The biology and fishery of the velvet swimming crab, *Necora puber* (L.) (Brachyura, Portunidae) in the Orkney Islands, UK

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Submitted to Heriot-Watt University (International Centre for Island Technology, Dept. Civil & Offshore Engineering) for the degree of Doctor of Philosophy

September 2001

THESIS CONTAINS

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ABSTRACT

The velvet swimming crab, *Necora puber*, is fished in various locations throughout the United Kingdom for export to southern Europe. In the Orkney archipelago, the fishery began in the mid-1980s as a response to demand from Spain, where catches had fallen. Orkney currently supports a fishery valued at over £1m per year.

This work aimed to increase the local and global understanding of the species, which has been little studied previously. It comprised a range of studies, including rearing of larvae, juveniles and adults; plankton sampling; market and vessel sampling and a tagging programme. The study focused on the reproduction, growth and stock assessment of *N. puber.*

Females become sexually mature at 43mm carapace width (CW) and males at 51mm. Reproduction showed an annual pattern, with mating occurring in late August-September, coinciding with the annual female moult period. Eggs were spawned in January and hatched in June. The planktonic larval stages lasted for 60-90 days, after which settlement and metamorphosis occurred.

The von Bertalanffy growth parameters were estimated ($L\infty = 98.4$mm; $K = 0.268$), with no discernible differences found between the sexes at the juvenile stages. The life span was estimated at 8-10 years. Animals entered the fishery at 4 years (65mm Minimum Landing Size). Total mortality (Z) was estimated to be 1.01 for males and 1.15 for females.

The state of the stock was investigated. Length cohort analysis indicated that current levels of fishing effort were close to the optimum. The uncertainty of the results suggests that, while reduction in effort may not be necessary at present, caution should be exercised if expansion of the industry is considered.

Acknowledgements

I would like to thank the following for their help in carrying out this work:

My supervisor, Prof. Jon Side
Dr. Mark Baine for all his help (and the squash games)
Ann Cross and Effy Everiss in the library
Jeannine Hazlehurst for finding large numbers of juveniles
John Vincent and the crew of the Velvet Crab
Colin Mainland and the crew of the Double Twos
Billy Seatter and Alan Moar
Alan Coghill at OFA
Morris, Ian, Johnny, Lynn, Elaine Mate and all at OFS
Ciaran Delaney for help with measuring crabs
Alberto Naveira and Dan Hart for the advice
All at ICIT
Juan Freire and Francesc Sarda
Peter Williams and the staff at OWTC (Flotta)

PESCA, OIC and ICIT (Heriot-Watt University) for the funding

I would also like to thank the following people for their support and for making Stromness as much a home to me as Spain:

The Delaney family
Sonya and Elaine "Mate", both ex-Stromness Hotel
All the staff at the Royal Hotel
The Stromness Drama Club
The St. Magnus Players
Graham Adamson
Neil and Sarah Taylor
Roy Seatter
Roy Temple
Orkney Youth Field Club

Finally, thanks to my parents and family without whose support none of this would have been possible.

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INTRODUCTION

A. Focus of Research

This thesis addresses the biology and fishery for the velvet swimming crab (*Necora puber*, Brachyura, Portunidae) in waters surrounding the Orkney Islands, UK. The thesis focuses on those aspects of the biology of the species which affect the fishery and the sustainability of the resource. This comprises the following:

- Background research made up of:
    - A review of the biology of *Necora puber* from studies carried out on stocks elsewhere and identification of gaps in the knowledge of the species with special focus on those aspects displaying geographical plasticity.
    - An analysis of the methodology used in different studies as a background for determining the methods to be used in this study.
    - An analysis of the development of the fishery in Orkney and its importance to the Orkney shellfish sector and to the general economy as a whole.
    - A description of the current legislation regarding the velvet swimming crab fishery in the UK.

- A detailed analysis of the reproduction, larval and juvenile stages, growth and population dynamics of the Orkney stock.

- An analysis of the fishery, including fishing methods, stock assessment and other factors relating to the quality of the catch and market considerations.

- A discussion of the management options for the sector, in the light of the results obtained by this thesis and the future implementation of a regulating order to allow for local management of shellfish species (including *Necora puber*).

B. Terms of Inquiry

The general objective of this study is to examine the life cycle of the Orkney stock of the velvet swimming crab, paying particular attention to those factors that might influence the fishing industry. A review of the current state of the fishery and its management is also included as a primary objective.

