An assessment of biological and population parameters of the Common whelk, *Buccinum undatum* (L.) in the region of the North West Irish whelk fishery

By

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Submitted to Galway-Mayo Institute of Technology,
November 2006

GMIT
GALWAY-MAYO INSTITUTE OF TECHNOLOGY
INSTITIÚID TEICNEOLAÍOCHTA NA GAILLIMHE-MAIGH EO

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Acknowledgements

This project has been made possible through funding from Bord Iascaigh Mhara (BIM) and the Galway-Mayo Institute of Technology (GMIT) under the National Development Project.

My sincere thanks go to my supervisors, in particular Dr Pauline King and Dr David McGrath of GMIT. Your support while I have studied by distance has been invaluable. Thank you to Dr Oliver Tully of BIM for arranging data and sample collection from the fishing fleet and advice on stock assessment. Thanks also to Brian Ottway of GMIT for special assistance with ageing analysis.

For assistance with collection of samples and data, my thanks to Eoghan Kelly of BIM, Gavin Power of GMIT and Orla Lee of Trinity College, Dublin. For field support to conduct the mark re-capture experiment, thanks to Brendan Allen of GMIT, Dr Stephen Robson of GMIT and Marianne Green, formerly of GMIT. Thanks to all the staff at BIM for storage of samples and GIS support, in particular Emer O'Keefe. Thank you to Owen Doyle of BIM in Greencastle for arranging sample collection and storage. My thanks to the Skippers and Crew of FV Michelle, FV Jennifer Constance, FV Kilbrogan, FV Ave Maria, FV Swilling Star, FV Nuala Girl, FV Molly Oige, and the Common whelk fishing fleet in Greencastle, Bunagee and Portaleen, Co. Donegal, for allowing me to spend time on their vessels collecting data and samples.

For support and advice in preparation of histological samples and analysis, and for your friendship, thanks to Dr Deirdre Brophy. Thanks to Dr Martin Robinson of GMIT for advice on Common whelk fisheries. Thanks to Prof. Peter MacDonald of McMaster University, Canada for support with MIX software for age analysis. Thank you to the University of Wollongong (Marine Ecology) in Australia for providing the opportunity for mollusc discussion. Thanks to Dr Mark Hemer, formerly of NUI Galway and currently of CSIRO Australia, for assistance in the preparation of maps, and mathematical advice in determining size at maturity in Common whelks.

Thank you to the Marine Institute of Ireland for allowing sample and data collection on board the Irish Ground Fish Survey in 2003. My thanks also to staff at the Marine Institute of Ireland for support in fisheries statistics, and providing contacts for sample collection. Thank you to Hans Gerristson of the Marine Institute for photographs.

Thank you to Ed Fahy and Susan Grogan of the Marine Institute, and Margaret O'Toole of Trinity College, Dublin for participating in the observer analysis of operculums.

Thank you to the Australian National Botanic Gardens for use of a microscope to analyse histological slides. Thank you to Jessie Mahony in the Dept. of Physics at GMIT for assistance in the use of the SEM.

Thank you to Noirin Burke for assistance in the laboratory, and with canonical scores analysis. Thank you to laboratory and IT technical support staff at GMIT for assistance, particularly in maintaining aquaria for live samples. Thank you to administration staff at GMIT for arranging travel and registration.

I would like to thank my employers at the Australian National Botanic Gardens, Canberra, Australia and North West Waterwatch Inc., Tasmania for their support when I have required extra time to dedicate to this project.

My special acknowledgement and thanks to the GMIT Commercial Fisheries Research Group, Molecular Ecology Research Group and Physics Post-Graduate students and Post-Docs for support, friendship and laughs, particularly during early 2004. Thank you for making my time living in Ireland so memorable and enjoyable. Thank you to Jim and Sarah Morrissey for arranging accommodation in Galway and lots more during my 2005 trip. Thank you to my husband, Mark Hemer, for your support, advice and encouragement, particularly when we have lived on other sides of the world during the completion of this project.

Abstract

The Common whelk, *Buccinum undatum* (L.) is a conspicuous benthic scavenger in Irish waters, and is a valuable fisheries resource in South East Ireland. *B. undatum* is fished in many parts of its range, and previous studies have shown that certain life history parameters, which vary with location, make this species vulnerable to overexploitation. This makes research into each exploited stock essential to ensure sustainable fisheries management of the species. In 2003, interest in *B. undatum* as a complementary species in the inshore fishery east of the Inishowen Peninsula, North West Ireland, initiated investigation into fisheries related biological and population aspects of the species in this region. The current study presents estimates of spatial variation and density of the stock, size at age and growth rates, size and age at onset of sexual maturity, and timing of reproductive events in the region of the North West Irish whelk fishery for the period of June 2003 to May 2004. Analysis of variance of the total shell length of whelk landings to the fishery was conducted over spatial scales of fishing pot, fishing string and landings to vessels. Landings varied significantly in shell length at the spatial scale at which whelks are attracted to baited pots, but did not vary significantly over larger spatial scales. Depletion estimates of stock density from fisheries derived Catch per Unit Effort data and a mark re-capture experiment estimate 0.134 – 0.227 whelks per m^2. Two independent methods of age determination found similar growth logistics functions for *B. undatum*. Modal analysis of length frequency distribution of landings to the fishery estimated asymptotic length, $L\infty$ = 151.64 mm and Brody growth coefficient, K = 0.04. Analysis of the striae in individual opercula, where each stria was found to represent annual growth, estimated $L\infty$ = 137.73 mm and K = 0.12. Common whelks in the region of the North West Irish whelk fishery grow slowly and are long-lived, with 19 opercula striae recorded in one individual. Onset of sexual maturity is late, and no sex-specific differences in size or age at maturity were determined in the present study. Males were found to achieve sexual maturity at 83.30 ± 10.77 mm, and 8.9 – 11.1 years of age, and females at 82.62 ± 10.68 mm and 8.8 to 11.1 years of age. Systematic observations of reproductive events, including histological changes to the female ovary and male testis, and changes in the size and mass of body components, suggest that breeding occurred between the autumn and winter months of October and December 2003. Biological aspects of *B. undatum* in the study region are compared with previous studies from other regions, and discussed in relation to sustainable management of the fishery.

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Introduction

The Common whelk, *Buccinum undatum* (Linneaus, 1758) is an important element of the benthic fauna in waters surrounding the coast of Ireland. High demand for its meat induced the exploitation of the species in the 1990's on the southeast coast of Ireland in the Irish Sea. The stock found east of the Inishowen Peninsula, North West Ireland, is captured in high numbers as by-catch of the Brown Crab (*Cancer pagurus*) creel fishery. Until 2003 however, *B. undatum* remained unexploited by a targeted commercial fishery in this region. There is very little biological information pertaining to *B. undatum* in the region of the new North West Irish whelk fishery. Descriptions of biological parameters relevant to fisheries stock assessment are available for *B. undatum* in other regions. However, evidence of local variation in biological parameters, which make the species susceptible to over-fishing, warrant the investigation of these parameters in emerging fisheries for Common whelk.

The neogastropod whelk, *B. undatum*, is common in continental shelf waters throughout the North Atlantic (Golikov, 1968, Taylor and Taylor, 1977). *B. undatum* is a sub-tidal species, occurring at depths of 5 – 600 metres, and tolerating a wide range of salinities (Staaland, 1972; Hansson, 1998). It is found on a variety of sub-strata, and commonly occurs on mixed mud and sand where it lives either on the surface or buried (Himmelman, 1988; Valentinsson *et al.,* 1999). In European waters, fishing for the species typically occurs in the shallower parts of the range, where densities are greatest (Hansson, 1998).

Determination of population density and spatial location of *B. undatum* is of great importance regarding the development of a new fishery (Kideys, 1993). There are difficulties, however, in estimating population density or describing the stock structure of Common whelks, which occur at depths too great for direct observation. Tagging experiments have shown that adult *B. undatum* are relatively sedentary (Hancock, 1963; Himmelman and Hamel, 1993). Depletion analyses of Catch per Unit Effort have been used as indicators of population density and to map the stock size (Himmelman, 1988;

Kideys, 1993; Valentinsson *et al.,* 1999; Fahy *et al.,* 2000; Morel and Bossy, 2004). Size distributions of whelk differ substantially between regions (Thomas and Himmelman, 1988), however, and the population density and stock structure of whelk in the region of the North West Irish whelk fishery has not been described.

In order to analyse the population dynamics of a species, the age structure of the population must be known. In gastropod molluscs, measurable increases in shell length occur during growth as retained energy is incorporated into the biomass of the organism (Kideys and Hartoll, 1991; Kideys, 1996). *B. undatum* displays an indeterminate growth pattern, such that shell growth continues at a decreasing rate during the lifetime of the animal (Kideys *et al*, 1993). *B. undatum* is a slow growing and long-lived species, and efforts to define a system of predicting age and growth rate in commercially exploited populations of *B. undatum* have been reported (Hancock, 1963; Santarelli and Gros, 1985; Kideys, 1996; Fahy *et al.*, 2000). However, Common whelks have been shown to demonstrate geographical variation in size and growth rate over short distances (Kideys, 1996; Valentinsson *et al.*, 1999; Fahy *et al.*, 2000). Therefore, size at age estimates derived from geographically separated whelk populations may not provide reliable estimates for the purpose of stock assessment in developing fisheries.

A number of studies have sought to determine the size and age at the onset of sexual maturity in male and female *B. undatum* (Hancock and Simpson, 1962; Martel *et al.*, 1986a; Santarelli *et al.*, 1986; Gendron, 1992; Gunarrson and Einersson, 1995; Bell and Walker, 1998; Valentinsson *et al.*, 1999; Fahy *et al.*, 2000). Knowledge of maturity indices is important in the assessment of commercially exploited populations of whelk. Combined with catch data, biologists can determine the proportion of stock contributing to reproduction. Sex specific differences in size of maturity have been observed in Common whelk from the Gulf of St Lawrence, Eastern Canada (Martel *et al.,* 1986a; Gendron, 1992). Although, Valentinsson *et al.* (1999) found that this is not the case for whelk in Swedish waters. The size at onset of sexual maturity has been shown to vary significantly between locations, and age at sexual maturity in *B. undatum* is high. It is also unknown for the population of Common whelk in the region of the North West Irish whelk fishery.

The neogastropods are considered to display the most advanced reproductive strategy of the gastropods (Webber, 1977; Himmelman, 1999). *B. undatum* is a dioecious species, which demonstrates a distinct annual reproductive cycle that varies in timing with location (Martel *et al.,* 1986; Gendron, 1992; Valentinsson, 2002. Early studies suggested that *B. undatum* undertakes egg-laying year round (Thorson, 1946). However, later research provides evidence that in European populations, breeding occurs between autumn and winter, and eggs are laid from winter to early spring (Fretter and Graham, 1984; Kideys *et al.,* 1993). Following internal fertilization facilitated by copulation, females lay eggs contained in capsules directly on to hard substrates of the benthos during a major egg-laying period. Fecundity is low and the trochophore and veliger larval stages of *B. undatum* occur within the egg capsules. Juveniles emerge to begin their benthic life directly, after 3-8 months of development, and demonstrate fast early growth (Martel *et al.*, 1986a; Kideys *et al.*, 1993). The sedentary adult life of *B. undatum* and the absence of a planktonic larval stage is likely to encourage reduced gene flow, which could result in local adaptations and genetic divergence between populations (Hancock, 1963, Valentinsson *et al.*, 1999).

Common whelk populations are regulated by a number of influencing factors. The key predators of *Buccinum undatum* comprise various species of asteroid, decapods (including crabs and lobsters), and humans. Cod and dogfish have also been reported to prey on Common whelk (Thomas and Himmelman, 1988). The morphology of whelk populations is highly variable with location in Canadian waters, with shell thickness and elongation varying most significantly in the presence of crustacean predators (Thomas and Himmelman, 1988). Demersal beam trawl and dredging fisheries have been associated with damage and high mortality rate in epibenthic invertebrate populations (Ramsay and Kaiser, 1998; Mensink *et al.*, 2000; Bergmann *et al.*, 2002). The phenomenon of imposex, whereby female gastropods develop male sexual characteristics and ultimately resulting in sterility has been reported in *B. undatum* at

Killary harbour on the west coast of Ireland, and on the east coast, in the Irish Sea (Nicholson and Evans, 1997). Larval trematode endoparasites have been reported in *B. undatum*, and affect the ability of individuals to reproduce, but do not cause mortality directly (Køie, 1965).

B. undatum is both an active predator and an opportunistic scavenger in epibenthic environments (Nielsen, 1975, Hughes, 1986, Himmelman and Hamel, 1993). The main diet is a mixture of polychaetes, molluscs, echinoderms, and a variety of smaller crustaceans (Nielsen, 1975; Taylor, 1978; Jalbert and Himmelman, 1989; Himmelman and Hamel, 1993). The species is highly sensitive to odour and will actively seek live prey and carrion to fulfill its energetic requirements (Nielsen, 1975; Himmelman, 1988; Sainte-Marie, 1991; Lapointe and Sainte-Marie, 1992; Morissette and Himmelman, 2000). Fishermen have long exploited the attraction of scavenging whelks to baited pots for commercial purposes, and capture is easy.

Commercial fisheries for Common whelk occur in inshore waters off the coast of Scotland, the Isle of Jersey and the Isle of Man, United Kingdom. These fisheries were fuelled by developments in the market in Asia in the mid 1990's (Morel and Bossy, 2004). Markets for Common whelk exist in France, and are supported by a local French commercial fishery. Interest in a complementary fishery for Common whelk in the inshore waters off the coast of Sweden saw the initiation of a controlled trial fishery in 1995. A study of the trial fishery found that stocks on the Swedish west coast may be of commercial value, but would be vulnerable to over-fishing (Valentinsson *et al.*, 1999). A Common whelk fishery operates in the Gulf of St Lawrence, Canada, with fluctuating landings since 1949 in response to local and international market demands. There is evidence that local stocks have been depleted and not recovered in the Canadian fishery (Gendron, 1992).

The southwest Irish Sea Common whelk fishery is one of Ireland's largest inshore fisheries in recent years (Fahy *et al.*, 2000). Depletion of parallel species of Pacific stocks and opening markets in Asia, particularly Korea, has encouraged the fishery to expand. At the height of the fishery up to 80 vessels operated from ports in Waterford, Wexford, Wicklow and Dublin. Between 1990 and 1996 catches in the fishery steadily increased. By 1998 landings to the fishery had declined due to trading difficulties, fluctuating prices and locally exhausted stocks. While the fishery fleet has declined by up to fifty percent, the existing vessels still fish intensively, with increasing effort each year (Fahy *et al.,* 2000).

The life history characteristics of *B. undatum*: slow growth, high age at sexual maturity, low fecundity, sedentary life, entirely benthic reproductive strategy, ease of capture, and slow genetic mixing between adjacent populations, suggest that Common whelk are vulnerable to over exploitation in commercial fisheries. Depletion of local populations has been reported in European and Canadian commercial fisheries (Gendron, 1992; de Jong *et al.*, 1993; Fahy *et al.,* 2000). Relevant to fisheries, a reduced gene flow suggests that a depleted local population will be slow to recover (Valentinsson *et al.*, 1999).

In the region east of Inishowen Peninsula, Ireland, fishermen target the benthic dwelling Brown crab for the claw industry and for bait. *B. undatum* comprise a significant proportion of the by-catch of Brown crab fishery. From time to time fishermen in the east Inishowen Peninsula region experience low profitability, and diversification to include a complementary Common whelk fishery may ease economic pressure, as well as pressure on other targeted commercial stock species. However, in spite of general abundance and economic interest, little is known about the population of Common whelks local to this area. Moreover, given the biological characteristics of the species and its susceptibility to over fishing, further investigation is necessary towards consideration of management and conservation strategies for the stock. Therefore, in 2003 the present investigation was initiated to study some fisheries related aspects of whelk biology in the region of the new North West Irish whelk fishery.

To better understand the population dynamics and biological characteristics that regulate the stock of *B. undatum* in the region of the North West Irish whelk fishery, the following study aims to:

- Describe stock spatial and temporal variation, and density,
- Determine the size at age and growth rate of *B. undatum*,
- Determine the size and age at onset of sexual maturity in male and female Common whelk, and
- Make systematic observations of the timing of reproductive events of *B. undatum*.

Chapter 1

Assessment of Stock of Common whelk, Buccinum undatum in the Region of the North West Irish Whelk Fishery

INTRODUCTION

In recent years, interest in expanding the existing Irish Common whelk fishery has increased. A fishery for Common whelk, *Buccinum undatum* has traditionally operated on the East coast of Ireland. The fishery expanded rapidly in the Irish Sea in the 1990s, reaching record landings in 1996 of 6575 t, and stabilising thereafter as the number of vessels supported by the fishery declined (Fahy *et al.,* 2000). Irregular fisheries for Common whelk in waters off England, the Isle of Man, the Isle of Jersey and Scotland have also undergone expansion since the 1990s (Fahy *et al.*, 1995). In Sweden, assessment of Common whelk populations has taken place to assess the fisheries potential of the species in these waters as a means of diversifying inshore catch for profitability (Valentinsson *et al.,* 1999). Fisheries for Common whelk around Ireland, England and Sweden have expanded due to economic interest in the species from Asian markets (Nicholson and Evans, 1997; Valentinsson *et al.,* 1999; Fahy *et al.,* 2000; Morel and Bossy, 2004). Fishing Common whelks in France and the Gulf of St. Lawrence, Canada has long occurred, where demand is driven by local markets.

International market demands, coupled with the opportunity to diversify catch and improve profitability in North West Ireland, have seen the Irish Common whelk fishery expand to inshore waters in this region. *B. undatum* had been frequently caught as a by-catch species of the Brown crab (*Cancer pagurus*) fishery East of the Inishowen Peninsula in North West Ireland (see Map 1.1). One to two vessels are also thought to have fished Common whelks in the region during the 1990s (Pers. Comm., whelk Fishermen), and in 2003 the number of operating vessels increased to at least five to actively fish the species from April to July. Presumably, *B. undatum* as a by-catch species was discarded, and with high survival rate from baited traps (Mensink *et al.,* 2000), fishing mortality was low prior to the commencement of the current North West Irish whelk fishery. There is however, very little information pertaining to the life history and habit of *B. undatum* in North West Ireland, in spite of general abundance and economic interest. Therefore, the current study was initiated with the aim of assessing biological aspects of *B. undatum* in the region of the North West Irish whelk fishery, towards evaluating the potential of the emerging fishery.

Common whelks are a relatively sedentary species which tolerate a variety of soft, sandy and rocky substrata; salinities down to 20‰; and depths from 5 – 600 m (Hancock, 1963; Staaland, 1972; Himmelman and Hamel, 1993; Hansson, 1998; Valentinsson *et al.,* 1999). The species demonstrate fast early growth, high age at sexual maturity, low fecundity, an entirely benthic reproductive strategy, ease of capture, and slow genetic mixing between adjacent populations (Martel *et al.,* 1986; Gendron 1992, Kideys *et al.,* 1993; Valentinsson et al., 1999). Common whelks are a scavenging species (Nielsen, 1975, Hughes, 1986, Himmelman and Hamel, 1993), and their capture is easy. These life history characteristics suggest that *B. undatum* is vulnerable to over exploitation in commercial fisheries. Depletion of local populations has been reported in European and Canadian commercial fisheries, including Ireland (de Jong *et al.*, 1993; Gendron, 1991; Fahy *et al.,* 2000). Relevant to fisheries, a reduced gene flow suggests that a depleted local population will be slow to recover (Valentinsson *et al.*, 1999).

Numerous studies have demonstrated the movement of whelk upstream towards a potential food source by chemoreception (Fretter and Graham, 1962; Nielsen, 1975; Hughes, 1986; Himmelman, 1988; Sainte-Marie, 1991; Lapointe and Sainte-Marie, 1992; Himmelman and Hamel, 1993; Moore and Howarth, 1996; Morissette and Himmelman, 2000; Bergmann et al, 2002). Fishermen utilise *Buccinum's* habit of scavenging by baiting whelk pots with newly dead crabs and fish (Fretter and Graham, 1962). Sainte-Marie (1991) and Lapointe and Sainte-Marie (1992) used the tag-recapture method to attempt to measure the field of attraction and effective fishing area of baited traps for *B. undatum.* The area of attraction of a baited trap is a physical area within which at least some of the animals present actively move towards the trap in response to the odour plume of the bait. The shape and size of the area of attraction are determined by advective and diffusive processes and by chemosensory thresholds in target species (references within Sainte-Marie, 1991). The effective area fished by a baited trap is a theoretical area within which the probability of capturing all individuals of the target species is 100% (Miller, 1975). The effective area differs from the area of attraction because the proportion of animals responding to bait may decrease with time and distance from bait, and because some trapped animals may originate from beyond the defined field of attraction.

Himmelman (1988) determined that the area of attraction to bait was irregularly shaped and determined by current direction in tag-recapture experiments with *B. undatum*. Himmelman showed that in strong currents, the area of attraction was elongated in the direction of the current and reduced, thus recapture rates were low, and that the area further declined with increasing depth. However, with increasing soak time of the baited pots at depth, peak catch could be achieved. This was particularly the case in weak currents. The area of attraction did not vary with bait type. Himmelman (1988) also suggests that the area of attraction varies seasonally due to behavioural changes associated with temperature and whelk reproduction.

Mark Re-Capture techniques have been employed as a tool to determine growth and mortality in gastropod molluscs (Hancock, 1963; Forster, 1967; Sire, 1984; Kraeuter et al., 1989; Kideys, 1991) and area of attraction to baited pots (Himmelman, 1988; Sainte-Marie, 1991; Lapointe and Sainte-Marie, 1992). Population abundance and density of *B. undatum* have also been estimated from mark recapture methods (Lincoln, 1930; Hancock, 1963; Kideys, 1993), under the assumption that if a population is closed, and the probability of capture constant, the total population can be estimated from an index of removal. Depletion estimates of stock assessment are also demonstrated appropriate indicators of population size and decrease in exploited finfish and cephalopod mollusc populations (Royer *et al.,* 2002). Depletion methods are based on the analysis of the influence of the cumulative catch (Leslie and Davis, 1939), or cumulative effort (DeLury, 1947) on an abundance index Catch Per Unit Effort (CPUE) (Royer *et al.,* 2002). Two studies have employed depletion methods of stock analysis in the assessment of Common whelk populations (Valentinsson *et al.,* 1999; Morel and Bossy, 2003). Mark re-capture and depletion estimates of population abundance and density are therefore appropriate tools in the study of *B. undatum*, which dwell at depths too great for direct observation.

To effectively assess the fisheries potential of the new North West Irish whelk fishery, the current study aims to describe spatial and temporal variation, population size and density in Common whelk stock in the area of interest. Spatial scales will be compared within and between the level of the fishing pots and fishing strings, and within discrete locations in the fishing area as defined by the operation of fishing vessels. Depletion estimates of stock assessment will be used to map the stock size of whelks in the area of interest and express variation in the stock of *B. undatum* on a temporal scale. A mark re-capture experiment, coupled with depletion analysis, will also be used to determine the population and density of the target stock of Common whelk.

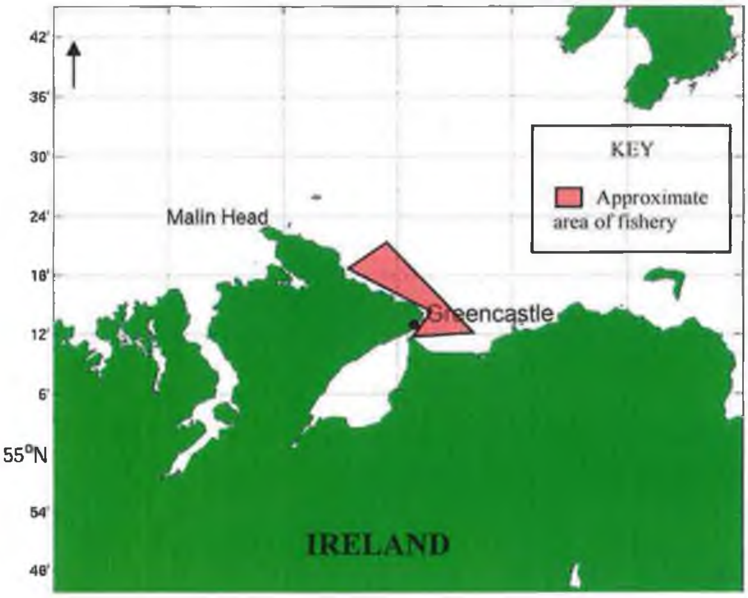
MATERIALS AND METHODS

The region of the North West Irish whelk fishery covers an area of approximately 128 km^2 (55°18'N, -7°10'W; 52°20'N, -7°00'W; 55°12'N, -6°55'W; 55°12'N, -6°50'W). Up to six small vessels fished *B. undatum* from the ports of Greencastle and Portaleen, and from Bunagee Pier, on the Eastern Inishowen Peninsula, Co. Donegal from March to July 2003. The fishing gear used to target Common whelks consists of pots fashioned from industrial plastic containers, drilled with multiple drainage holes of approximately 15 mm diameter, and weighted generally with cement (see Photo 1.1). The gear is deployed from the rear of fishing vessels in lines of up to 100 pots, with a floating buoy at the end of each string of pots. Pots were baited with a combination of dogfish (*Scyliorhinus spp.*) and Brown crab (*Cancer pagurus*). Pots are lifted every 24 hours, weather permitting, re-baited and deployed. Fishing occurs at depths of approximately 44 metres. Upon landing, whelks were removed from pots to standard plastic fishing boxes, supplied by the Foyle and Greencastle Fishermen's Co-op.

Photo 1.1 Common whelk fishing pots. Note the drainage holes and top access for whelk capture and removal.

Data Collection

Catch data was collected on board fishing vessels by direct observation and logbooks for 13 weeks from March to July 2003, in the region of the North West Irish whelk fishery (see Map 1.1). Information including time, day, bottom type, depth, soak time, number of strings, number of pots per string and location of buoys was collected for each string of pots. Where the principal observer (J. Hemer) made observations (June 4, 5 and 11, 2003), pots were selected randomly using a numbers generated by www.random.org to examine the total number of Common whelks landed per pot, and the total shell length of each animal contained therein. Total shell length was measured from the tip of the apex to the end of the siphonal canal (see Photo 1.2), to the nearest mm with plastic calipers. Where other observers (appointed as observers to the fishery but not dedicated to the methods of the present study) collected data, pots were opportunistically selected, and the total number landed and shell length recorded. The total number of boxes of whelk landed per string was recorded. Observations were made, where possible, of by-catch and discards of the fishery. The day's total quantity (boxes) of whelk landed on-board vessels and caught (removed to land for processing) was recorded.



Map 1.1 Map of Ireland indicating the approximate area of the North West Irish whelk fishery

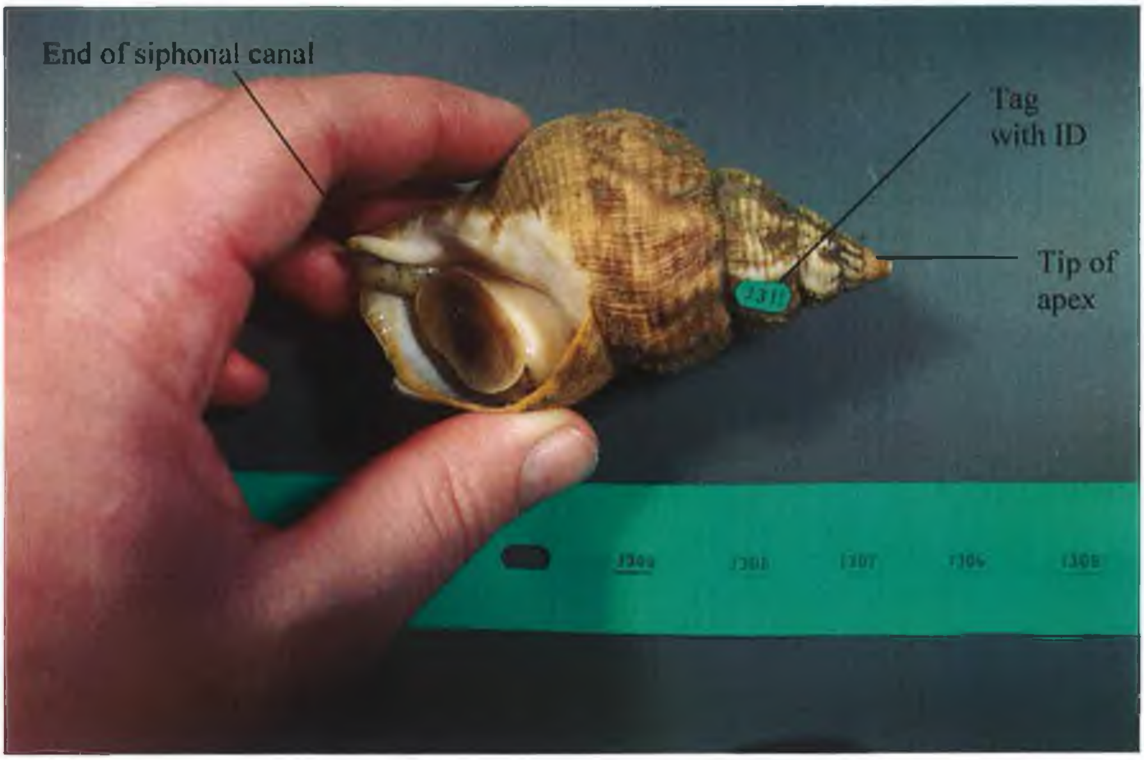


Photo 1.2 *Buccinum undatum* and the position of the hall print tag used in the mark re-capture analysis. The tip of the shell apex and end of siphonal canal are indicated as a measure of total shell length.

Spatial Variation

Spatial variation in catch total shell length within the region of the North West Irish whelk fishery was analysed. Differences in spatial variation of the shell length and population density of the stock were tested at the level of pot, string and vessel fishing area. The null hypothesis (Ho) for analysis of variance is no variation in the total shell length between and within pots, strings and vessels. Randomly selected replicates of the total shell length of landed whelks were available, and between pots, within strings, between strings and within vessel variation were determined by One-Way Analysis of Variance and Fully Nested Analysis of Variance. Analysis of Variance was also conducted to determine the importance of position of pots on strings. Levene's tests were conducted to determine homogeneity of variances, and mean plotted against standard deviation to determine the appropriate transformation if data were found to be heteroscedastic (variance in errors over the sample.) Anderson-Darling tests were conducted on total shell length measurements in pots and on strings to determine if the size of the catch was normally distributed, and normality of residuals was checked. The density of Common whelk in the region of the North West Irish whelk fishery was determined from average catch per pot, and estimated effective area of attraction.

Depletion Estimates of Stock Assessment

Total population and density of the stock were estimated using a Leslie-Davis Catch Effort Model (1939) of depletion analysis. Temporal variation in the size of the stock was also observed by a Leslie plot of catch data. A Ricker plot (DeLury, 1947; Ricker, 1975) of Catch per Unit Effort was also employed to determine population size.

The Leslie-Davis (1939) Catch Effort Model estimates total population by the decline in Catch per Unit Effort (CPUE) with time. Catch of boxes removed at sample time *i* (c_i), accumulated catch (K_i), fishing effort expressed as pots per day (f_i), and accumulated effort (F_i) were collated, and CPUE (Y_i) calculated from c_i/f_i. The initial population total, *N,* is estimated from a linear regression of K_i against Y_i. The slope of the regression line gives an estimate of the catchability, *C*, of individuals (the probability than an individual will be caught with one unit effort of catch). Density of the stock is estimated from the calculated population in the area of the fishery. The Ricker model employs the same parameters as the Leslie model, but uses semi-logarithmic linear regression relationship between the log of CPUE and accumulated fishing effort to assess underlying assumptions.

Mark Re-Capture Experiment

An area of approximately 60800 m^2 was selected to conduct a Mark Re-capture Experiment (MRE) in the region of the North West Irish whelk fishery during July 2004. The area was estimated by determining the total distance of sampling equipment, plus a 10 m area of attraction (Himmelman, 1998) for Common whelks. A Petersen table (Robson and Reiger, 1964) was used to determine the number of whelks required for marking to achieve a statistically robust experiment, given the estimated population size in the area from the Leslie-Davis Catch Effort Model. Assuming whelk density is uniform over the area of the fishery, approximately 10000 whelks should be marked and re-captured, according to the Petersen estimate.

The tag and the position of the shell to be tagged (see Photo 1.2) were tested in the laboratory for practicality on the species *B. undatum*. The tagged position is beyond the foot cleaning area and is downward-angled to reduce visibility to predators. As Common whelks are predominately a scavenging species, the position of the tag was thought to have no effect on food collection. It was observed that the tag did not to impede usual movement and behaviour in whelks, and it was anticipated that the tag would not adversely affect the reproductive behaviour of whelks. Hallprint Tags™ were used in this experiment, and have been found by mollusc researchers to be durable and discrete, and not to hinder growth (Lemarié *et al.,* 2000; Ross *et al.*, 2001). The area of the shell to host the tag was dried with a towel. The shell does not need to be very dry as a small amount of moisture aids the binding of the glue, which contains the active ingredient cyanoacrylate. An individual tag was removed from the roll, and held with forceps to apply a small amount of glue on the reverse side to the identification. The tag was placed on the dried area of the shell and pressed lightly with forceps. Total shell length was record in millimeters against tag identification. The animal was left a further 2 – 4 minutes for the glue to bind, and returned to water.

The MRE was conducted over 5 days from July 12 – 16, 2004, in the North West Irish whelk fishery on the fishing vessel *Lady Nuala*. Fishing effort remained constant in the research area for the period of the marking program, with 4 strings of 75 pots (total 225 pots) deployed daily in the same location and left to soak for 24 hours. On Day 1, baited pots that had soaked in the area for 24 hours were lifted, and 2770 captured whelks tagged and returned to the water during Day 1 and Day 2. Pots were re-baited and deployed in the same location as on Day 1 and for a further three days of fishing. During each day of fishing from Day 2 to Day 5, hauled pots were checked for tagged whelks, and the total catch for the day recorded for depletion analysis. A Petersen-Lincoln Estimate (Lincoln, 1930) and Bailey Estimate (Bailey, 1951) of population size, $\acute{N}$, were calculated from the number of whelks marked, sampled and recaptured.

