Dwivedi, 1963; 1964; Sanchez et al. 1998). It prefers soft muddy bottoms and is rarely found near the surface (Wheeler, 1969). The diet of L. whiffiagonis consists predominantly of crustaceans and fish (Rae, 1963; Morte, 1999).

The four spot megrim, Lepidorhombus boscii is similar to the common megrim in general, with a moderately large mouth to the left of the eyes. The lower jaws project, but not strongly. The eyes are large and the lower eye is slightly in front of the upper eye (Dwivedi, 1964; Wheeler, 1969). The length of the snout is less than the eye diameter. The body is moderately long and narrow, and the head length is equal to the width at the level of the rear of the eye. The pectoral fins are unequal in length as in *L. whiffiagonis* and the pelvic fins are broad based but equal in length. Both the dorsal and anal fins end at the proximal end of the lower side of the tail (Wheeler, 1969). Lepidorhombus boscii is a yellowish brown colour without definite markings on the body except for a pair of large, rounded and very distinct spots near the end of the dorsal and anal fins (Dwivedi, 1964; Wheeler, 1969).

Lepidorhombus boscii is normally distributed in southerly waters as far south as the Mediterranean, but has been recorded as far north as 58°N (Sanchez *et al.* 1998). It is common on soft bottoms at depths of 293-730m off the west coast of Ireland (Wheeler, 1969). The diet of *L. boscii* consists mainly of crustaceans such as decapods and mysids (Sartor and De Ranieri, 1996).

Meristic characters such as fin ray, vertebral and gill raker counts play an important part in racial studies of fish in distinguishing species, subspecies and populations within species (Taning, 1952; Purdom and Wyatt, 1969). Morphometric characters are those that are measured, *i.e.* lengths of various body parts (Caillet *et al.* 1986). Much work has been done on the different reasons for the variation in meristics in fish. Studies by Hubbs (1924), Johnsen (1936), Weisel (1955), Sagnes *et al.* (1997) and Kovac *et al.* (1999) concluded that not only genetic factors can determine meristic characters, but environmental factors also, such as water temperature, salinity and seasonality.

Meristic work has been carried out on several species of flatfish, primarily to distinguish between populations of the same species. Purdom and Wyatt (1969) used meristic characters to differentiate between Irish Sea and North Sea plaice (*Pleuronectes platessa* L.). Meristics have been used to demonstrate that the racial character of plaice altered from year to year in the North Sea (Jensen, 1939). The influence of environmental factors such as temperature and geographic location, which can cause variation in meristic characters, has been studied for flatfish species such as plaice (Dannevig, 1950; Molander and Molander Swedmark, 1957). In Ireland, the only flatfish meristics published is that for witch (*Glyptocephalus cynoglossus* L.) from off the west coast (Robson *et al.* 2003).

There are several studies on the morphological and meristic characteristics of the two megrim species, L. whiffiagonis and L. boscii elsewhere in Europe. Furnestin (1935) gives a detailed examination of the meristics of L. whiffiagonis from the Atlantic and the North Sea and the differences between the populations. Dwivedi (1963) examined the morphological differences between a population of L. boscii from the Atlantic and one from the Mediterranean. Another study by Dwivedi (1964) compared the ecology, morphology and biology of L. whiffiagonis with L. boscii from the Atlantic (in the Bay of Biscay), and also the North Sea and Mediterranean. Meristic characters were used to distinguish the populations in the different areas. Wheeler (1969) briefly reviewed megrim meristics in his definitive study of the fishes of north west Europe. Clingy (1905) cited by Furnestin (1935) examined meristics of fish from the Lepidorhomus genus. Finally, Nielsen (1986) details some megrim meristics in a study of several Scophthalmidae species.

As no work has been published to date on megrim morphometrics and meristics in Irish waters, the purpose of the present work was to conduct a baseline study in order to allow further comparisons to be made by others at a later date or for a different area. The results are compared with similar works carried out by authors elsewhere in Europe.

MATERIALS AND METHODS

For this investigation, 200 fish were examined, *i.e.* 100 common megrim, *Lepidorhombus whiffiagonis*, and 100 four spot megrim, *Lepidorhombus boscii*. The fish were obtained from commercial catches landed at the port of Rossaveal, Co. Galway and were taken on four different sampling occasions *i.e.* November 1998, March, May and July 1999. The fish were caught on prawn grounds (*Nephrops norvegicus* L.) off the west coast of Ireland in ICES Divisions VII_b mainly on fishing grounds behind the Aran Islands, and VII_c, particularly off the Porcupine Bank. The fish were caught at depths of approximately 150m, by commercial trawlers using an otter board bottom trawl with a standard mesh size of 80mm at the cod-end. The fish were preserved at -18° C pending further examination at the laboratory.

Each fish was examined morphometrically and meristically. Morphometric measurements consisted of total length (T.L.) which was determined by measuring from the tip of the snout of the fish to the most extreme part of the tail fin when the tail was fully extended. Standard length (S.L.) was taken by measuring from the tip of the snout to a region of the tail which acts as a wrist and can be identified by touch, while head length (H.L.) was determined by measuring from the tip of the snout to the furthest point posteriorly on the gill operculum. Snout length (Snt.L.) was taken by measuring the distance from the most anterior point of the upper lip to the anterior edge of the orbit of the eye on the dorsal fin side of the fish. Eye diameter (E.D.) was determined by measuring the distance across the body at a point in

the bend of the lateral line on the fish. All fish were measured to the nearest millimetre below.

The meristic examination was carried out by counting the number of soft fin rays on the dorsal, anal, caudal, pelvic and pectoral (eyed side of fish) fins. Vertebral counts were taken by removing the flesh from above the lateral line on the eyed side of the fish and counting each vertebra from the beginning of the spine to the base of the tail fin. The number of gill rakers were counted on the first gill arch of each fish.

RESULTS

100 L. whiffiagonis and 100 L. boscii were examined morphometrically and meristically. Male and female fish were combined. A summary of results is presented in Table 1.

Morphometric Measurements

Total Length

The total length for *L. whiffiagonis* ranged from 23.6cm to 40.7cm with a mean value of 30.63cm (\pm s.d. of 3.45cm), while total length for *L. boscii* ranged from 24.2cm to 41.9cm and had a mean value of 28.64cm (\pm s.d. of 2.97cm). Standard Length

Standard length ranged from 20.1cm to 33.4cm for *L. whiffiagonis*, with a mean value of 25.49cm (\pm s.d. of 2.88cm). The standard length for *L. boscii* ranged from 19.6cm to 34.8cm with a mean value of 23.69cm (\pm s.d. of 2.54cm). *Head Length*

For *L. whiffiagonis* head length ranged from 5.2cm to 9.3cm with a mean value of 6.73cm (\pm s.d. of 0.83cm), while for *L. boscii* a range of 4.9cm to 9.4cm and a mean of 6.21cm (\pm s.d. of 0.72cm) was obtained.

Snout Length

A range of 1.6cm to 2.8cm was obtained for *L. whiffiagonis* snout length with a mean value of 2.0cm (\pm s.d. of 0.25cm). For *L. boscii* a range of 1.3cm to 2.5cm was recorded with a mean of 1.6cm (\pm s.d. of 0.20cm).