The aims of this thesis were elaborated from a combination of a detailed literature review on past studies carried out into the biology of *Necora puber* in other areas and from conversations with local stakeholders. This information is set out in Section 1.7. An outline of the aims of this thesis is provided below:

1. Reproduction: from previous studies it would appear that general reproductive behaviour is similar for different stocks, but that particular aspects, which may affect managerial decisions relating to the fishery, vary from place to place. It is therefore necessary to determine these for this stock. Size at sexual maturity will be determined for both sexes. The timing and duration of egg development will be ascertained, as will the fecundity of females, change in egg size and egg loss during the incubation period. The timing of the reproductive cycle in terms of mating, spawning and egg release will also be determined.

2. Larval Development: morphometric measurements on larvae have shown some variation between different areas. The cooler nature of Orkney and its shorter summer leads to the assumption that the larval period of this stock may be different to that of its southern, warm water counterparts. Presence of larvae in the water column will be investigated. In addition to this, larvae will be reared in the laboratory in order to determine the duration of each larval stage, its particular characteristics, the survival during development and the feasibility of rearing larvae for release as a hypothetical enhancement scheme.

3. Juveniles: this part of the life cycle has been largely neglected in past studies. The aim of this part of the study is to find juveniles and examine their

occurrence on the shore as well as their growth and recruitment into the fishery.

4. Growth: the moult cycle of both males and females will be determined. Growth at each moult stage will be measured, directly and indirectly. Size will be related to age, and the von Bertalanffy growth parameters will be ascertained for this stock. These include asymptotic size and the growth coefficient. This information will be used to examine recruitment and the population dynamics (e.g. natural mortality) of the stock. The validity of different methods to do this will be examined.

5. The fishery: the fishery will be examined in two ways. Firstly, the methods of capture will be studied, in terms of bait use and soak time. Secondly, the state of the stock as a whole will be examined, using the surplus yield model as a framework to assess the change in yield and effort over the development of the fishery. Length cohort analysis and yield per recruit analysis will be used to examine potential effects of changes in fishing practice (mesh size, effort, etc.). A market study will include information as to the demand for the product, the changing monthly situation, regarding both catch and mortality, and an investigation into some of the proposed management tools of the regulating order for Orkney, currently under development.

From these aims, a series of questions were devised. These questions are summarised in Section 1.10. At the start of each section, those questions to be addressed are restated.

C. Methodological Justification

Considerable literature exists on the methods to assess fish stocks, and in particular, to overcome the problems inherent in assessing growth parameters of crustaceans and other animals which periodically shed their exoskeletons.

A discussion of methodologies is provided in Section 1.8. The methodology used in this thesis combines the conclusions from the discussion with the time and resource availability of the study.

Most of the experimental work carried out during this thesis was field based. The main sampling programme was carried out using commercial fishing catches before landings (so as to include undersized individuals). This was carried out on a regular basis for a two-year period. Fisheries-independent data was obtained by carrying out shore searches (this mainly concerned the collection of juvenile velvet crabs).

Laboratory work was limited to the rearing of larvae and the *in situ* observation of the moult process and egg development.

Throughout the study, conversations were held with various stakeholder bodies, including OFA (Orkney Fisherman's Association), OFS (Orkney Fisherman's Society), Lurreitxaso SA (a Spanish shellfish company dealing in Orkney) and a number of local fishermen. These were aimed at obtaining some insight into the processes and problems faced by the industry, and to explore views on potential management tools for the stock.

Various experiments and sampling programmes were carried out during the course of this study. Table A summarises each dataset, explaining how the data was obtained, the parameters measured and what they were used for. Appendix A contains a diskette with the raw data for each dataset for consultation. Each dataset is referred to in the main text when it is used for analysis.

Dataset	Method of collection	Dates	Location	Measurements	Use	Ref in text
1. General Sampling Programme	Baited creels on commercial fishing vessels	Monthly from Jan99 to Dec00 with weekly sampling in summer	Eynhallow Sound, North Rousay, Wass Wick, Hoy Sound (specified on each occasion). General location: 59°N 03°W	Sex Carapace width Carapace length Limb loss Water temperature Ovigerous state Moult stage	Monthly sex ratio Grouped for Powell-Wetherall estimation of Linf. Separate for gear selection Von Bertalanffy Growth parameters Bhattacharya analysis for modal sizes To determine losses at catch stage: limb loss, discards, undersized. To determine moult cycle	4.2.6 4.3.1 4.3.2 4.3.3 4.3.5 5.11.2
2. Juvenile searches	Shore searches Experimental creels Bottle traps	Monthly at low spring tides	Various beaches throughout Mainland Orkney (specified each month).	Date Location Method of capture Sex Carapace width	For growth and temporal and spatial distribution of juveniles	3.7.2
3. Plankton Hauls	200µm, 30cm mesh net, 5 minute tow	Monthly Jan99-Dec00, but weekly in summer	Eynhallow Sound, surface waters, by Tingwall Harbour	Number individuals Larval stage Water temperature Vol. Water sampled	For periodicity and development of larvae in plankton	3.3.5