RESULTS

It is assumed that the pots, weighted with cement, remained in an upright position during fishing, and thus there were no escapes from the trap. Kideys (1993) confirmed the upright position of pots weighted with cement over a 6-month period with visual aid. However, there was no study of the efficiency of pots in retaining catch in this study. It was also assumed that small animals of less than 15 mm diameter were either able to escape from the pots through drainage holes of larger diameter than shells, or did not respond to bait within the 24 hour soak period, as these animals are not represented in the catch. Gear saturation, whereby catch rates decrease with increasing soak time, was not observed in this study. By-catch of the fishery was low, with the gastropod *Neptunea antiqua*, hermit crabs (*Eupagurus bernhardus*), a number of sea star species, and Brown crab (*C. pagurus*) occasionally appearing in the contents of landed pots.

Spatial Variation

The total catch of 115 pots was measured for shell length over 4 days of fishing on May 20 and June 4, 5 and 11, 2003. Each pot held on average 50 whelks. Variation in total shell length of catch between pots within strings was determined for each day of fishing. Results are summarised in Table 1.1. The null hypothesis, that there is no variation in total shell length between pots within strings, was accepted in 50% of cases, and rejected in 50% of cases. Total shell length replicates were tested for homogeneity of variances. Where a Levene's test result of $P<0.05$ was found, the means and standard deviations were plotted and the appropriate form of transformation determined. This was typically a log transformation. An Anderson-Darling test for normality of shell length in pots found that 38.26% of the pot catch was normally distributed to the 95% confidence limit.

Variation between Pots within Strings

(Ho: There is no variation in shell length between pots on the same string)

String	Date	Vessel	No. Pots	P	Test	Ho
41	20-May-03	Michelle	2	0.073	Mann-Whitney	Accept
47	20-May-03	Michelle	4	0.089	One-Way ANOVA	Accept
50	20-May-03	Michelle	2	0.084	Two Tailed t-test	Accept
51	20-May-03	Michelle	2	0.057	One-Way ANOVA	Accept
52	20-May-03	Michelle	9	0.000	One-Way ANOVA	Reject
55	20-May-03	Michelle	9	0.000	One-Way ANOVA	Reject
60	20-May-03	Michelle	9	0.000	One-Way ANOVA	Reject
62	20-May-03	Michelle	9	0.000	One-Way ANOVA	Reject
65	20-May-03	Michelle	7	0.000	One-Way ANOVA	Reject
67	20-May-03	Michelle	7	0.000	One-Way ANOVA	Reject
72	20-May-03	Michelle	9	0.468	One-Way ANOVA	Accept
4	5-Jun-03	Jennifer Constance	2	0.046	Mann-Whitney	Reject
10	5-Jun-03	Jennifer Constance	4	0.089	One-Way ANOVA	Accept
13	5-Jun-03	Jennifer Constance	2	0.076	Two Tailed t-test	Accept
14	5-Jun-03	Jennifer Constance	3	0.049	One-Way ANOVA	Reject
2	11-Jun-03	Kilbrogan	3	0.140	One-Way ANOVA	Accept
7	11-Jun-03	Kilbrogan	3	0.806	One-Way ANOVA	Accept
9	11-Jun-03	Kilbrogan	3	0.004	One-Way ANOVA	Reject

Table 1.1 Variation in the size of landed whelks between pots and within strings. The string number, date, vessel, number of pots analysed for contents, P value, analysis of variance and response to the null hypothesis at the 95% confidence limit are indicated.

Whelk landing size was analysed in a total of 84 strings of pots during the 4 days of fishing. The average number of whelks landed per string was 149.38. Normal distribution of total shell length per string was observed in 10.71% of strings (Anderson-Darling test for normal distribution).

A single Fully Nested Analysis of Variance between 20 randomly selected replicates of total shell length of landed whelks per pot, 2 pots per string, 3 strings per vessel and 3 vessels fishing location were conducted using data from May 20, June 5 and June 11 2003. Insufficient replicates of pots were available for analysis for June 4, 2003 data. For each of the three analysed vessel locations per day of fishing, the null hypothesis was accepted at the level of string (there is no variation in the total shell length of landed whelks between strings within vessels and within strings between vessels; Fully Nested ANOVA, $P>0.05$), and rejected at the level of pot (there is significant variation in the total shell length of landed whelks between pots, within strings, within and between vessels; Nested ANOVA, $P<0.05$). The null hypothesis was rejected at the level of vessels fishing location where all three vessels were compared (Fully Nested ANOVA, $P=0.014$), however, no significant difference was found in total shell length of landings to vessels on June 5 and June 11 (Fully Nested ANOVA, $P=0.106$). Analysis of variance between size of landings of strings on June 4 and June 5, 2003 found no significant difference (non-parametric Kruskall-Wallace, $P>0.05$), however, June 4 string landing size varied significantly with other dates (non-parametric Kruskall-Wallace, $P<0.05$). Data were tested for homogeneity of variances (Levene's test) and normality (Anderson Darling test) and transformation was not required.

Analysis of variance between pots positioned at the string end and string middle found no significant difference in mean shell length or number landed (non-parametric Mann-Whitney; $P=0.0857$). Analysis of grouped end pots towards middle pots on strings landed on May 20, 2003, found significant difference in number and size of landed whelks (One-way ANOVA; $P=0.000$). However, post-hoc pooling (Tukey's family error rate) reveals that there is no pattern in numbers or size landed along strings.

Himmelman (1988) estimated the effective area of attraction for Common whelks to be 10 m over a 24-hour period in the Gulf of St Lawrence, Canada. It is therefore assumed that for pots spaced 6 fathom, or approximately 11 m along the centre of a string, the effective area of capture is 10 m either side of the pot, and 5.5 m along the string, or 220 m^2. Over the 13 week period of fishing, an average of 50 whelks were captured per pot, thus yielding a density of 0.227 whelks per m^2. Gros and Santarelli (1986) estimated the effective area of attraction to be 373 m^2 for *B. undatum* in the region of the Channel Islands, and Kideys (1993) concurs with this estimate for the Isle of Man in the Irish Sea. A density of 0.134 whelks per m^2 is found when applying this effective area of attraction on the stock of Common whelk in the current study.

Depletion Estimates of Stock Assessment

A Leslie plot of CPUE from FV Jennifer Constance against accumulated catch, K*i*, in boxes shows a steady rate of catch over seven weeks of fishing, with a total of 758 boxes of whelk landed to the fishery (see Fig. 1.1). During the eighth week of fishing, CPUE begins to decline. Following 13 weeks of fishing, the total accumulated catch is 1535 boxes (see Table 1.2). The slope of the declining CPUE represents catchability, Ĉ, and is determined using the linear regression equation:

$$Catchability = \hat{C} = \frac{-\sum_{i=1}^{s} Y_i\left(K_i - \bar{K}\right)}{\sum_{i=1}^{s}\left(K_i - \bar{K}\right)^2}$$

$$PopulationSize = \breve{N} = \bar{K} + \left(\frac{\bar{Y}}{\hat{C}}\right)$$

$$Variance(\breve{N}) = \frac{s_{yx}^2}{\hat{C}^2}\left[\frac{1}{s} + \frac{\left(\breve{N} - \bar{K}\right)^2}{\sum_{i=1}^{s}\left(K_i - \bar{K}\right)^2}\right]$$

where

$$s_{yx}^2 = \sum \frac{\left[Y_i - \hat{C}\left(\breve{N} - K_i\right)\right]^2}{(s-2)}$$

The total population, Ń, is thus determined where Yi = ci/fi (see Table 1.2), K = mean value of Ki = 883.77, and s = total number of samples = 13. Ĉ was found to be 1.126^{-4} and N = 5877.74 boxes. The Variance of N was determined to be 3.334x10^6, Standard Error of Ń = √Variance of Ń = 1827, and 95% CI of Ń = N±1.96(SE(N)) = 2.106X10^{7}to

-2.105×10^7. It was estimated throughout the 13-week fishing period that the average number of whelks landed per pot is 50, and the average number of pots per box is 15. Furthermore, up to 5 fishing vessels were fishing at similar rates. For the area of the fishery, the total population of Common whelk is estimated to be 2.204×10^7, and density 0.172 whelks per m^2.

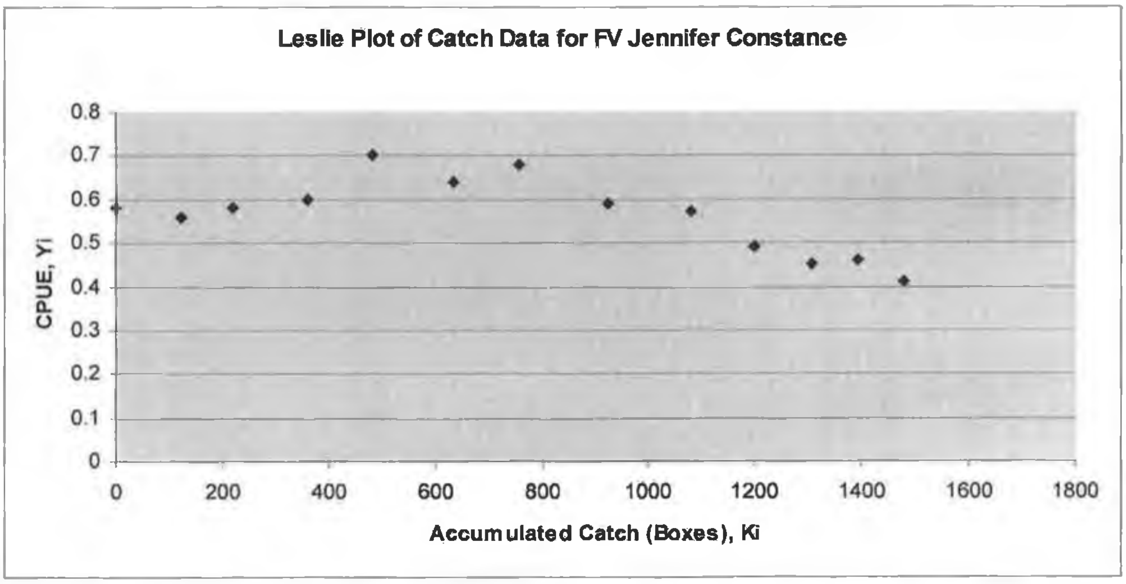


Figure 1.1 Leslie plot of Catch per Unit Effort and Accumulated Catch in Boxes, as estimated from catch data collated from the fishing records of FV Jennifer Constance during the 13-week period of fishing from March to July 2003, in the region of the North West Irish whelk fishery. CPUE begins to decline after 7 weeks of fishing.

Week Number, *i*	Catch in Boxes, C*i*	Accumulated Catch, K*i*	Effort (Pots per Day), f*i*	Accumulated Effort, F*i*	CPUE C*i*/f*i*+Y*i*
1	122	0	210	0	0.58
2	97	122	171.4	210	0.56
3	142	219	242.8	381.4	0.58
4	121	361	200	624.2	0.6
5	151	482	214.3	824.2	0.7
6	125	633	195.7	1038.5	0.64
7	165	758	242.8	1234.2	0.68
8	158	923	265.7	1477	0.59
9	119	1081	208.5	1742.7	0.57
10	108	1200	220	1951.2	0.49
11	82	1308	182.8	2171.2	0.45
12	87	1390	188.6	2354	0.46
13	58	1477	140	2542.6	0.41

Table 1.2 Parameters of the Leslie-Davis Effort Model, as estimated from catch data collated from the fishing records of FV Jennifer Constance during the 13-week period of fishing from March to July 2003, in the region of the North West Irish whelk fishery.

A Ricker plot (Ricker, 1975) of the log of CPUE against accumulated effort, Fi (see Fig. 1.2), shows a decline in catch of whelks over the 13-week fishing period. $\acute{N}$ is then determined from the equation log $\acute{N}$ = Flog(1 – $\hat{C}$) – log $\hat{C}$, where F = mean value of Fi = 1479.5, and $\acute{N}$= 765545. When pots per box, whelk per pot and number of vessels are factored, the total population is estimated at $2.87\text{X}10^9$, and a density of 22 whelks per m^2 for the area of the North West Irish whelk fishery.

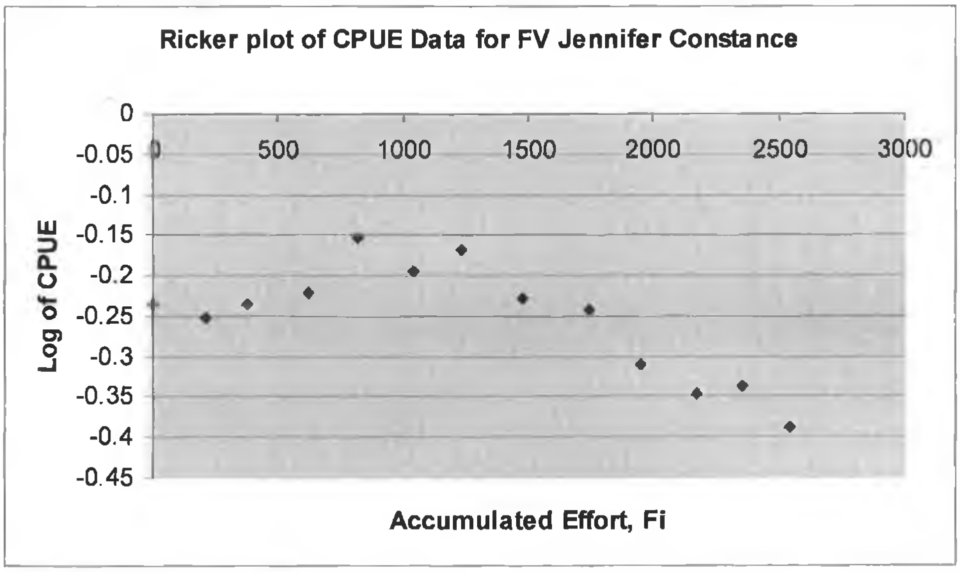


Figure 1.2 Ricker plot of log Catch per Unit Effort and Accumulated Effort in Pots, as estimated from catch data collated from the fishing records of FV Jennifer Constance during the 13-week period of fishing from March to July 2003, in the region of the North West Irish whelk fishery.

Mark Re-capture Experiment

The Petersen estimate of marked population size of 10,000 for this experiment was not met due to the logistical constraints of working on board a small fishing vessel. Those whelks that were tagged were done so on board the fishing vessel *Lady Nuala*, and on land at the local Fishermen's Co-operative. Whelks were returned to sea at the same location as collected. Those whelks tagged on land were stored in fishing catch boxes, and covered with dark, damp hessian fabric bags. Of those whelks tagged on land, small quantities have been reported in post-experiment fishing operations up to at least 11 months post-marking (MaryAnne Green, Pers. Comm.; Mary Hayes, Pers. Comm.). This suggests that the selected tag is durable, and also that whelks landed during fishing operations and returned to sea can survive.

Catch per Unit Effort declined over 4 days of intensive fishing, following the marking of whelks (see Table 1.3). Regression analysis of a Leslie plot (see Fig 1.3) of CPUE against accumulated catch estimates catchability, $\hat{C} = 7.259^{-2}$ and $\acute{N} = 13325$. Variance about the regression is 1162.98, SE of $\acute{N} = 3472$, and 95% CI is $9.068\text{x}10^6$ to $-9.066\text{x}10^7$. When the area of the depletion analysis defined by the Mark Recapture Experiment is scaled to the size of the fishery, the population of Common whelk is found to be $2.809\text{x}10^7$, and density 0.219 whelks per m^2.

The size of whelks landed did not decline over Days 2-5 of fishing, however, the size of whelks landed per day were not normally distributed (Anderson-Darling; $P<0.005$) and varied significantly (non-parametric Kruskal-Wallis; $P=0.000$). Further analysis of the size of whelks landed on Strings 1, 2, 3 and 4 on Days 3-5 of fishing indicated that size varies significantly between strings (One-way ANOVA; $P=0.003$), and post-hoc analysis indicated that the size of landings on String 1 are significantly larger (mean = 93.65 mm total shell length) than those on String 4. Data were log transformed for homoscedasticity.

Recapture of marked whelks following tagging was low, reducing precision. 2770 Whelks were marked on Day 1, and released on Days 1 and 2 at separate locations within the area of analysis. Fishing operations commenced on Days 2, 3, 4 and 5. On Day 3, 4 marked whelks were returned, all on the one string (String 4). On Day 5, 7 more whelks were returned, again on a single string, in the same location as the Day 3 marked landings. A further 9 marked whelks were returned over 2 days of fishing on August 3 and 5, 2004. A Petersen-Lincoln Estimate (Lincoln, 1930) of total population, Ń, was made using the equation N=an/r, where a = the total number marked in the first sample = 2270, n = the total number of individuals in the second sample = 3189, and r = the total recapture = 4. The population, Ń, was estimated to be $2.208x10^{6}$ in the area of the experiment. When the area of the experiment is factored to the area of the fishery, the population is $4.656x10^{9}$, and density 36.32 per m^{2}. As the value of r is very small, a Bailey estimate of Ń was also determined, using the equation Ń = n(a+1)/r+1. The population of whelk in the area of the experiment was then Ń = $1.767x10^{6}$, and the Variance of Ń estimated to be $2.479x10^{13}$. When factored to the area of the whole fishery, the total population is estimated at $3.725x10^{9}$, and density of 29.07 per m^{2}.

Day Number, i	Catch in Numbers, Ci	Accumulated Catch, Ki	Effort (Pots per Day), fi	Accumulated Effort, Fi	CPUE Ci/fi=Yi
2	4230	0	75	0	56.4
3	3189	4230	75	75	42.52
4	2714	7419	75	150	36.1866667
5	977	10133	75	225	13.0266667
		11110		300	

Table 1.3 Parameters of the Leslie-Davis Effort Model, as estimated from catch data collected from the depletion analysis conducted over 4 days of fishing in July 2004 on board the FV Lady Nuala, simultaneously with the MRE.

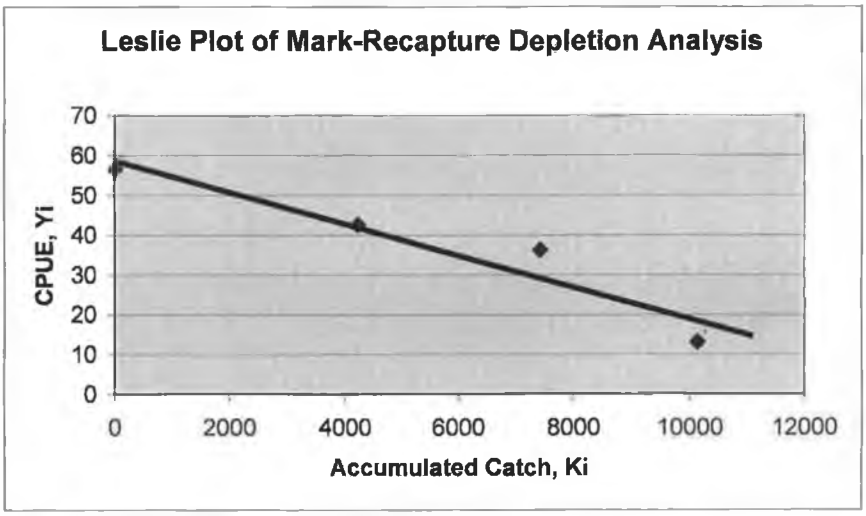


Figure 1.3 Leslie plot of Catch per Unit Effort and Accumulated Catch in Boxes, as estimated from catch data collected from the depletion analysis conducted over 4 days of fishing in July 2004 on board the FV Lady Nuala, simultaneously with the MRE.

DISCUSSION

The area of the North West Irish whelk fishery, 128.2 km^2, was estimated from the maximum and minimum coordinates of latitude and longitude from Fishermen's logbooks and records of on board observers. It is a conservative estimate of the total area fished. Within the area of the fishery, pots are generally left to soak for a period of 24 hours. However, in poor weather conditions, pots may be left for twice or three times this period. Pot immersion time and catch rates have been the focus of benthic fish and shellfish population analyses (Hanckock, 1963; Bennet, 1974; Brown, 1979; Skud, 1979; Kennelly, 1989; Himmelman, 1988; Sainte-Marie, 1991; Valentinsson *et al.,* 1999). Hancock (1963) reports little change in catches of *B. undatum* between pots lifted after 1 day and up to 7 days. Similarly, Davis and Sisson (1988) found that catches of Channeled whelk (*Busycotypus canaliculatus*) were not significantly different after 48 hours than 24 hours. However, Valentinsson *et al.*, (1999) found increasing CPUE with soak time, while Fahy *et al.* (2000) described falling catch rates with increased soak time greater than 24 hours due to predation pressure and physical conditions. In the current study, there was equal treatment in the analysis of variation in the size and number of whelks caught in pots with a soak time of 24 hours and greater than 24 hours (up to 72 hours in extreme weather conditions.)

During the period of the current study two types of bait, Dogfish (*Scyliorhinus spp.*) and Brown crab (*C. pagurus*) were preferred by fishermen and generally deployed in pots to attract *B. undatum*. Brown crab occasionally appeared as by-catch to the Common whelk fishery, and was subsequently re-used as bait. Dogfish was purchased as by-catch from a different fishery and used. Where bait was not entirely consumed, it would on occasion be re-deployed in pots. Neither species of bait was directly targeted to support the Common whelk fishery. When necessary, such as a shortage in supply of preferred bait, fishermen baited pots with various unsold white fish species, such as haddock and plaice. Again, these species were not targeted to support the whelk fishery. It is assumed that bait type varies with supply, and therefore with season. Bait preferences were not determined in the current study, and the effects of bait type have been disregarded in other studies due to anecdotal evidence of equal attraction to mixed species of bait (Kideys, 1993). While the type of by-catch to the whelk fishery was described as low in diversity, quantity was not described. This is because in most cases, the volume (in numbers) of by-catch was much less than the target species. Where possible, fishermen hosed by-catch from the decks of boats with salt water in the same location as landings were taken. Survival is unknown, but it is possible that by-catch may be utilised by benthic scavengers such as *B. undatum* (Bergmann *et al.*, 2002).

While every effort was made in this study to ensure random analysis of catch per pot, this was not always achievable. Up to six observers other than the principle observer, and fishermen collected a large proportion of data made available to the study. It is not certain that random selection of pots was always adhered to. While on board working fishing vessels, it is difficult to monitor the movement of randomly pre-selected pots, due to the efficient nature of the work and a lack of working and storage space for crew and scientific observers. Occasionally pot contents were combined, or the closest pot to the randomly selected pot surveyed. Consequently, the number of pot contents observed for variation is lower than it might be in a dedicated scientific survey.

The size of the catch per pot was shown to vary significantly between pots on different strings, within the same string, and between vessels on different fishing days. Only a small proportion of pots contained a size selection of Common whelks that were normally distributed. These results suggest that the size of whelks is not uniformly distributed at the spatial scale of pot area of attraction across the region of this fishery. However, the size of landings between strings, within and between vessels fishing location, shows no variation. The significance of variation in the size of whelks landed between vessel fishing locations should be treated with caution as data were collected on different days. The results of this analysis may be confounded by time, physical conditions, or some other parameter. Further evidence of non-uniformity of distribution is provided by the finding that although CPUE was shown to decline, the mean size of the catch was not, and that vessels fishing different locations at successively later dates landed whelks of mean sizes not proportional to declining catch rates. Few very small whelks were represented in the catch, possibly due to the ability to escape through pot drainage holes, or by not achieving access to bait in the soak period due to slower response abilities associated with a smaller foot. The possible selection against small whelks by the fishing gear demonstrates bias in the results. Valentinsson *et al.,* (1999) describe a trend of increasing shell length with depth. This relationship was not observed in the current study, as depth measurement was not always available during operations on board small fishing vessels. However, it is noteworthy that on June 4, fishing depth was greater than on June 5, 2003, yet mean size of the catch was less than the following day. Fahy (1999) discusses the occurrence of whelk in discrete patches in the Irish Sea whelk fishery, arguing that density distribution and condition (size and mass) varies throughout the fishery (Fahy *et al.,* 2000). There was no significant difference found between the numbers of whelks landed in end pots or grouped end pots, although the effective area of attraction for end-string pots should be greater than for mid-string pots. These results also suggest that the population of whelk is not uniformly distributed on the benthos, as end pot numbers would be higher if this were the case.

The nature of observing catch on board fishing vessels has resulted in a lack of replicates in fishing vessels operating in the same location to determine spatial and temporal variability. However, the total estimated catch from one vessel, FV Jennifer Constance, throughout the fishing season has allowed an assessment of CPUE, and thus changes in catch with time. CPUE is an index to fish population density, and a measure of species relative abundance (Hubert, 1996). However, CPUE is also criticised because of the high variability among catches at various sites (Hubert, 1996). The Leslie plot of CPUE against accumulated catch demonstrates that following a period of stable to increasing CPUE, decline in catch is seen toward the end of the fishing period.

The following assumptions are integral to the success of Leslie-Davis Effort Models: the population is closed, the probability of each individual being caught is equal, and the probability of capture is constant throughout the fishing period. Under these assumptions, CPUE is directly proportional to population size. However, Leslie Davis effort models may be restrictive in their prediction of population parameters because a large enough fraction of the population must be removed so that a decline in CPUE is observed, and the depletion estimate will not work if the population is large relative to removals. Estimates of population parameters in the current study could be affected by the period of stable fishing catch for a portion of the fishing period. Additionally, the number of whelk landed per pot, and per box, could be estimated at higher or lower numbers than the conservative estimate used in the current study. Other factors effecting catch of whelk have been identified, and these are principally either biological (mating, spawning, feeding, recruitment, immigration and/or emigration), or physical (temperature, speed and direction of currents) (Hancock, 1963; Gros and Santarelli, 1986; Martel et al., 1986; Himmelman, 1988; Kideys, 1993). Some of the assumptions of the Leslie-Davis Effort Model have been violated in the current study due to both biological and physical factors. It has already been described that smaller whelks are not well represented in the catch, thus the probability of each individual being caught is not equal. Himmelman (1988) demonstrated that the area of attraction changes in direction and distance according to physical conditions and as such, the probability of capture is not constant throughout the fishing period. Fishermen in the region of the North West Irish whelk fishery report anecdotal evidence of reduced catch in Spring tides (Pers. Comm), and Fahy *et al.* (2000) report that strong tidal currents influence whelk catch in the Irish Sea. The violation of these assumptions is evident in the extremely high variation of N, Standard Error, and Confidence Intervals estimated for this analysis.

The Ricker plot of log CPUE against accumulated effort to predict catchability and population follows the same assumptions, and therefore violations as the Leslie-Davis Effort Model. The Ricker method is also sensitive to the population being large relative to removals, possibly illustrated by CPUE<1, and therefore negative log of CPUE. CPUE is a widely used abundance index in the study of *B. undatum* stocks, and frequently expressed as mass (e.g., kg or t) (Valentinsson *et al.*, 1999; Fahy *et al.*, 2000; Morel and Bossy, 2003). Estimates of catch in mass were not available to the current study, and thus standardised comparison between CPUE and stock in the North West Irish whelk fishery and other Common whelk fisheries was not possible.

The depletion analysis conducted during the MRE occurs over a shorter space of time, and within a smaller region, thus possibly eliminating some variation in biological parameters such as immigration and emigration affecting catch in this slow moving species. Changes in physical parameters affecting catch are likely reduced within the MRE period of less than a week, compared with the 13-week period of fishing for FV Jennifer Constance. In the Leslie plot of MRE data, an immediate decline in CPUE with accumulated catch is identified, though there are fewer samples. CPUE data collated from the FV Jennifer Constance for the region of the fishery are multiplied up to the level of the fishing fleet to determine N. CPUE data from the MRE are multiplied to the area of the fishery to determine N. However, fishing may have occurred over a larger or smaller area than estimated, given that not all coordinates of deployed gear were made available to this study. Potential bias in the assumption of fishing area size is consistently embedded in all estimates of population density throughout the study.

Four assumptions underpin Lincoln index MRE techniques. These are: a) marked animals are not affected in either behaviour or life expectancy as a result of marking and the marks will not be lost, b) marked animals become completely mixed when returned to the population, c) the probability of capture and mortality is equal, and d) sampling must be at discrete time intervals after marking (Southwood, 1966; Krebs, 1994; Henderson, 2003). The return of marked whelks from the MRE was very low, and comparable to returns found by Kideys (1993) in the Irish Sea. Similarly, Kideys (1993) reports that MRE yielded an overestimate in population, N. The inefficiency of mark recapture methods in density estimates of *B. undatum* was also reported by Sainte-Marie (1991).

In the current study, whelks were marked with a small plastic tag attached with cyanoacrylate glue. The attaching of the tag did not appear to affect the feeding activity of whelk in laboratory trials, and has been recommended by other researchers because it is less invasive than some methods (Lemarié *et al.,* 2000; Ross *et al.*, 2001). Other methods of attaching tags to *B. undatum* have included painting shells (Hancock, 1963), drilling and wiring plastic tags (Kideys, 1994) and wrapping labeled elastic bands around the shell (Himmelman, 1988). In a study of Common whelk movement following release after tagging, Sainte-Marie (1991) reports that tagged whelk behave differently to undisturbed whelks, and will move away from the area of release. The observed changes in behaviour and mixing will likely contribute to the low rate of recapture in the 3 days following release, and violate the assumptions of the MRE method. However, such response does not account for the low rate of recapture in fishing efforts in early August 2004, 3 weeks after whelks were marked and released. While every effort was made to sample at discrete, regular periods following release, marked animals were not collected in each sampling effort. As such, more complex methods of modeling open populations (Bailey, 1951; Jolly, 1965) were not available to the current study. Mark re-capture methods are poor tools in the estimation of large populations as approximately 20% of the population must be captured and marked if the accuracy of the estimation is to be more than an order of magnitude approximation (Henderson, 2003). It was not possible to mark the estimated 10,000 whelks to achieve accuracy in the current study, and the resulting estimates of population numbers and density were larger than other methods employed in this study.

Table 1.4 shows estimates of population and relative density achieved through the various methods of analysis employed in this study. Absolute density cannot be measured in this study, as the precise area of attraction to the baited trap is unknown. Methods of pot catch area of attraction, and the two Leslie-Davis Effort Models have revealed density estimates of between 0.134 and 0.227 whelks per m^2. These estimates fall within the range of density estimates of Kideys (1993) in the Irish Sea (Isle of Man), which were achieved by pot sampling, MRE, underwater television survey and SCUBA diving survey. Himmelman (1988) also achieved similar estimates of density (0.05 – 0.24 whelks per m^2) in the Gulf of St Lawrence, Canada. The current study and the studies by Kideys (1993) and Himmelman (1988) all took place during summer months. However, Kideys (1993) observed a significant change in density estimates with season, possibly due to fishing effort or some other biological parameter. Hancock (1963) observed reduced feeding in Common whelk in summer months in English waters, suggesting a temperature impact on attraction to baited pots. In the current study, the number of landings per pot varied significantly over the period of analysis, and revealed no pattern of decline or otherwise during this time. As such, comparison of density over the period of this study has not been presented. It is recommended however, that in order to attain a complete understanding of population and density in the area of the North West Irish whelk fishery, that seasonal variation be assessed. Furthermore, to validate results and eliminate the effect of bias by attracting larger whelks to baited pots, dredging, SCUBA diving or visual assessment by remote means should be employed in the study of *B. undatum*.

Method	**Catchability, $\hat{C}$**	**Population, $\acute{N}$**	**Area of Attraction, m^2**	**Density, per m^2**
Pot Catch Effective Area of Attraction			220 (Himmelman, 1988)	0.227
Pot Catch Effective Area of Attraction			373 (Kideys, 1993)	0.134
FV Jennifer Constance Leslie-Davis Model Depletion Estimate	1.126^{-4}	$2.204\text{x}10^7$		0.172
FV Jennifer Constance Ricker Model Depletion Estimate		$2.87\text{x}10^9$		22.39
MRE Leslie-Davis Model Depletion Estimate	7.259^{-2}	$2.809\text{x}10^7$		0.219
MRE Petersen-Lincoln Estimate		$4.656\text{x}10^9$		36.32
MRE Bailey Estimate		$3.725\text{x}10^9$		29.07

Table 1.4 Summary of methods used and estimates of population size, $\acute{N}$ and density, whelks per m^2. Estimates of Catchability, $\hat{C}$, and Area of Attraction, m^2, are given where applicable.

Chapter 2

Age and Growth in the Common whelk, Buccinum undatum, in the region of the North West Irish Whelk Fishery

INTRODUCTION

In fisheries resource management, knowledge of the age composition of a population is essential. Age information is necessary for longevity predictions, to establish records for rates of growth, to know age at maturity, and to understand critical life history stages (Everhart and Youngs, 1975). Gastropod molluscs are however, a difficult group to age with the traditional methods that are used in fish or bivalve molluscs. The most conspicuous potential growth marks in gastropod molluscs are the striae in the operculum, which have been shown to correspond to annual growth rings in a small number of Neogastropod species (Kobu and Kondo, 1953; Santarelli and Gros, 1985; Cledón *et al.,* 2005).

Efforts to define a system of predicting age and growth rate in commercially exploited wild populations of the Common whelk *Buccinum undatum* have been reported (Hancock, 1963; Santarelli and Gros, 1985; Kideys, 1996; Fahy *et al*., 2000). *B. undatum* displays an indeterminate growth pattern, such that shell growth continues at a decreasing rate during the lifetime of the animal (Kideys *et al.,* 1993). Common whelks also demonstrate geographical variation in biological characteristics such as size at age and growth rate over short distances (Gendron, 1992; Kideys, 1996; Valentinsson *et al.*, 1999; Fahy *et al*., 2000). In assessments of wild commercial populations of *B. undatum*, age is unknown, and as such, growth parameters are difficult to measure. Therefore, where a new fishery for *B. undatum* is initiated, the age structure of the exploited population should be investigated.

Using oxygen isotope analysis, Santarelli and Gros (1985) confirmed records of seasonal temperature fluctuations in 3 Common whelks, and suggested that the formation of the operculum striae in *B. undatum* is an annual event. Subsequent studies employing this technique have found that very few Common whelks actually show clear striae in the operculum, which indicates uncertainty in the accuracy of striae number representing year class and size at age data (Kideys, 1996; Fahy *et al.,* 2000).