Eye Diameter

L. whiffiagonis had an eye diameter range of 1.8cm to 3.0cm and a mean of 2.1cm (\pm s.d. of 0.24cm), while L. boscii had a range of 1.9cm to 3.0cm and a mean value of 2.2cm (\pm s.d. of 0.20cm).

Body Width

A range of 6.5cm to 13.4cm with a mean value of 9.27cm (\pm s.d. of 1.28cm) was recorded for *L. whiffiagonis*, while *L. boscii* had a range of 7.2cm to 14.4cm and a mean value of 9.02cm (\pm s.d. of 1.18cm).

Head Length / Total Length Ratio

The head length / total length ratios for each species was examined, with a mean head length / total length ratio for *L. whiffiagonis* at 0.219 (\pm s.d. of 0.0085) being recorded. For *L. boscii*, a mean head length / total length ratio of 0.216 (\pm s.d. of 0.0061) was observed.

Meristic Counts

Dorsal Fin Rays

The number of soft fin rays in the dorsal fin of *L. whiffiagonis* ranged from 80 to 96 rays with a mean number of 88.74 rays (\pm s.d. of 3.19). For *L. boscii*, dorsal fin rays ranged in number from 79 to 89 rays, with a mean value of 82.88 rays (\pm s.d. of 2.15) The number of dorsal fin rays for both species is presented in Fig 1. *Anal Fin Rays*

Anal fin rays for *L. whiffiagonis* ranged in number from 60 to 74 rays with a mean number of 69.14 rays (\pm s.d. of 2.44), while the anal fin ray range for *L. boscii* was 63 to 71 rays with a mean number of 66.61 rays (\pm s.d. of 1.82). The number of anal fin rays for *L. whiffiagonis* and *L. boscii* is presented in Fig. 2. *Caudal Fin Rays*

A constant number of 17 rays was recorded for both species during the investigation.

Pectoral Fin Rays

Pectoral fin ray counts were taken from the eyed side only of both species. For *L. whiffiagonis* a range of 11 to 13 rays was recorded, with a mean number of 11.66 rays (\pm s.d. of 0.55). *L. boscii* had a pectoral fin ray range of 10 to 12 rays and a mean number of 11.65 rays (\pm s.d. of 0.50).

Pelvic Fin Rays

A constant number of 6 rays was recorded for both species for pelvic fin rays, without any variation.

Vertebrae

A range of 40 to 43 vertebrae was recorded for *L. whiffiagonis* with a mean number of 41.68 vertebrae (\pm s.d. of 0.55), while a range of 39 to 43 vertebrae was recorded for *L. boscii* and a mean number of 40.79 vertebrae (\pm s.d. of 0.70). The number of vertebra counts recorded during the study for both species is presented in Fig. 3.

Gill Rakers

For L. whiffiagonis, a range of 17 to 21 gill rakers and a mean number of 18.47 rakers (\pm s.d. of 0.82) was obtained, while a range of 16 to 20 gill rakers with a mean number of 17.95 rakers (\pm s.d. of 0.89) was recorded for L. boscii. The number of gill rakers recorded for both L. whiffiagonis and L. boscii is presented in Fig. 4.

DISCUSSION

The meristic counts for L. whiffiagonis and L. boscii obtained in this study are comparable with those recorded by other authors elsewhere. The range of 80 to 96 dorsal fin rays recorded in the present investigation for L. whiffiagonis is closest to the range of 80 to 94 rays found by Furnestin (1935) in the Atlantic for the same species. It is considerably different from that found by Wheeler (1969) in the north east Atlantic who recorded a dorsal ray range of 85 to 94. Furnestin (1935) and Wheeler (1969) do not state how many fish were examined during their respective studies. It can be assumed that the range is likely to increase as a greater number of fish are examined so the lower range of Wheeler (1969) may be a reflection of sample size. The range of anal fin rays for L. whiffiagonis in this study was 60 to 74. This result was very close to the 61 to 74 rays recorded by Furnestin (1935). The number of caudal fin rays for L. whiffiagonis as well as L. boscii, was constant at 17 rays. This number has also been recorded without variation, by Furnestin (1935) and Cligny (1905) in the Atlantic, off the coasts of Spain and Portugal. Like the caudal fin, the number of pelvic fin rays for both species remained at 6 rays. The latter is consistent with results recorded by other authors elsewhere (Furnestin, 1935; Dwivedi, 1964; Wheeler, 1969). The range of pectoral fin rays recorded during the investigation for L. whiffiagonis was 11 to 13 rays. Furnestin (1935) recorded 12 as the most common number of rays, rarely 11 rays. It was also noted by Furnestin (1935) that the number of pectoral fin rays diminished with age. Fish were not examined with regard to age and its relationship with the number of fin rays during the present study. Only the pectoral fin on the eyed side of the fish was examined during this study, whereas both pectorals were studied in other works. It was observed during the present investigation that there is a very small first ray, on the anterior part of the pectoral fin which is quite easy to omit from the meristic count for the fin. This may result in lower pectoral fin ray counts overall in some studies and may perhaps present a greater difficulty when counting fin rays for older fish.

The number of vertebrae have been studied by Furnestin (1935), Dwivedi (1964) and Wheeler (1969) in the Atlantic and North Sea, Atlantic and Mediterranean and the north east Atlantic respectively. The authors recorded ranges of 40-43, 38-42 and 40-42 respectively for *L. whiffiagonis*. These results are similar to the range of 40-43 vertebrae recorded during the present study. The range of gill raker numbers in this study cannot be compared with elsewhere, as no other work appears to have been published on this particular meristic characteristic.

The number of dorsal fin rays for L. boscii in this investigation is slightly higher than the ranges found by Cligny (1905) and particularly Dwivedi (1963) in the Atlantic and Mediterranean (Table 1.). Variation in the number of fin rays is a common occurrence within species of fish. Studies by Molander and Molander Swedmark (1957), for example, showed that the mean numbers of rays varies with different populations. Several stocks of plaice exist in the English Channel, North Sea and Baltic Sea. Stocks can be distinguished by varying meristic counts on dorsal and anal fins as well as vertebrae (Molander and Molander Swedmark, 1957). Considerable variation exists in anal fin ray counts for L. boscii from various locations. Cligny (1905) recorded a range of 65-70 rays from the Atlantic. Dwivedi (1963) recorded ranges of 60-69 rays for populations in the Atlantic and the Mediterranean. Wheeler (1969) gives a range of 64-74 rays for the L. boscii anal fin. The anal fin ray range for fish from the west coast of Ireland was 63-71, which is closest to the results recorded by Cligny (1905). A range of 10-12 (mean of 11.65 rays $(\pm$ s.d. of 0.50)) for pectoral fin rays for L. boscii was recorded during the present investigation. This is an identical mean value to that recorded by Dwivedi (1964). Vertebrae number variation is quite small in L. boscii as can be determined from examination of previous works (See Table 1.). All previous mentioned authors recorded vertebrae numbers in the range of 39-42, while the present study shows a range of 39-43 (mean number of 40.79 vertebrae (± s.d. of 0.70)) was recorded. Vertebrae number are more conservative than the number of fin rays (Itazawa, 1959) as they are determined during early development. It is generally considered that fish subjected to low temperature tend to have more vertebrae than those in warmer waters (Itazawa, 1959). This would probably explain why a slightly higher range of vertebral counts were recorded in this study, as the present samples were from the Atlantic, off the Irish coast, as opposed to the warmer waters of the Mediterranean or more southern areas of the Atlantic.