4. Larval Rearing	Hatchery observations	June-July 2000	Flotta hatchery OWTC	Date Developmental stage Numbers surviving For 10 individuals at each stage, these measurements: Dorsal spine length Total length Carapace width Carapace length	For mortality rate estimation For development rate For morhpometric analysis	3.3.2 3.3.3 3.3.4
5. Market Sampling	Individuals measured at marketplace	Monthly Sep99-Dec00	OFS Pierhead, Stromness	Sex Carapace width Carapace length Weight Limb loss Mortality	Market sex ratio and size distribution For use with length cohort analysis and Yield per recruit analysis To determine losses due to mortality, ovigerous state and limb loss at packing stage For length-weight and length-width analysis	4.3.1 Section 5B 5.11.2

6. Bait and selectivity	Baited creels and prawn creels for comparison	April 2000 Daily for 11 days	Wass Wick	Type of creel Type of bait Length of soak Sex Number Carapace width Ovigerous state Other species	For determination of preferred bait and best soak regime for fishery For determination of selectivity of fishing gear	Section 5A 4.X
7. Sexual maturity	Individuals obtained from datasets 1 and 2	Jan99-Dec00 (300 individuals)	Eynhallow Sound and Inner Holm, Stromness	Sex Carapace width Carapace length Chelar height and width Width of abdominal segments Gonad stage	For functional and physiological determination of sexual maturity	2.2.1, 2.3.1
8. Brood size and egg development	Individuals obtained from daraset 1	Subsample of 10 ovigerous females from every monthly/weekly survey, when found (Jan99-Dec00)	Depending on weather and fishery: Northern Rousay, Eynhallow Sound	Date Carapace width and length weight Fecundity Limb loss Egg stage 3 radii of egg (mean diameter)	For determination of fecundity and factors affecting it For determination of increase in egg size over time	2.2.3 and 2.3.3 2.2.4 and 2.3.4
9. Laboratory egg development	Direct observation	March-April 2000	Laboratory	Date Egg mean diameter Egg long diameter Egg stage	For direct observation of egg development	2.2.4 and 2.3.4

10. Mating Pairs	Pairs obtained from dataset 1	Jan99-Dec00 monthly samples; weekly during summer	Depending on weather and fishery: Northern Rousay, Eynhallow Sound	Date Sex and carapace width of each individual	For determination of size relationship between mating pairs	2.2.2. and 2.3.2
11. Moult stages	Laboratory tanks (individuals obtained from datasets 1 and 2)	Jan99-Dec00 whenever moulting occurred	Laboratory, ICIT	Premoult carapace width Postmoult carapace width Sex Moult stage Date	To determine the length of each stage in the moult cycle and the growth increment at moulting	4.3.3 4.3.5
12. Tagging	Baited creels	Release during spring 1999 (1000 individuals)	Eynhallow Sound, Wass Wick	Sex Carapace width Date of release and recapture Limb loss Location of release and recapture	For observation on growth and movemvents	4.3.4

Table 1.3 Summary of datasets used throughout this study.

D. Structure of the Thesis

This thesis is divided into 6 sections, and is structured so that biological issues are discussed before assessing the fishery. A brief summary of the sections is given below.

Introduction

This part lays out the framework of the thesis.

Part 1 Background

This part provides a description of portunid fisheries worldwide and shellfish fisheries in the UK. In addition, it reviews the development of the fishery and its importance to Orkney, with a summary of the legislation surrounding the fishery. A detailed literature review of previous work carried out on *Necora puber* in other areas and the methodologies used follows. The aims of the thesis are laid out in question form and a description of the main study areas is provided.

Part 2 Reproduction

This part focuses on the reproduction of the local stock, placing emphasis on factors that may affect managerial decisions regarding the control of the fishery. These include sexual maturity, brood size, egg development and the timing of the reproductive cycle.

Part 3 Larvae and Juveniles

Section A Larvae

Section A deals with the larval stages of *Necora puber*. Batches of larvae were reared under laboratory conditions at the Orkney Water Test Centre on the island of Flotta. The development time and survival through each larval stage is studied, as well as the feasibility of rearing larval on an economic scale as a basis for possible future enhancement schemes. The presence of larvae in the water column throughout the year is also monitored.

Section B Juveniles

This section studies the occurrence of juvenile stages of *Necora puber* using shore searches as the main sampling technique. Distribution, growth and moulting are the main aspects focused upon, as well as the potential for using juveniles to assess the state of the stock.