Representative size frequency analysis offers a demographic analysis of size frequency distributions, and has been used to determine age classes and growth rates of marine organisms where there are no age samples, or where an ageing method is unknown or difficult to implement. Size frequency analysis may also be used where age samples exist, but where the coverage is incomplete, or may be used to model the age structure of a population (Parrack and Cummings, 2003). Kideys (1996) reports agreement in the estimation of age of *B. undatum* from the Irish Sea (Isle of Man) from the opercula striae and size frequency distribution.

Mark re-capture is another method for determining age and growth in animals, allowing animals to continue their life cycle in the natural environment. The Jones (1976) method of mark re-captures measures incremental growth per unit of time. Mark re-capture analysis has been performed on wild populations of *B. undatum* (Hancock, 1963; Kideys, 1996). The latter study was however, unsuccessful in determining growth using this technique because the tag used to mark individuals was found to impede growth, and recapture rates were low (Kideys, 1996). A limited number of studies report the determination of age and growth in *B. undatum* through laboratory rearing experiments (Kideys, 1996). However, laboratory reared whelk grew at a greater rate than wild populations of whelk, and therefore estimated growth constants were not applicable to wild populations of *B. undatum*.

Nothing is known about the age structure of a newly exploited population of Common whelk in North West Ireland, in the area east of the Inishowen Peninsula. The aim of this study was to analyse age and growth in the target stock to provide parameters of population dynamics, which are required in order to manage sustainable exploitation of the resource.

Three independent methods were employed to determine size at age and rate of growth in *B. undatum*:

- Size (length) frequency analysis
- Operculum analysis
- Mark re-capture experiment.

METHODS

Length Frequency Analysis

Shell length-frequency data were collected over a total of one days fishing in May 2003, four days in June 2003, and one day in July 2004, from the area of the North West Irish whelk fishery (see Map 1.1), and for samples collected on a monthly basis for the 12-month period between June 2003 and July 2004 from the same region. Samples were not collected in September 2003, March 2004 or June 2004 due to commercial fishing vessels not operating or being unavailable to observers. Independent observers measured the total shell length, from the siphonal canal to the tip of the apex, of un-sexed landed individual whelks to the nearest 1.0 millimetre using plastic calipers while at sea.

Graphical and mathematical methods of separating age classes from length frequency distribution were applied to data collected on June 4, 5 and 11 2003, and a size interval of 3 mm was chosen for size frequency histograms. Other sampling days (May 20 and June 12, 2003 and July 14, 2004) were not selected for age class separation because the chief observer (J.Hemer) did not make measurements and there is concern over the correct identification of *B. undatum* among the stock, particularly where smaller individuals were recorded. Single cohorts of a size frequency are identified by eye from size frequency graphs.

Age classes from these data were subsequently separated using the NORMSEP mathematical model (Hasselbald, 1966). The NORMSEP model was run using FiSAT II software, developed by the Food and Agriculture Organisation of the United Nations (Version 1.1.3, 2000-2004; Abrahamson, 1971; Pauly and Caddy, 1985). This method applies the maximum likelihood concept to separation of the normally distributed components of the size frequency samples, and the expected number of age groups and mean lengths are derived from the results of Bhattacharya's method (Bhattacharya, 1967). The model outputs mean length, population size (n), standard deviation and a separation index (SI) for identified age groups. Parameters of the von Bertalanffy equation were then computed for the data collected on June 5, 2003, $Lt= L_{\propto} (1-exp[-k(t-t_0)]$ with their standard errors, where L_t is the estimated length at age t. These data were selected because they show the best fit between modes in the histogram and those generated by the model. The mean lengths derived from the closest fit between graphical and mathematical methods were used to find the asymptotic length ($L\infty$) and Ford's growth coefficient (k) using a Ford-Walford plot (Walford, 1946), and the hypothetical age that the animal would have been at zero length, t_0, was determined. The Brody growth coefficient was calculated using the equation $-\ln k = K$ (Ricker, 1975).

Operculum Analysis

Samples of *B. undatum* were collected from fishing vessels in the area of the North West Irish whelk fishery at approximately monthly intervals for the 12-month period from June 2003 to May 2004. Where possible, 30 unsexed individuals were randomly collected from each of the size categories: ≤49 mm, 50-69 mm, 70-89 mm, 90-109 mm and ≥110 mm total shell length. Once euthanased by freezing, individual total shell length and sex were determined, and the operculum was removed and placed in a small paper envelope to dry completely. The number of clear striae was counted from the underside of the operculum using a light microscope. Where striae were unclear, no result was recorded.

Analysis of variance of male and female mean striae number at size was conducted to test the null hypothesis that male and female whelk show no variation in mean number of opercula striae at size, and assess whether the sexes should be treated independently in further analysis. To perform this analysis, 20 replicates of striae number were randomised at 5 size categories between the 2 sexes, and tested for homogeneity of variances and normality of residuals. Analysis of variance of mean number of striae at size per month was conducted for the period of the present study to test the null hypothesis that there is no variation in monthly number of opercula striae, and to assess whether a discrete period of recruitment could be detected. Data were tested for homogeneity of variances and normality of residuals.

The number of striae counted was plotted against total shell length for the period of the study. The plot was transferred into a linear model, where it was assumed that each striae counted represents a constant unit of growth, 1 year. Parameters of the von Bertalanffy model were estimated, where the average total shell length, L_t was calculated for each number of striae counted, and $L\infty$ and K calculated from a Ford-Walford plot. These parameters were compared with the results of the Length Frequency Analysis. The frequency, and variation in the mean number of striae, was observed and plotted with time.

Mark Re-capture Experiment

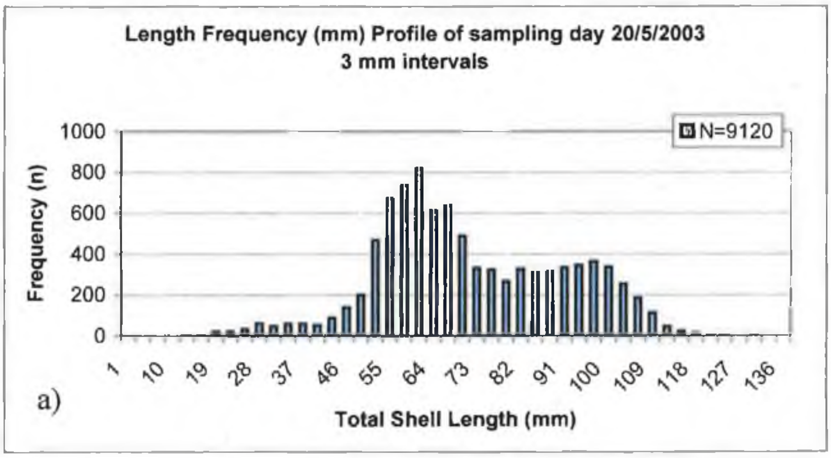
Whelks tagged during the Mark Recapture Experiment (see Methods in Chapter 1) and subsequently caught during fishing operations were returned for analysis to assess size increment data. The total shell length (mm), L_t of the animals was recorded against a pre-defined identification tag at the commencement of the program. Length was recorded again at capture, $L_t + x$ (where x = constant time interval). While these data do not contain information on individual age, the growth over elapsed time may be used to determine growth rate. Where L_t and L_t+x are constant, a growth function may be linearised, and parameters of the von Bertalanffy equation estimated through a Ford-Walford plot. However, insufficient numbers (4) of returned tagged whelk were recovered in the subsequent 12-month period to determine growth rate. Of those that were returned, x was either not constant or unknown.

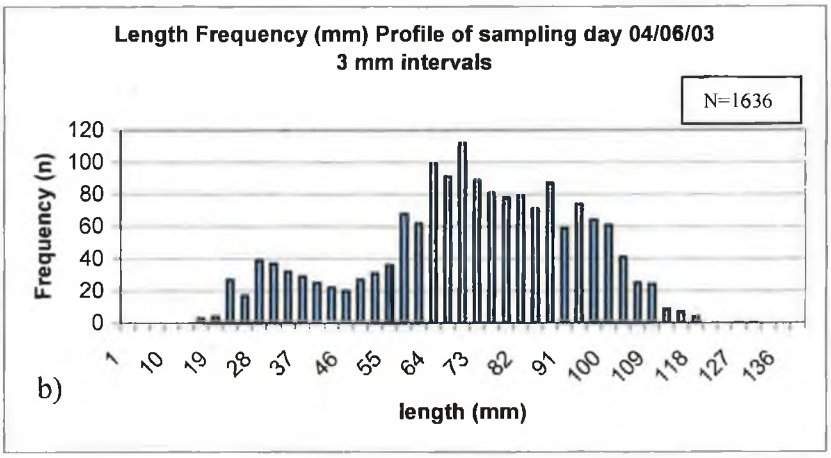
RESULTS

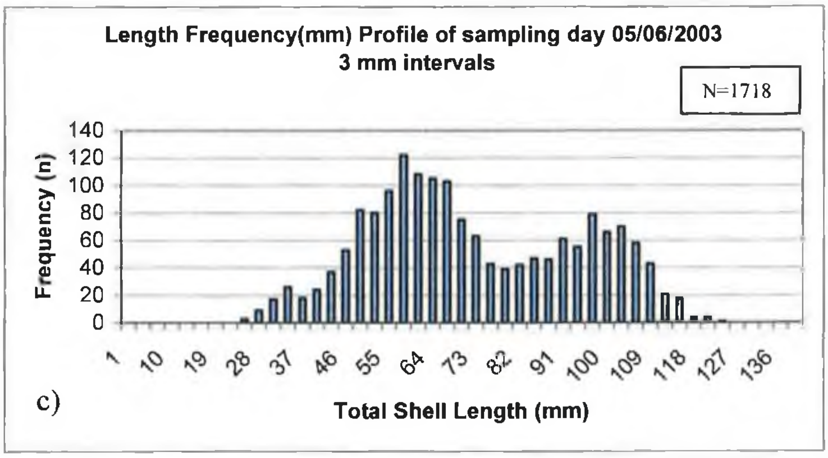
Length Frequency Analysis

Fishing Survey Data

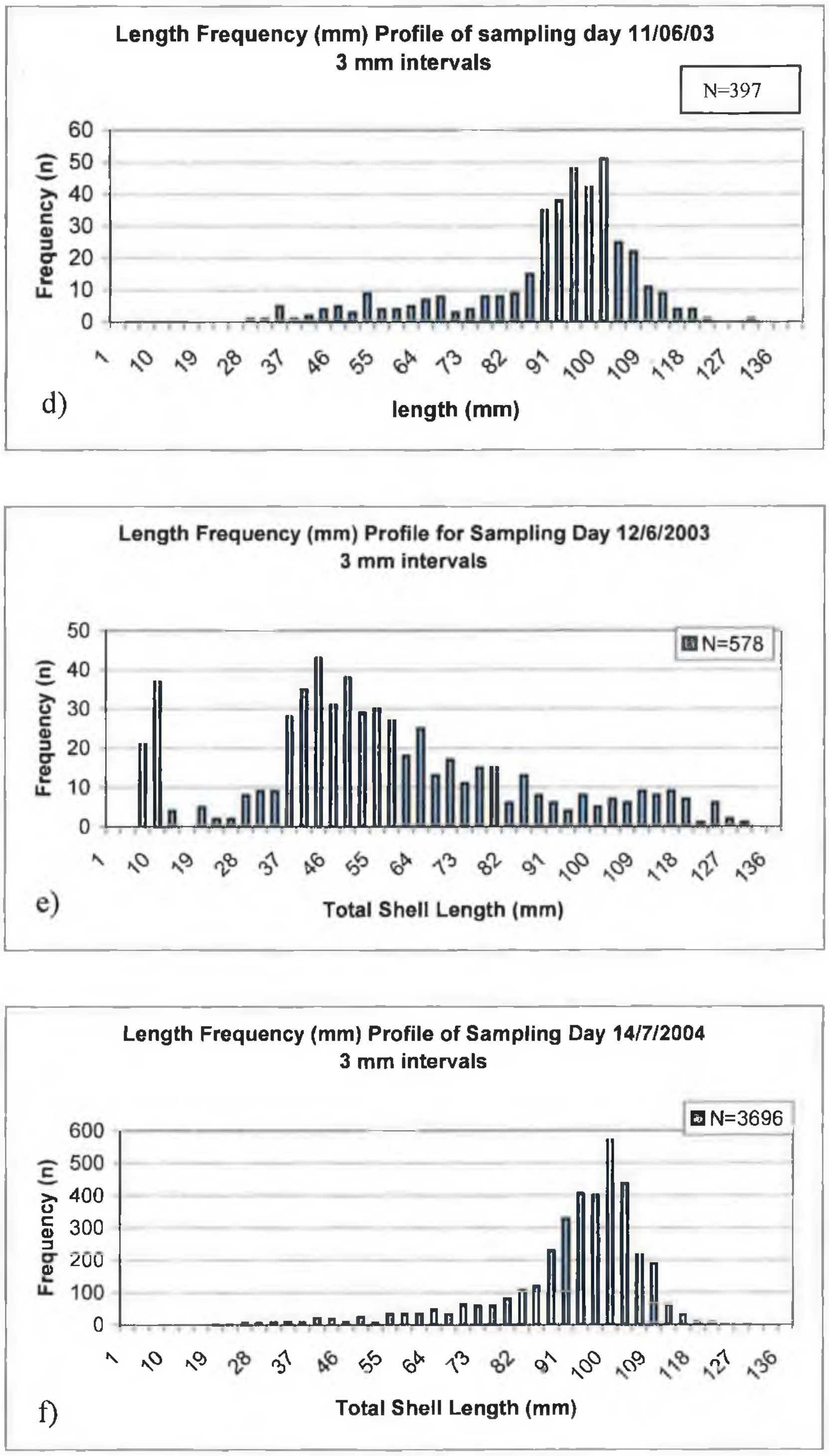
Length frequency histograms of whelks collected during fishing surveys on May 20, June 4, 5,11 and12, and July 14, 2003, were plotted (see Figs 2.1 a-f). A total of 17,065 whelks were used to construct length frequency histograms. The smallest and largest whelks collected during length frequency analysis of fishing survey data had a total shell length of 15.0 mm and 130.0 mm respectively, and both were collected on June 4, 2003. The length frequency histograms showed at least 3 peaks, generally at around 25 – 35, 55 – 65 and 95 – 105 mm total shell length. The data comprised 84.05% of animals larger than or equal to 50 mm total shell length (fully juvenile; Kideys, 1996).


Length Frequency (mm) Profile of sampling day 20/5/2003
3 mm intervals
N=9120
Frequency (n)
1000
800
600
400
200
0
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
Total Shell Length (mm)
a)


Length Frequency (mm) Profile of sampling day 04/06/03
3 mm intervals
N=1636
Frequency (n)
120
100
80
60
40
20
0
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
length (mm)
b)


Length Frequency(mm) Profile of sampling day 05/06/2003
3 mm intervals
N=1718
Frequency (n)
140
120
100
80
60
40
20
0
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
Total Shell Length (mm)
c)

d)


Length Frequency (mm) Profile of sampling day 11/06/03
3 mm intervals

Length Frequency (mm) Profile for Sampling Day 12/6/2003
3 mm intervals

Length Frequency (mm) Profile of Sampling Day 14/7/2004
3 mm intervals

Fig 2.1 a-f: Length Frequency profiles for landed catch at sea on fishing vessels in the region of the North West Irish whelk fishery. Dates are specified.

Mean lengths of modes were derived using the Bhattacharya method (Modal Progression Analysis available in FiSAT II) and used as initial input data for NORMSEP. A total of nine models of several iterations were conducted to obtain a good fit. For each of three survey days on June 4, 5 and 11, 2003, histogram data were modeled at 3 mm intervals, beginning at 0 – 3 mm bins, 1 – 4 mm bins and 2 – 5 mm bins. The best fit was determined by eye for data collected on June 5, 2003, where 3 mm groups commenced at 1 mm – 4 mm length (see Fig 2.1 c and Fig 2.2). A total of 10 age components were found from 1613 individuals. NORMSEP calculates a mean, standard deviation, population size, and separation index (see Table 2.1). When the means were linearised to lie along a von Bertalanffy growth curve (Fig 2.3 a-b), the asymptotic length, *L*∞, value of 151.64 mm and a Brody growth coefficient, *K*, value of 0.04 were found for the June 5, 2003 sample.

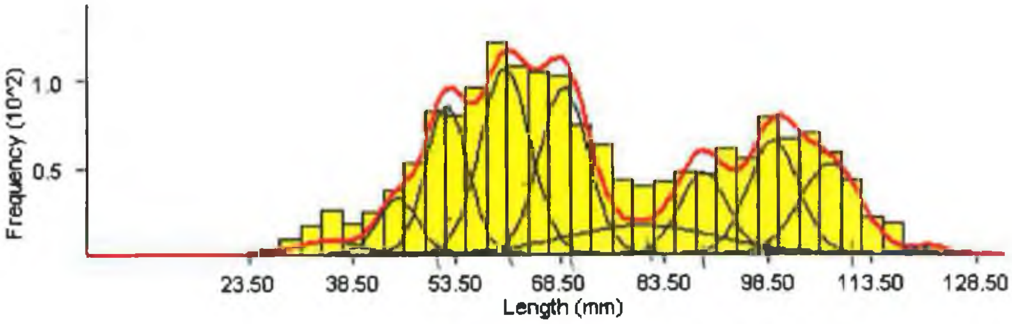


Fig 2.2: NORMSEP Length Frequency Analysis results, indicating modal progression of catch landed on June 5, 2003.

Group	*Mean mm*	*SD*	*Population n*	*SI*
1	35.12	4.41	29	0
2	45.08	2.93	79	2.71
3	52.16	3	215	2.39
4	60.62	3.64	326	2.55
5	69.11	3.53	283	2.37
6	80.07	10.7	145	1.54
7	89.18	3.42	135	1.29
8	99.26	3.64	200	2.86
9	107.51	4.42	192	2.05
10	121.65	2.28	9	4.22

Table 2.1: Group Means, Standard Deviation, Population Size and Separation Index of NORMSEP results.

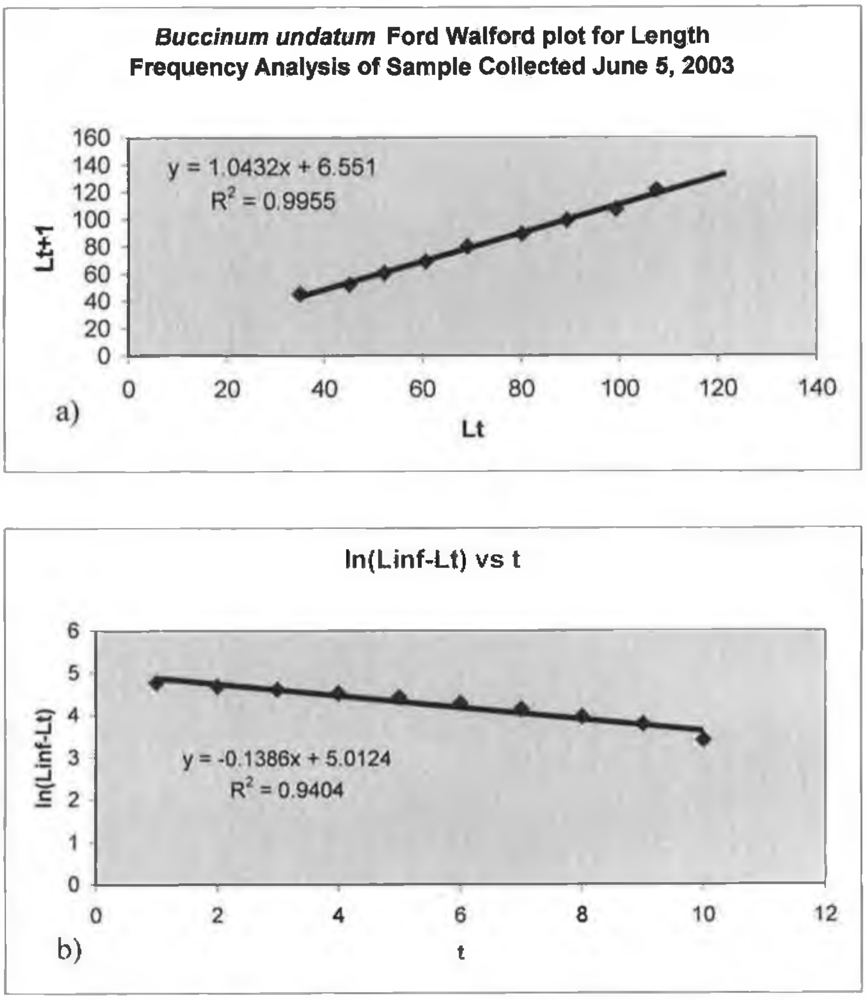
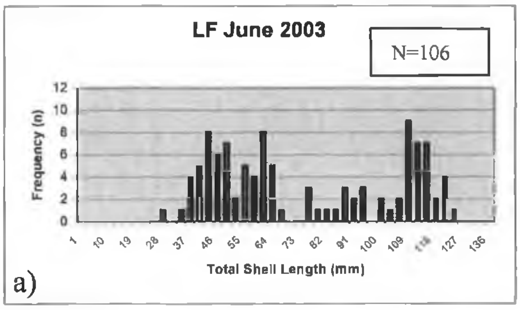


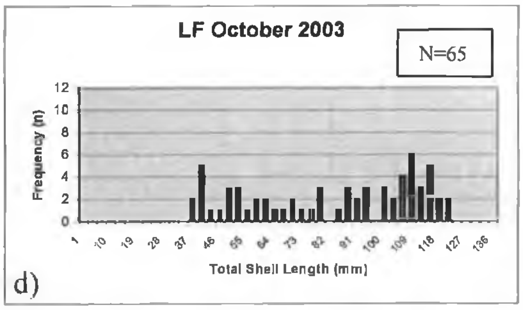
Fig 2.3 a-b: Ford-Walford plots of Lt and Lt+1, and ln(L∞-Lt) and t for the NORMSEP Length Frequency Analysis.

Monthly Sample Collection Data

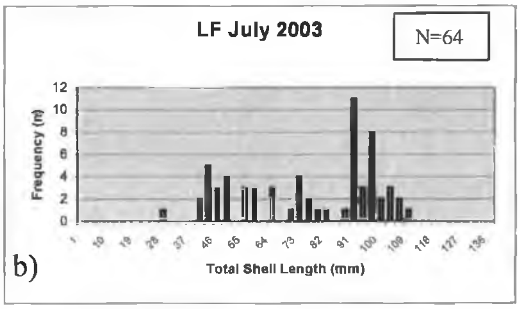
Length frequency (LF) histograms of whelks collected monthly for between June 2003 and July 2004 were plotted (see Figs 2.4 a-j). The timing of recruitment is not clear from monthly length frequency histograms, and whelks measuring <50 mm total shell length (fully juveniles, Kideys, 1996) were represented in June, July and August 2003, and April and May 2004 (see Fig 2.5). This may suggest that recruitment occurs in the spring to summer months of April to August. The highest representation of smaller size groups was in June 2003.



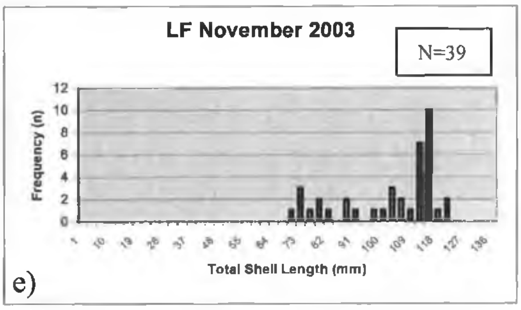
a)



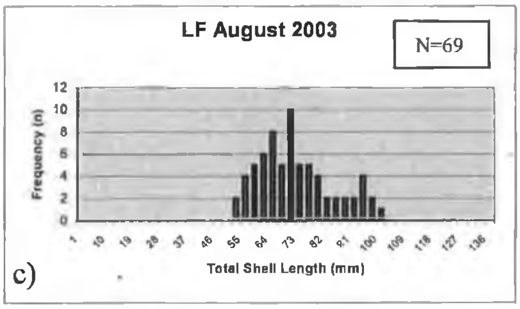
d)



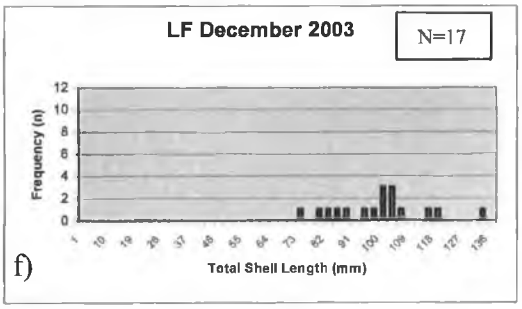
b)



e)



c)



f)

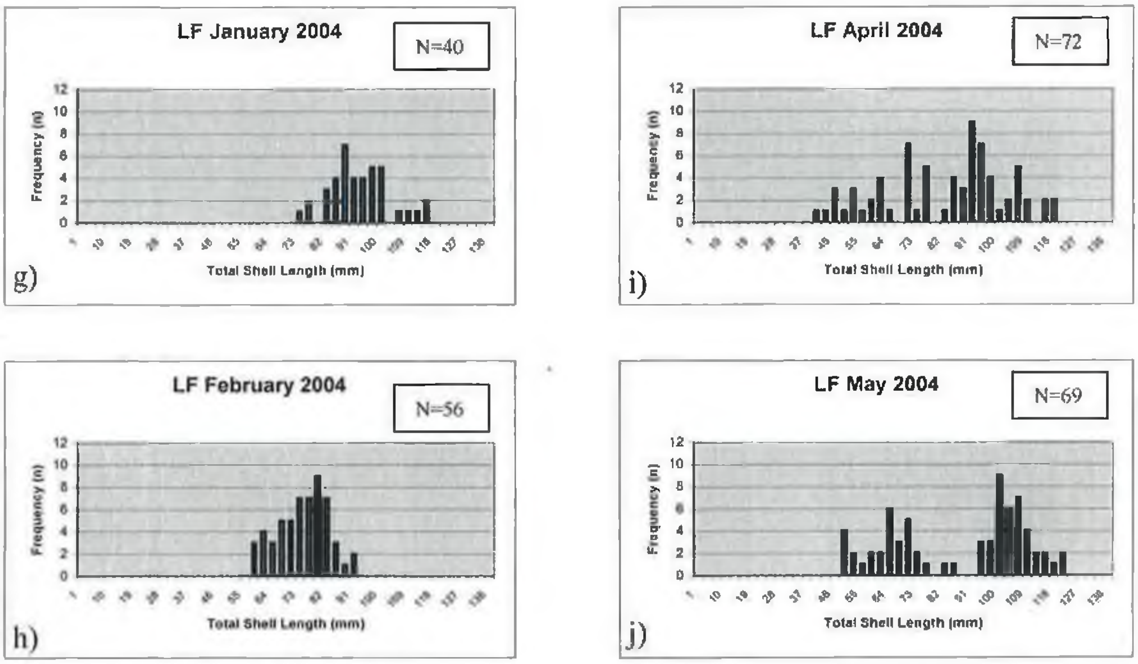


Fig 2.4 a-j: Length Frequency histograms of samples collected each month between June 2003 and May 2004.

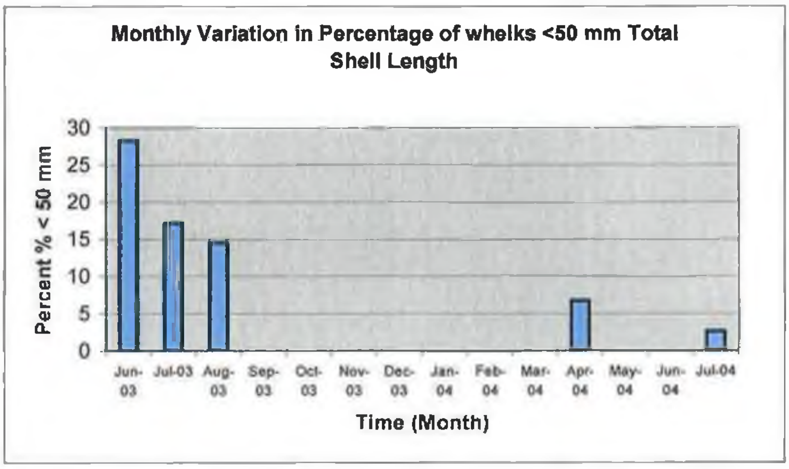


Fig 2.5: Variation in the proportion (%) of Common whelks < 50 mm Total Shell Length observed in samples collected each month between June 2003 and May 2004.

Operculum Analysis

An increasing number of operculum striae were observed with increasing shell length in Common whelks from the region of the North West Irish whelk fishery (see Fig 2.6). However, not all opercula striae were discernible, and of the 602 individuals collected for observation, 552 (91.7%) were used in further analysis. There were also large overlaps in length at number of striae. The maximum number of opercula striae observed was 19, and the minimum 3. A frequency distribution of the proportion of individuals at number of opercula was prepared (see Fig 2.7) with Chi-Square Goodness of Fit to normal distribution value P=0.001 (data are normally distributed; Anderson-Darling test P>0.05).

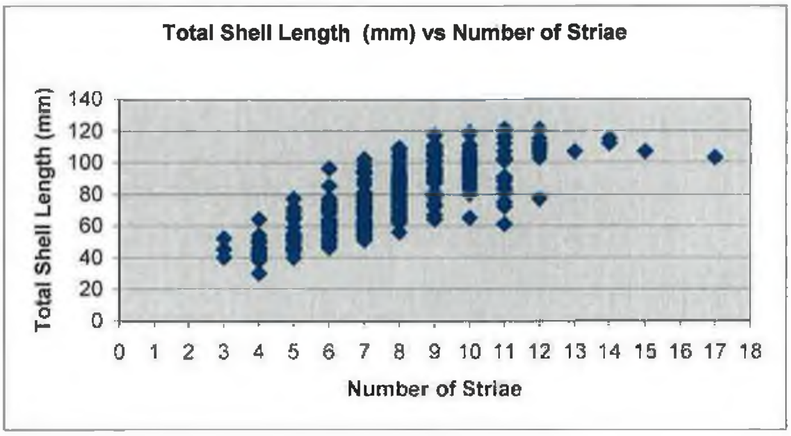


Fig 2.6: Scatter plot of Number of Opercula Striae counted at Total Shell Length (mm).

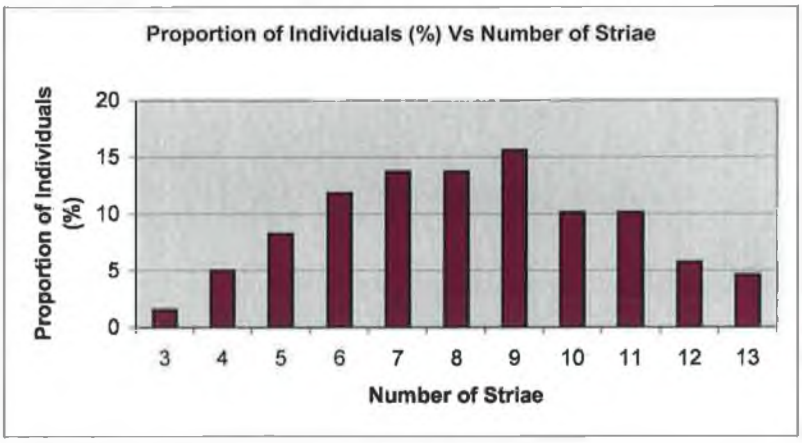


Fig 2.7: Proportion of Individual Common whelks (%) with Observed Number of Opercula Striae.

Male and Female number of opercula striae at total shell length were compared (see Figs 2.8 and 2.9 respectively). No significant difference between male and female mean number of striae at size was found (Two-Way ANOVA, P=0.646; data were randomised and balanced, and were found to be homoscedastic and residuals normal). Data collected from male and female whelk are therefore treated equally (not separated) in further analysis of opercula striae.

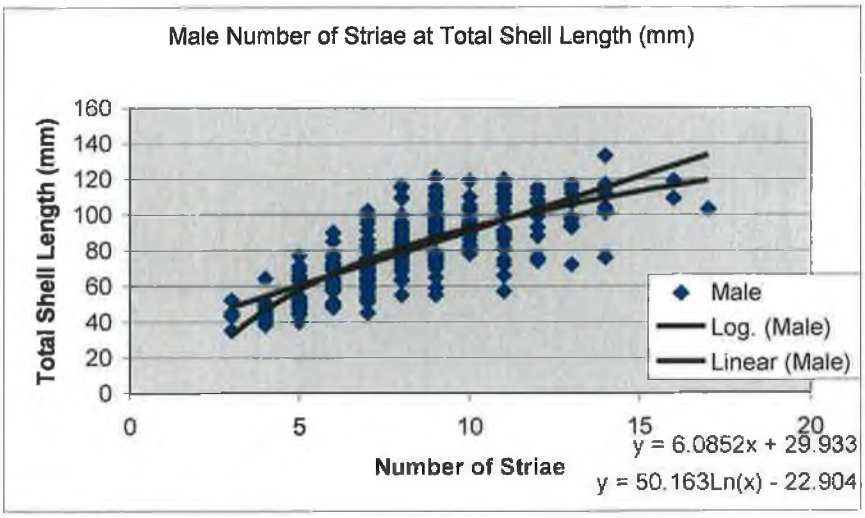


Fig 2.8: Scatter plot of Observed Number of Opercula Striae at Total Shell Length for Male Common whelks.