The only morphometric character of interest identified in works elsewhere was a head length / total length ratio carried out by Furnestin (1935) on L. *whiffiagonis*. Furnestin (1935) recorded a mean ratio value of 0.251. This is considerably higher than the 0.219 mean value obtained for the same species off the west coast of Ireland, though a value of 0.250 was obtained for a single fish in the present study.

The differences recorded between this study and other works, primarily Furnestin (1935), Dwivedi (1963, 1964) and Wheeler (1969) are probably due to factors such as temperature, geographic variation and genetic composition. As shown in studies by Purdom and Wyatt (1969), racial differences occur between populations of the same species. In the present study, eye diameter is greater than snout length, which is different to that stated by Wheeler (1969) who described eye diameter as less than snout length for both species. This may reflect the choice of measurements and measuring procedure used in this investigation. The meristic traits found in this study are probably specific to the populations of L. whiffiagonis and L. boscii inhabiting the waters off the west coast of Ireland.

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Table 1.	Meristic and morphometric characteristics recorded by several authors for
	L. whiffiagonis and L. boscii.

Author & Year	Character	Lepidorhombus	Lepidorhombus	Location of
	Examined	whiffiagonis	boscii	Study
Cligny 1905	Dorsal Rays	80-92 (85.5)	82-89	Atlantic (from
	Anal Rays	64-71 (67.3)	65-70	off the coast of
	Caudal Rays	17	17	Spain and
	Pelvic Rays	6	6	Portugal)
	Pectoral Rays	12	11	
Furnestin 1935	Dorsal Rays	80-94		Atlantic and the
	Anal Rays	61-74		North Sea
	Caudal Rays	17		
	Pelvic Rays	6		
	Pectoral Rays	12, rarely 11		
	Vertebrae	40-43 (41.31)		
	HL/TL Ratio	0.251		
Dwivedi 1963	Vertebrae		40.26 (mean)	Atlantic and
	Total Length		13.0-34.0	Mediterranean
	Dorsal Rays		72-87 (81.30)	Sea
	Anal Rays		60-69 (64.18)	
Dwivedi 1964	Vertebrae	41.21 (mean)	39.83 (mean)	Atlantic, Bay of
	Dorsal Rays	86.85 (mean)	79.67 (mean)	Biscay, North
	Anal Rays	67.28 (mean)	63.19 (mean)	Sea and
	Pectoral Rays	11.60 (mean)	11.65 (mean)	Mediterranean
Wheeler 1969	Dorsal Rays	85-94	79-86	North Western
	Anal Rays	64-74	65-69	Europe
	Vertebrae	40-42	39-42	
Nielsen 1986	Dorsal Rays	85-94	79-86	North Eastern
	Anal Rays	64-74	65-69	Atlantic
Fishbase 1996	Dorsal Rays	85-94		Location
	Anal Rays	64-74		Unspecified
Robson et al. 1999	Dorsal Rays	80-96 (88.74)	79-89 (82.88)	The Atlantic
	Anal Rays	60-74 (69.14)	63-71 (66.61)	from off the
	Caudal Rays	17	17	west coast of
	Pelvic Rays	6	6	Ireland.
	Pectoral Rays	11-13 (11.66)	10-12 (11.65)	
	Vertebrae	40-43 (41.68)	39-43 (40.79)	
	Gill Rakers	17-21 (18.47)	16-20 (17.95)	
	Total Length	23.6-40.7	24.2-41.9	
	Standard Lth.	20.1-33.4	19.6-34.8	
	Head Length	5.2-9.3 (6.73)	4.9-9.4 (6.21)	
	Snout Length	1.6-2.8 (2.00)	1.3-2.5 (1.61)	
	Eye Diameter	1.8-3.0 (2.16)	1.9-3.0 (2.25)	
	Body Width	6.5-13.4 (9.27)	7.2-14.4 (9.02)	
	HL/TL Ratio	0.219	0.216	

All morphometric measurements in cm. Numbers in brackets represent mean values.

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MEGRIM MORPHOMETRICS & MERISTICS PAPER FIGURES 1-4.









Appendix III

AGE AND GROWTH OF A SAMPLE OF FOUR-SPOT MEGRIM, *LEPIDORHOMBUS BOSCII*, FROM OFF THE WEST COAST OF IRELAND

Stephen M. Robson, Pauline A. King, Joan Hannan and David McGrath

ABSTRACT

A sample of 150 four-spot megrim, Lepidorhombus boscii (Risso 1810), was collected from the port of Rossaveal, Co. Galway, between June 1997 and July 1999. Age was determined by examining the sagittal otoliths, and the oldest fish was estimated to be an eleven-year-old female measuring 33.4cm in total length. Six-year-old fish were the most frequently recorded age class in the sample (40.5%). The von Bertalanffy growth parameters of k=0.27, $L \infty = 34.39$ cm and $t_0 = -1.997$ years were determined, as well as the weight (W) to length (TL) relationship of W (g) = 0.0062TL (cm)^{3.367}. More females than males were recorded during the investigation, giving a female to male sex ratio of 1:0.293 (P < 0.05), which significantly departs from the expected ratio of 1:1. Females lived longer and attained a greater length than males. The age of full recruitment to the fishery was determined as seven years.

Stephen M. Robson (corresponding author), Pauline A. King, Joan Hannan and David McGrath, Department of Life Sciences, Galway–Mayo Institute of Technology, Dublin Road, Galway, Ireland.

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INTRODUCTION

The four-spot megrim, Lepidorhombus boscii (Risso 1810), is a demersal flatfish of the family Scophthalmidae. It is commercially exploited, along with its close relative the common megrim Lepidorhombus whiffiagonis (Walbaum 1792), off the west coast of Ireland. Currently, L. boscii is not separated from L. whiffiagonis in the Irish catches, and no work has been published to date on its biology in Irish waters.

Both the four-spot megrim and the common megrim have the mouth to the left of the eyes and are moderately large. The lower jaw projects but not strongly (Wheeler 1969). The eyes of *L. boscii* are large, and the length of the snout is less than the eye diameter. The body is long, narrow and yellowish-brown, without definite markings, except for a pair of large, rounded and very distinct spots near the end of both dorsal and anal fins (Wheeler 1969). *Lepidorhombus boscii* has been recorded up to 44cm long by Santos (1995).

The four-spot megrim is normally distributed in southerly waters but has been fished as far north as 58°N (Sanchez *et al.* 1998). It is common on soft bottoms on the deeper grounds to the west of Ireland at depths of 293-730m (Wheeler 1969). *Lepidorhombus boscii* replaces *L. whiffiagonis* within its area of distribution, with *L. whiffiagonis* occupying northern waters and *L. boscii* found in the south (Sanchez *et al.* 1998). The diet of *L. boscii* consists mainly of crustaceans (Sartor and De Ranieri 1996) and small fish (Morte *et al.* 1999).