Part 4 Growth and Population Dynamics

This section focuses on the growth of the stock, based mainly from data derived from unsorted catches from commercial vessels. The moult frequency and timing is analysed as well as moult increments from laboratory individuals and from analysis of size-frequency distributions. Growth and mortality parameters are estimated. A tagging programme is carried out and discussed.

Part 5 Factors Affecting the Fishery

Section A Fishing Practice

This section deals with the differences in catch efficiency depending on whether bait is fresh, frozen or salted. It also focuses on the relative efficiency of 24 hour and 48 hour soak times. The relationship between lobsters and velvet crabs in the catch is also explored.

Section B Fishing Effort and Stock Assessment

This section focuses on the state of the fishery regarding catch and changes in effort. Models are used to predict the effects of changes in legislation such as increasing the minimum landing size.

Section C Market Considerations

This section describes the fluctuations in prices both at first sale and at the marketplace, the changing demand for velvet crabs throughout the year, and the changing quality of the catch with regards to limb loss, mortality and proportion of discards.

Part 6 Final Discussion and Conclusions

This chapter analyses the discussions from the previous chapters, relating them to the focus of the research and the terms of inquiry as set out above. Future management options are discussed, and recommendations for further studies are also made.

PART 1: BACKGROUND AND AIMS

Section A: Shellfish Fisheries

This section aims to discuss portunid fisheries around the world and in Europe, before discussing the UK and Scottish shellfish fisheries and the industry in Orkney. The importance of the velvet swimming crab (*Necora puber*) is placed into context on a local, national and international level. The current legislation governing the fishery in Orkney is also discussed.

1.1 Portunid Fisheries Around the World

Crabs and spider crabs make up around 1.15% of the total world fish catch (FAO, 1995). Of the crabs, important portunid species include the blue crab, *Callinectes sapidus*. This supports both a commercial fishery and an important recreational fishery from which reliable catch data is unavailable (Rugolo, *et al.* 1998) on the eastern coast of the USA. It is fished mainly with pots but also with trotline and dredges, and is the most important fishery in localised areas such as Chesapeake Bay. *Portunus trituberculatus*, is one of the most important species fished in Pacific countries such as Japan, China and Korea. The Indo-Pacific mud crab, *Scylla serrata*, which is mainly estuarine, is the most important commercial shellfish species in India, and is also mainly caught in pots and traps. Table 1.1 shows the worldwide catches for portunid species between 1985-1991. The category named "*Portunus spp.*" includes *Necora puber* and *Liocarcinus* species, and is small relative to some of the others.

Species	1985	1986	1987	1988	1989	1990	1991
Cancer pagurus	29826	26214	29003	29258	26998	28208	26232
Portunus pelagicus	33573	41466	48253	52538	49100	46716	49855
P. trituberculatus	29188	36255	142780	134518	174885	162890	171522
Portunus spp	2006	2114	2431	2700	4081	6521	5743
Callinectes sapidus	93829	90072	96584	107488	101953	100494	111771
C. danae	4734	4913	4597	4018	4119	4100	4191
Carcinus maenas	115	134	253	320	421	393	349
Scylla serrata	12663	13041	12279	12561	14385	12824	15436

Table 1.1 World landings of important crab species (source: FAO, 1995). Data in metric tonnes.

In the northeast Atlantic, the main countries involved in portunid fisheries are Spain and France, along with the UK. In addition to *Necora puber*, the other commercially exploited species are *Liocarcinus depurator* and *Carcinus maenas*, both of which have their main market in Spain. Table 1.2 shows the landings of swimming crabs (including *Necora puber*) for European countries over the past few years:

Year	**1982**	**1984**	**1986**	**1988**	**1989**	**1990**	**1992**	**1995**
France	994	983	918	637	637	637	326	241
Portugal	14	25	48	49	38	147	36	32
Spain	151	210	278	229	229	258	206	400
UK		330	695	1584	448	1690	2442	3835
Total	1159	1548	1939	2499	1352	2732	3010	4508

Table 1.2 Catches of swimming crabs in metric tonnes (source: FAO Yearbook, vol.80, 1995).

The UK fishery has only recently developed, largely as a result of the depletion of Spanish stocks. This apparent collapse was due to a combination of lax enforcement of regulations and continuous heavy exploitation of the stocks. In the UK, portunid fisheries are based mainly in Cornwall and the west coast and islands of Scotland.

The figures show how the fishery in France has decreased steadily and rapidly over the last twenty years and can no longer be considered as an important part of that sector in France. In Portugal, the velvet crab fishery is anecdotal. The Spanish figures show a gradual increase in catch, but levels are still lower than in the 1970s, when catches were consistently over 500 tonnes (MacMullen, 1983). The Spanish fishery is a multispecies fishery including the octopus (*Octopus vulgaris*), which has recently gained in importance as the velvet fishery declined. The regulations in recent years have, therefore, been geared more towards the octopus than the velvet crab, and have thus sometimes been disadvantageous to velvet crabs (pers. comm. Freire, University of Vigo). The importance of Orkney in the fishery is demonstrated by the fact that the catch levels in Orkney alone (650 tonnes in 1995) are of the same order of France, Portugal and Spain added together.