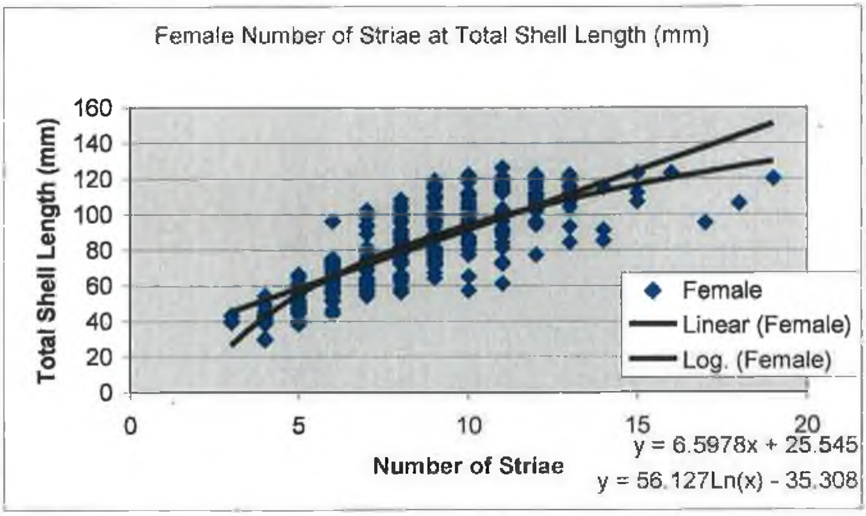
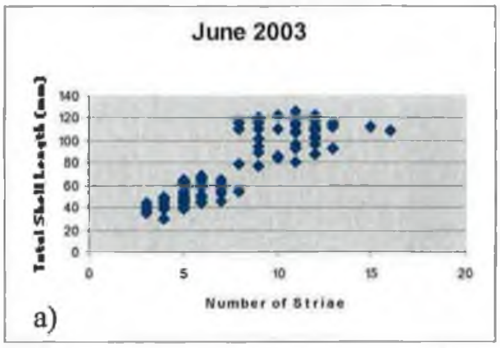
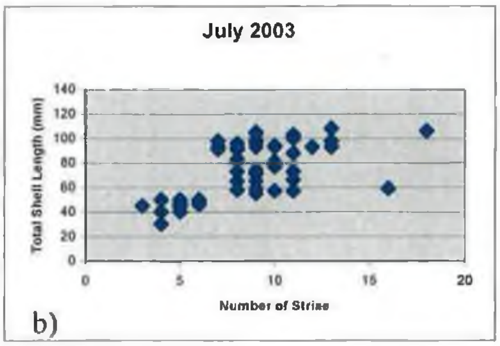
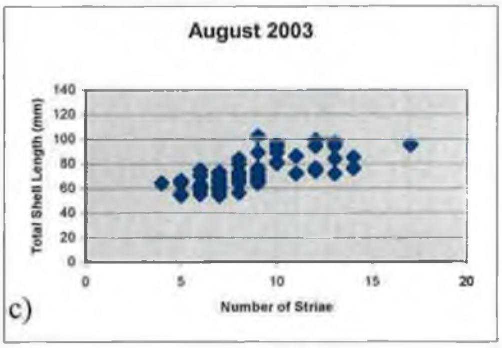


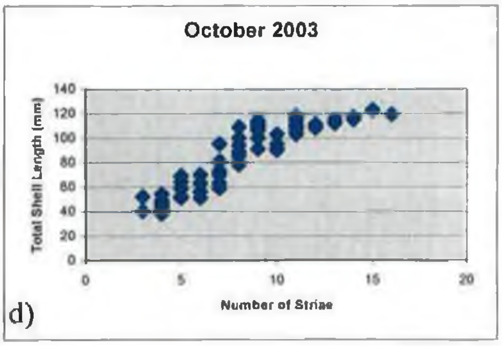
Fig 2.9: Scatter plot of Observed Number of Opercula Striae at Total Shell Length for Female Common whelks.

Frequency distributions of number of striae per month, and plots of number of striae at total shell length per month, were prepared (see Figs 2.10 a-j and 2.11 a-j). The mean and median number of striae per month was determined (see Fig 2.12 and Tables 2.2 and 2.3), and a one-way ANOVA performed to test the null hypothesis that there is no variation in mean number of striae per month in Common whelk (P=0.000; data were log transformed for homoscedasticity and normality). A Tukey's post-hoc test showed significant difference to the 99% confidence interval between June and November 2003, and June 2003 and January 2004. These results demonstrate that the number of striae per month is greater between November 2003 and January 2004. These results support the findings of the present study that recruitment occurs during the spring to summer period.









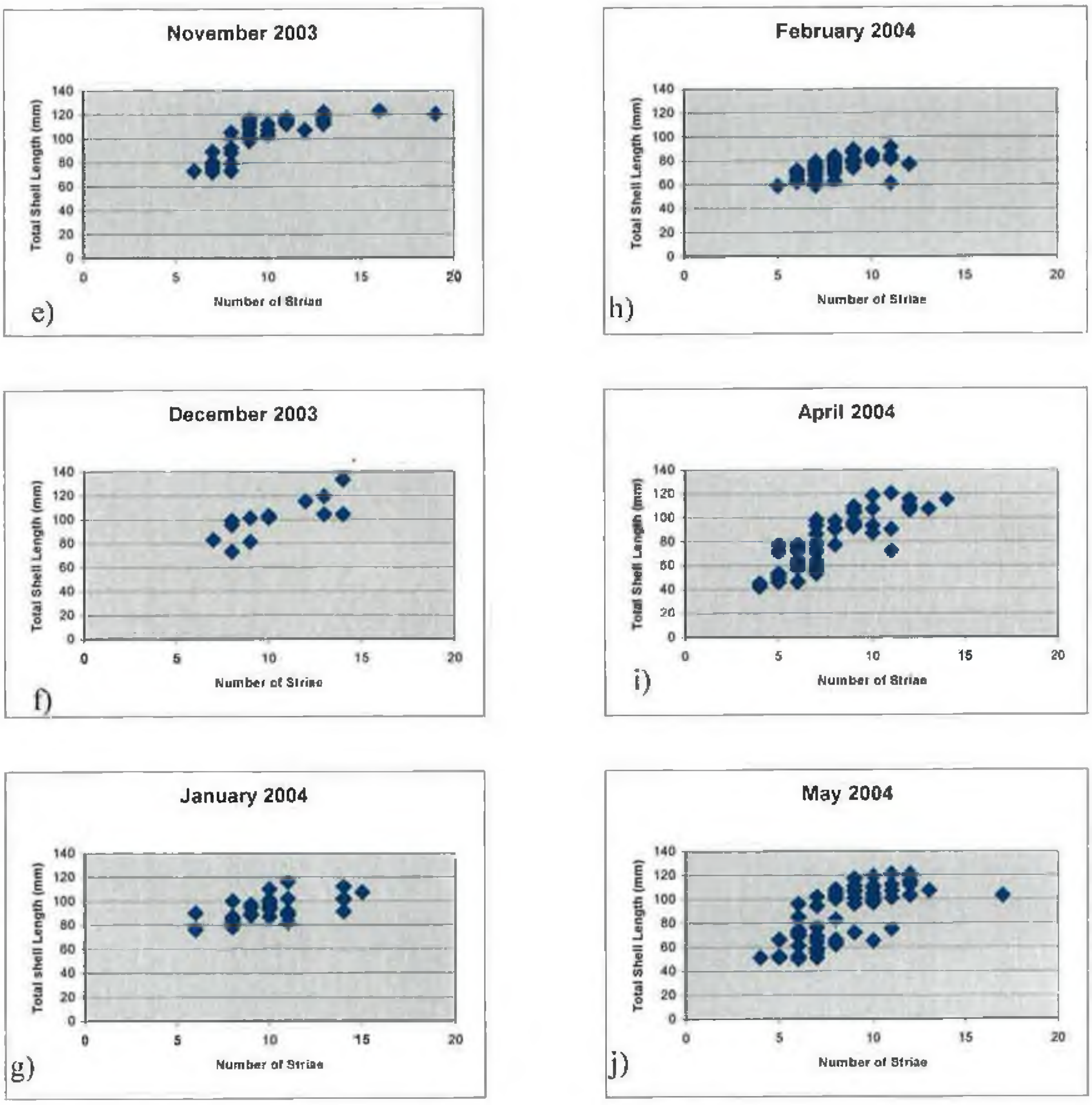
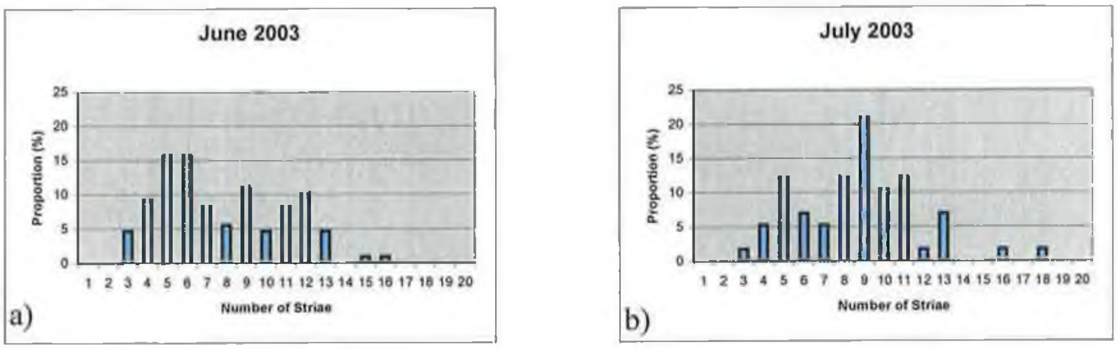


Fig 2.10 a-j: Scatter plots of Observed Number of Opercula Striae at Total Shell Length for Common whelks collected at monthly intervals from June 2003 to May 2004.



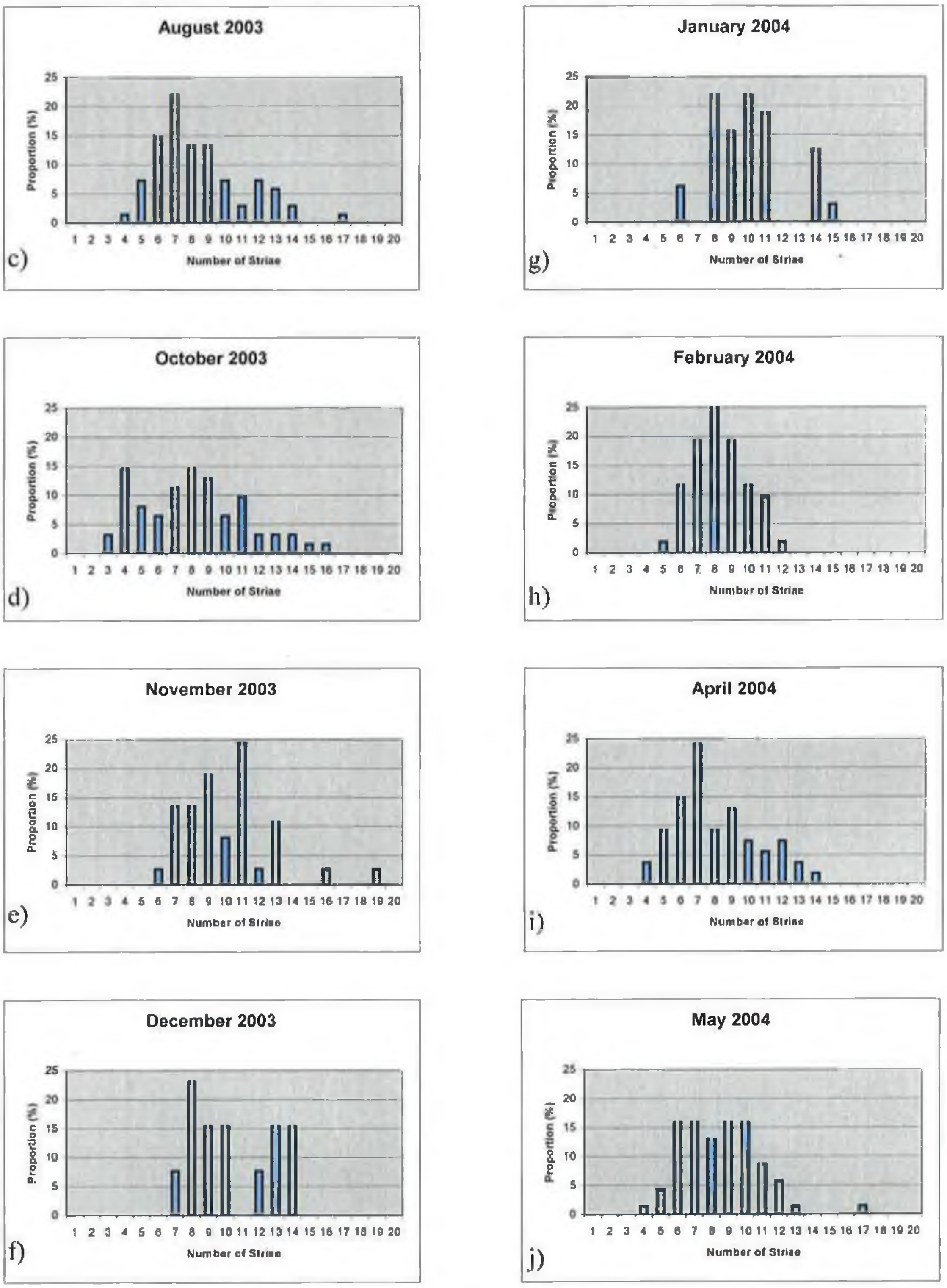


Fig 2.11 a-j: Histograms of the Frequency of Number of Opercula Striae observed at monthly intervals from June 2003 to May 2004.

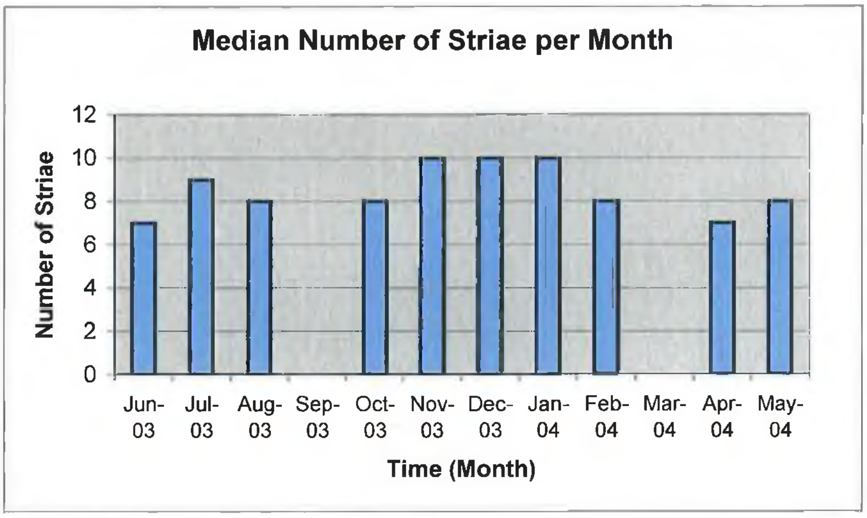


Fig 2.12: The Median Number of Opercula Striae observed at monthly intervals from June 2003 to May 2004.

Group	Mean	Std Dev.	Std Err	N
June 2003	7.759	3.111	0.299	108
July 2003	8.667	3.014	0.399	57
August 2003	8.471	2.679	0.325	68
October 2003	8.048	3.154	0.401	62
November 2003	10.054	2.656	0.437	37
December 2003	10.385	2.501	0.694	13
January 2004	10.000	2.272	0.402	32
February 2004	8.308	1.615	0.224	52
April 2004	8.074	2.464	0.335	54
May 2004	8.507	2.298	0.277	69

Table 2.2: Mean, Standard Deviation, Standard Error and Population of Number of Opercula Striae per month from June 2003 to May 2004.

		Normal Distribution Results, DF=17	
Time	*Median*	*Chi-square Value*	*Chi-square P*
Jun-03	7	33.473	0.010
Jul-03	9	29.943	0.027
Aug-03	8	29.581	0.030
Oct-03	8	16.346	0.499
Nov-03	10	62.212	0.000
Dec-03	10	8.635	0.951
Jan-04	10	20.135	0.267
Feb-04	8	2.812	1.000
Apr-04	7	11.052	0.854
May-04	8	74.743	0.000

Table 2.3: Goodness-of-Fit to Normal Distribution tests for Frequency of the Number of Opercula Striae Observed per Month from June 2003 to May 2004. Median and Chi-Square Values, and Probability are shown.

Von Bertalanffy growth parameters were calculated using 106 individuals with discernible striae on the operculum, from the June 5, 2003 sample. Following linearisation, an asymptotic length, $L\infty$, value of 137.73 mm and a Brody growth coefficient, K, value of 0.12 was found, and t_0 estimated to be –2.18 mm (see Figs 2.13 a-b). However, Kideys (1996) reports that in the Irish Sea, hatching occurs in April-May. With this correction, t_0=-0.36 mm. The mean length values calculated for each Class correlate well with respective data from the Length Frequency Analysis (two-tailed t-test, P>0.05; see Table 2.4). Furthermore, 99% Confidence Interval results for mean length at class in the NORMSEP Length Frequency Analysis, and Operculum Analysis, overlap in 70% of cases, with the exception of Classes 5, 7 and 10 (see Fig 2.14). If it is assumed that 3 opercula striae represent 3 years of age, it can therefore be assumed that the first age at landing is during the 4th year, at 3 years of age. An adjustment of the Von Bertalanffy parameters estimated in the Length Frequency Analysis for age and time of hatching produces t_0=-0.32 mm, which is comparable with the results of the Operculum Analysis, and the two tests were conducted independently.

		CLASS										**von Bertalanffy Parameters**		
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	***L∞***	***K***	***t₀***
NORMSEP	**Lt**	35.12	45.08	52.16	60.62	69.11	80.07	89.18	99.26	107.51	121.65	151.64	0.04	0.07
	Lt+1	45.08	52.16	60.62	69.11	80.07	89.18	99.26	107.51	121.65				
	ln(Linf-Lt)	4.76	4.67	4.60	4.51	4.41	4.27	4.13	3.96	3.79	3.40			
	SD	4.41	2.93	3.00	3.64	3.53	10.70	3.42	3.64	4.42	2.28			
	N	29.00	79.00	215.00	326.00	283.00	145.00	135.00	200.00	192.00	9.00			
	CI	1.64	0.66	0.41	0.40	0.42	1.78	0.59	0.51	0.64	1.52			
Operculum Analysis	**Number of Striae**	3.00	4.00	5.00	6.00	7.00	8.00	9.00	10.00	11.00	12.00			
	Lt	40.00	42.70	49.50	57.50	57.40	94.80	101.20	102.40	105.90	107.60	137.73	0.12	-2.18
	Lt+1	42.70	49.50	57.50	57.40	94.80	101.20	102.40	105.90	107.60	110.40			
	ln(Linf-Lt)	4.58	4.55	4.89	4.38	4.39	3.76	3.60	3.56	3.46	3.41			
	SD	3.32	6.41	8.76	6.97	7.09	27.18	15.51	16.64	13.87	9.78			
	N	5.00	10.00	17.00	16.00	7.00	5.00	12.00	5.00	9.00	11.00			
	CI	2.97	4.06	4.25	3.48	5.36	24.31	8.96	14.88	9.25	5.90			

Table 2.4: Von Bertalanffy Growth Equation Parameters, L∞, K and t_0 estimated from NORMSEP Length Frequency Analysis and Operculum Analysis for landed catch sampled on June 5, 2003. Class Mean Length, L_t, Standard Deviation, Population and Confidence Intervals are shown.

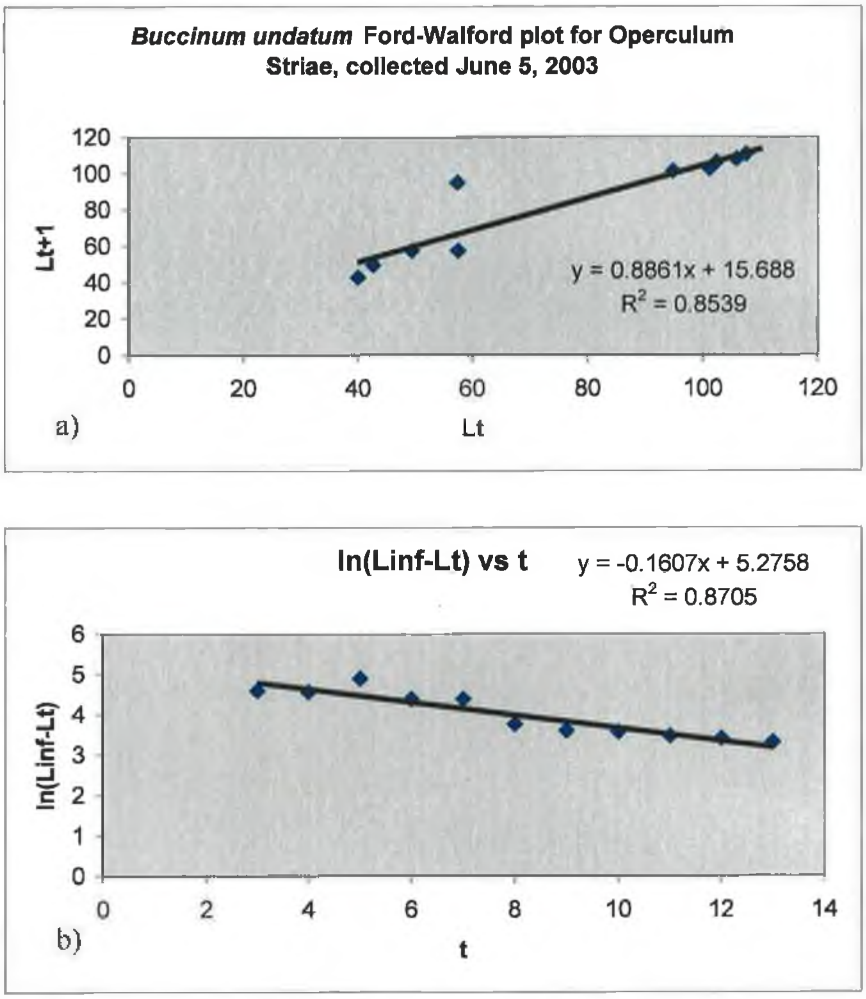


Fig 2.13 a-b: Ford-Walford plots of Lt and Lt+1, and ln(L∞-Lt) and t for the Operculum Analysis.

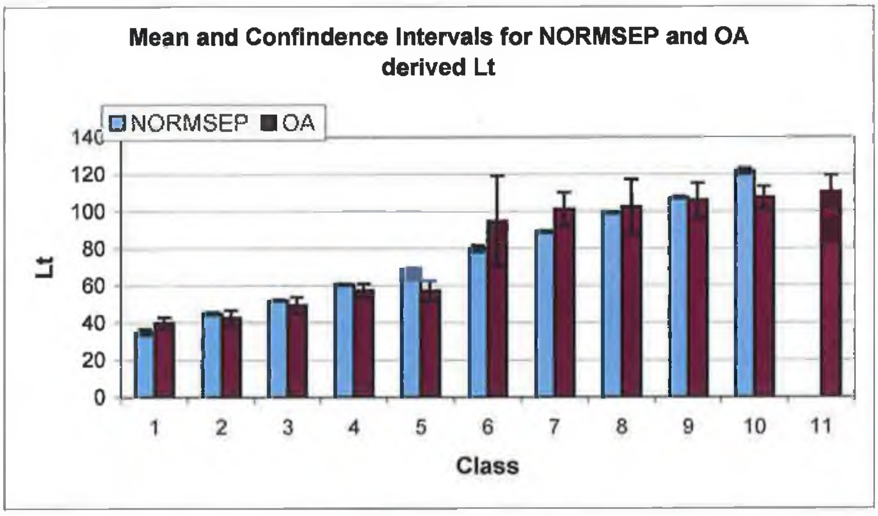


Fig 2.14: Overlapping 99% Confidence Intervals and Mean Length of Class Sizes as Estimated from NORMSEP Length Frequency Analysis and Operculum Analysis.

Age at Length

Von Bertalanffy growth values were substituted into the equation:

$t(L)=t_0-(1/K)ln(1-(L/L_\infty))$ (Sparre *et al.*, 1989; Kideys, 1996)

and the mean age at length determined according to the results of the Length Frequency Analysis and the Operculum Analysis (see Table 2.5). Age at length results for Length Frequency Analysis show a declining rate of increase in size with age, while Operculum Analysis results demonstrate accelerated rate of increase in length at age. Common whelks are described as having an indeterminate growth pattern (Kideys *et al.,* 1993). Therefore, to determine the age of the population of Common whelk in the NW Irish whelk fisheries, parameters of the Von Bertalanffy growth equation, derived from Length Frequency Analysis, are used. However, it is noteworthy that the number of opercula striae is comparable with age at length, in younger ages, up to a size of approximately 110 mm total shell length. When whelks reach a size greater than 110 mm total shell length, the relationship between age and length diverges rapidly.

The minimum size whelk captured during fishing and sampling operations was 15 mm total shell length, where $t(L)$ = 1.9 years. The maximum size was 130 mm total shell length, where $t(L)$ = 14.3 years. At 50 mm total shell length, $t(L)$ = 6.4 years, and 84% of the landed population are above this age. The age at onset of sexual maturity in males is calculated to be 8.9 – 11.1 years, and in females 8.8 – 11.1 years.

Total Shell Length (mm)	0	10	20	30	40	50	60	70	80	90	100	110	120	130
NORMSEP Age	-0.32	1.19	2.61	3.95	5.21	6.42	7.56	8.65	9.70	10.69	11.65	12.57	13.46	14.32
OA Age	-0.36	0.26	0.93	1.67	2.47	3.37	4.37	5.51	6.83	8.40	10.34	12.89	16.59	23.45

t(L)=t0-(1/K)ln(1-(L/Linf)) (Sparre *et al.*, 1989; Kideys, 1996)

Table 2.5: Age at Length Key from the equation, t(L)=t0-(1/K)ln(1-(L/Linf)), using Von Bertalanffy parameters derived from NORMSEP Length Frequency Analysis and Operculum Analysis.

DISCUSSION

To implement Length Frequency Analysis (LFA), the observer needs to ensure that cohorts are distinct and differ in average size, and that growth is fast in relation to the accuracy of size measurements. In the current investigation, growth should be greater than 1 mm per year to satisfy the assumptions of the analysis. A summary of Von Bertalanffy growth parameters (length at time) derived from the NORMSEP model and operculum analysis suggest that this assumption has been met in the present study (see Table 2.4). A number of methods exist for separating age-classes and predicting growth rates from a size frequency distribution, as described by Parrack and Cummings and references therein (2003):

1) The Petersen (1891) method, whereby the modes of a histogram are interpreted as single classes. This is accomplished by separating length frequency modes by eye, and is widely used.
2) Further graphical techniques that fit procedures to determine modes. These assume that the lengths of individuals at the same age are normally distributed.
3) Mathematical procedures have been adopted in recent years. These allow confidence limits to be applied to account for the variation in individual lengths with at each age.

The methods of determining demographic parameters in a LFA generally assume a discrete period of recruitment (Grant *et al*, 1987 in Kideys, 1996). However, for *B. undatum,* recruitment may fluctuate with time. Kideys (1996) found that the timing and recruitment of *B. undatum* was not clear and appeared to be a year round event with an escalation in the frequency of recruits from March 1989 to September 1989. Similar results were found in the current investigation, with recruitment increasing in the spring to summer months, and a discrete period of reproduction was found for the sampling period (see Chapter 4). In their paper reviewing transformation of length samples to age frequencies without age samples, Parrack and Cummings (2003) conclude that a priori knowledge of recruitment age is necessary because the procedure estimates the presence of ages that are younger than those present in a sample. Furthermore, Parrack and Cummings suggest that no more than the youngest half of the age span can be estimated reliably using LFA as variation in size does not remain constant with variation in age. Modal analysis methods can be misused if applied to size-frequency samples of insufficient sample size (MacDonald and Pitcher, 1979), to species with slow growth compared with size, or to species with continuous, irregular or poly-annual recruitment. The suggested minimum number of 50 individuals for each mode representing age group was met using the June 5, 2003 sample, with the exception of the smallest and largest modal groups (MacDonald and Pitcher, 1979). Sparre *et al.,* (1989) recommend 50 – 100 length groups where possible. The 3 mm intervals selected for the current study gave 33 length groups.

Grant *et al* (1987) suggest that if the Petersen method of LFA does not work, accurate estimates of demographic parameters are unlikely to be obtainable using more rigorous methods. The results of LFA methods are uncertain because sample size may be insufficient, and/ or there is a discrepancy between the basic assumptions of the applied model (e.g., Normal Distributions) and reality (Grant et al., 1987). Furthermore, there is difficulty in separating modes by visual inspection (Kideys, 1996). In his study of age and growth determination in *B. undatum*, Kideys (1996) compared the Petersen; graphical and mathematical model methods of LFA. Sixteen monthly size frequency distribution diagrams were constructed, and only one month showed clear modes of possible age classes. This was used to perform LFA. Kideys (1996) used and compared two computer length frequency analysis programs (mathematical models), MIX and ELEFAN. Similar modal lengths were found with all methods of analysis and all methods revealed a good fit of the von Bertalanffy growth curve (1938) for the observed population of *B. undatum*. However, this was only possible due to initial data derived by the Petersen method, and this is perhaps the principal reason for the similarity in results from different methods. Kideys is most satisfied with the results of the MIX analysis as this technique gives confidence intervals for the estimated values.

In the current study, the Bhattacharya (1967) method was employed to separate modes to use in the NORMSEP model. Methods such as Petersen and Bhattacharya are difficult and subjective because the user decides which possible solutions for the same data set to accept (Sparre *et al.,* 1989). Consequently, they have been subject to severe criticism (Grant *et al.,* 1987).

The current study found an increase in the number of striae with length, although there was variation in the size of whelks showing the same number of striae. Kideys (1996) also observed a trend of increasing striae number with increasing length, which appears logical with respect to age. However, significant variation between shell length and age estimated using operculum analysis (OA) was also cited in Kideys (1996) results. For example, Kideys found that individuals with 2 striae varied between 26.4 to 86.5 mm in length. Where whelk have been held live in the laboratory over a 12 month period, a small proportion clearly showed an increase by one stria, while one whelk showed no increase at all and others showed a decreased number of striae (Kideys, 1996). In the current study, opercula were physically removed from the foot of the Common whelk, and the underside examined, where striae are more clearly visible. To record opercula change in the 12-month period, Kideys could not have performed this procedure.

Ageing from the operculum requires counting striae with the naked eye, however, the striae are not always clear. In age determination studies, the operculum is removed from the snail and stored to dry, and is then interpreted, according to Santarelli and Gros (1985). The age is expressed as the number of clear striae counted. Kideys (1996) suggests that operculum could be a good indicator of age if a greater proportion of whelk showed more clear striae. Yet with regard to the results of laboratory rearing, Kideys states that it is ‘difficult to accept the number of striae are proportional to age’. Valentinsson *et a.l* (1999) also report reduced OA samples due to striae that were impossible to read. Santarelli and Gros do not indicate the proportions of clear striae in their research area. Fahey *et al* (1995, 2000) are confident with the results of OA, stating that in the southwest Irish Sea research area, only one animal with one stria was encountered and few 2 striae animals. The maximum number of striae and therefore age in this area was 15. Kideys found the maximum number of striae off Douglas, Isle of Man, to be 11. Clarity in striae appears to be an important factor in the accurate determination of growth parameters from OA and may vary with location. Fahy *et al* (2000) and Kideys (1996) both found large variation in size for estimated age of whelk, using the operculum ageing technique.

To fit growth models, size at age data derived from growth marks should cover the whole range of sizes present in the population. In the current study, individuals were not represented with 0, 1 and 2 opercula striae. This is probably because of pot selection against juveniles, and therefore these individuals are not represented in fisheries landing stock. Kideys (1996) also suggests that poor representation of juveniles may be due to diet selection differences between smaller and larger whelks, with bait in pots not meeting the nutritional or other demands of juvenile whelks. Additionally, smaller whelks cannot respond as quickly to bait due to their smaller foot size, and thus pots may select for larger individuals (Kideys, 1996). Low representation of juveniles in the catch and sample may also explain the lack of an obvious recruitment period, despite a distinct reproductive cycle (Chapter 4). It is assumed that large individuals with greater numbers of opercula striae are adequately represented. For future analysis, it is recommended that small, young individuals are represented, and could be collected by rearing from egg masses, or hand collected by SCUBA. There are no studies on the growth of juveniles in *B. undatum*.

To successfully apply size increment data obtained in MRE experiments to growth models, the observer must 1) eliminate bias due to tagging; 2) ensure a consistent rate of recapture; and 3) the observed data should cover the whole range of sizes in the population. In the current study, the second and third requirements were violated.

Logistics growth functions reported in a variety of aging analyses of *B. undatum* are summarised in Table 2.6. K and L_∞ values found by Kideys (1996) are higher than those in previous studies undertaken for *B. undatum* in northeastern England and northern France. Fahy *et al.* (2000) compared average L_∞ values in four Common whelk fishery sectors in the southwest Irish Sea to overcome confounding in growth parameters due to sub-populations of the species. Fahy's study (2000) found significant differences in the mean length at age for the four sectors. *K* and $L_{\propto}$ values determined in the present study, for both methods of analysis, are higher than in other studies, although the *K* value determined by OA compares favourably with Santarelli and Gros (1985). It is suggested that growth parameters vary markedly between relatively close populations, and that for fisheries stock assessment and management purposes, growth parameters of target stock populations should be determined by stock location, and appropriate conservation measures developed.

Author	**Location**	**Method**	**Estimated Asymptotic Length, $L\infty$**	**Brody Growth Coefficient, *K***
Kideys, 1993	Isle of Man, Irish Sea	Length Frequency Analysis, MIX	123.8 mm	0.20
Hancock, 1963	Northeastern England	Mark Re-Capture	68 mm	0.8
Santarelli and Gros, 1985	Northern France	Operculum Analysis	112.5 mm	0.13
Fahy *et al.*, 2000	Southwest Irish Sea	Operculum Analysis	106 mm	
Present Study	East Inishowen Peninsula, Northwest Ireland	Length Frequency Anlaysis, NORMSEP	151.64 mm	0.04
Present Study	East Inishowen Peninsula, Northwest Ireland	Operculum Analysis	137.73 mm	0.12

Table 2.6 Reported logistical growth function estimates for *Buccinum undatum* with location and method.