Studies on the growth of *L. boscii* in European waters include work in the southern Adriatic (Bello and Rizzi 1987), in the eastern Mediterranean (Vassilopoulou and Ondrias 1999), off the Portuguese continental coast (Castilho *et al.* 1993; Santos 1994; 1995) and along the northern Spanish shelf (Landa 1999). Other studies, such as that of Dawson (1991) in the Celtic Sea and Pineiro *et al.* (1993) in the north-east Atlantic, deal with growth of both species of megrim combined and are therefore not directly relevant to this investigation.

The purpose of the present work was to study the age, growth and population structure of the four-spot megrim, *Lepidorhombus boscii*, off the west coast of Ireland and to compare the results with those of similar studies undertaken in other parts of Europe.

MATERIALS AND METHODS

A total of 150 four-spot megrim were obtained from catches landed at the commercial fishing port of Rossaveal, Co. Galway. Samples were taken on three days during June 1997, November 1998 and July 1999. The fish were

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caught on Nephrops grounds in ICES Division VIIb, off the Porcupine Bank off the west coast of Ireland, at depths of ϵ . 150m, by commercial trawlers using an otter board trawl with a standard mesh size of 80mm at the cod-end. The fish were preserved by freezing at -18° C pending further examination in the laboratory. Total length (TL) and standard length (SL) for each fish were measured to the nearest millimetre below. Each fish was surface dried and weighed to the nearest gram. The fish were sexed by macroscopic examination of the gonads. Paired sagittal otoliths were removed, immersed in water to remove surrounding membranes, cleaned and stored dry. Age readings were taken by examining the otoliths under a stereoscopic microscope, using reflected light against a black background with the whole otoliths immersed in water. Under low magnification, a series of successive concentric opaque and hyaline bands was noted radiating out to the otolith edge. The opaque bands are known to be laid down during summer, while the dark, or hyaline, bands are laid down during winter. Therefore an opaque band and a hyaline band together represent one year's growth (Caillet et al. 1986). Age was determined by counting the number of hyaline bands (Williams and Bedford 1974).

The growth rate for L. boscii was calculated using the simple and precise method of Rafail (1973), and the data were used to construct a von Bertalanffy growth curve, which is represented as $Lt = L\infty (1 - e^{-k(t-t_0)})$. Insufficient data were present to obtain growth values for males separately, so males and females were combined. From this, values for $L\infty$, k and t_0 were determined. $L\infty$ is the maximum size that the fish would achieve if unaffected by fishing effort, predation, disease and natural mortality; k is the rate at which the fish reaches the limiting size; and to is the age at which the fish is theoretically 0mm long. The first k value was estimated by the resulting slope from a log, plot of annual increments in growth against mid-age points. This k value was used in the equation

$$\frac{L\infty = {}^{ck}\Sigma Lt - \Sigma Lt}{(N-1)(e^k - 1)}$$

to estimate $L\infty$, the value of which was used in the equation $(\log_r (1 - Lt/L\infty))$. From this equation a second estimate of k was determined and then a more accurate second value for $L\infty$ (Rafail 1973). The value for t_0 was estimated by using the k value in the equation

$$\frac{t_0 = y \text{ intercept}}{k}$$

The length-weight (W) relationship repre-

sented by the formula $W = aTL^b$ was log transformed to $\log_c a + b(\log_c TL)$, where b is an exponent with a value nearly always between 2 and 4, and often close to 3 (Ricker 1971). The value of b = 3 indicates that the fish grows isometrically, while values other than 3 indicate allometric growth: if b > 3 the fish becomes 'heavier for its length' as it grows larger (Ricker 1971). The variance (S^2) of the slope (b) was calculated using the equation of King (1995).

A plot of the \log_e of numbers against ages was constructed, resulting in a dome-shaped curve, commonly referred to as a catch curve (Gulland 1985). Because the age group representing the peak of the dome may or may not be totally vulnerable to the fishing gear, the portion of the descending leg used to estimate Z (the mortality coefficient) is shifted one age group to the right of the dome (Gulland 1985). The latter age group is then taken to be that at which the fish are fully recruited to the fishery.

RESULTS

From the sample of 150 fish, two fish were not included in the statistical analysis because of difficulties in ageing the otoliths, and another two were missing caudal fins, so a total length measurement could not be taken from them.

SEX RATIO

Females comprised 77.3% (n = 116) and males 22.6% (n = 34) of the sample, resulting in a male to female ratio of 0.293:1. This was significantly different from the expected male to female ratio of 1:1 ($\chi^2 = 44.8$, P < 0.05).

LENGTH FREQUENCIES

The length frequency distribution for the sample of *L. boscii* (males and females combined) is shown in Fig. 1. The largest percentage of fish (32.43%) is within the length class of 26–27.99cm TL. The largest specimen recorded was a female measuring 41.9cm TL, while the smallest was a male of 24.2cm TL. Males ranged from 24cm to 34cm TL, while females ranged from 24cm to 42cm TL. All specimens of greater than 34cm TL were female.

The relationship between total length and standard length was highly significant ($R^2 = 0.98$, P < 0.01). This relationship can be written as $SL = 0.0057 TL^{0.8478}$.

The relationship between log_c total length and log_c body weight (Fig. 2) was also highly significant ($R^2 = 0.94$, P < 0.01). The slope of the relationship b = 3.367 and log_ca (the intercept





Fig. 1-Length frequencies for male and female four-spot megrim off the west coast of Ireland.



Fig. 2-Regression analysis showing the relationship between log (weight) and log (total length) for four-spot megrim off the west coast of Ireland.

of the line with the y axis) = -6.262. The relationship can therefore be written as $W(g) = 0.0062TL (cm)^{3.367}$. The variance (S^2) of the slope (b) is given as $S_b^2 = 0.004967$, and the 95% confidence intervals of the slope b (3.37) = ± 0.138 . As the confidence intervals for b (from 3.23 to 3.50) are greater than 3, growth is determined as allometric for this species.

AGE FREQUENCIES, CATCH CURVE AND GROWTH

The age frequency distribution for the sampled population is shown in Fig. 3. The most frequently recorded age was six years. Ages for male *L. boscii* ranged from five to nine years, and for females from four to eleven years.





Fig. 3-Age frequencies for male and female four-spot megrim off the west coast of Ireland.



Fig. 4—Catch curve for four-spot megrim captured off the west coast of Ireland; arrow indicates average age of full recruitment.

A catch curve was calculated, and the age of full recruitment was determined to be at Age Group 7 for the fishery (Fig. 4).

Growth of *L. boscii* can be described by the von Bertalanffy growth equation as follows: $Lt = 34.39 \ (1 - e^{-0.2703} \ ^{(t+1.997)}) \ (n = 148, \ R^2 = 0.94, \ P < 0.01)$, where *Lt* is the total length in cm at time *t*, and *t* the age in years.