1.2 UK and Scottish Shellfish Fisheries

The term "shellfish" describes invertebrates of both crustacean and molluscan origin. The main species of commercial shellfish in the UK are the Norway lobster, *Nephrops norvegicus*, the European lobster, *Homarus gammarus*, the edible crab, *Cancer pagurus*, the velvet swimming crab, *Necora puber*, and the king scallop, *Pecten maximus*.

The most important species which make up the Scottish catch are shown in Figure 1.1 below:

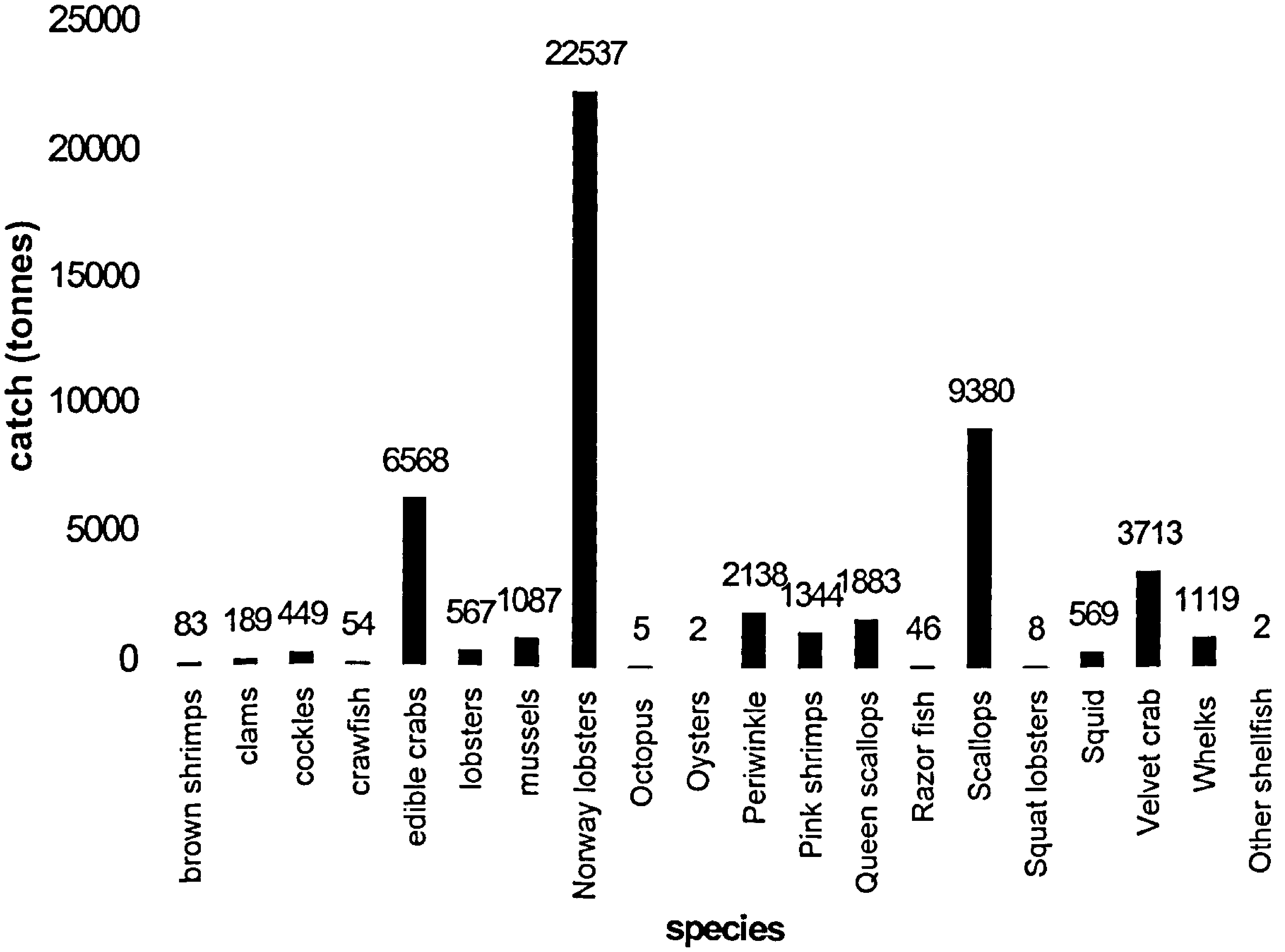


Figure 1.1 Catch by weight of shellfish species by UK vessels in Scotland (data from SOAEFD, Scottish Sea Fisheries Statistics Tables, 1995)