Independent estimates of size at age using LFA and OA results were comparable to a maximum size of approximately 110 mm total shell length, at which point OA derived estimates of *t(L)* depart from an indeterminate to infinite growth pattern. These results suggest that for the purpose of stock assessment and fisheries management, either LFA or OA could be employed to assess the age of *B. undatum* target stock.

The von Bertalanffy parameters determined in the current study suggest that Common whelk in the region of the North West Irish whelk fishery grow at slower rates, and achieve larger sizes than in other studied populations. Fahy *et al.* (1995 and 2000) describe high densities of animals and the Lee phenomenon (stunting due to overcrowding) in sectors of the Irish Sea whelk fishery, attributing smaller lower $L_{\propto}$ values to these factors.

Chapter 3

Sexual Maturity in the Common Whelk, Buccinum undatum in the region of the North West Irish Whelk Fishery

INTRODUCTION

A number of studies have sought to establish the size and age at which the Common whelk, *B. undatum* reaches sexual maturity (Hancock *et al*., 1962; Martel *et al*., 1986b; Santarelli *et al*., 1986; Gendron, 1992; Kideys *et al*., 1993; Gunnarrson and Einarsson, 1995; Bell and Walker, 1998; Valentinsson *et al*., 1999). The size at onset of sexual maturity is an important parameter in fisheries stock assessment. Combined with catch data, biologists can use known size and age at maturity to determine the proportion of a population contributing to reproduction, and thus make forward predictions regarding the sustainability of commercially exploited populations. For *B. undatum*, the size at onset of sexual maturity has been used to establish minimum catchable size limits in Common whelk fisheries across the Northern hemisphere (Gendron, 1992, Valentinsson *et al*., 1999). However, the size at onset of sexual maturity varies with location and between sexes in this species, and thus published results are not applicable in fisheries stock assessment in locations that have not previously been examined. Furthermore, the phenomenon of imposex, affecting sexual maturation and reproduction in female whelks (Blaber, 1970; ten Hallers-Tjabbes *et al.,* 1994), and parasite infection, may impact upon the proportion of sexually mature stock contributing to future generations.

Gendron (1992) studied eight sites within the Gulf of St Lawrence, eastern Canada, and found that the size of onset at sexual maturity varied significantly between all sites for male and female whelks. Valentinsson *et al.* (1999) compared the size at onset of sexual maturity between two sites on the Swedish west coast and also found significant variation with location. However, this latter study found no variation in the size at the onset of sexual maturity between the two sexes. Bell and Walker (1998) found different sizes in the onset of sexual maturity in male and female Common whelk between the east and south coast of England. Fahy *et al.* (2000) determined the size of onset of sexual maturity for male whelk only in the southwest Irish Sea Common whelk fishery, and found that in the Dublin sector maturation occurred at approximately 83 mm shell length, while in other parts of the fishery lengths at maturity onset ranged from 63 to 68 mm. The biological characteristics of *B. undatum*, including sedentary lifestyle and entirely benthic reproductive cycle are likely to produce local populations with reduced gene flow, which could result in local differences in traits such as the size at onset of sexual maturity. Furthermore, the existing literature indicates a late age for the onset of sexual maturity in this species (Valentinsson *et al.*, 1999). Coupled with other biological parameters, this may make stocks vulnerable to local extinction.

Santarelli-Chaurand (1985) classified as mature, males having a penis greater than or equal to half the total length of the shell. This was based on observations made by Køie (1969) that penis length increased when sexual maturity was attained. Gendron (1992) further examined the relationship between penis size and sexual maturity in male Common whelks to confirm the validity of the criteria. Gendron (1992) presented the frequency distribution of the seminal vesicle index (ratio seminal vesicle mass to somatic tissue mass) for mature and immature males (according to relative penis size), confirming the association between a large penis and gonad development.

The present investigation, detailed in the following chapter, aims to:

- Validate the use of the penis-shell length index as a method for determining male maturity in *B. undatum* for the region of the present investigation;
- Determine the size at onset of sexual maturity for male and female whelk in the region of the North West Irish whelk fishery;
- Determine the age at onset of sexual maturity in male and female Common whelks from the region of the North West Irish whelk fishery;
- Assess the variability in size at onset of sexual maturity on temporal and spatial scales; and
- Compare the results from the present investigation with previous results from Irish waters and international waters.

MATERIALS AND METHODS

Sample Collection

Sampling of *B. undatum* took place in the North West Irish whelk fishery, during fishing operations for Common whelk and Brown crab on a variety of vessels, at monthly intervals, from June 2003 through to May 2004. While every effort was made to ensure consistency in fishing method, elapsed time between collection and sample size, sample collection occurred opportunistically. For each sample, up to ten individuals were randomly collected from 5 size classes, measured with calipers from the end of the siphonal canal to the tip of the apex. These size classes were: <49 mm, 50 – 69 mm, 70 – 89 mm, 90- 109 mm and >110 mm. Samples were collected throughout the area of the new fishery, East of the Inishowen Peninsula, Co. Donegal. Samples of other populations of *B. undatum* were also made from around the coast of Ireland (see Map 3.1) at irregular intervals throughout the same period. During off-season periods, samples were collected as by-catch from the Brown crab fishery, which operates in the same geographic region. Sampling depth was on average 44 metres and sediment was a soft bottom ranging from mud, to sand and coarse grains. After collection, freshly landed whelks were transported from fishing vessels in woven bags covered with ice cubes in a large plastic or polystyrene sealed container. As soon as possible and within 24 hours of landing the whelk samples were transferred to a domestic chest freezer and stored at -10°C for a period of up to 4 months.

Laboratory Analysis

Whelks were defrosted by placing them inside a sealed plastic bag and immersing in cool water for up to 2 hours. Defrosting time varied with air temperature. The total shell length (TSL) from the tip of the siphonal canal to the apex was measured using vernier calipers and recorded to the nearest millimeter. Shell width and aperture length were also measured and recorded in millimeters. The whole animal was then placed on a digital balance and mass was recorded to the nearest 0.01 grams. Gentle cracking in a bench vice and piece-by-piece extraction with pliers and forceps removed the shell of the whelk. Each sample was drained on paper towel for 2 minutes and the soft weight recorded in grams. Shell weight was determined to the nearest 0.01g.

Once the soft mass of the animal was exposed, the mantle was removed and the sex of each individual determined, predominately by the presence or absence of a conspicuous penis. Penis length was measured with vernier callipers and recorded to the nearest millimetre. Female whelks were examined for imposex by searching for growth of a penis or vas deferens. The colour of the gonad was recorded. The digestive gland and gonad were removed and weighed together to the nearest 0.01g. In mature animals, the gonad was removed from the animal and preserved for further analysis. In female whelk, the colour of the capsule gland was recorded and the size measured with vernier callipers and recorded in millimetres. The shell, digestive gland and gonad were also examined for any signs of parasitism and recorded when observed.

Validation of Male Maturity Index and Determining Size at Onset of Sexual Maturity

For the purpose of validating the published penis-shell length maturity index in male *B. undatum*, the relationship between total shell length, penis length and gonadal development was examined. Samples of individual male gonad were preserved and examined using histological methods for the presence of mature sex cells. See Chapter 4 for histological methodology. The proportion of male whelks with penis length ≥ 0.5 total shell length was plotted against the proportion of male whelks classified as either immature or mature by the presence of mature sex cells in the gonad.

The percentage of mature male animals in each 5 mm size class was determined and a logistic curve fitted to the data:

$$y = ymax/1+e^{b(a-x)}$$

where $ymax$ equals 100 %, y is the percentage of mature animals in a size class, a is the inflexion point, b is the constant of the curve and x is the mid point of the shell length size class (mm). The parameters *a* and *b* were determined by fitting a linear trend to a plot of shell length (mm) against $log((ymax-y)/y)$, with the straight line equation $y=mx+c$, where $m=-b$ and $c=ab$. Values of y were adjusted where $y=100\%$ and $y=0\%$ to 99.9% and 0.1% respectively. Size at onset of sexual maturity was derived from the inflexion point, *a*. An estimate of the fitting error of the size at onset of sexual maturity was determined by calculating the standard deviation between the *x* value of the logit curve and the *x* value of the data.

To assess a minimum size at onset of sexual maturity in female *B. undatum*, gonads were removed for histological examination. See Chapter 4 for histological methodology. Where mature oocytes were found to be present, the percentage of mature female animals in each 5 mm size class was determined. A logistic curve was fitted to the data and the size at onset of sexual maturity derived from the inflexion point, and standard deviation calculated, as above.

Temporal Variation in Size at Onset of Sexual Maturity

The size at onset of sexual maturity in male and female Common whelks was determined for each month of sample collection from June 2003 to May 2004. Variation with time was determined by comparing the overlap in 95% Confidence Intervals for size at onset of sexual maturity. The null hypothesis is that there is no variation in mean size at onset of sexual maturity with time.

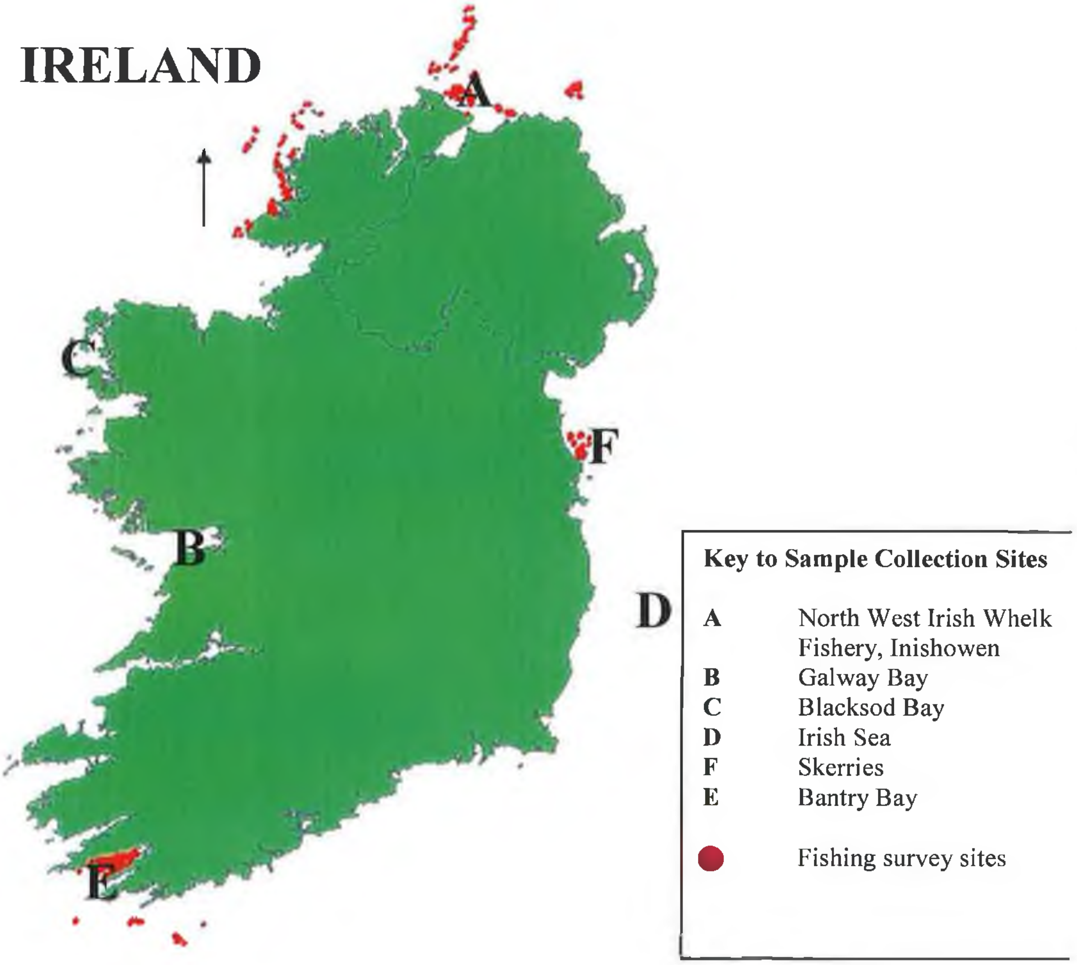
Spatial Variation in the Size at Onset of Sexual Maturity and Shell Morphometry

The mean size and standard deviation at onset of sexual maturity was determined for male and female whelks from four geographically separated locations around the Irish coast, in addition to the region of the North West Irish whelk fishery (see Map 3.1), using the methods previously described. Variation with location was determined by comparing the overlap in 95% Confidence Intervals for size at onset of sexual maturity, where the null hypothesis is that there is no variation in mean size at onset of sexual maturity between populations. Variation in the mean size at onset of sexual maturity in male and female whelks may be an artifact of time or location. A comparison of 95% Confidence Intervals were made between samples collected from a variety of locations, and from the North West Irish whelk fishery, simultaneously to avoid temporal confounding.

Three morphometric characteristics were examined on the shell of each whelk from the North West Irish whelk fishery and other locations around the Irish coast (see Map 3.1). The shell characteristics were: shell length, shell width and aperture length. To assess the null hypothesis that there were no morphological differences in shell characteristics between different populations, variability was examined using a canonical discriminant function analysis (Gendron, 1992), based on a correlation matrix of the three morphometric variables.

Age at Onset of Sexual Maturity

Age at length of whelks was calculated by length frequency analysis, and derived parameters of the von Bertalanffy equation, as described in Chapter 2, and shown in Table 2.6. The minimum and maximum age of onset of sexual maturity in male and female whelks was derived from estimates of size at onset of sexual maturity, and maturity ogives are presented.



Key to Sample Collection Sites

A	North West Irish Whelk Fishery, Inishowen
B	Galway Bay
C	Blacksod Bay
D	Irish Sea
F	Skerries
E	Bantry Bay
●	Fishing survey sites

Map 3.1 Location of Common whelk sample collection sites around the coast of Ireland. Samples from Site A, North West Irish whelk fishery, were collected on board fishing vessels operating in the region. Samples from Sites B, C and F were collected on board fishing vessels commissioned by Bord Iascaigh Mhara (BIM) for whelk fishing surveys. Samples from Site D, Irish Sea, were collected on board the Celtic Explorer as part of the Marine Institute of Ireland Irish Ground Fish Survey 2003. Samples from site E, Bantry Bay, were collected by an independent fishing vessel operating in that region (Skipper: Gavin Power). Fishing survey sites show location of some whelk fishing gear deployed as part of BIM commissioned whelk-fishing surveys.

RESULTS

Validation of Male Maturity Index and Size at Onset of Sexual Maturity in Males

A total of 76 individual male whelks from the area of the North West Irish whelk fishery were used to compare the penis-shell length index with histological samples of the gonad. In over 90% of cases male whelks with a penis-shell length index of ≥ 0.50 were found to have mature sex cells (see Fig 3.1). Males with penis length ≥ 0.50 TSL were therefore classified as sexually mature in the present investigation. In contrast, males with penis length < 0.50 were found to have mature sex cells in 25% of cases (see Fig 3.1), and males with penis length <0.50 TSL were classified as sexually immature in the present investigation.

Penis length increases with total shell length in male Common whelks from the area of the North West Irish whelk fishery throughout the period of sampling (see Fig 3.2). The relationship between penis length and total shell length is non-linear, initially with a shallow slope representing small-shelled whelks with small penis length, followed by a steep slope representing rapid rise as penis length and shell length increase. The later, rapid rise in penis-shell length suggests the onset of sexual maturity. The mean size at onset of sexual maturity in male Common whelks for the 12-month sampling period in this area was found to be 83.30 mm total shell length, and standard deviation 10.77 mm (Fig 3.3). Therefore male whelks in the area of the fishery generally attain sexual maturity between 72.6 and 94.0 mm total shell length. Mean size at onset of sexual maturity was determined by the inflexion point of the curve, % mature at length against length (see Fig 3.3), and was derived from the straight-line equation fitted to the curve (see Fig 3.4).

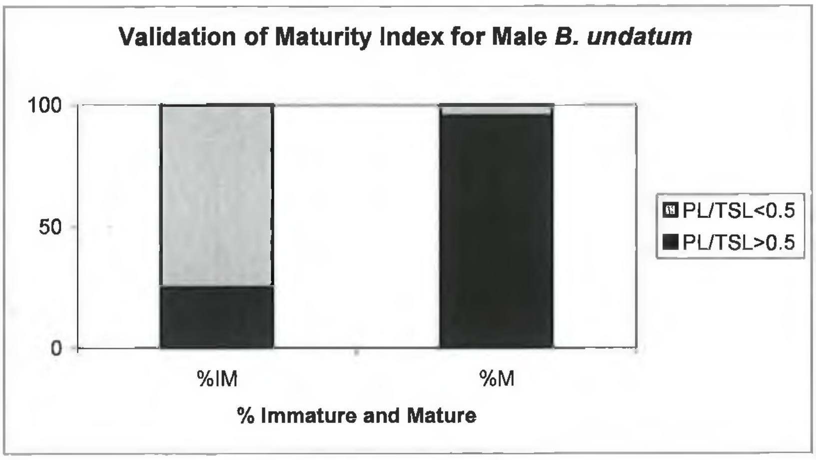


Figure 3.1 Proportion (%) of immature and mature male *B. undatum*, as determined by histological analysis of the gonad, against the maturity index, PL/TSL ≥ 0.5.

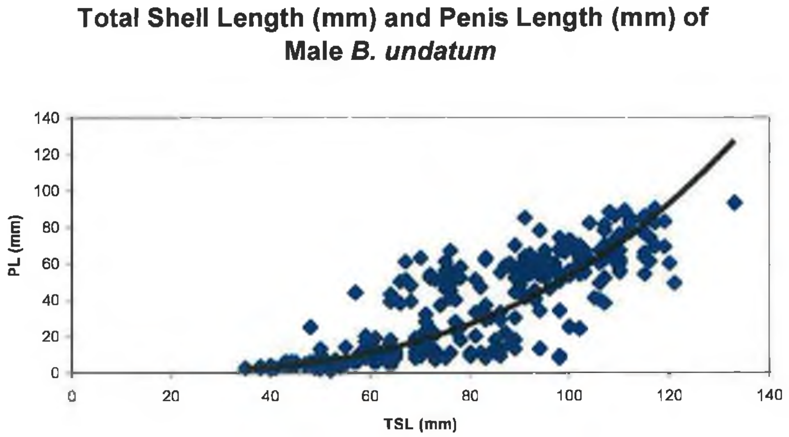


Figure 3.2 Relationship between Total Shell Length (mm) and Penis Length (mm) in male *B. undatum*, sampled from the area of the North West Common whelk Fishery.

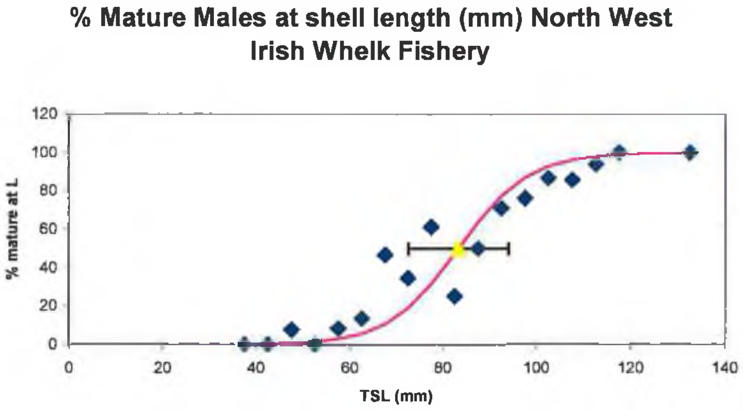


Figure 3.3 Logistic curve ($y = ymax/1+e^{b(a-x)}$) describing the probability of maturity in relation to total shell length (mm), shown in relation to observed proportions of mature individuals summarised by 5 mm shell length classes. Standard error around the mean (inflexion point) was derived from the distance between the curve and scattered data points.

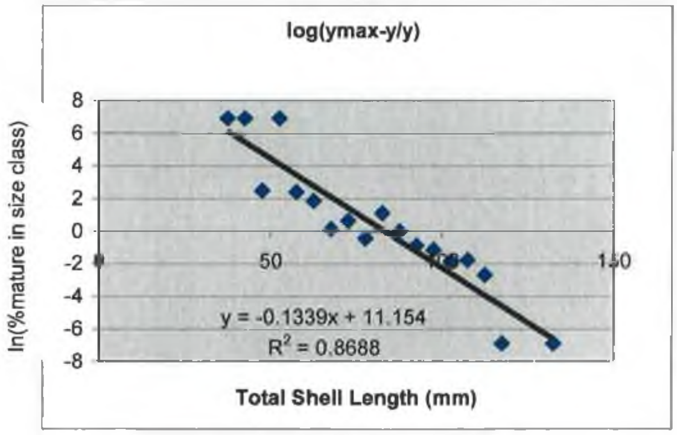


Figure 3.4 Straight line equation from which point of inflexion and curve constant are derived to determine mean size at onset of sexual maturity for male Common whelks in the area of the North West Common whelk fishery.

Temporal Variation in Size at Onset of Sexual Maturity in Males

The size at onset of sexual maturity was determined for each month of sampling, with the exception of September 2003 and March 2004 when samples were unavailable for analysis. While the number of observed male Common whelks varied between months, the previously described relationship between increasing penis length and total shell length was observed for each month of sampling. Results of mean shell length at onset of sexual maturity and standard deviation are summarised in Table 3.1 and presented graphically in Figures 3.5 a-j, Figures 3.6 a-j, and Figure 3.7. Analysis of overlap between 95% confidence intervals shows that in 60-90 % of months sampled there is an overlap in the mean size at onset of sexual maturity with all other months. However, in July 2003 the mean total shell length at onset of sexual maturity was 60.07 mm with 95% CI 50.65 – 69.50 mm, forming an overlap only with the sample collected in August 2003.

Size at Onset of Sexual Maturity in Male *B. undatum*

Month	Year	Mean TSL (mm)	St Dev TSL (mm)	*n* mature observed	95% CI	
June	2003	97.59695	14.55498	13	89.52331	105.6706
July	2003	60.07605	21.075	20	50.65102	69.50107
Aug	2003	77.38661	23.43361	21	67.15934	87.61388
Sept	2003	No Observations				
Oct	2003	84.79204	13.0663	22	79.22055	90.36353
Nov	2003	93.7405	22.18405	8	78.05401	109.427
Dec	2003	99.30628	9.805598	5	90.53589	108.0767
Jan	2004	89.15164	6.974206	15	85.55018	92.75311
Feb	2004	77.16167	4.741159	10	74.1631	80.16024
Mar	2004	No Observations				
Apr	2004	83.48817	7.353859	19	80.11399	86.86235
May	2004	83.87745	17.01458	13	74.43946	93.31544

Table 3.1. Summary of male size at onset of sexual maturity for each month of the 12 month sampling period between June 2003 and May 2004.

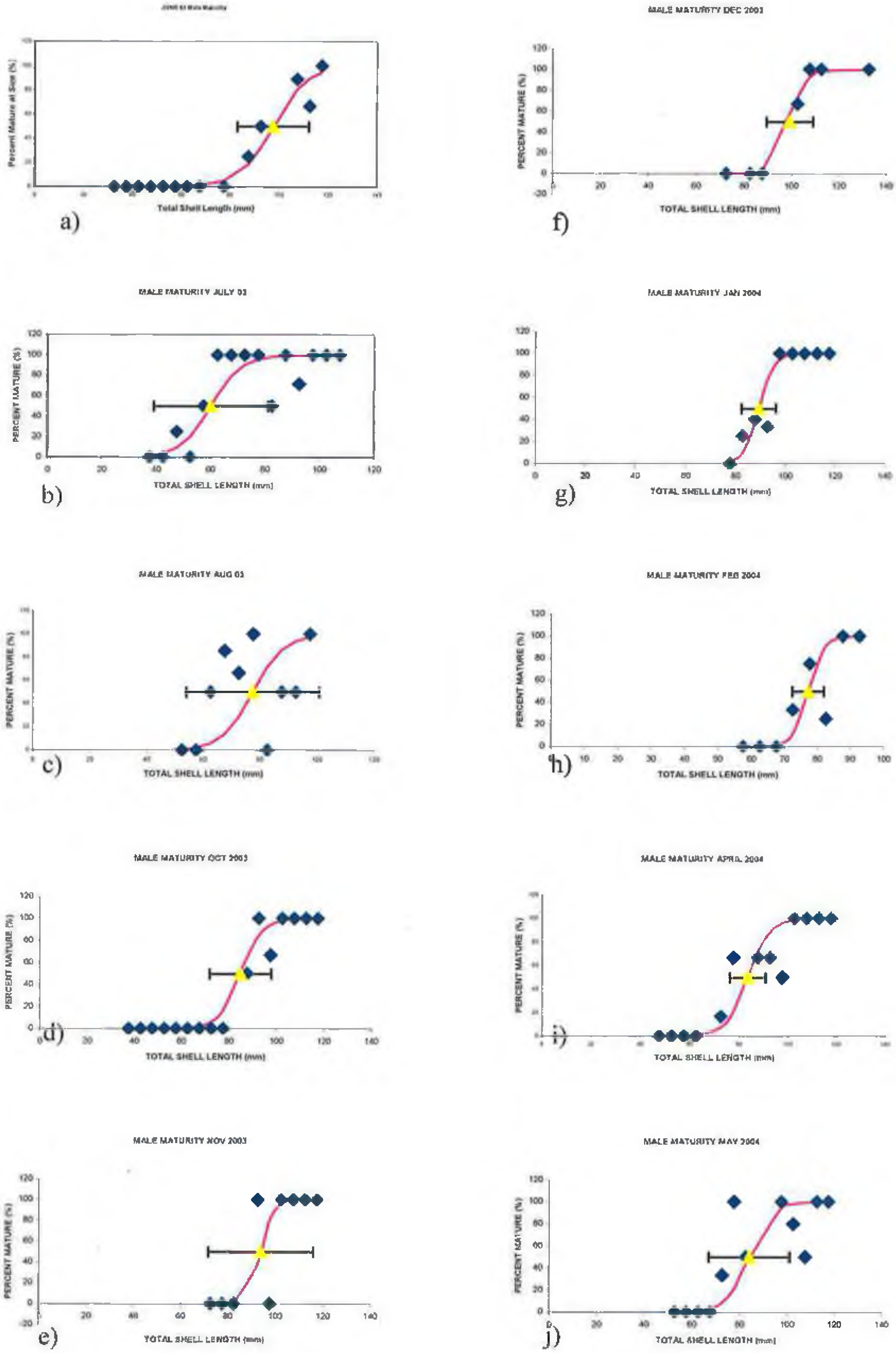
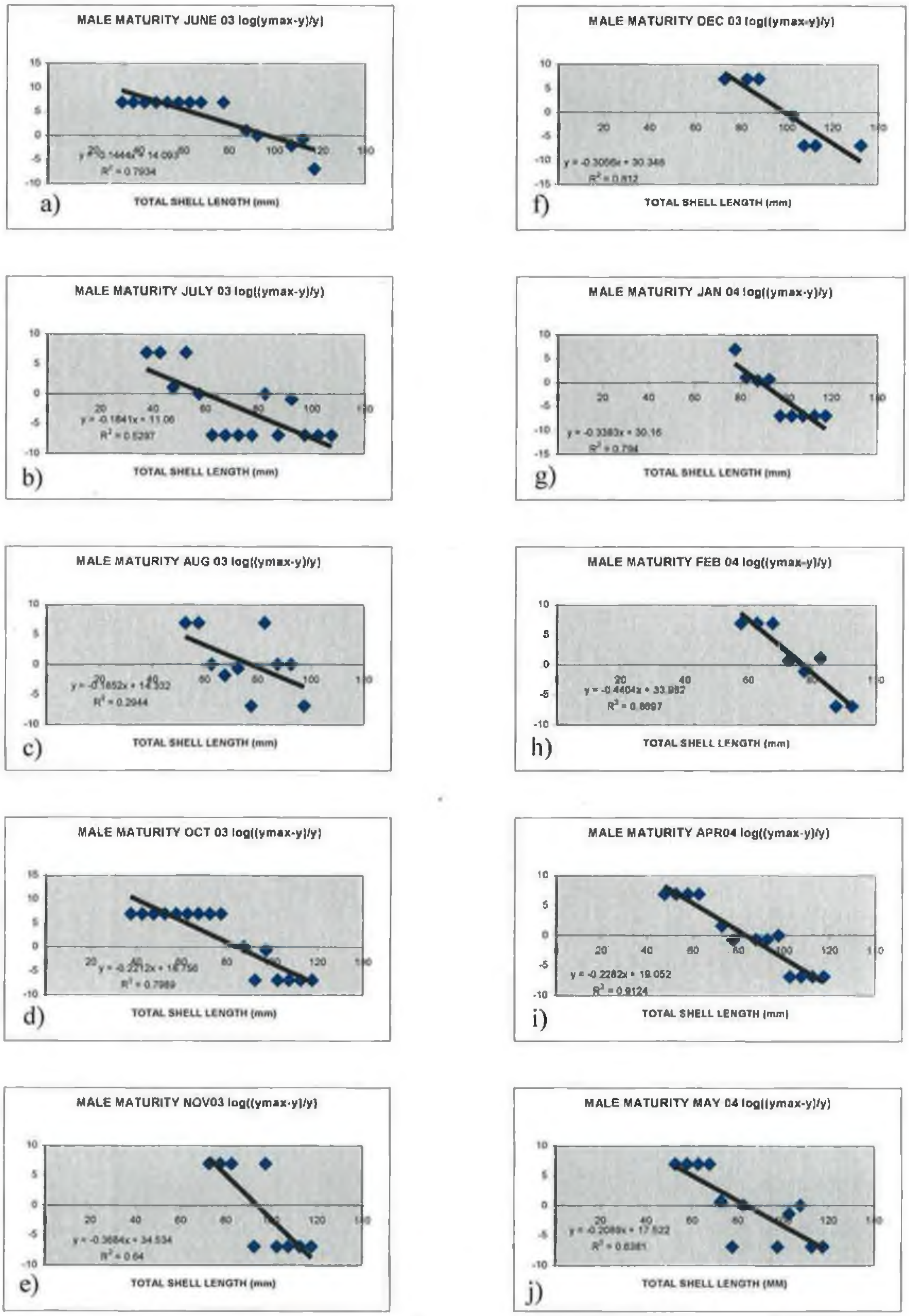


Figure 3.5 a-j Logistic curve of monthly size at onset of sexual maturity for the region of the North West Irish whelk fishery, where the point of inflexion indicates the means size at first maturity.



MALE MATURITY JUNE 03 log(ymax-y)/y)

MALE MATURITY JULY 03 log((ymax-y)/y)

MALE MATURITY AUG 03 log((ymax-y)/y)

MALE MATURITY OCT 03 log((ymax-y)/y)

MALE MATURITY NOV03 log((ymax-y)/y)

MALE MATURITY DEC 03 log((ymax-y)/y)

MALE MATURITY JAN 04 log((ymax-y)/y)

MALE MATURITY FEB 04 log((ymax-y)/y)

MALE MATURITY APR04 log((ymax-y)/y)

MALE MATURITY MAY 04 log((ymax-y)/y)

Figure 3.6 a-j Derivation of the straight-line equation for determining size at onset of male sexual maturity for each month of sample collection between June 2003 and May 2004.

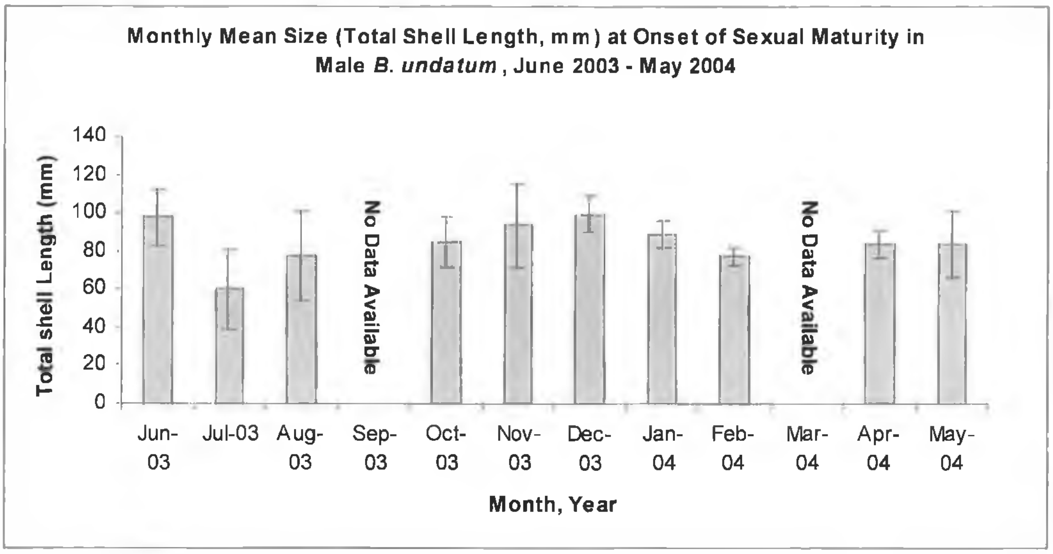


Figure 3.7 Monthly mean total shell length (mm) and standard deviation at onset of sexual maturity in male *B. undatum* from the region of the NW Irish Common whelk fishery.

Spatial Variation in Size at Onset of Sexual Maturity in Males

Under the assumption that male Common whelk become sexually mature when penis length is ≥0.5 total shell length, the mean size at onset of sexual maturity in male Common whelks varies between populations (presented in Table 3.2; figures 3.8 a-d and 3.9 a-d). The largest size at onset of sexual maturity was observed in samples collected from Bantry Bay, at 95.08 mm TSL (SD 12.48 mm). The observed size at onset of sexual maturity decreases respectively in Blacksod Bay, Inishowen Peninsula (North West Irish whelk fishery), the Irish Sea and Galway Bay, where size at onset of sexual maturity in observed individuals occurred at 64.53 mm TSL (SD 11.12 mm). Comparison of 95% Confidence Intervals indicates the mean size at onset of sexual maturity overlaps in all locations and at all times similar to samples collected from the North West Irish whelk fishery, with the exception of Galway Bay (see Fig 3.11). The confidence intervals in mean size at onset of sexual maturity in male *B. undatum* from Galway Bay do not overlap in time or space with any other population examined.