DISCUSSION

The growth parameters for L. boscii obtained in this study are similar to those found by other authors. The value of $L\infty = 34.39$ cm obtained for L. boscii during the present investigation is within the range (28-41cm) obtained by Dawson (1991) for the Celtic Sea and by Santos (1994) for the Portuguese continental coast. Similarly, the *k* value (0.27) and the t_0 value (-1.997) are within the ranges found elsewhere (0.14 to 0.31, -1.06 to -3.64, respectively) (Fuertes 1978; Bello and Rizzi 1987; Castilho *et al.* 1993; Santos 1995).

Length frequency distributions for the sampled population showed that female fish are bigger than males, a feature that is common in other flatfish species and a finding similar to those of other *L. boscii* growth studies (Santos 1994; 1995).

The length-weight relationship obtained during the present investigation gave values of a =0.0062 and b = 3.367, and growth of *L. boscii* is determined as allometric, i.e. the fish becomes heavier for its length as it grows larger (Ricker 1971). This length-weight relationship is similar to that found by Santos (1994; 1995) in Portuguese coastal waters. The catch curve shows the age of full recruitment to be seven years for *L. boscii* off the west coast of Ireland. There are no comparable Portuguese data on catch curves for *L. boscii*. A full recruitment age of seven years corresponds with a mean length of 29.18cm TL and a mean body weight of 170.35g for the sampled population.

The male to female sex ratio for the four-spot megrim in the present study indicated that males were outnumbered by almost three to one. Santos (1994) found a male to female ratio of 0.955:1 in Portuguese coastal waters. This considerable difference between the two data sets is probably due to different sampling strategies. Santos (1994) collected data on board a research vessel using a 10m otter trawl with a stretched mesh size of 40mm in the cod-end. In contrast, the present results were obtained from a commercial trawl with an 80mm mesh size at the cod-end. The smaller male fish were probably retained by the 40mm mesh in the cod-end in Portuguese waters, while the 80mm mesh probably allowed the majority of males to escape from the west of Ireland catches. Sanchez et al. (1998) found that sex ratios for L. boscii on the northern Spanish shelf vary with the age of individuals: similar numbers of males and females of up to four years old were caught, and more females than males of over four years. In the present investigation males were more frequently recorded in Age Groups 4 and 5; however, from Age Group 6 onwards females were predominantly caught. No information is available for the west coast of Ireland for fish less than four years of age.

The growth rate of the four-spot megrim off the west coast of Ireland is within the lower part of the ranges recorded by authors in southern parts of Europe. This may be due to the fact that the present investigation was carried out near the northern limit of distribution for the species (Sanchez *et al.* 1998), where colder water temperatures may have retarded the rate of growth (Caillet *et al.* 1986).

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Appendix IV

					A	Age (ye	ears)							
Length Class (cm)	2	3	4	5	6	7	8	9	10	11	12	15	16	Tota
15-15.99														1*
16-16.99										<u> </u>				0
17-17.99	-													0
18-18.99														0
19-19.99	1								1					0
20-20,99														0
21-21.99		3												3
22-22.99		7	2	1										10
23-23.99		15	7	3										25
24-24.99	1	31	38	13										83
25-25,99		56	65	38	11	2	1							173
26-26.99	1	70	115	60	22	9	2							279
27-27.99		72	171	99	30	17	2	1						392
28-28.99		32	215	151	107	31	8							544
29-29.99	-	19	181	157	122	52	16	1	1					549
30-30.99		4	121	144	133	68	22	2						494
31-31.99		1	108	168	112	58	13	2	2					464
32-32.99		1	76	158	115	60	14	3						427
33-33.99			38	89	107	66	16	7	2					325
34-34.99			16	68	78	48	22	6		1				239
35-35.99			5	52	55	48	28	4	3	1				196
36-36.99			2	28	34	26	14	6	2	1				113
37-37.99			1	13	19	23	9	14	5	2				86
38-38,99				7	19	19	16	7	1					69
39-39.99					11	20	7	4	4	2				48
40-40.99					3	7	2	5	2	1				20
41-41.99					6	8	4	1	2		[21
42-42.99					3	6	5	5			1			20
43-43.99							2	2						4
44-44.99					1		6	2	3					12
45-45.99							2	2			1			5
46-46.99								1				1		2
47-47.99						1		1						2
48-48,99							1						1	2
49-49.99														0
50-50.99														0
51-51.99												1		1
52-52.99									1					0
53-53.99							1		1					1
Total	2	311	1161	1249	988	569	212	76	28	8	2	2	1	4609

* (No age available for a 15.1cm TL female, as the otolith was removed by the Marine Institute as part of their routine port sampling programme).

						Age	(yea	rs)						
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)					1									
15-15.99						1	1							0
16-16.99		1							-					1
17-17.99	-													0
18-18.99					1		1							0
19-19.99												1 I		0
20-20.99		1												1
21-21.99							1							0
22-22.99			2	1										3
23-23.99		2	2	1										5
24-24.99			2	4	3	2								11
25-25.99		1	7	5	3	1								17
26-26.99		1	10	2	6	3								22
27-27.99			5	12	6	1	1							25
28-28.99			7	8	5	2								22
29-29.99			3	4	4	3								14
30-30.99			1	5	5									11
31-31.99				3	2									5
32-32.99					1	4								5
33-33.99						1								1
34-34.99														0
35-35.99						2								2
36-36.99														0
37-37.99							1							1
38-38.99														0
39-39.99														0
40-40.99														1*
41-41.99														0
42-42.99														0
43-43.99														0
44-44.99														0
45-45.99														0
46-46.99														0
47-47.99														0
48-48.99														0
49-49.99														0
50-50.99														0
51-51.99														0
52-52.99														0
53-53.99														0
Total	0	6	39	45	35	19	2	0	0	0	0	0	0	146

Table 15b. Age at length key for male L. whiffiagonis sampled from 1997-2001.

* (No age available for a 40.0cm TL male, as the otolith was unreadable and omitted).

					Age	(yea)	rs)							1
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
15-15.99														0
16-16.99														0
17-17.99														0
18-18.99								T						0
19-19.99					Τ									0
20-20.99														0
21-21.99		1												1
22-22.99		6		1										7
23-23.99		8	2											10
24-24.99	1	14	11	6										32
25-25.99		11	12	13	5		1							42
26-26.99		8	21	20	5	3								57
27-27.99		7	36	29	11	6	1							90
28-28.99		5	45	43	25	11	6							135
29-29.99		2	26	47	42	13	4							134
30-30.99		1	13	41	29	20	9							113
31-31.99		1	8	48	36	13	6		1	<u> </u>				113
32-32.99	1	-	7	52	36	11	4	1						111
33-33.99	1		2	28	28	14	4	2	1	<u> </u>				79
34-34.99				21	23	12	5	2						63
35-35.99	+		1	8	19	18	9		1					56
36-36.99				10	8	8	3	1						30
37-37.99					2	8	3	4						17
38-38.99	-			1	3	4	5	4						17
39-39.99	+				6	4	1		2					13
40-40.99		-			1	1	1	3	1					7
41-41.99					1	6	2		1					10
42-42.99	1				1		1	5			1			8
43-43.99						<u> </u>	-				-			0
44-44.99		+			1		3	1	3					8
45-45.99					-		2		-					2
46-46.99					-			-						0
47-47.99				-		1		1						2
48-48.99	1					-	<u> </u>					-	1	1
49-49 99	+	-						-					-	0
50-50 99	+				-									0
51-51 99					1							1		1
57_57 00		+												0
53_53 00	1								1					1
JJ-JJ.77	1	61	104	260	1202	152	70	24	10	0	1	1	1	1161

Table 16a. Age at length key for female L. whiffiagonis sampled during 1997.