The most important species by weight is clearly the Norway lobster, followed by scallops, edible crabs and velvet crabs, the subject of this study. However, it must be taken into account that this graph shows only weights landed, and not market value. Value at first sale is shown in Figure 1.2, below:

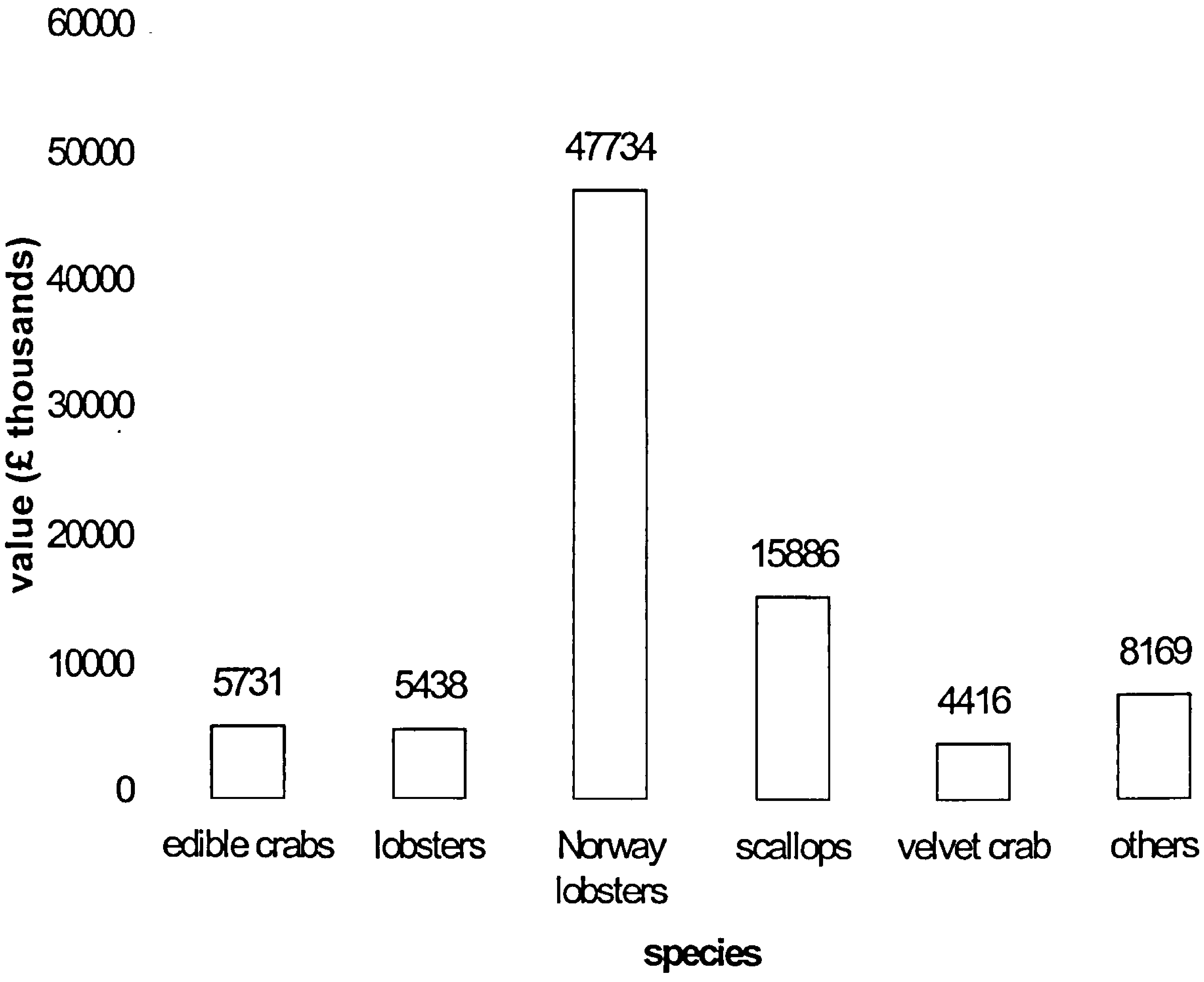


Figure 1.2 Value of shellfish landed by UK vessels in Scotland in 1995 (from SOAEFD, Scottish Sea Fisheries Statistics Tables, 1995)

In terms of value, the Norway lobster brings in the most revenue due to its quantity in terms of weight. However, European lobsters and scallops stand out in terms of value with comparison to their catch by weight. This relates to their status as luxury food items and hence, to their higher value per unit of weight in comparison with other species such as edible crabs. The velvet crab also shows a significant contribution to the value of landings, a fact that demonstrates how quickly it has become incorporated into the shellfish industry since its commencement in the mid-1980s.