Male *B. undatum*

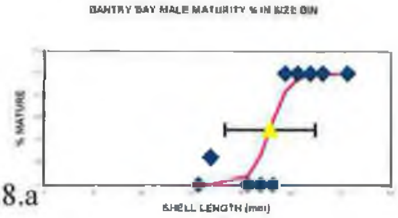
Month/Year	Location	Mean TSL (mm)	St Dev (mm)	N Mature	CI	95% CI	
Oct-03	Inishowen Peninsula	84.79	13.07	22	5.57	79.22	90.36
	Blacksod bay	90.51	5.85	18	2.76	87.76	93.27
Nov-03	Inishowen Peninsula	93.74	22.18	8	15.69	78.05	109.43
	Irish Sea	83.10	24.34	15	12.57	70.53	95.67
Dec-03	Inishowen Peninsula	99.31	9.81	5	8.77	90.54	108.08
	Bantry Bay	95.08	12.48	20	5.58	89.50	100.67
Apr-04	Inishowen Peninsula	83.49	7.35	19	3.37	80.11	86.86
	Galway Bay	64.53	11.12	14	5.94	58.59	70.47

Female *B. undatum*

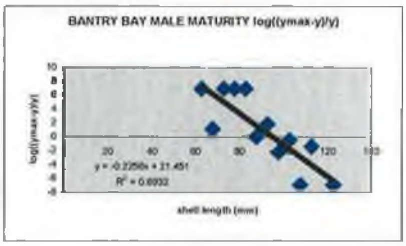
Month/Year	Location	Mean TSL (mm)	St Dev (mm)	N Mature	CI	95% CI	
Oct-03	Inishowen Peninsula	92.29	17.46	9	11.64	80.64	103.93
	Blacksod bay	90.63	9.71	14	5.19	85.44	95.82
Nov-03	Inishowen Peninsula	93.08	9.46	20	4.23	88.85	97.31
	Irish Sea	68.94	17.24	32	6.10	62.85	75.04
Dec-03	Inishowen Peninsula	98.99	8.94	4	8.94	90.05	107.92
	Bantry Bay	88.25	11.23	27	4.32	83.93	92.57
Apr-04	Inishowen Peninsula	76.69	11.83	21	5.16	71.52	81.85
	Galway Bay	64.52	6.26	9	4.18	60.35	68.70

Table 3.2 Summary of Male and Female mean size at onset of sexual maturity, standard deviation and 95% Confidence Intervals for variously sampled locations and times within the 12-month sampling period between June 2003 and May 2004.

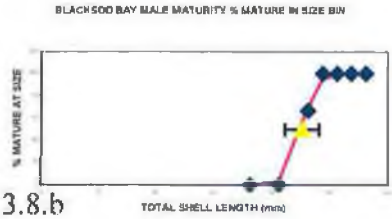
3.8.a



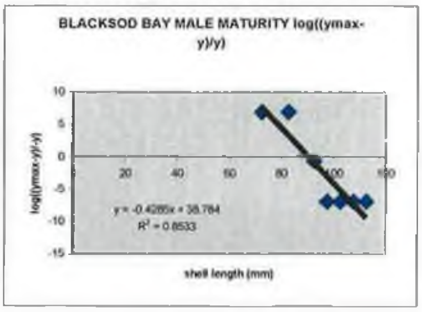
3.9.a



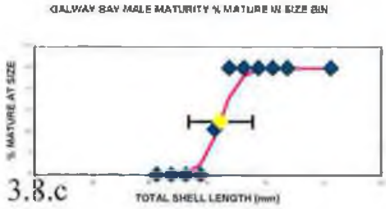
3.8.b



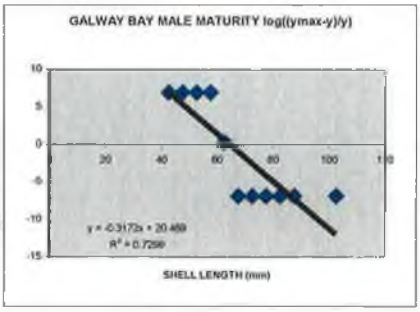
3.9.b



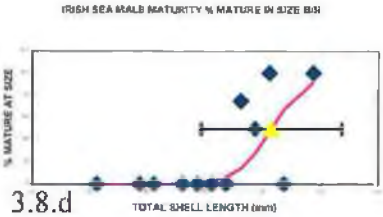
3.8.c



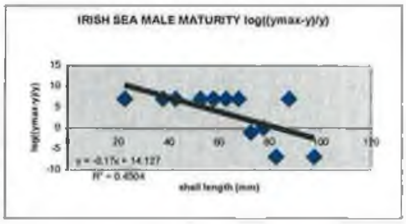
3.9.c



3.8.d



3.9.d



Figures 3.8 a-d Logistic curve of size at onset of sexual maturity for male *B. undatum* for locations sampled around the coast of Ireland, where the point of inflexion indicated mean size at first maturity.

Figures 3.9 a-d Derivations of straight-line equations for determining size at onset of sexual maturity in male *B. undatum* from locations sampled around the coast of Ireland.

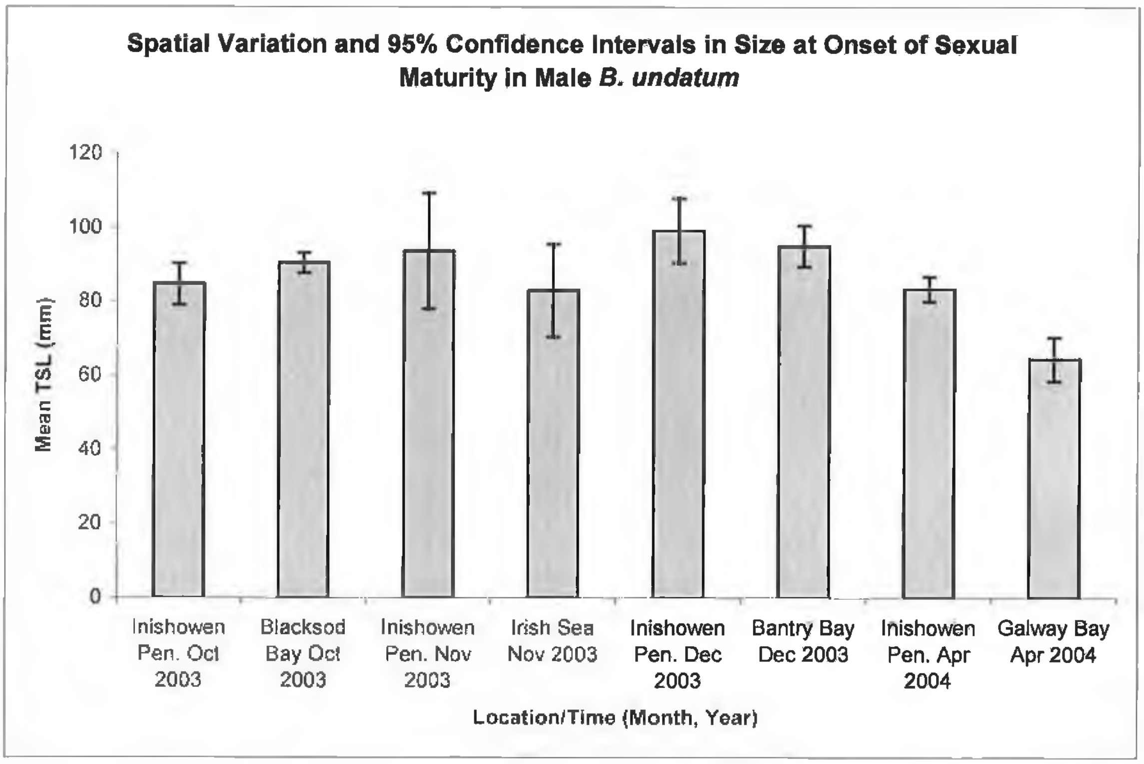


Figure 3.10 Spatial variation in mean size at onset of sexual maturity for male Common whelk is represented by overlapping 95% confidence intervals for pairs of samples collected simultaneously between the North West Irish whelk fishery and other locations (Blacksod Bay, Bantry Bay, the Irish Sea and Galway Bay).

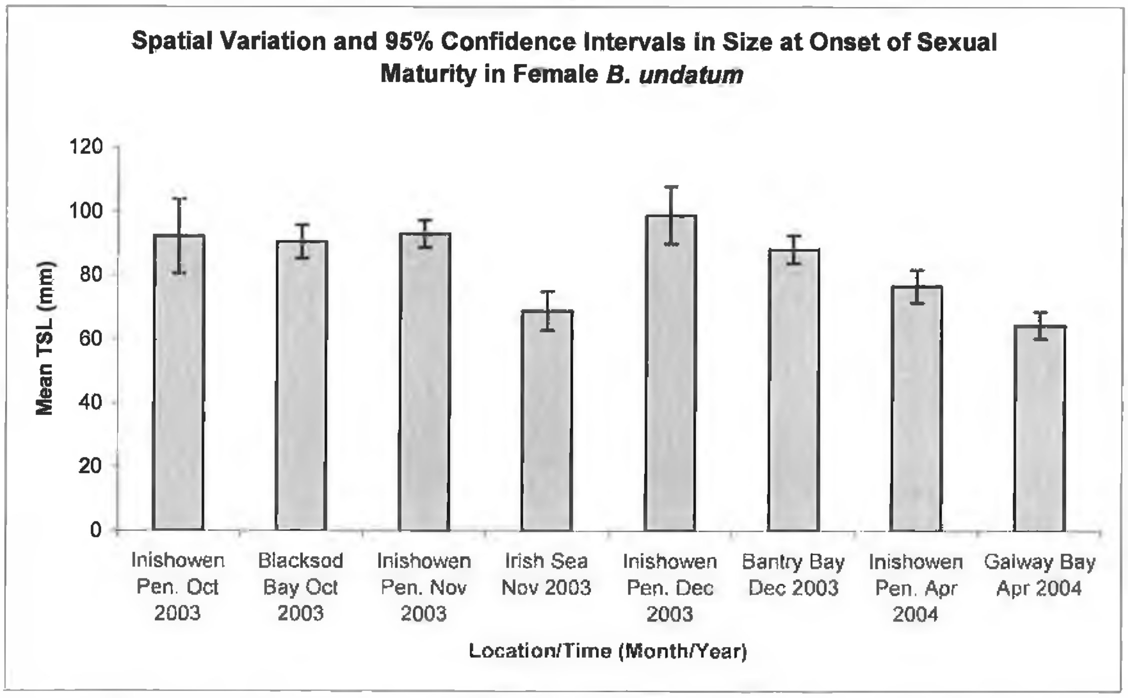


Figure 3.11 Spatial variation in mean size at onset of sexual maturity for female Common whelk is represented by overlapping 95% confidence intervals for pairs of samples collected simultaneously between the North West Irish whelk fishery and other locations (Blacksod Bay, Bantry Bay, the Irish Sea and Galway Bay).

Age at Onset of Sexual Maturity in Males

The age of onset of sexual maturity in male *B. undatum* was determined from a transformation of the von Bertalanffy equation, $t(L) = t_0 - (1/K)\ln(1-(L/L\infty))$, where the parameters $t_0 = 0.007$, K = the growth coefficient = -0.04, and $L\infty$ = the asymptotic length = 151.64 were determined by length frequency analysis (see Chapter 2). Male *B. undatum* in the region of the North West Irish Whelk fishery, achieve sexual maturity at a minimum age of 8.9 years, and maximum age of 11.1 years growth. The proportion of mature male individuals per year of growth, sampled from the fishery catch, is represented in Fig 3.12.

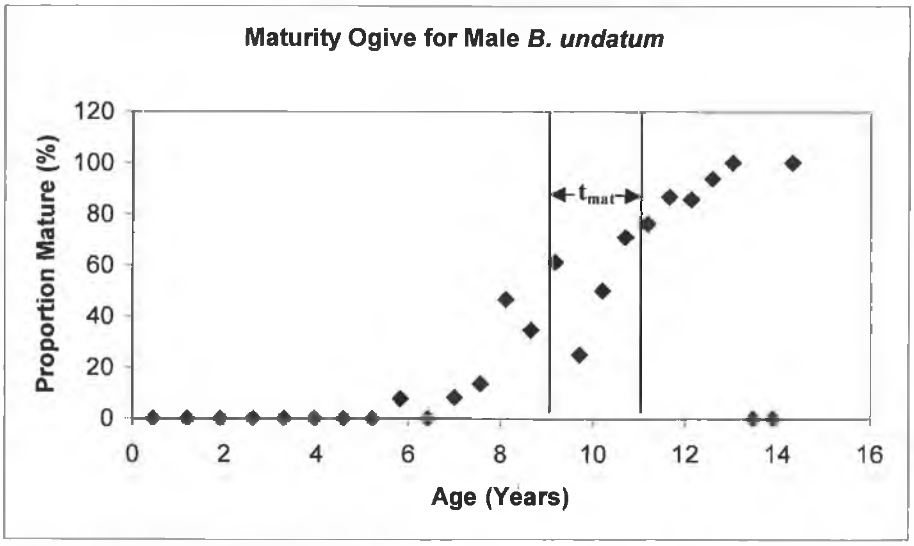
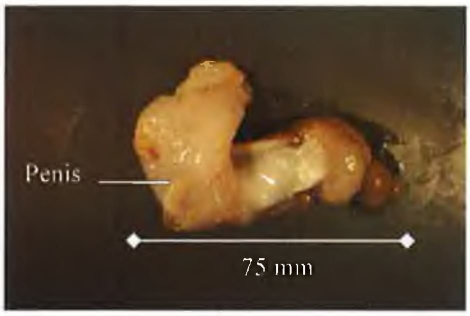
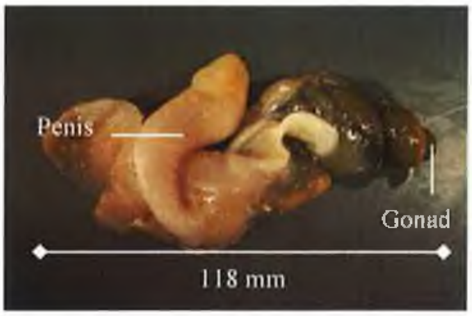


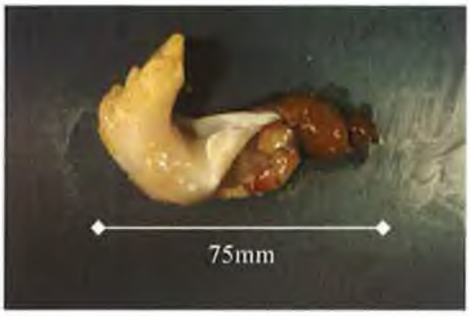
Figure 3.12 Male maturity ogive demonstrating proportional maturity at age for the region of the North West Irish whelk fishery, and indicating time at first maturity, t_{mat}.

Size at Onset of Sexual Maturity in Females

Prior to the onset of reproductive maturity, the female ovaries were underdeveloped and lacked mature oocytes (Martel *et al.*, 1986a). Histological analysis determined that in female *B. undatum*, the gonad contained mature sex cells when it was also highly visible and coloured. In female specimens, the mature gonad was bright to pale yellow (see Photo 3.D). The colour of the mature gonad in female *B. undatum* was distinctly different to the colour of the adjoining digestive gland, however, in immature specimens, the gonad and digestive gland may be indistinguishable by colour (see Photo 3.C). Female maturity was assessed by the presence or absence of large, bright yellow gonads, and used to give a minimum shell length size above which female whelks are likely to achieve sexual maturity. A total shell length of 60 mm was selected as the minimum size above which onset of sexual maturity is likely to occur, based on the presence-absence assessment (see Fig 3.13). An increase in relative ovary weight also showed that females attained sexual maturity above 60 mm total shell length (see Fig 3.14). Where mature ovaries were present, the total mass of the ovary and digestive gland (attached) was recorded. Where the ovary was absent the mass was recorded as 0.0 g (digestive gland mass not recorded). The mean size at onset of sexual maturity in female Common whelks for the 12-month sampling period in this area was found to be 82.62 mm total shell length and standard deviation 10.68 mm. Female whelks attain sexual maturity between 71.9 and 93.9 mm total shell length in the area of the examined fishery. Mean size at onset of sexual maturity was equal to the inflexion point of the curve % mature against length (see Fig 3.15), and was derived from the straight-line equation fitted to the curve (see Fig 3.16).







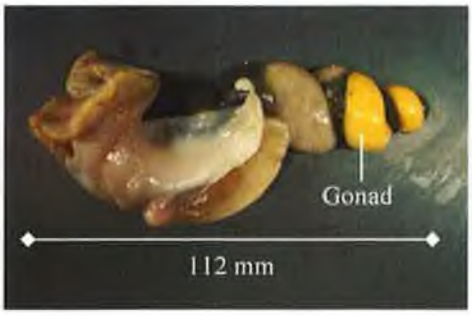


Photo 3.A	Immature Male, indicating penis <0.5 Total Shell Length
Photo 3. B	Mature Male, indicating penis ≥0.5 Total Shell Length and coloured gonad
Photo 3.C	Immature Female, no colouration in gonad
Photo 3. D	Mature Female, indicating colouration in gonad

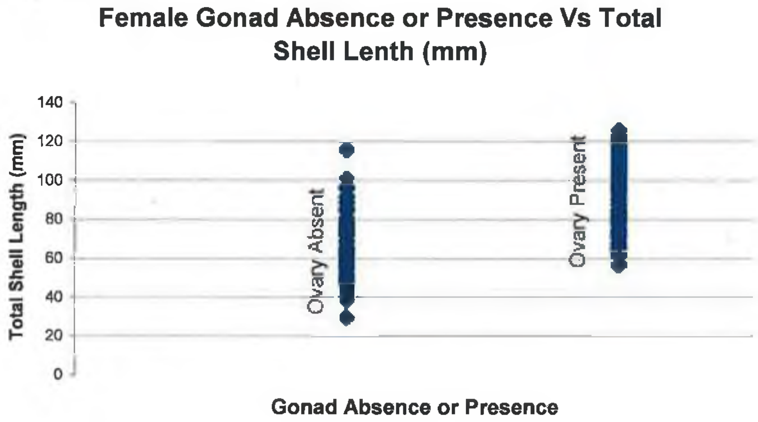


Figure 3.13 Presence and absence of a conspicuous and coloured gonad in female *B. undatum*, where presence indicates sexual maturity has been attained.

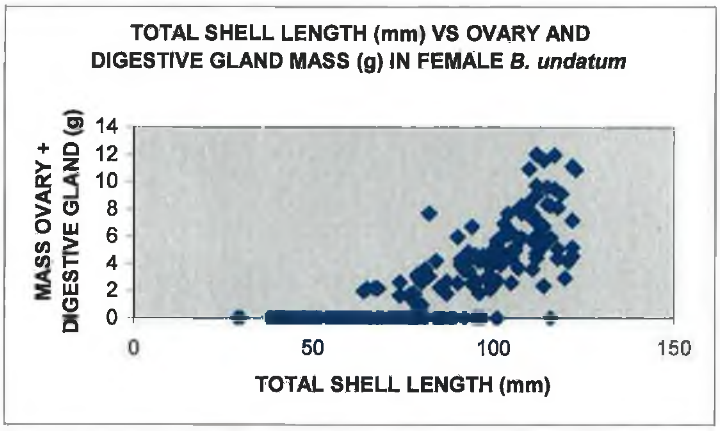


Figure 3.14 Mass of ovary and digestive gland plotted against total shell length in female *B. undatum*. Where ovary was not present, mass indicated as 0.0 g.

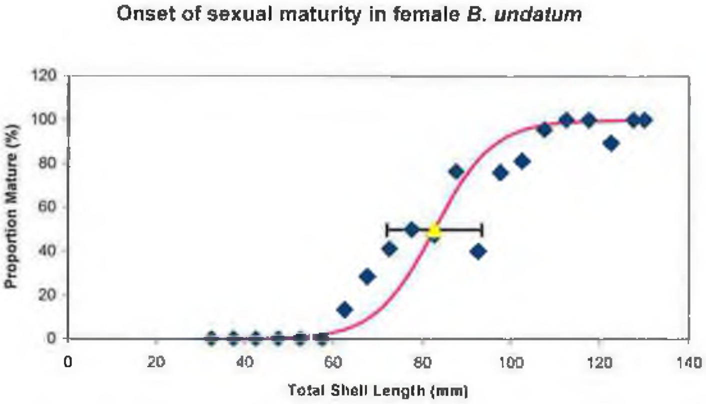


Figure 3.15 Logistic curve ($y = ymax/1+e^{b(a-x)}$) describing the probability of female maturity in relation to total shell length (mm), shown in relation to observed proportions of mature individuals summarised by 5 mm shell length classes. Standard error around the mean (inflexion point) was derived from the distance between the curve and scattered data points.

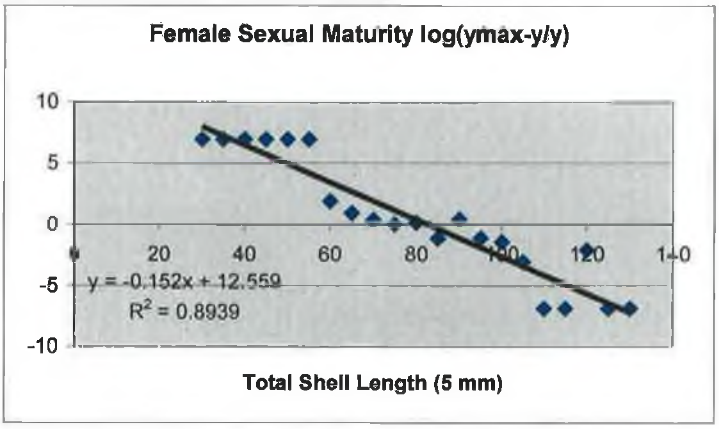


Figure 3.16 Straight line equation from which point of inflexion and curve constant are derived to determine mean size at onset of sexual maturity for female Common whelks in the area of the North West Common whelk fishery.

Temporal Variation in Size at Onset of Sexual Maturity in Females

The size at onset of sexual maturity was determined for each month of sampling, with the exception of September 2003 and March 2004 when samples were unavailable for analysis. Results of mean shell length at onset of sexual maturity and standard deviation are summarised in Table 3.3 and Fig 3.17. Figures 3.18 a-j and 3.19 a-j indicate the point of inflexion and the straight line equation used to find the mean size and standard deviation at onset of sexual maturity in female Common whelks from the area of the North West Irish whelk fishery. Analysis of overlap between 95% confidence intervals shows that in July 2003 the mean total shell length at onset of sexual maturity was 65.61 mm with 95% CI 56.37 – 74.85 mm, forming an overlap with the samples collected in August 2003, February, April and May 2004. The pattern of decreased size at onset of sexual maturity between June and July 2003, increasing in December 2003, and subsequently declining in January and February 2004 was also observed in male samples (see Fig 3.7 and Fig 3.17).

Size at Onset of Sexual Maturity in Female *B. undatum* from the North West Irish whelk fishery

Month	Year	Mean (mm)	St Dev (mm)	*n* Mature Observed	95% CI	
June	2003	86.23794	17.73654	21	78.49708	93.9788
July	2003	65.61508	20.66295	20	56.37433	74.85583
Aug	2003	70.07424	24.20078	21	59.51216	80.63633
Sept	2003			No Observations		
Oct	2003	92.28509	17.46266	9	80.64332	103.9269
Nov	2003	93.08446	9.458343	20	88.85456	97.31436
Dec	2003	98.98609	8.937745	4	90.04835	107.9238
Jan	2004	89.17538	3.764139	10	86.79473	91.55603
Feb	2004	71.52327	4.598276	21	69.51642	73.53012
Mar	2004			No Observations		
Apr	2004	76.68841	11.83299	21	71.52407	81.85275
May	2004	77.69072	15.17242	29	72.05583	83.32562

Table 3.3 Summary of size at onset of sexual maturity in female *B. undatum* for each month of the 12-month sampling period between June 2003 and May 2004.

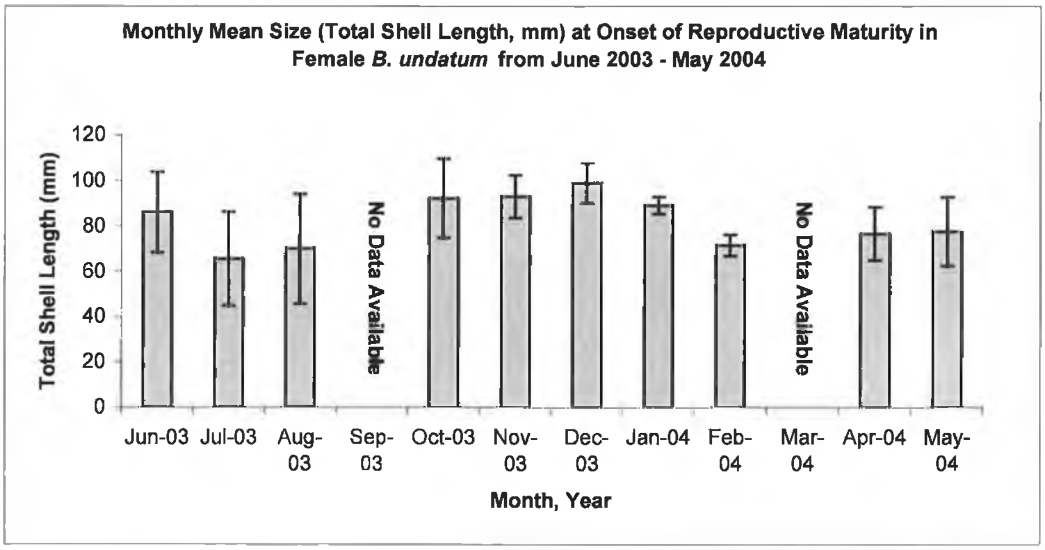
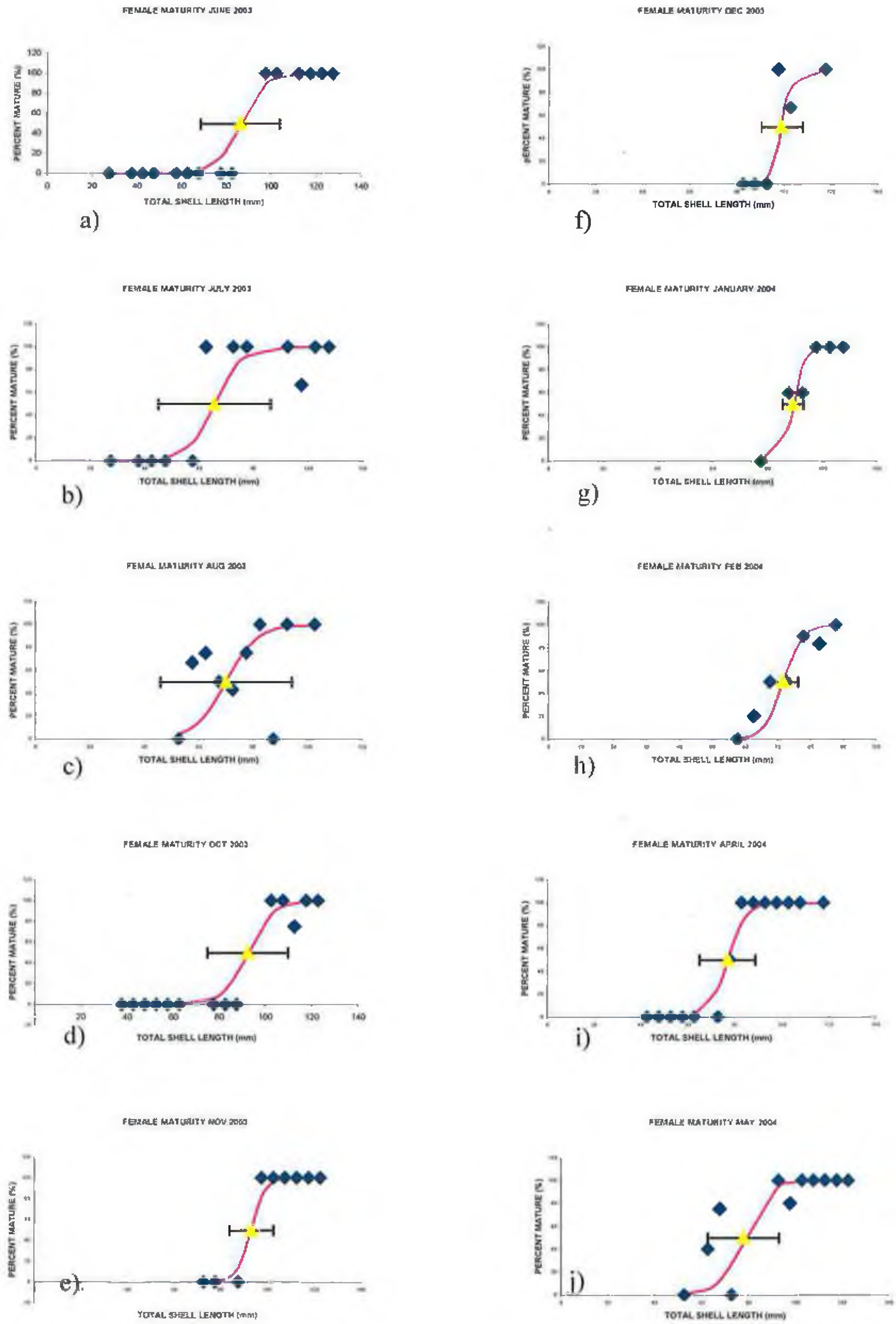
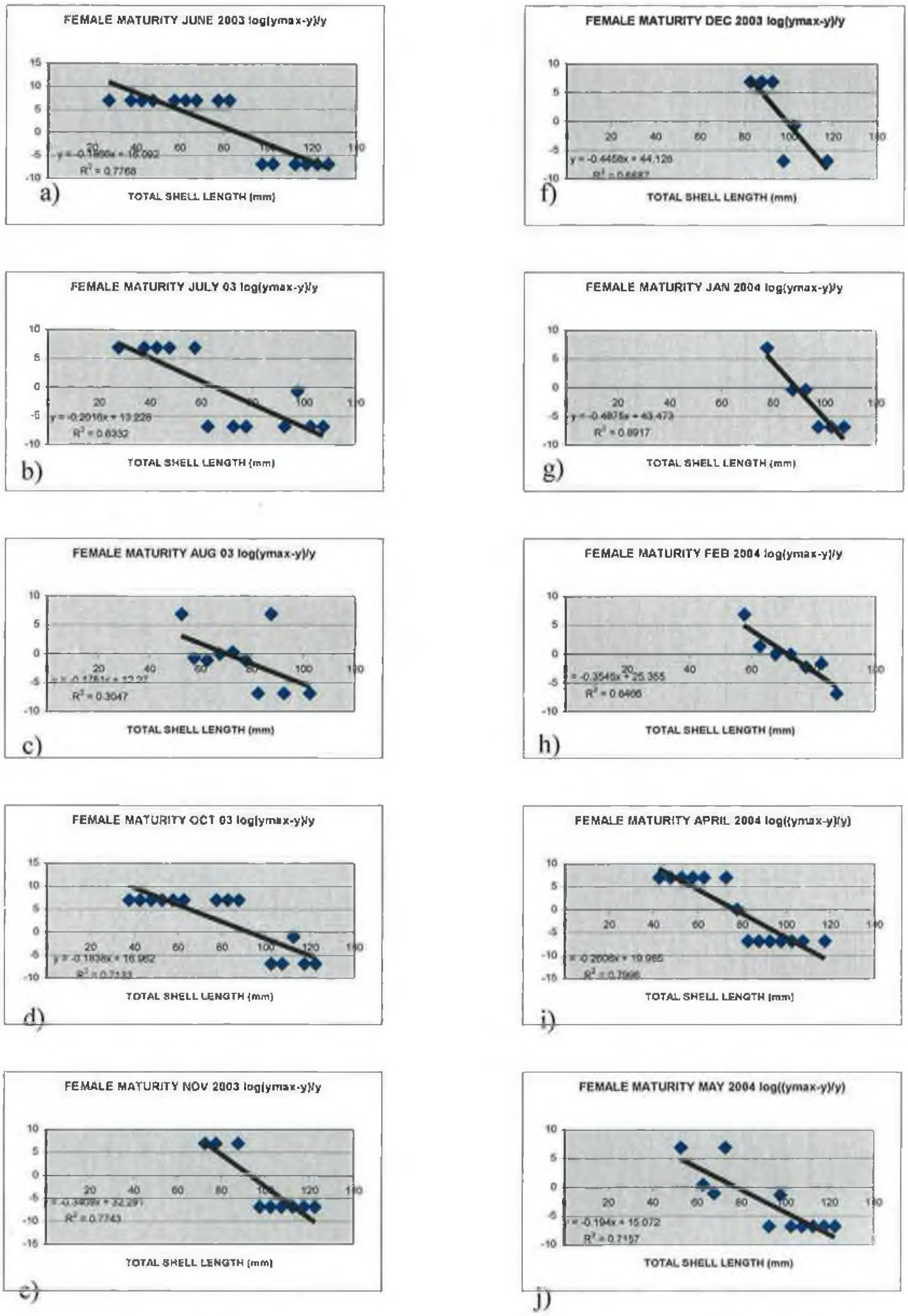


Figure 3.17 Monthly mean total shell length (mm) and standard deviation at onset of sexual maturity in male *B. undatum* from the region of the NW Irish Common whelk fishery.



Figures 3.18 a-j Logistic curve of monthly size at onset of sexual maturity in female whelk for the region of the North West Irish whelk fishery, where the inflexion point indicates mean size at first maturity.