	_					Age	(year	s)						
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
15-15.99			1		1				1					0
16-16.99														0
17-17.99														0
18-18.99						1						1		0
19-19.99														0
20-20.99		1	1											1
21-21.99														0
22-22.99														0
23-23.99			2	1										3
24-24.99				1		1								2
25-25.99		1	2	1		1								5
26-26.99			1		2									3
27-27.99			1		1	1								3
28-28.99			2		2	1								5
29-29.99				1	1									2
30-30.99				2	3									5
31-31.99				1	2									3
32-32.99						1								1
33-33.99														0
34-34.99						1								0
35-35.99						1								1
36-36.99														0
37-37.99							1							1
38-38.99														0
39-39.99														0
40-40.99	T													0
41-41.99														0
42-42.99														0
43-43.99														0
44-44.99														0
45-45.99														0
46-46.99														0
47-47.99														0
48-48.99														0
49-49.99														0
50-50.99														0
51-51.99														0
52-52.99														0
53-53.99														0
Total	0	2	8	7	11	6	1	0	0	0	0	0	0	35

Table 16b. Age at length key for male L. whiffiagonis sampled during 1997.

					1	Age (y	ears)							
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)										1		ĺ		
15-15.99														0
16-16.99									_					0
17-17.99		1 -												0
18-18.99														0
19-19.99					1									0
20-20.99														0
21-21.99		2							-			İ		2
22-22.99		1	2											3
23-23.99		5	5	3					1					13
24-24.99	+	9	22	6			1		+					37
25-25.99		12	32	17	5	2								68
26-26.99	1	22	33	21	12	4								92
27-27.99	-	12	34	28	10	4		1						89
28-28.99		8	43	30	20	11	1		+					113
29-29.99		3	11	28	34	12	4	1	1					94
30-30.99			8	33	30	17	3	2	-					93
31-31.99		1-	9	29	28	15	3	1	1					86
32-32.99	+		8	20	27	17	4		-					76
33-33.99			4	10	22	16	6	2	-					60
34-34.99		-		11	20	13	10	2		1				57
35-35 99	+			4	10	13	5	2	-					34
36-36 99	1			1	5	5	4	4	2	1				22
37-37 99	-			2	1	6	3	4	2	1				19
38-38.99			<u> </u>	4	2	4	3	1		-				10
39-39-99		<u> </u>				3	2	2	1	1				9
40-40.99						2		1	1					4
41-41 99	+				1	1	1	1	1					5
47-47.99		+				1	2		1	-				3
43-43.99		-				1		1						1
44-44 99	-							1	-					1
45-45 99	+	+	-											0
46-46 99									1					0
47-47 99		-												0
48_48 00							<u>+</u>							0
49_40 00		+												0
50-50 00	+								-					0
51-51 00								+						0
57_57 00		-							-					0
53-53.00										-				0
<u></u>	0	74	211	212	227	1/6	51	26	0	4	0	0	0	001

Table 16c. Age at length key for female L. whiffiagonis sampled during 1998.

Table 16d. Age at length key for male L. whiffiagonis sampled during 1998.

					Age	e (yea	rs)							
Length Class (cm)	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
15-15.99		+					+	1	1					0
16-16.99	+	1	-			1		1						1
17-17.99		<u> </u>				1		-						0
18-18.99				+		1		1						0
19-19.99	-			-				1				<u> </u>		0
20-20.99		1	-		-		+							0
21-21.99			-				1		1					0
22-22.99			2	1		1	1				1	1		3
23-23.99	-	2				-	1-	1						2
24-24.99		+	1	2	2	1	<u> </u>	1						6
25-25.99			2	1	2	-	+	-						5
26-26.99		1	3	1	3	2	1			-				10
27-27-99				3	1	+	1				1			5
28-28.99			-	1	1	1	- <u> </u>		1				-	3
29-29-99		1	2	2	2	1	-		+					7
30-30.99				3	-			1						3
31-31 99		+			+	+	-	+						0
32-32.99	+				1	1	+		+					2
33_33 99					-	1								1
34_34 99				1		1								0
35_35 99		+				1								1
36-36.99	-		-			1	-				-			0
37-37 99		+				+		-						0
38-38 00	+			-		1	+				<u> </u>			0
30-30.00	+		-	+	+	-	+				1			0
40-40.99					-		-			-				0
40-40.99					+	+		+						0
41-41.99	+						+							0
42-42.99	+					+	+							0
43-43.33			-											0
44-44.77				-		-	-							0
45-45.77	+		-	-	+	-				-				0
40-40.77			-	-	-									0
4/-4/.77								-	+		-			0
40-40.77 10 10 00	1								-			-		0
47-47.77 50 50 00	+									-				0
50-50.99 51 51 00														0
51-51.99			-		+		+	-						0
52-52.99	-								-					0
53-53.99	-		10	14	10	-			-	0	0	0	0	40
LOTAL	10	4	- IU-	14		18		1.0	10	1 U	I U -	I U -	U U	47

					Ag	e (vear	s)							
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
15-15.99			1											0
16-16.99			-					1	<u> </u>					0
17-17.99	1							1						0
18-18.99						-			1			1		0
19-19.99	1	1						1	1		1			0
20-20.99								1						0
21-21.99									<u> </u>					0
22-22.99									1			1		0
23-23.99		1	1		1			1	1	-				1
24-24.99		4	4	1					<u> </u>					9
25-25.99	1	20	15	8	1									44
26-26.99	1	30	48	16	4	1	1		†			1		101
27-27.99		37	82	39	9	6	1		1					174
28-28.99		14	106	70	59	9	1	1					-	259
29-29.99		8	121	71	43	26	7	1	1				1	276
30-30.99		3	85	59	70	29	10		1					256
31-31.99			64	67	45	27	4	1	1					208
32-32.99	1	1	46	64	48	31	6	2						198
33-33.99	1		20	41	50	31	6	2	1					151
34-34.99			13	29	29	20	6	2	1				1	99
35-35.99			2	32	21	16	11	2	2	1				87
36-36.99			2	12	17	10	6				1			47
37-37.99	1-			7	13	9	3	5	3	1				41
38-38.99				3	11	7	8	1	1					31
39-39.99	-				4	10	4	2	1	1				22
40-40.99					2	4	1	1	1	1				9
41-41.99	1				3	1	1							5
42-42.99			1		2	5	2		1			1		9
43-43.99					1		2	1		-				3
44-44.99		1					2	1	1		1		1	2
45-45.99			1					1	1	-	1	1		2
46-46.99		1		1			1	1		1		1	1	2
47-47.99	1					1								0
48-48.99	1		1				1		1					1
49-49.99	-	1	-			1			1					0
50-50.99	-	1		1						-		1		0
51-51.99	-						-				1	1		0
52-52.99		1	-		1	1		—			1	1		0
53-53.99	1	1	1			1			1	<u> </u>		1		0
Total	1	118	608	519	431	242	83	21	8	4	1	1	0	2037

Table 16e. Age at length key for female L. whiffiagonis sampled during 1999.