The current (2000) relative importance of the shellfish fishery within the UK fishery sector is shown in Figure 1.3. The proportion of 24% refers to a catch of 127 700 tonnes compared to 152 100 tonnes for pelagic fisheries and 246 500 tonnes for demersal fisheries (Scottish Office, 2000).

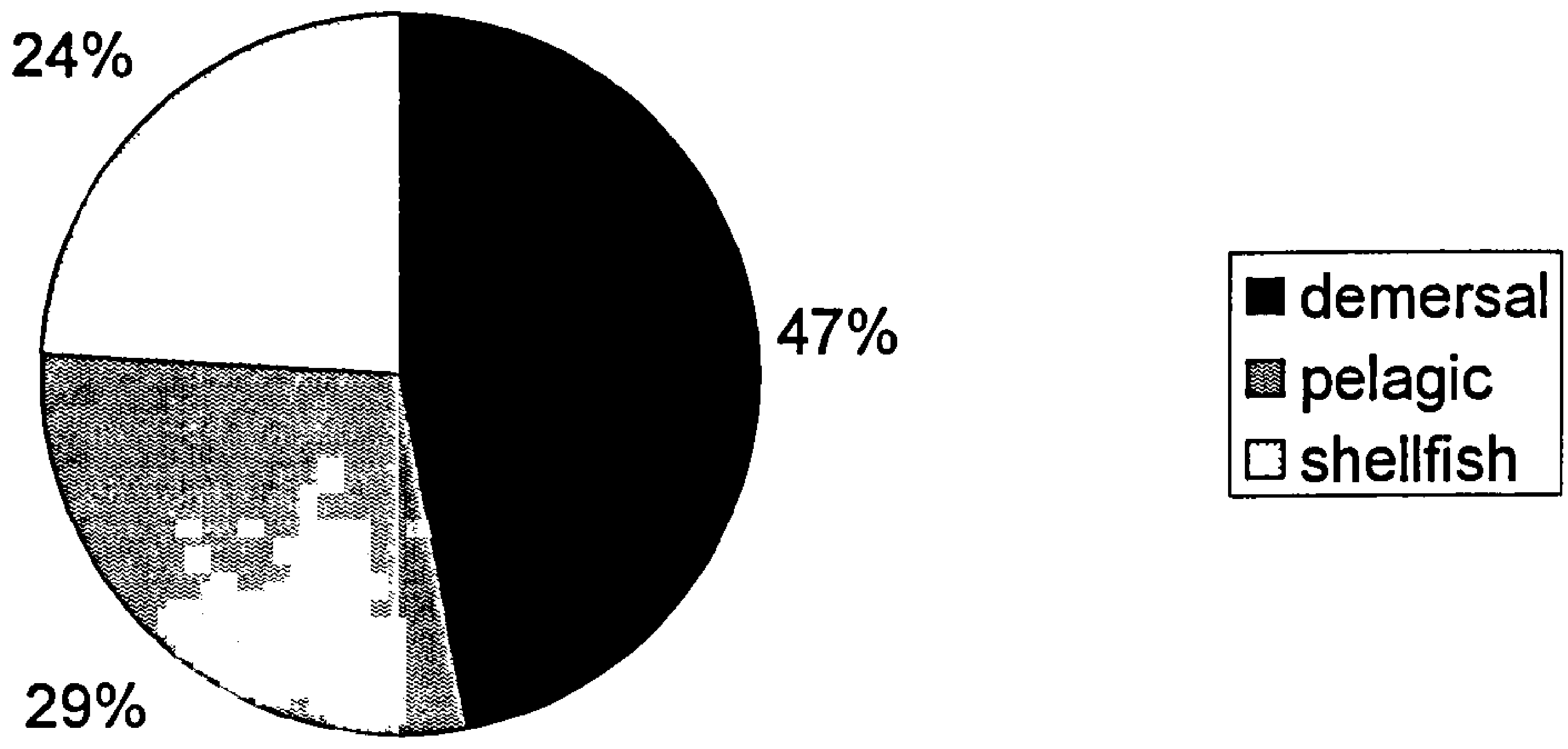


Figure.1.3 Relative importance of fisheries in UK. All landings into the UK (data from Scottish Executive website: www.scotland.gov.uk/library3/fisheries/sfs2-26.asp, 2000)

Figure 1.4 shows the Scottish landings of the most important shellfish species since 1983.