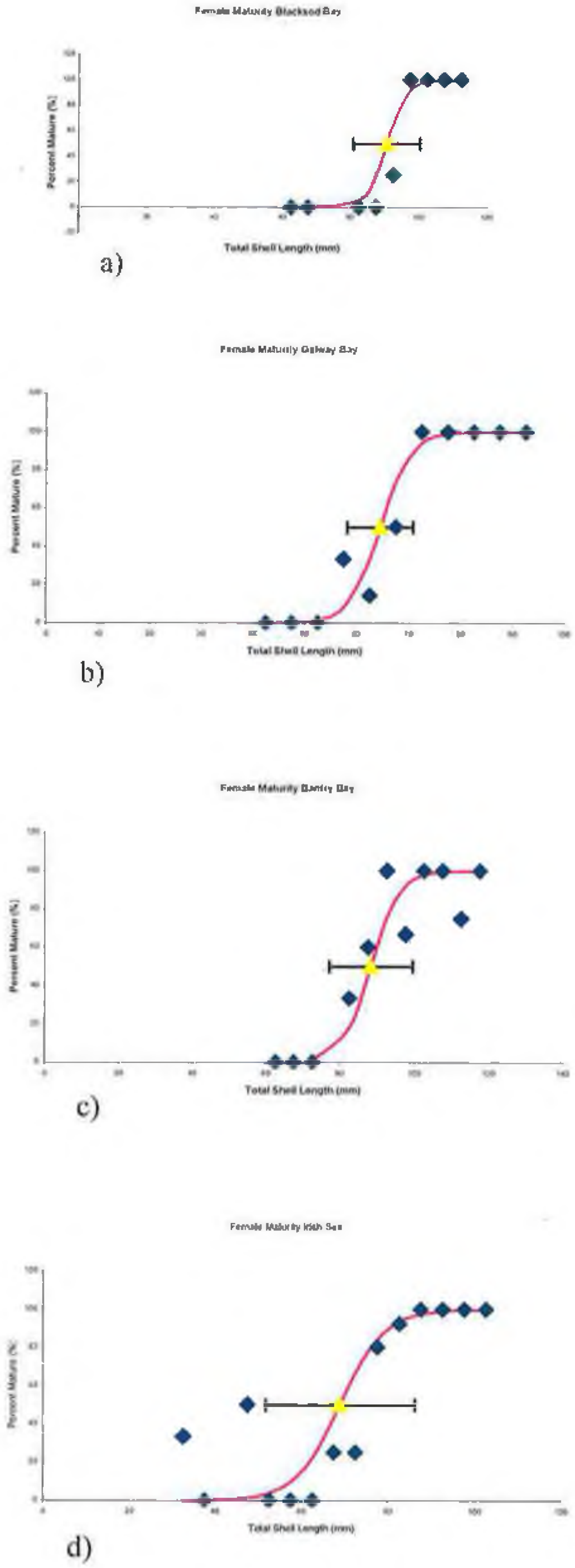
Figures 3.19 a-j Derivation of straight-line equations for determining size at onset of sexual maturity in female whelks in the region of the North West Irish whelk fishery throughout the 12-month sampling period from June 2003 to May 2004.

Spatial Variation in Size at Onset of Sexual Maturity in Females

The mean size at onset of sexual maturity in female Common whelks (presented in Table 3.2) varies between populations (see Figs 3.20 a-d and 3.21 a-d for mean size at onset of first maturity and derivation of the standard deviation for each population). The largest size at onset of sexual maturity was observed in samples collected from Blacksod Bay, at 90.93 mm TSL (SD 9.70 mm). The observed size at onset of sexual maturity decreased respectively in Bantry Bay, Inishowen Peninsula (North West Irish whelk fishery), the Irish Sea and Galway Bay, where size at onset of sexual maturity in observed individuals occurred at 64.52 mm TSL (SD 6.26 mm). Comparison of 95% Confidence Intervals reveals overlap in mean size at onset of sexual maturity in female *B. undatum* from Blacksod Bay and Bantry Bay populations, and from the Irish Sea and Galway Bay populations (see Fig 3.11). Furthermore, confidence intervals of female size at sexual maturity in samples from Blacksod Bay and Bantry Bay overlap with samples from the area of the North West Irish whelks fishery in the same month. However, confidence intervals of samples collected from the Irish Sea and Galway Bay do no overlap with samples collected at the same time from the North West Irish whelk fishery.

Age at Onset of Sexual Maturity in Females

The age of onset of sexual maturity in female *B. undatum* was determined from a transformation of the von Bertalanffy equation, $t(L) = t_0 - (1/K)\ln(1-(L/L\infty))$, where the parameters $t_0 = 0.007$, K = the growth coefficient = -0.04, and $L\infty$ = the asymptotic length = 151.64 were determined by length frequency analysis (see Chapter 2). Female *B. undatum* in the region of the North West Irish Whelk fishery, achieve sexual maturity at a minimum age of 8.8 years, and maximum age of 11.1 years growth. The proportion of mature female individuals per year of growth, sampled from the fishery catch, is represented in Fig 3.22.



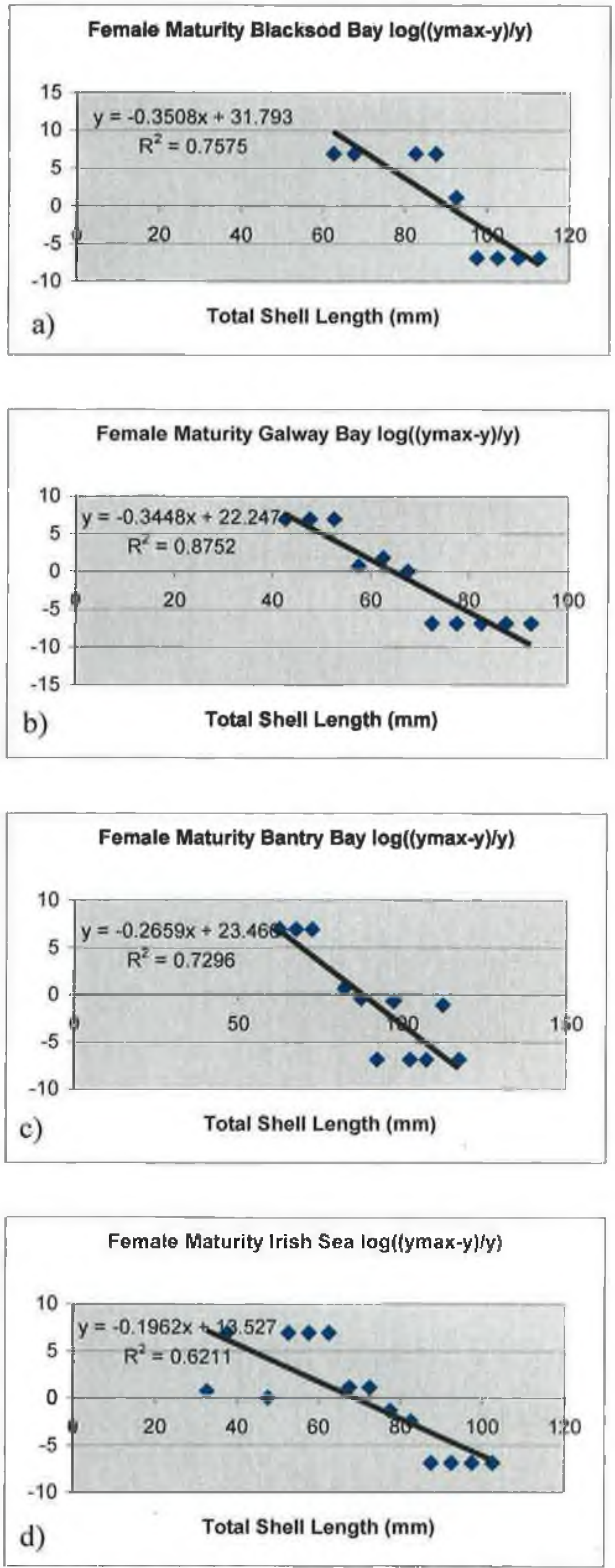


Figure 3.20 a-d Logistic curve of size at onset of female sexual maturity for locations sampled around the coast of Ireland, where the point of inflexion indicates mean size at first maturity.

Figure 3.21 a-d Derivation of a straight-line equation for determining size at onset of female sexual maturity for locations sampled around the coast of Ireland.

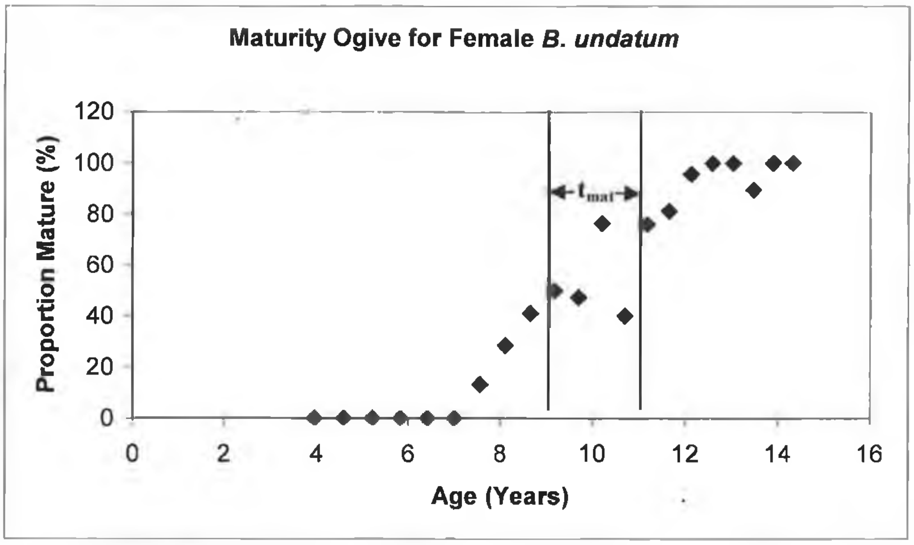


Figure 3.22 Female maturity ogive demonstrating proportional maturity at age for the region of the North West Irish whelk fishery, and indicating time at first maturity, t_{mat}.

Shell Morphometry

Canonical discriminant function analysis revealed no significant difference in TSL, width and aperture length between any of the sampled populations from the Inishowen Peninsula (North West Irish whelk fishery), Galway Bay, Blacksod Bay, Bantry Bay and the Irish Sea. Male and female whelks were not distinguished in the analysis.

Imposex and Parasitism

The phenomenon of imposex was not observed in any female Common whelks from the region of the North West Irish whelk fishery. Swelling and discolouration of the digestive gland and gonad in a small proportion (0.83%) of observed male and female Common whelk suggest infection by trematode sporocycsts.

DISCUSSION

Martel *et al.* (1986a) and Gendron (1992) determined sexual maturity in female whelks from a gonado-somatic index (GSI), defined as the ratio of gonadal weight (ovary + albumen and capsule glands + seminal receptacle + bursa) to the total eviscerated weight (total body weight – (gonad + digestive gland)). The eviscerated weight was used instead of total body weight to eliminate the effect of the highly variable weight of the digestive gland. Martel *et al.* (1986a) report that three factors justify the use of eviscerated weight as the denominator for body component indices: 1) the correlation coefficient (r) was significantly greater between eviscerated weight and shell length than for that of total weight and shell length (Wilcoxon's test, $P<0.05$); 2) the eviscerated weight had a significantly lower coefficient of variation than the total weight (Wilcoxon's test, $P<0.05$); and 3) the eviscerated weight was the most seasonally stable body component and a stable denominator is particularly important when examining variations of small organs such as the seminal vesicle. Both Martel *et al.* (1986a) and Gendron (1992) observed that females having GSI ≥ 0.6 were considered mature, and this was further supported by histological examination of the ovaries. GSI was not determined for male or female whelks in the current study. This is due to the sampling method adopted, whereby whelks were frozen and transported. It was observed that in frozen samples, the digestive gland is extremely fragile and difficult to remove from the ovary. Furthermore, the delicate structures of the albumen, capsule gland, bursa and seminal receptacle deteriorate with freezing and thawing. Immediate preservation of samples in formalin and seawater, as described by Gendron (1992), is advised for future analyses. However, this latter method was not adopted in the current investigation due to the nature of sample collection from working fishing vessels, i.e. where time and space were unavailable to remove the hard shell and prepare solutions. An alternative method of determining sexual maturity in female whelks is to screen for the presence of recent sperm deposition in the seminal receptacle and pallial oviduct at the time of reproduction. Evidence of sexual maturity in female whelk may be identified by the presence of sperm in the pallial oviduct, representing recent copulation (Martel *et al.*, 1986a). Sperm was unable to be recovered from the samples collected from the North West Irish whelk fishery, and again this may be an artifact of freezing. Female whelk are said to be mature when mature oocytes are present in the ovary. Prior to the onset of reproductive maturity, the ovaries are underdeveloped and lack mature oocytes (Martel *et al.*, 1986a). In the present investigation, mature oocytes were found in yellow-coloured ovaries, and the presence or absence of the mature ovary was employed as an indicator of reproductive maturity. A single observer, thus reducing bias in the assessment of ovarian colour, consistently prepared all collected samples. As observations of sperm in the seminal receptacle were not possible, it is assumed for the purposes of the current investigation that sexual maturity occurs simultaneously with reproductive maturity in female *B. undatum*.

Where mean size at onset of sexual maturity was observed for the 12-month sampling period of the North West Irish whelk fishery, male and female Common whelks matured within 1.00 mm, and both with a standard deviation of 10.7 mm total shell length. Simultaneous size at onset of sexual maturity between the sexes has been observed in a variety of studies in European waters (see Table 3.4) (Hancock and Simpson, 1962; Santarelli *et al.*, 1986; Valentinsson *et al.*, 1999; Fahey *et al.*, 2001). In Swedish waters, Valentinsson *et al.* (1999) determined that male size at onset of sexual maturity occurred from 53.5 – 71.9 mm total shell length, and ages 7.4 – 9.2 years, while female whelks matured from 51.5 – 71.5 mm, and ages 7.3 – 9.1 years. Valentinsson *et al.* (1999) concluded, that no apparent sex specific difference in size at onset of sexual maturity was found, supporting the results of the current study. However, Martel *et al.* (1986a) and Gendron (1992) observed sex-specific differences in size at onset of sexual maturity in Canadian waters. Furthermore, Gendron (1992) reported that at a number of locations in Canadian waters, the percentage of mature animals decreased as size increased. This phenomenon was not observed in the present study.

Imposex has been defined as the development of male primary sexual characteristics in female gastropods, causing sterility (Blaber, 1970; ten Hallers-Tjabbes *et al.,* 1994). The phenomenon is caused by exposure to tributyltin (Bryan *et al.,* 1988), which has been used as an anti-fouling paint on ship hulls since the early 1970's (ten Hallers-Tjabbes *et al.,* 1994). Consequently, imposex in *B. undatum* frequently occurs in regions of high shipping traffic (ten Hallers-Tjabbes *et al.,* 1994), and has been reported across Europe (Knickmeyer and Steinhart, 1989; Cadée et al., 1995; Mensink *et al.,* 1996b; Poloczanska and Ansell, 1999; Strand and Jacobsen, 2002; ten Hallers-Tjabbes *et al.,* 2003). Imposex has been recorded in *B. undatum* from the Irish Sea (Knickmeyer and Steinhart, 1989), although it does not seem to affect the stock of Common whelks in the Irish Sea whelk fishery (Fahy *et al.,* 2000). Imposex was not found in the present study of the North West Irish whelk fishery stock, and thus has no impact on size at onset of sexual maturity, or breeding performance. A small proportion of the sampled stock was, however, infected with parasites. The most likely parasite in *B. undatum* is trematode sporocysts of the species *Zoogonoides viviparus*, which are common in the North Atlantic (Køie, 1987). Trematode parasite infections are known to cause destruction of the gonad tissue as well as reduction of the penis (Køie, 1969), and may result in immaturity in some larger animals. Parasite infection is unlikely to affect the size at onset of sexual maturity and breeding performance in Common whelks in the North West Irish whelk fishery at the time of the present investigation.

Temporal variation in the size at onset of sexual maturity in common whelks is not described often in the literature. In the present study, variation in the size at maturity between monthly samples of male and females in the region of the North West Irish whelk fishery may arise for a number of reasons. There is a possible pattern of declining size at onset of sexual maturity between June and July 2003, increase in December 2003, and subsequent decline again in January and February 2004. The observed variation may be due to the appearance of a cohort of recently matured individuals, which decrease the size at onset of maturity. Alternatively, because of existing variability in the population, the removal by fishing of larger individuals may produce the appearance of maturation at a smaller size. It is widely accepted that feeding declines dramatically during the breeding period in Common whelks (Martel et al, 1986a; Himmelman, 1988; Himmelman and Hamel, 1993). However, Rochette *et al.* (2001) demonstrated that large, sexually mature whelks take increased risks to obtain food during the breeding season due to increased energy requirements for reproduction. The current study found that the reproductive period occurred in late 2003 (see Chapter 4), and elevated feeding requirements may explain why larger whelks were captured in baited pots at this time. In July 2003 the ≥ 110 mm sampling size range was not represented in collected samples because individuals of this size order were not landed in fisheries catch. This sampling period coincided with the end of the 3-month whelk fishing season in the region of the fishery. Results of the analysis of onset of sexual maturity in July 2003 indicate that female whelks matured at a mean size of 65.6 mm TSL (SD 20.66 mm), and male whelks 60.1 mm TSL (SD 21.1 mm). These figures indicate the least amount of overlap in confidence interval with any other month for both sexes during the 12-month sampling period, and for the mean annual size at first maturity. Studies of predation pressure on the size at maturity in *B. undatum* have suggested that intense pressure can select for smaller size at maturity (Gendron, 1992), implying a high level of fishing mortality on the examined population. However, apparent temporal variation in size at onset of sexual maturity may also be an artifact of sampling. While every effort was made to ensure a full representation of sizes in monthly sampling, this was not always possible and some size classes may not have been included in analysed data.

The present investigation found that Common whelks from the area of the North West Irish whelk fishery reach sexual maturity at larger sizes than from other investigated waters (see Table 3.4). However, overlapping confidence intervals in size at maturity between whelks from the North West Irish whelk fishery and those of other locations suggest that there is little spatial variation. Variation was found in the size at sexual maturity between the population of male and female Common whelks from Galway Bay, and the four other sampled locations (Bantry Bay, Blacksod Bay, the Irish Sea and the North West Irish whelk fishery stock). Female Common whelks from the Irish Sea become sexually mature at a smaller size than in the other sampled locations, however this was a sex-specific observation. Evidence of size at sexual maturity in the present study suggests therefore that the population of Common whelks in Galway Bay may be distinctly different from those in other locations, including the North West Irish whelk fishery. Similar differences between populations have been reported from other waters (Valentinsson *et al.*, 1999; Martel *et al.*, 1986a; Gendron, 1992).

Author	*Size at Maturity Females (mm)*	*Size at Maturity Males (mm)*	*Age at Maturity (years)*	*Location*
Santarelli *et a.l* (1986)	55	55		France
Hancock and Simpson (1962)	55	55		Britain
Gendron (1992)	Unavailable	49 - 76	5 - 6	Eastern Canada
Gunarrson and Einersson (1995)	Unavailable	45 - 80		Iceland
Valentinsson *et al* (1999)	51.5 – 71.5	53.5 – 71.9	6 - 9	Sweden
Fahey *et al* (2001)	Agrees with all above	Agrees with all above		Irish Sea
Martel *et al.* (1986a)	70 - 80	70		Eastern Canada
Bell and Walker (1998)	Not assessed	55		South Coast England
Bell and Walker (1998)	Not assessed	Poorly determined in relation to size		Thames Estuary, England
Bell and Walker (1998)	Not assessed	71		East Coast England and Wales

Table 3.4 Reported estimates of Size and Age at Maturity for *Buccinum undatum*, determined by gonado-somatic indices.

The influence of predation pressure, either from natural predators, or from fisheries, could account for variation in size at onset of sexual maturity (Martel *et al.*, 1986; Gendron, 1992). Gendron (1992) observed that *B. undatum* matured at smaller sizes and ages in the presence of large crustacean predators, such as lobsters, when compared to populations from benthic assemblages where these predators are not represented. Gendron (1992) also reports variation in shell morphometry within the region of the Gulf of St. Lawrence, Canada, suggesting that growth of robust shells, for example, may delay the onset of sexual maturity in affected populations. There was no variation found in shell morphometry between locations by canonical discriminant analysis in the present study, however. Martel *et al.* (1986a) reports smaller size at sexual maturity in regions of long-term selective pressure, a consequence of heavy fishing, than compared to populations subjected to reduced predation. Fisheries select for the reproductive portion of the population in the Martel *et al* analysis, and also in the present study of the North West Irish whelk fishery. Around the coast of Ireland, the Irish Sea has the longest history of whelk exploitation, with peak landings in the mid 1990's (Fahy *et al.*, 2000). Smaller size at first maturity was observed in the Irish Sea than in the region of the more recently exploited North West Irish whelk fishery. The findings of the current investigation support the findings of Fahy *et al.* (2000) and Kideys *et al.* (1993) for size at onset of sexual maturity in the Irish Sea. Anecdotal evidence of increased crustacean predator influence in the North West Irish whelk fishery as opposed to the Irish Sea (Fahy, Pers. Comm.), does not appear to influence the size at onset of sexual maturity, as suggested by Gendron (1992). However, with increasing commercial pressure in the region of the North West Irish whelk fishery, mature individuals may be fished before contributing to the stock. The smaller size in the onset of sexual maturity observed in Galway Bay, observed in the present study, is unlikely to be due to intensive exploitation of the mature population (as fishing operations are not extensive) but rather suggest the effects of local conditions.

That variation in the size at onset of sexual maturity in *B. undatum* may be influenced by local conditions, such as different food, habitat preferences, or a combination during different life stages, has been referred to in the past by numerous authors (Himmelman, 1988; McQuinn *et al.*, 1988; Himmelman and Hamel, 1993; Rochette and Himmelman, 1996). Valentinsson *et al.* (1999) observed that smaller individuals live in shallower waters than larger ones, reflecting differences in growth, and size and age at first maturity. Onsite whelk density and food availability have also been put forward as hypotheses for the regulation of size at sexual maturity. In the Gulf of St Lawrence, Canada, Gendron (1992) found the smallest size at first maturity at the most southerly site examined, Magdalen Island, suggesting latitudinal variation in water temperature. Further, results of the present analysis suggest that whelks in the region of the North West Irish whelk fishery mature at larger sizes and higher ages than those in Canadian waters (see Table 3.4), despite European winter waters being warmer than Canadian summer water temperatures (Martel *et al.*, 1986a; Gendron, 1992). If the potential artifact of temporal variation between sampling of locations is ignored, the current study does not support the hypothesis that the size at onset of sexual maturity in Common whelks varies with latitudinal variation in water temperature. Factors such as current speed and direction, and exposure to regular storm effects were not investigated in the current study, and yet may contribute to local variation in the observed results. A number of studies cite benthic development and sedentary adult habit as factors reducing the movement of *B. undatum* populations (Valentinsson *et al.*, 1999; Morel and Bossy, 2003), creating stocks likely to be highly responsive to location conditions. Some variation between populations may be due to the presence of distinct local stocks. Gendron (1992) suggests that distinctly different stocks may occur over very short distances. It is recommended therefore that further investigation of spatial scales be taken within the region of the fishery in order to take into account the possible influences of sediment type and depth.

Chapter 4

Reproductive Cycle of the Neogastropod Buccinum undatum, in the Region of the North West Irish Whelk Fishery

INTRODUCTION

Studies of reproduction in subtidal neogastopods have historically focused on the examination of reproductive anatomy and egg-laying bahaviour (Dakin, 1912; Hancock, 1967). Increasingly, systematic observations of the seasonal patterns of reproductive events, including changes in the size of body components and gonadal histology, are described for neogastropods. Takmaru and Fuji (1981) and Takahashi *et al.* (1972) first described systematic seasonal patterns of reproductive events in *Neptunea arthritica.* More recently, Ward and Davis (2002) described systematic seasonal reproductive patterns in *Turbo torquatus*, Olabarria and Ramirez-Llondra (2004) in *Amphissa acutecostata* and *Gymnobela subaraneosa*, and Cledón *et al.* (2005) described the gonadal cycle of *Adelomelon brasiliana.*

Aspects of reproductive anatomy and strategy of the Common whelk, *Buccinum undatum* have been described in detail. Mating begins with the aggregation of whelks caused by the movement of males toward gravid females of the species (Martel *et al.*, 1986a,b). During copulation, spermatozoa from the male seminal vesicle are deposited in the female bursa, where shortly afterwards they are transferred to the seminal receptacle. Fertilization occurs as eggs are passed through the pallial oviduct (Webber, 1977). Mating whelk exhibit a high degree of polygamy, and the reproductive strategy allows eggs to be released over a prolonged period, thus ensuring the reproductive success of this species (Martel *et al.*, 1986a). During a major egg-laying period, eggs contained in capsules are laid directly on to hard substrates of the benthos by females of the species. The larval stages of *B. undatum* occur within the egg capsules and juveniles emerge to begin their benthic life directly (Fretter and Graham, 1962). A number of studies have investigated copulation and egg laying in *B. undatum* (Hancock, 1967;

Martel *et al.,* 1986b; Himmelman and Hamel, 1993; Kideys *et al.,* 1993; Valentinsson, 2002) and it is widely accepted that the timing of these events varies with location (Valentinsson, 2002).

Martel *et al.* (1986a) first described systematic observations of the timing of reproductive events in *B. undatum* from the Gulf of St. Lawrence, Canada. In an annual event at the onset of breeding, the mass of the female ovary and pallial oviduct increases steadily, with the production of lipid-rich oocytes. The mass of these organs declines abruptly again when egg masses are deposited following fertilization. Concurrently in male Common whelk, the mass of the testes increases as a result of sperm production. The size of the testes decline again when sperm are transferred to the seminal vesicle prior to copulation, and this is represented by an increase in the size of the latter organ (Martel *et al.,* 1986a). More recently, the use of gonadal indices, based on the pattern of the reproductive cycle in *B. undatum,* have been used in the analysis of feeding behaviour and energetic costs in this species (Himmelman and Hamel, 1993, Kideys *et al.,* 1993; Brokordt *et al.,* 2003).

B. undatum is a commercially important species in Irish coastal waters (Fahy *et al.,* 2000). Historically, it has been fished on the East coast of Ireland, in the Irish Sea, and in recent years the fishery has expanded to include the area east of the Inishowen Peninsula, in North West Ireland. However, very little is known about the timing of reproductive events in this region, or for any of the waters surrounding the coast of Ireland. Systematic observations of the timing of reproductive events in the region of the North West Irish whelk fishery are required for a better understanding of the population dynamics that regulate the stock. Knowledge of the reproductive cycle of an exploited species has implications for determining vulnerability to overexploitation and the implementation of control measures (Ward and Davis, 2002). The present study will use variation in the size and mass of body components, and gonadal histology to determine the annual pattern of reproductive events, and describe the reproductive cycle in the population of *B. undatum* in the region of the North West Irish whelk fishery. The sex ratio of the exploited stock will also be determined.

METHODS

Field collection and laboratory dissection

Samples were collected during commercial fishing operations on a variety of fishing vessels at approximately monthly intervals from June 2003 through to May 2004. Samples were not collected in September 2003 and March 2004 due to a cessation in commercial fishing operations and lack of independent sampling opportunities. Approximately ten individuals were arbitrarily collected from 5 pre-defined size classes, measured with calipers from the end of the siphonal canal to the tip of the apex; <49 mm, 50 – 69 mm, 70 – 89 mm, 90- 109 mm and >110 mm. Samples were collected throughout the area of the North West Irish whelk fishery, east of the Inishowen Peninsula, Co. Donegal. During off-season periods, samples were collected as by-catch from the brown crab fishery, which operates in the same geographic region. Sampling depth was typically 44 m and sediment was a soft bottom ranging from mud, to sand and coarse grains. After collection, samples were frozen in a domestic freezer to temperature of -10°C and transported to the laboratory at GMIT, Galway.

Samples were completely defrosted in sealed plastic freezer bags for further analysis. Defrosting time varied with air temperature. The total shell length was measured using calipers and recorded to the nearest millimeter. Individuals were weighed to the nearest 0.01 g. The shell was then cracked under gentle pressure in a bench vice and fragments of the shell removed piecemeal with forceps. Each sample was drained on a paper towel for 2 minutes and the soft weight determined. The mantle was removed and the sex of each sample determined, predominately by the presence or absence of a conspicuous penis. In female whelk, the colour of the capsule gland, which encapsulates eggs after fertilization, was recorded and size measured in millimeters. An analysis of variance was conducted to test the null hypothesis that there is no variation in capsule gland size with time. In male and female whelks, the digestive gland and gonad were removed and weighed together to the nearest 0.01 g. The mass of the combined digestive gland and gonad were determined as a proportion of the total soft body mass. An analysis of variance was conducted to test the null hypothesis that there is no variation in combined gonad and digestive gland mass with time in male and female Common whelks.

The sex ratio of the sampled stock was determined for the whole sampled population, and for the sexually mature sampled population, deemed to be greater than 70 mm total shell length (see Chapter 3). A Chi-Square test was conducted test the null hypothesis that there is no departure from a 1:1 ratio in numbers of male and female Common whelk in the sampled population.

Histology

The female ovary and male testis were dissected away from sexually mature whelk were preserved in buffered formalin for a minimum of 24 hours. The tissue was then divided into sections of approximately 0.25 cm^2 thickness and prepared for sectioning by placing in a solution of 3.5 mol DMSO in 0.5M sucrose and buffered saline until saturation (approximately 1 hour). Sections of tissue were removed from the solution and covered with embedding compound. The sections were then plunged into hexane and dry ice to freeze at -70°C. For each individual sample, sections 7 µm thick were cut using a Leica Kryostat and collected on slides coated in albumen, and left for a period of 24 hours. Slides were then stained with eoisin in a Leica stainer and mounted for examination.

The female ovary was examined at 200x magnification for the condition of oocytes; immature, growing and mature. The diameter of oocytes cut through the nucleus was determined where possible. The male testis was examined at 400x magnification to detect seasonal changes in the testicular tubules (cavities of tissue where gametogenesis proceeds) through the identification of spermatogonia, spermatocytes and spermatozoa.

RESULTS

Seasonal Change in Female Organ Size and Histology

One-way analysis of variance demonstrates that female whelks show variation in the size of the capsule gland with time (ANOVA, P=0.000; see Fig 4.1). Data were log transformed to meet the assumption of homogeneity of variances, and data were normally distributed (Anderson-Darling, P>0.05). The capsule gland increased progressively in size in August and October 2003, and reached maximum mean size in November 2003. The capsule gland was observed to be bright white during October and November 2003, whereas in previous and subsequent monthly samples, it was observed to be off-white in colour. Post-hoc comparison of 95% confidence intervals show that the mean size of the capsule gland in October and November 2003 was significantly different to each of the other 6 months sampled in the current study (Tukey's family error rate). This was likely to reflect the loss of encapsulated eggs following an egg-laying period, and this was supported by anecdotal evidence of fishermen hauling egg-masses attached to fishing equipment from November 2003 to the early months of 2004. From November 2003 through to February 2004, the size of the capsule gland declines progressively. In April and May 2004, the capsule gland appeared to show a trend of increasing size. No observations of capsule gland size were recorded in June and July 2003, as the organ was not obvious in laboratory dissections.

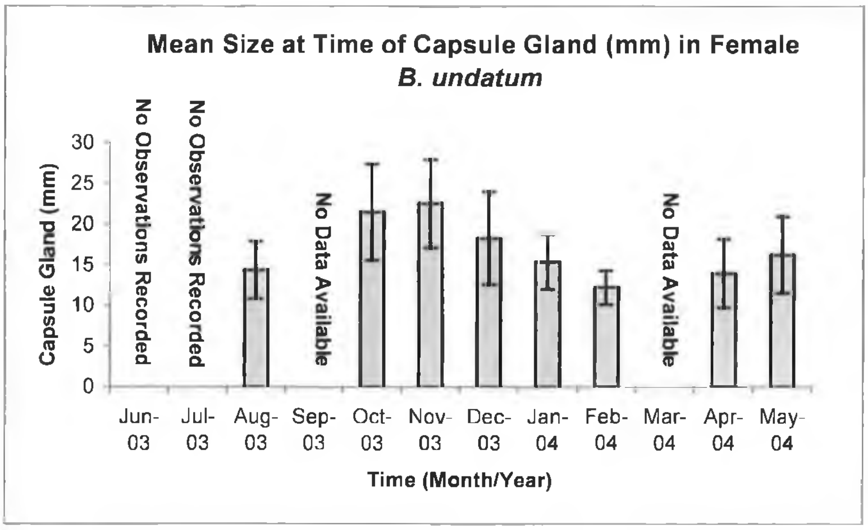


Figure 4.1 Mean size and standard deviation of female capsule gland with time. No observations were recorded in June and July 2003, and data were not available in September 2003 and March 2004.

One-way analysis of variance demonstrates that the combined mass of the female gonad (ovary) and digestive gland as a proportion of the total soft body mass shows variation with time (ANOVA, P=0.021; see Fig 4.2). Data were log transformed to meet the assumption of homogeneity of variances, and are normally distributed (Anderson-Darling, P>0.05). The ovary and digestive gland reached maximum mass in October and November 2003, simultaneously with the maximal size of the capsule gland. The mass of the combined ovary and digestive gland declined slightly in December 2003, and dramatically in January 2003. Post-hoc analysis of 95% confidence intervals shows that the mass of the ovary and digestive gland is significantly higher in October and November 2003 than in January 2004 (Tukey's family error). The decrease in combined organ mass may reflect a loss of oocytes from the ovary at reproduction. A trend of gradually increasing mass of the combined organs is observed from January 2004 through to May 2004, and to decline from June to August 2003.