						Age	(year	s)						
Length Class (cm)	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
15-15.99	+					1					1		1	0
16-16.99	+			1										0
17-17.99	1			1			1					1		0
18-18.99	1		1				+			1				0
19-19.99														0
20-20.99									-			-		0
21-21.99						1						-	-	0
22-22.99				-										0
23-23.99														0
24-24.99			1	1	1								1	3
25-25.99			2	3										5
26-26.99		_	4	1	1	1								7
27-27.99		-	4	7	4									15
28-28.99			4	3	2									9
29-29.99			1	1	1	1				1				4
30-30.99			1		2									3
31-31.99		-		2							-			2
32-32.99						2								2
34-34.99														0
35-35.99											1			0
36-36.99							1							0
37-37.99														0
38-38.99														0
39-39.99	1					-			1					0
40-40.99														0
41-41.99														0
42-42.99														0
43-43.99														0
44-44.99	1											1	1	0
45-45.99	1													0
46-46.99												1		0
47-47.99														0
48-48.99														0
49-49.99								1						0
50-50.99												1		0
51-51.99	1			1		-								0
52-52.99	1									1				0
53-53.99								1						0
Total	0	0	17	18	11	4	0	0	0	0	0	0	0	50

Table 16f. Age at length key for male L. whiffiagonis sampled during 1999.

					A	lge (y	ears)							
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99														0
22-22.99														0
23-23.99														0
24-24.99		2	1	2										5
25-25.99		4	1	2	2		1							10
26-26.99		2	3	8	2	1		Τ						16
27-27.99		3	9	7	2	1	1							23
28-28.99		2	12	10	3	1	3							31
29-29.99		2	6	9	7	3	3							30
30-30.99			5	9	4	3	4							25
31-31.99			2	11	9									22
32-32.99		1	2	15	6	2	2	1						28
33-33.99			1	8	6	2								17
34-34.99				3	5	3	1							12
35-35.99	+			1	11	5								17
36-36,99				4	3	3								10
37-37.99					1	3	2	3						9
38-38.99		1	1		1	1	1				1		-	3
39-39.99		1	1		5	2			1		1			8
40-40.99		1			1	1		1						2
41-41.99	-					2								2
42-42.99		1	-		1		1	2			1			5
43-43.99								1						0
44-44.99	1	-			1		2							3
45-45.99					1		1							1
46-46.99	1				1							ĺ	1	0
47-47.99				-		1					1			1
48-48.99			1		1	<u> </u>						1		0
49-49.99	1	+	1	+	+	-			-					0
50-50.99							1							0
51-51.99							-							0
52-52.99		1	+		1	1			+					0
53-53.99	-					1			1		1			1
Total	0	15	42	89	69	34	22	7	2	0	1	0	0	281

Table 17a.Age at length key for female L. whifflagonis sampled during the 2ndquarter of 1997.

xxxiii

					1	Age (years))						
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99														0
22-22.99			T											0
23-23.99		2	1											3
24-24.99	1	3	5	1										10
25-25.99		2	3	1	2									8
26-26.99		2	7	4	1	1								15
27-27.99		3	10	10	6	3			1					32
28-28.99	1	2	14	16	14	8	3							57
29-29.99			8	15	24	7	1							55
30-30.99	1		2	15	18	11	5							51
31-31.99		1	1	17	21	10	3		1					54
32-32.99				17	20	7	2							46
33-33.99				11	13	11	4	2	1					42
34-34.99				8	11	9	3	2						33
35-35.99	1		1	3	4	9	7		1	1				25
36-36.99				3	2	4	2	1						12
37-37.99					1	4	1							6
38-38.99				1	1	2	2	3						9
39-39.99					1	1	1		1					4
40-40.99	1				1		-	2	1					4
41-41.99					1	2	2							5
42-42.99				T				3						3
43-43.99														0
44-44.99								1	3	1				4
45-45.99	1						1							1
46-46.99	1	1							1					0
47-47.99	-							1	-		1			1
48-48.99					1	1	1		1				1	1
49-49.99						<u> </u>								0
50-50.99		1						-			1			0
51-51.99			1					+				1	<u> </u>	1
52-52.99	1					1		1						0
53-53.99	1-					1								0
Total	1	15	52	122	141	89	37	15	8	0	0	1	1	482

Table 17b. Age at length key for female L. whiffiagonis sampled during the 3rdquarter of 1997.

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Age (years)														
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99		1												1
22-22.99		6		1				T						7
23-23.99		6	1											7
24-24.99		9	5	3										17
25-25.99		5	8	10	1									24
26-26.99		4	11	8	2	1		1						26
27-27.99		1	17	12	3	2		1						35
28-28.99		1	18	17	8	2								46
29-29.99			12	23	11	3								49
30-30.99		1	6	17	7	6							[37
31-31.99			5	20	6	3	2							36
32-32.99			5	20	10	2								37
33-33.99			1	9	9	1								20
34-34.99				10	7		1							18
35-35.99				4	4	4	2							14
36-36.99				3	3	1	1							8
37-37.99						1		1						2
38-38.99					1	1	2	1						5
39-39.99						1								1
40-40.99							1					T		1
41-41.99						2			1					3
42-42.99														0
43-43.99														0
44-44.99							1							1
45-45.99														0
46-46.99														0
47-47.99						ľ								0
48-48.99														0
49-49.99														0
50-50.99														0
51-51.99														0
52-52.99								Ī						0
53-53.99														0
Total	0	34	89	157	72	30	10	2	1	0	0	0	0	395

Table 17c. Age at length key for female L. whiffiagonis sampled during the 4thquarter of 1997.