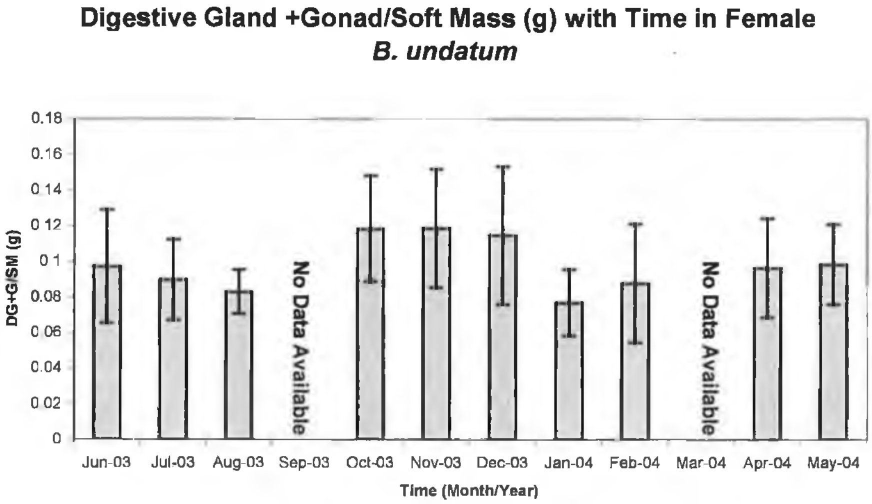


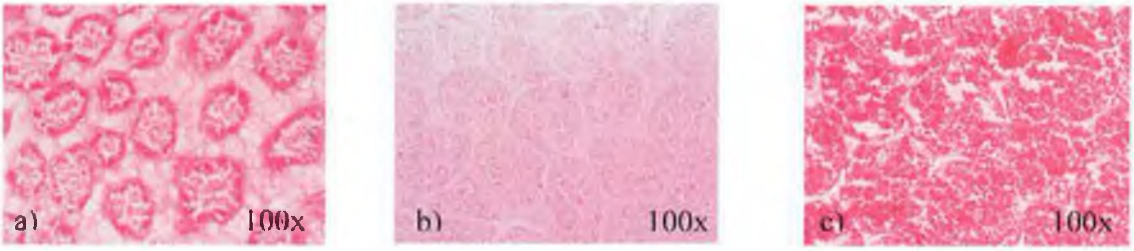
Figure 4.2 Mean mass and standard deviation of female digestive gland and ovary, as a proportion of total soft mass, with time.

Oogenesis

Oogenic condition in female *B. undatum* varied with time in the present study. Females in different stages of oogenic development could be found at any given time throughout the 12-month period of analysis. However, most individuals showed distinctive, synchronous changes in oogenic condition with time. At the commencement of the present analysis, in June 2003, and through to December 2003, the majority of female ovaries contained mature oocytes. During this time oocytes were large, at 120 – 270 μm in diameter (see Photo 4.1.c). Oocytes were observed to be largest from October to December 2003, indicating vitellogenesis and the production of granular yolk globules. Histological sampling was more difficult at this time due to the large size, consistency and fragility of the ovary. From November 2003 to February 2004, tubules of immature oocytes were observed in female ovaries (see Photo 4.1.a), and follicular cells at the pallial epthelium surround young oocytes. During November and December 2003, female ovaries showed either exclusively fully mature oocytes or exclusively immature oocytes. The incidence of both stages at the same time suggests that reproduction has occurred in some, but not all individuals. The appearance of immature oocytes also coincided with declining size of the capsule gland and mass of the ovary in January and February 2004. In January and February 2004, and through to May 2004, oocytes were observed to be small and developing around the ova, with most being < 120 μm in diameter and suggesting growth in the ovary. This period coincided with increasing mass of the combined ovary and digestive gland. Three successive stages of developmental oogenesis were defined in the present study, and described in Table 4.1 and Figure 4.3.

Stage of Oogensis	**Description of Oogenic Stages**	**Photographic Description**	**Major Time of Observation (see Fig 4.3)**
A	Immature oocytes; thickening of the pallial epithelium	Photo 4.1.a	November 2003 – February 2004
B	Growth phase; oocytes small and developing, < 120 μm	Photo 4.1.b	January and February 2004
C	Mature oocytes, > 120 μm	Photo 4.1.c	June to December 2003; April 2004

Table 4.1 Description of 3 stages of oogenic development in female *B. undatum* from the region of the North West Irish whelk fishery, and reference to photographic description and proportions of observations.



Photos 4.1 a-c: Histological photographs of mature female *B. undatum* gonads from individuals >90 mm total shell length: a) November 2003, oocytes absent following reproduction and egg-laying ; b) June 2003, oocytes immature and developing; c) November 2003, oocytes mature.

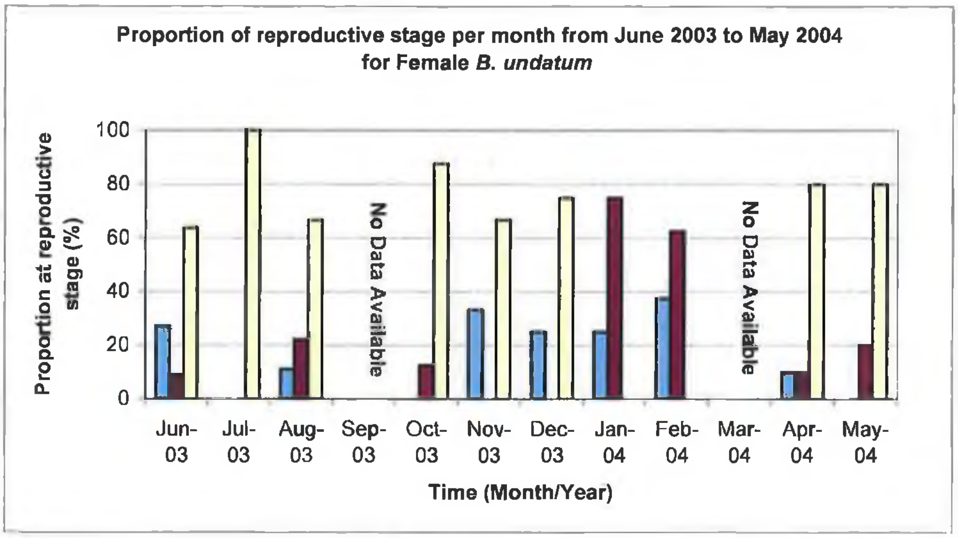


Figure 4.3 Proportion of mature female *B. undatum* samples at reproductive stage. Blue - Immature oocytes; thickening of the pallial epithelium; Red - Growth phase; oocytes small and developing, < 120 μm; Yellow - Mature oocytes, > 120 μm. N = 50.

Seasonal Change in Male Organ Size and Histology

One-way analysis of variance demonstrated that the combined mass of the male gonad (testis) and digestive gland as a proportion of total soft body mass varied significantly with time (ANOVA, P=0.000; see Fig 4.4). Data were log transformed to meet the assumption of homogeneity of variances and were normally distributed (Anderson-Darling, P>0.005). The mass of the combined organs reached two peaks, in June 2003 and October 2003. The minimum mass of the combined organs occurred in January 2004. Post-hoc analysis of 95% confidence intervals found that the mass of the combined organs varied significantly between June 2003 and January 2004, and between October 2003 and January 2004, but that there was no difference between all other months (Tukey's family error). From October 2003 through to January 2004, a trend was observed in the mass of the combined testis and digestive gland, which progressively decline, and increase from January 2004 through to May 2004.

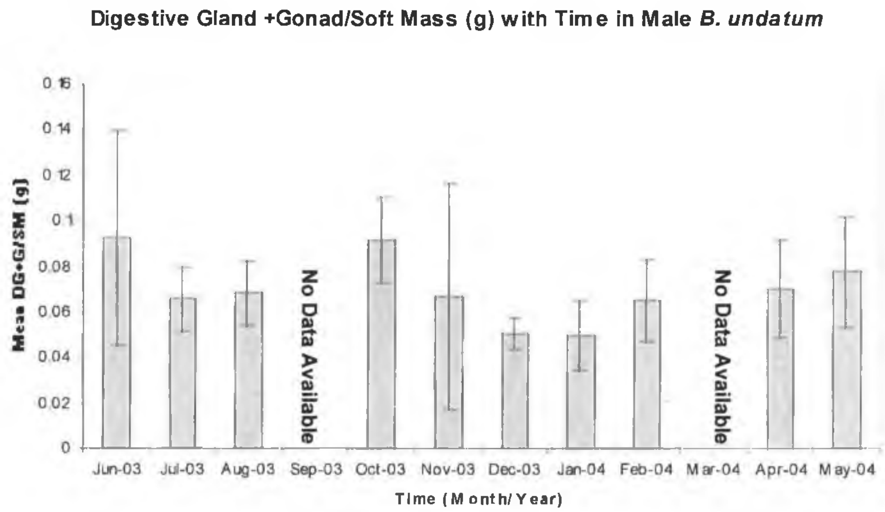
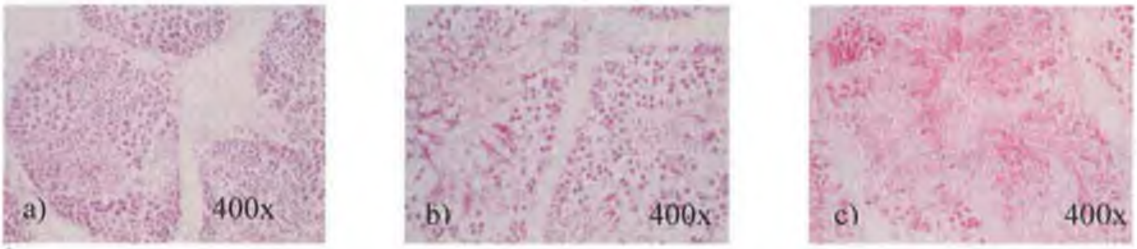


Figure 4.4 Variation in mean mass of male digestive gland and testis, as a proportion of total soft mass, with time.

Spermatogenesis

Histological analysis of male *B. undatum* testis showed variation in gametogenic development throughout the period of the present study. At the commencement of the present investigation in June 2003, the majority of individual male testis showed small tubules with phagocytic cells clustered at the centre, and separated from the germinal epithelium. Some individuals in June and July 2003 demonstrated development of the germinal epithelium, and an absence of phagocytic cells, with the appearance of small, undifferentiated cells that are likely to be spermatogonia and nutritive cells. In July 2003, small spermatogonia cells and spermatozoa appeared in the centre of tubules in samples of male testis. From August to October, and in November and December 2003, spermatozoa are abundant and fill the centre of large tubules in most male testis samples. The germinal epithelium was also observed to decrease in thickness compared with previous months. Testes containing misshapen tubules, reduced in cytoplasmic volume, void of any cells, or containing only phagocytic cells, were observed in almost half of November and December 2003 samples, and dominated the samples observed in January – April 2004. During November and December 2003, two gametogenic stages of development were observed simultaneously: abundant in spermatozoa or void of any cell type. The incidence of both these developmental conditions suggests that sperm has been transferred for reproductive purposes in some, but not all, individuals. This coincides with the maximal size and loss of mature oocytes from the female ovary at this time, and suggests that reproduction in the species *B. undatum* occurred in early winter, November and December 2003.



Photos 4.2 a-c: Histological photographs of mature male *B. undatum* gonads from individuals >90 mm total shell length. a) June 2003, cells are reorganising to the germinal epithelium and beginning to differentiate; b) August 2003, further differentiation of the cells and appearance of spermatozoa; c) November 2003, spermatozoa are plentiful and accumulating in the lumen.

Four successive gametogenic stages were defined for male *B. undatum* in the present study, and described in Table 4.2 and Figure 4.5.

Stage of Spermatogenesis	Description of Spermatogenic Stage	Photographic Description	Major Time of Observation (see Fig 4.5)
A	Aggregation of phagocytes in the centre of tubules	Not Available	June 2003; November 2003 – May 2004
B	Development of the germinal epithelium; absence of cells in the centre of the tubules; undifferentiated cells (spermatogonia)	Photo 4.2.a	June – July 2003; May 2004
C	Spermatozoa appear in lumen of tubule	Photo 4.2.b	July 2003
D	Spermatozoa abundant and accumulating in lumen; germinal epithelium decreases in thickness	Photo 4.2.c	August – December 2003

Table 4.2 Description of 4 stages of gametogenic development in male *B. undatum* from the region of the North West Irish whelk fishery, and reference to photographic description and proportions of observations.

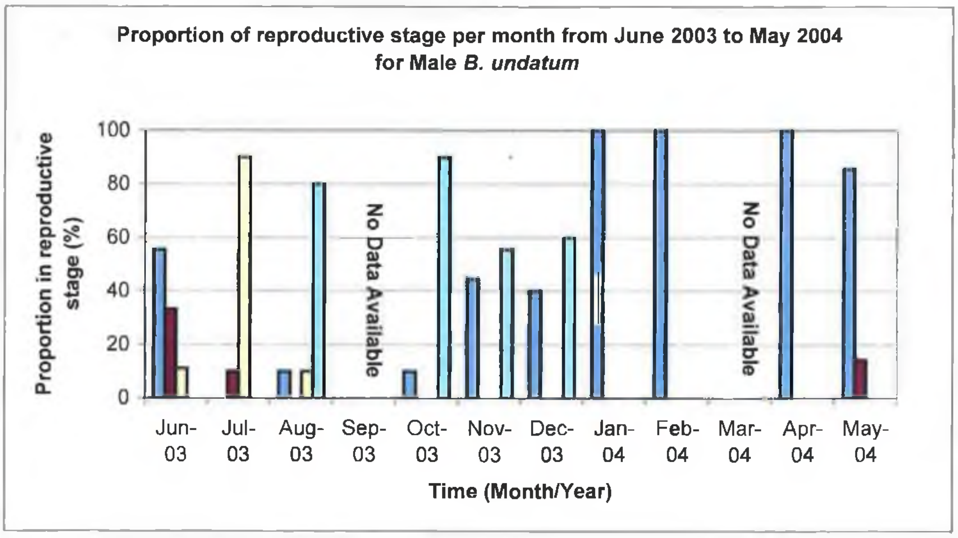


Figure 4.5 Proportion of mature male *B. undatum* samples at reproductive stage. Dark Blue - Aggregation of phagocytes in the centre of tubules; Red - Development of the germinal epithelium; absence of cells in the centre of the tubules; Yellow - Spermatozoa appear in lumen of tubule; Light Blue - Spermatozoa abundant and accumulating in lumen.

Sex Ratio of the Sampled Stock

The overall sex ratio of the sampled stock was determined with time (month) for the whole sample population (see Figure 4.6). For the sampled population, the observed ratio of male to female Common whelks does not depart from the expected 1:1 ratio at the 95% confidence limit for the duration of the present study (whole population χ^2 P=0.084). The overall ratio of whole numbers of individuals (f/m) = 1.05.

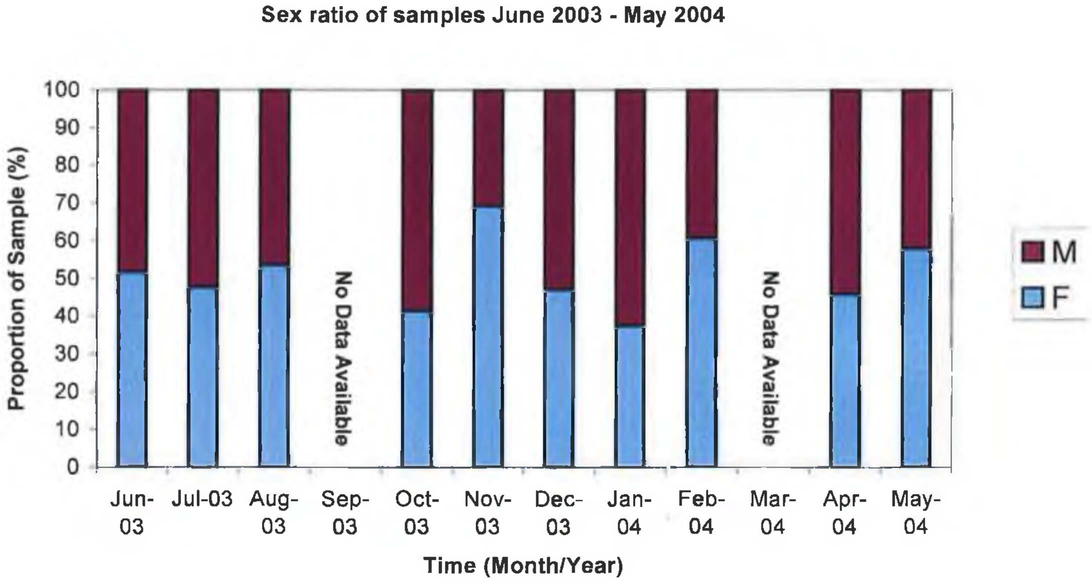


Figure 4.6 Variation in sex ratio (%) of sampled stock, with time. Chi Square test P=0.084.

DISCUSSION

Reproductive investigations from monthly samples of whelks in the present study, suggests that the egg laying period for *B. undatum* in the waters of the North West Irish whelk fishery occurred between October and December in 2003, and terminated prior to January 2004. This conclusion is supported by anecdotal evidence of *B. undatum* egg-masses appearing on fishing equipment during this time and into the early months of 2004. Early studies have suggested that egg-laying occurs throughout the year in *B. undatum* (Thorson, 1946). Recent research on European populations, which states that breeding occurs between autumn and winter, with egg laying occurring from winter to early spring (Fretter and Graham, 1984; Kideys *et al.*, 1993), provides evidence supporting that recorded in the current study (see Table 4.3). Breeding and egg laying have been reported to occur earlier in Swedish waters (Valentinsson, 2002). Studies from the Gulf of St. Lawrence, Eastern Canada, have determined that breeding occurs there in the spring, commencing in mid-May with a peak in mid-June, terminating prior to July, with egg laying in the summer months (Martel *et al.*, 1986; Himmelman and Hamel, 1993). Martel *et al.* (1986) suggest that variation in the timing of the reproductive cycle in *B. undatum* between European waters and those of Eastern Canada may be due to seawater temperatures, with recorded winter water temperatures in Europe higher than the average summer temperature in the Gulf of St. Lawrence.

Author	***Annual Time of Breeding***	***Annual Time of Egg-Laying***	***Location***
Fretter and Graham (1984)	Autumn - Winter	Winter – Early Spring	Europe
Kideys *et al* (1993)	Autumn - Winter	Winter – Early Spring (Late Dec - January)	Isle of Man
Martel *et al* (1986a)	Mid May	Late May – August	Eastern Canada
Himmelman and Hammel (1993)	Late May - June	June – August	Eastern Canada
Hancock (1967)	Unavailable	Early Winter	England
Valentinsson (2002)	September	Autumn (October – December)	Sweden
Thorson (1946)	Unavailable	Throughout Year	Sweden and Demark
Sykes (1903)	Unavailable	May - June	Scotland

Table 4.3 Reported annual time of breeding and egg laying in *B. undatum* at various locations.

The results of the present study suggests an annual breeding cycle, where reproduction occurs in early winter, for the whelk population in the region of the North West Irish whelk fishery. In Canadian waters, Himmelman and Hamel (1993) observed that reproduction occurred within the same period over 2 annual cycles, with 2 weeks variation. Valentinsson (2002) reports that in Swedish waters reproduction occurred in autumn over an 18-month study period. Hancock (1967) observes that in England, breeding in *B. undatum* occurs annually, during declining temperatures. Further breeding cycles need to be investigated for the North West Irish whelk fishery in future years to confirm that the cycle described in the present study is typical for this region.

A number of studies have reported parallel changes in the size of the female ovary and pallial oviduct to a maximum size prior to breeding, as indicators of reproductive activity (Martel *et al.,* 1986; Himmelman and Hamel, 1993; Valentinsson, 2002). The size of these two organs declined abruptly in the latter studies, following breeding and egg-laying. Evidence of recent copulation can also be seen by the presence of sperm in the bursa or seminal receptacle of female whelk (Martel *et al*, 1986b; Himmelman and Hamel, 1993; Valentinsson, 2002). Combined, variation in the mass of body components, and the presence of sperm in female whelks provide strong evidence of recent reproduction. The timing of reproduction was determined following detailed histological observation in the present analysis. Determination of eviscerated mass and the presence of sperm in the bursa were not possible in the present study, as the samples were frozen on collection from commercially operating fishing vessels. It is recommended that for future analysis, samples should be preserved immediately on capture in formalin and seawater as other researchers (Martel *et al.,* 1986a; Valentinsson, 2002) have found this method to be more successful.

The present study described three stages of oogenic development, and four stages of spermatogenic development for *B. undatum* in the region of the North West Irish whelk fishery. Martel *et al.* (1986a) described patterns of gametogenic development in *B. undatum* from the Gulf of St Lawrence, Canada, which vary in time of onset to the present analysis. Histological examinations of the male testis in the present study found that most male whelk are at the same gametogenic stage at any time, an observation also made by Martel *et al.* (1986a).

In Canadian waters, Martel *et al.*, (1986a) and Himmelman and Hamel (1993) observed that in male *B. undatum*, the seminal vesicle showed parallel development with the female ovary and pallial oviduct, increasing in size as sperm is transferred and stored from the testis in preparation for breeding at the end of winter. At the time of reproduction, the testes were described as small and undeveloped, having achieved maximum size in the previous summer (Martel *et al.*, 1986a; Himmelman and Hamel, 1993). The absence of sperm from the male seminal vesicle indicated that copulation had occurred in the Martel *et al.* (1986a) study. The maturation of male sex cells in the testis some months prior to the suggested timing of copulation, and the presence of immature sex cells at the time of copulation was not observed in the present study, due to a number of reasons: a) In histological analysis, parallel stages of development of spermatozoa and oocytes were observed between male and female samples in October, November and December 2003, with the absence of mature sex cells observed in both sexes in January and February 2004. This, coupled with a lack of mature male sex cells in the previous summer months, suggests simultaneous development of the ovary and testis. b) Sampling over the identified breeding period occurred at irregular intervals of between 3 and 5 weeks, and did not occur in September 2003. Thus sperm transfer from the testis to the seminal vesicle, prior to the loss of mature oocytes from female whelk, may not have been observed. However, this theory requires further investigation as the mean mass of the male testis and digestive gland increased from January to May 2004, further suggesting recent loss of sex cells due to copulation in December 2003. The sizes of the seminal vesicle, and independent analysis of the digestive gland and testes, are not presented in the current study due to the rapid deterioration of these organs with freezing.

Variation in the combined mass of the testis and digestive gland in the present study may be an artifact of the highly variable mass of the digestive gland, which decreases in size with reduced feeding activity at the onset of breeding, regardless of when breeding occurs (Hancock, 1967; Himmelman and Hamel, 1993; Valentinsson, 2002). The relatively high combined mass of the digestive gland and gonad in male and female whelks during the fishing period in June 2003 may be fishing-pot related, whereby whelks have recently fed on bait. Martel *et al.* (1986a) observed seasonal changes in feeding activity in *B. undatum*, and found that feeding activity followed a distinct annual pattern; feeding activity is much reduced during breeding activity.

Martel *et al.*, (1986a) observed no resting period for female whelks at the end of oogenesis, but rather, renewed ovarian development commenced shortly after gamete release. By contrast, in the male testis, following sperm transfer, there was a distinct period of phagocytosis. Similar patterns of development were observed between the sexes in the present investigation, where female ovarian development had occurred in most samples by April 2004, and male development delayed until at least May 2004 in some specimens.

Martel *et al.* (1986a) and Rochette *et al.* (2001) report that not all mature female whelks reproduce each year in the Gulf of St Lawrence, Eastern Canada. Further, Gendron (1992) observes that large whelk, during the breeding period often show lower gonadal indices than smaller individuals, indicating that larger animals may not reproduce every year. Valentinsson (2002) however, found that all mature female whelks in Swedish waters spawn equally as often, regardless of size, and that the number of hatchlings increases with maternal size. In the North West Irish whelk fishery, it is possible that those large mature female specimens observed in the present study to be in oogenic Stage A in November and December 2003, are perhaps abstaining from reproduction in that year. The present study demonstrated that the sex ratio of the sampled stock does not depart from the 1:1 ratio for male and female whelks for the overall period of the current study. However, a notable increase in captured females as a by-product of the brown Crab fishery in November 2003 may represent the greater risk taken by females to obtain food during the breeding months (Rochette *et al.*, 2001). As commercial whelk fishing does not take place in November, it is unlikely that selection of female whelks will bear any impact on the future of the stock at this time. However, it is recommended that fishing operations be monitored in the future to ensure that large, sexually mature females are not removed from the fishery during the breeding months.

The present study found that breeding and egg-laying occurred from October to December 2003 in *B. undatum* from the region of the North West Irish whelk fishery. Timing of breeding and egg-laying is supported by systematic observation of changes in the size and mass of body components, and gonadal histology. In female Common whelks, the capsule gland increased significantly in size during November 2003, suggesting activity in preparation of egg deposition. Further, the combined mass of the ovary and digestive gland peaked in October and November 2003, suggesting the gonad was ripe with lipid-rich oocytes, and coinciding with the presence of mature oocytes in the histological sections of the ovary in samples. Evidence of decline in capsule gland size, combined digestive gland and gonad mass, and the appearance of immature oocytes in January 2004 suggest that breeding activity has ceased. In male *B. undatum*, combined digestive gland and gonad mass peaked in October 2003 and declined thereafter. Spermatozoa were also found to be abundant in the male testis from August to December 2003, and replaced with phagocytic cells in the following months. The appearance and subsequent disappearance of mature sex cells occurred successively and simultaneously in both sexes. The sex ratio of the sampled stock did not depart significantly from the 1:1 ratio throughout the present study.

General Discussion

To sustainably manage the exploitation of fisheries resources, the population biology of fished species must be understood. In 2003, fishing for the Common whelk, *Buccinum undatum*, intensified in the region east of the Inishowen Peninsula, North West Ireland. Previous experience of Common whelk fisheries on the East Coast of Ireland, and the Gulf of St. Lawrence, Canada, indicates that populations of *B. undatum* are subject to overexploitation due to certain life history characteristics, including slow growth, high age at first reproduction, lack of a planktonic dispersal stage, and limited adult migration. Further, the species demonstrates local variations in biology, including size at maturity and size at age (Gendron, 1992; Valentinsson *et al.*, 1999). The population and life history parameters estimated in one location therefore cannot be reliably applied in another for the purpose of fisheries stock management. Very little is known about *B. undatum* in the region of the North West Irish whelk fishery, in spite of a general abundance and commercial interest. Therefore, in order to evaluate the potential of the fisheries resource in the area of the emerging fishery, the current study was initiated to investigate biological aspects of the species.

The current study assessed the spatial distribution of whelks and estimated stock density in the region of the North West Irish whelk fishery. Analysis of variance of randomly measured replicates of total shell length of whelks landed in fishing pots, fishing strings, and on board fishing vessels was conducted. The size range of the stock was found to vary significantly over the spatial scale of pot area of attraction. However, there was no variation in mean catch size at the spatial scale of string area of attraction. A number of methods were employed to determine the density of the stock, including area of attraction to baited pots. Two estimates of area of attraction were applied in the analysis from Kideys (1993) and Himmelman (1988), yielding results of 0.134 and 0.227 whelks per m^2 respectively. Leslie-Davis depletion estimate models of whelk abundance from Catch per Unit Effort (CPUE) to the fishery, and from a Mark Re-Capture program both yielded estimates of 0.172 and 0.219 whelk per m^2 respectively. CPUE from March to

July 2003 was steady for approximately half the observed whelk-fishing season from, and then gradually declined.

The size at age and growth of *B. undatum* was investigated in the region of the North West Irish whelk fishery. The results of two independent methods of age determination were presented in the current study. Firstly, modal separation of the length frequency of whelks landed to the fishery was modeled using the NORMSEP method. Secondly, numbers of striae in individual opercula were analysed, where each striae corresponds to annual growth. The sizes at age determined by these two independent methods were in strong agreement and an age at length key for the stock was presented (see Chapter 2). Von Bertalanffy growth parameters were estimated for the target stock in the region of the North West Irish whelk fishery. Asymptotic length, $L\infty$ values of 151.64 mm and 137.43 mm and Brody growth coefficient, K values of 0.04 and 0.12 were estimated from analysis of the length frequency distribution and striae in individual opercula respectively. Von Bertalanfy parameters values estimated in the current study compared well with those found in other European populations of *B. undatum*, including northern French waters (Santarelli and Gros, 1985). Common whelks in the region of the North West Irish whelk fishery grow at slower rates and achieve larger sizes than in other observed commercial populations.

The size and age at onset of sexual maturity were estimated for male and female Common whelks in the region of the North West Irish whelk fishery. Male size at onset of sexual maturity was determined following validation of the assumption that sexual maturity occurs when the penis is greater than or equal to half the individual total shell length. The presence of mature sexual cells in the yellow coloured ovary was taken to represent sexual maturity in female Common whelks. Size and age at onset of sexual maturity occurs simultaneously between the sexes in the area of interest. Male Common whelks achieve sexual maturity at 83.30 ± 10.77 mm total shell length, and 8.9 – 11.1 years of age. Female Common whelks obtain sexual maturity at 82.62 ± 10.68 mm total shell length, and 8.8 – 11.1 years of age. Maturity ogives of the proportion of male and female whelks landed to the North West Irish whelk fishery at age were presented (see

Chapter 3). The present study compared size at onset of sexual maturity in *B. undatum* in the region of the North West Irish whelk fishery, east of the Inishowen Peninsula, with other populations of Common whelk from Irish coastal waters. Whelks in the area of interest were shown to mature at larger sizes with respect to other Irish populations, and in comparison to European and Canadian commercial populations of Common whelk.

Systematic observations of changes in the reproductive cycle were described for *B. undatum*. The presence of mature sex cells in the majority of mature male and female gonads, coupled with development in mass and size of the female ovary and capsule gland, and the male testis in the autumn and winter months of October through to December 2003, indicated the onset of breeding activity. The subsequent reduction in mass and replacement of mature sex cells with immature cells, in the male and female gonads in January 2004 suggested that breeding is complete and egg-masses had been deposited. Evidence from other populations of Common whelk in European and Canadian waters suggested that annual reproductive events probably occur at the same observed time every year, with little variation (Fretter and Graham, 1984; Martel *et al.*, 1986a; Kideys *et al.*, 1993).

Common whelk is likely to be a valuable fisheries resource in North West Irish waters, in the region east of the Inishowen Peninsula. The present study demonstrated that the species occurs frequently, is easily fished, and grows to a large size in the region of interest. According to population growth logistical equations, sustainable stock exploitation is possible when population abundance decreases because of the compensatory mechanism of reduced competitive interaction (Stoner and Ray-Culp, 2000). In the present study, CPUE declined following a sustained period of exploitation. However, slow growth and late sexual maturation in *B. undatum* in the region of the North West fishery condition the resource to overexploitation. This is particularly so if the population were to fall below a critical size or density. The life history characteristics of *B. undatum* determined in the present study suggest a potentially slow recovery rate if over-fishing depletes the population. Many commercially exploited gastropod populations are vulnerable to unsustainable fishing pressure, for example, abalone species (Rogers-Bennett *et al.,* 2002), the Queen conch *Strombus gigas*, in the Carribean Sea (Stoner and Ray-Culp, 2000), and the Argentinean *Zidona dufresnei* (Giménez *et al.,* 2004). Commercially exploited populations of *B. undatum* in the Irish Sea and the Gulf of St Lawrence, Canada, have also shown evidence of depletion (Gendron, 1992; Fahy *et al.*, 2000). Additionally, analyses of the potential of *B. undatum* as a fisheries resource in England an Sweden have highlighted the risk of overexploitation due to biological characteristics of the species in those areas (Valentinsson *et al.,* 1999; Morel and Bossy, 2004). The present study found that reproduction in *B. undatum* occurs outside of the fishing period in the region of the North West Irish whelk fishery, facilitating contribution to the next generation. Furthermore, the present study suggests that the fishing gear selects against small individuals, including new recruits to the fishery during the fishing season. Overexploitation is unlikely to cause elimination of the resource, as demonstrated in long-term analysis of the whelk fishery in the Irish Sea (Fahy *et al.*, 2005). However, over-fishing could lead to undesirable economic and ecological consequences, including reduction in the average size of the stock.

To effectively assess and manage the Common whelk fishery in North West Ireland it is recommended that a dedicated scientific survey continue to evaluate population abundance and biological characteristics of the stock. The present study was conducted over a 12-month period, and does not account for variations in growing conditions in assessments of age and size at sexual maturity. Further, the present study is biased by selectivity of fishing pots as sampling devices. Long-term analysis of fishery effort is necessary to assess stock depletion, and make forward predictions to control and maintain levels of exploitation. Fisheries and species interactions, not assessed in the present analysis, should also be considered as the fishery progresses to understand the importance of these relationships to population fitness and stock rehabilitation.

To develop management strategies for exploitation without jeopardising the long-term sustainable yield of *B. undatum*, regulation of the North West Irish whelk fishery should be considered. Protection should be afforded to large, sexually mature individuals, and the establishment of a minimum catchable size, reflecting size at onset of sexual maturity, may be an appropriate management tool. In the region of interest, size at onset of sexual maturity does not differ between the sexes, and thus size management will protect the whole population. However, in practical terms, size restriction reflecting size at maturity would be difficult to implement, because of variation in this parameter between different populations around the coast of Ireland. An area-specific mesh to sort landings may provide a solution. For the period of the present investigation, fishing occurred outside of the observed reproductive season. However, seasonal fishery closures should be monitored in the future. Heavy exploitation in the absence of catch-size and seasonal fishery closure regulation, thus allowing continuous landings of whelks below the size at sexual maturity, may lead to over-fishing and negative economic growth of the fishery.

Conclusions

This study present results which will extend the knowledge of population dynamics and biological characteristics that regulate the stock of *B. undatum* in the region of the North West Irish whelk fishery:

- The size range of the targeted stock of Common whelk varies significantly over the spatial area of attraction to baited pots, but, does not vary significantly over the larger spatial area of attraction to baited strings of pots.
- The density of the stock was found to be 0.134 – 0.227 whelk per m^2, which compares well with different populations of whelk in locations across Europe and Canada.
- Catch per Unit Effort observed from March to July 2003 was demonstrated to decline following a steady period of fishing in the study region.
- Two independent methods of determining age at size, length frequency analysis and analysis of striae in individual whelk operculum, yielded asymptotic length, $L\infty$, values of 151.64 mm and 137.43 mm, and Brody growth coefficient, K, values of 0.04 and 0.12 respectively.
- There were no sex specific difference in the size at onset of sexual maturity between Male and Female Common whelks in the study region.
- Male Common whelks in the study region achieve sexual maturity at 83.30 ± 10.77 mm total shell length, and 8.9 – 1.1 years of age. Female Common whelks in the study region achieved sexual maturity at 82.62 ± 10.68 mm total shell length and 8.8 – 11.1 years of age.
- Breeding activity occurred in the autumn and winter months of October through to December 2003 in the region of the North West Irish whelk fishery.

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