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					A	ge (y	ears)							
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99		1					_							1
22-22.99		1	2											3
23-23.99		3	1	1										5
24-24.99		1	5	4										10
25-25.99		6	6	7	2	2								23
26-26.99		12	9	9	4	2								36
27-27.99		8	6	9	3	3								29
28-28.99		4	17	12	6	4	1							44
29-29.99		1	1	8	10	5	1	1	1		ļ			28
30-30.99			1	12	11	5		1						30
31-31.99			1	11	6	4	1		1					24
32-32.99			2	2	11	4								19
33-33.99			1	3	2	2	1							9
34-34.99				5	6	4	2	1						18
35-35,99				1		3	1	1						6
36-36.99						1	2	2	1					6
37-37.99			1			1		1			Γ			2
38-38.99			1				1							1
39-39.99			1											0
40-40.99													1	0
41-41.99							1	1	1					3
42-42.99							1							1
43-43.99														0
44-44.99														0
45-45.99					1					-				0
46-46.99														0
47-47.99	-													0
48-48.99														0
49-49.99		1			1									0
50-50.99	-			1						1	1			0
51-51.99		1	1	1	1					-			1	0
52-52.99		1		1	1	1								0
53-53.99		1						-						0
Total	0	37	52	84	61	40	12	8	4	0	0	0	0	298

<u>Table 17d.</u> Age at length key for female *L. whiffiagonis* sampled during the 1st <u>quarter of 1998.</u>

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xxxvi

Age (years)														
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)										}				
21-21.99		1					1							1
22-22.99												Γ		0
23-23.99			2	2				T					1	4
24-24,99		1	10	1										12
25-25.99		1	20	7	3									31
26-26.99		1	21	9	5	2								38
27-27.99			19	15	6	1		1						42
28-28.99			20	13	9	4				1				46
29-29.99			8	12	20	6	2							48
30-30.99			6	14	15	12	3	1				ĺ		51
31-31.99			7	15	19	11	2	1						55
32-32.99			4	14	15	13	4							50
33-33.99			3	6	19	14	5	2						49
34-34.99				4	12	8	8	1		1				34
35-35.99				3	10	10	3	1						27
36-36.99				1	5	4	2	2	1	1				16
37-37.99				2	1	5	3	3	2	1				17
38-38.99					2	4	2	1						9
39-39.99						2	2	2	1	1				8
40-40.99						2		1	1					4
41-41.99					1	1								2
42-42.99						1	1							2
43-43.99								1		1				1
44-44.99								1	-					1
45-45.99														0
46-46.99														0
47-47.99														0
48-48.99														0
49-49.99	1	1					1							0
50-50.99	1													0
51-51.99								1	1					0
52-52.99		1						1	-					0
53-53.99	-							-						0
Total	0	4	120	118	142	100	37	18	5	4	0	0	0	548

Table 17e.Age at length key for female L. whiffiagonis sampled during the 4thquarter of 1998.

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xxxvii

Age (years)														
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99								1						0
22-22.99														0
23-23.99		1								-				1
24-24.99		3	3	1										7
25-25.99		16	8	2										26
26-26.99	1	24	20	6		1							I	52
27-27.99		26	34	8	4	2	1							74
28-28.99		13	42	16	13	2	1							87
29-29.99		4	43	20	3	5	3							78
30-30.99		1	35	9	21	7	4							77
31-31.99			26	14	10	8								58
32-32.99		1	19	11	22	7	1							61
33-33.99			3	5	20	6	3	1						38
34-34.99			4	5	8	9	3	1						30
35-35.99				7	8	5	5	1	1	1				28
36-36.99			1	1	5	4	1							12
37-37.99				1	2	3	1	3	2	1				13
38-38.99				1	3	3	5	1	1	1				14
39-39.99	1				2	3	1		1	1				8
40-40.99								1		1				2
41-41.99														0
42-42.99		1			1	1								2
43-43.99								1						1
44-44.99							1							1
45-45.99								1						1
46-46.99												1		1
47-47.99														0
48-48.99							1							1
49-49.99							T							0
50-50.99														0
51-51.99														0
52-52.99														0
53-53.99			<u> </u>											0
Total	1	89	238	107	122	66	30	10	5	4	0	1	0	673

Table 17f. Age at length key for female L. whiffiagonis sampled during the 1stquarter of 1999.

xxxviii

Age (years)														
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99														0
22-22.99								T						0
23-23.99														0
24-24.99														0
25-25.99		2	3	2	1									8
26-26.99		4	10	7	3		1							25
27-27.99		9	32	23	4	4								72
28-28.99		1	34	29	36	6								106
29-29.99		4	44	35	31	16	3							133
30-30.99		2	32	28	35	16	6							119
31-31.99			26	26	17	13	3	1						86
32-32.99			19	25	13	9	3	1						70
33-33.99			12	11	18	13	3	1	1					59
34-34.99			7	10	11	6	2							36
35-35.99			1	14	7	2	3	1	1					29
36-36.99			1	4	8	2	2							17
37-37.99				3	5	2	2	2	1					15
38-38.99					5	2	3							10
39-39.99					1	3	2	2						8
40-40.99					1	3	1							5
41-41.99					1	1								2
42-42.99						1	2							3
43-43.99	1						2							2
44-44.99							1							1
45-45.99														0
46-46.99							T	1						1
47-47.99														0
48-48.99														0
49-49.99														0
50-50.99														0
51-51.99														0
52-52.99														0
53-53.99														0
Total	0	22	221	217	197	99	39	9	3	0	0	0	0	807

Table 17g. Age at length key for female L. whiffiagonis sampled during the 2ndquarter of 1999.

Age (years)														
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)			1											
21-21.99														0
22-22.99														0
23-23.99													1	0
24-24.99		1	1											2
25-25.99		2	4	3		1								9
26-26.99		1	16	3	1									21
27-27.99		2	13	8	1		1							25
28-28.99			26	23	10	1								60
29-29.99		1	28	11	6	4	1							50
30-30.99			10	17	12	3								42
31-31.99			11	20	9	2	1							43
32-32.99			4	21	8	5	1							39
33-33.99			4	19	9	2								34
34-34.99				10	5	3	1							19
35-35.99			1	8	1	2	1							13
36-36.99				4	2	2	1				1			9
37-37.99				3	4									7
38-38.99				1	1	1								3
39-39.99					1		1							2
40-40.99						1								1
41-41.99					2		1							3
42-42.99						2								2
43-43.99	1	1												0
44-44.99]		0
45-45.99											1			1
46-46.99														0
47-47.99		1									Ì			0
48-48.99										<u> </u>	1			0
49-49.99														0
50-50.99								-	1					0
51-51.99									1					0
52-52.99														0
53-53.99														0
Total	0	6	118	151	72	28	9	0	0	0	1	0	0	385

Table 17h.Age at length key for female L. whiffiagonis sampled during the 3rdquarter of 1999.

					A	ge (y	ears)							
Length	2	3	4	5	6	7	8	9	10	11	12	15	16	Total
Class (cm)														
21-21.99														0
22-22.99												1		0
23-23.99														0
24-24.99														0
25-25.99				1										1
26-26.99			2							1				2
27-27.99			3											3
28-28.99			4	2										6
29-29.99			6	5	3	1								15
30-30.99			8	5	2	3								18
31-31.99			1	7	9	4								21
32-32.99			4	7	5	10	1	1						28
33-33.99		T	1	6	3	10								20
34-34.99			2	4	5	2		1						14
35-35,99				3	4	7	2							16
36-36.99				3	2	2	2							9
37-37.99					2	4								6
38-38.99				1	2									3
39-39.99						4								4
40-40.99					1									1
41-41.99							1							0
42-42.99					1	1				1				2
43-43.99														0
44-44.99														0
45-45.99														0
46-46.99														0
47-47.99														0
48-48.99														0
49-49.99														0
50-50.99														0
51-51.99		1												0
52-52,99														0
53-53.99				1										0
Total	0	0	31	44	39	48	5	2	0	0	0	0	0	169

Table 17i.Age at length key for female L. whiffiagonis sampled during the 4thquarter of 1999.