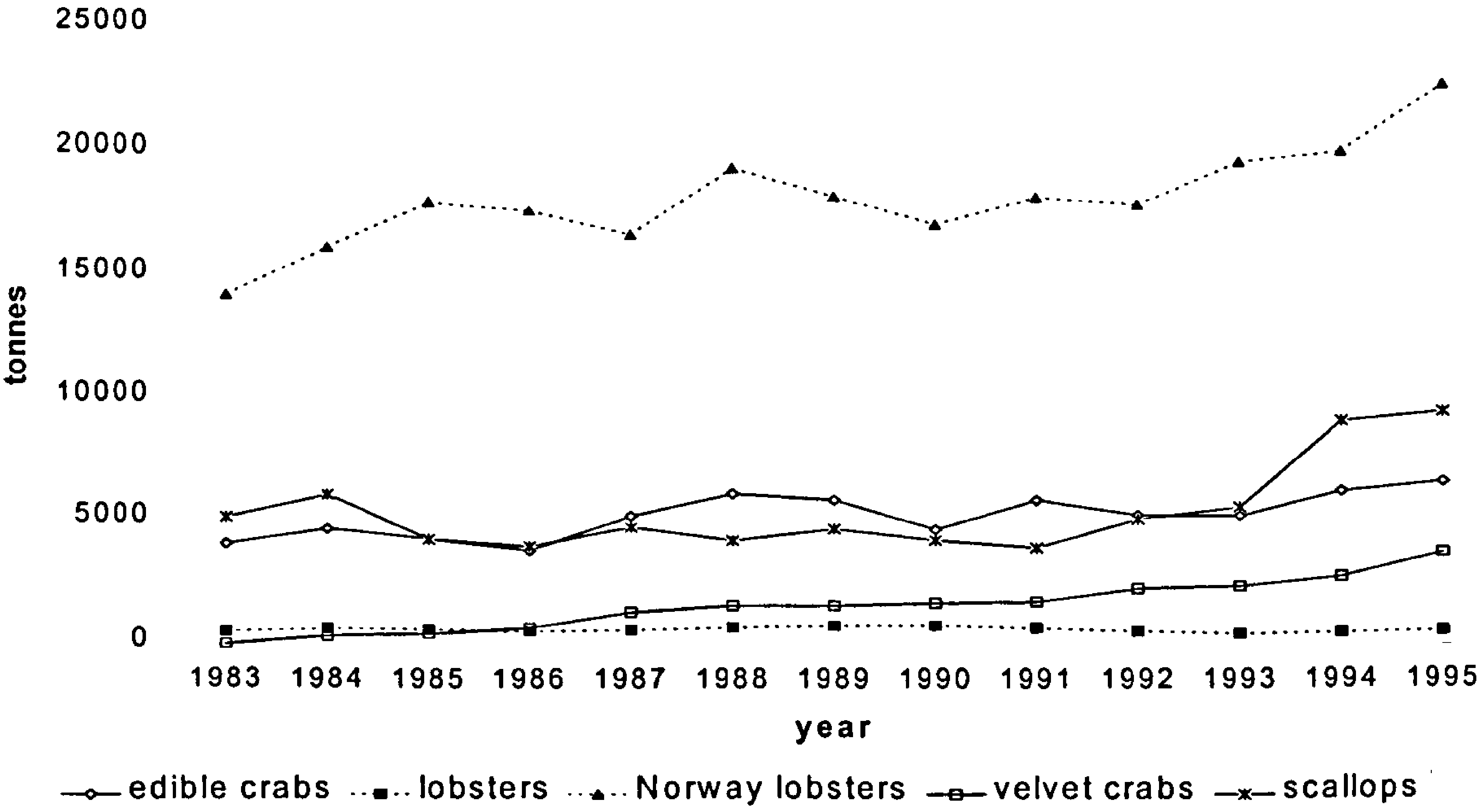


Figure 1.4 Landings into Scotland by species (Scottish Office Sea Fisheries Statistics Tables, 1985-1995)

The catch of Norway lobster sets the overall trend of increasing catch over the last few years. However, species such as the lobster and edible crabs have not increased substantially. Indeed, the Scottish lobster catch has decreased from a maximum of 781 tonnes in 1990 to 567 tonnes in 1995, having previously dropped to a minimum of 463 tonnes in 1993. The velvet crab fishery has increased dramatically from its birth in 1984, where the catch was 330 tonnes, to a total figure of 3717 tonnes in 1995, highlighting its increasing importance within the shellfish sector.

1.3 Orkney

The Orkney Islands are situated to the north of Scotland, separated from the mainland by the Pentland Firth. They are a group of around seventy low-lying islands (Figure 1.5), of which about twenty are inhabited.

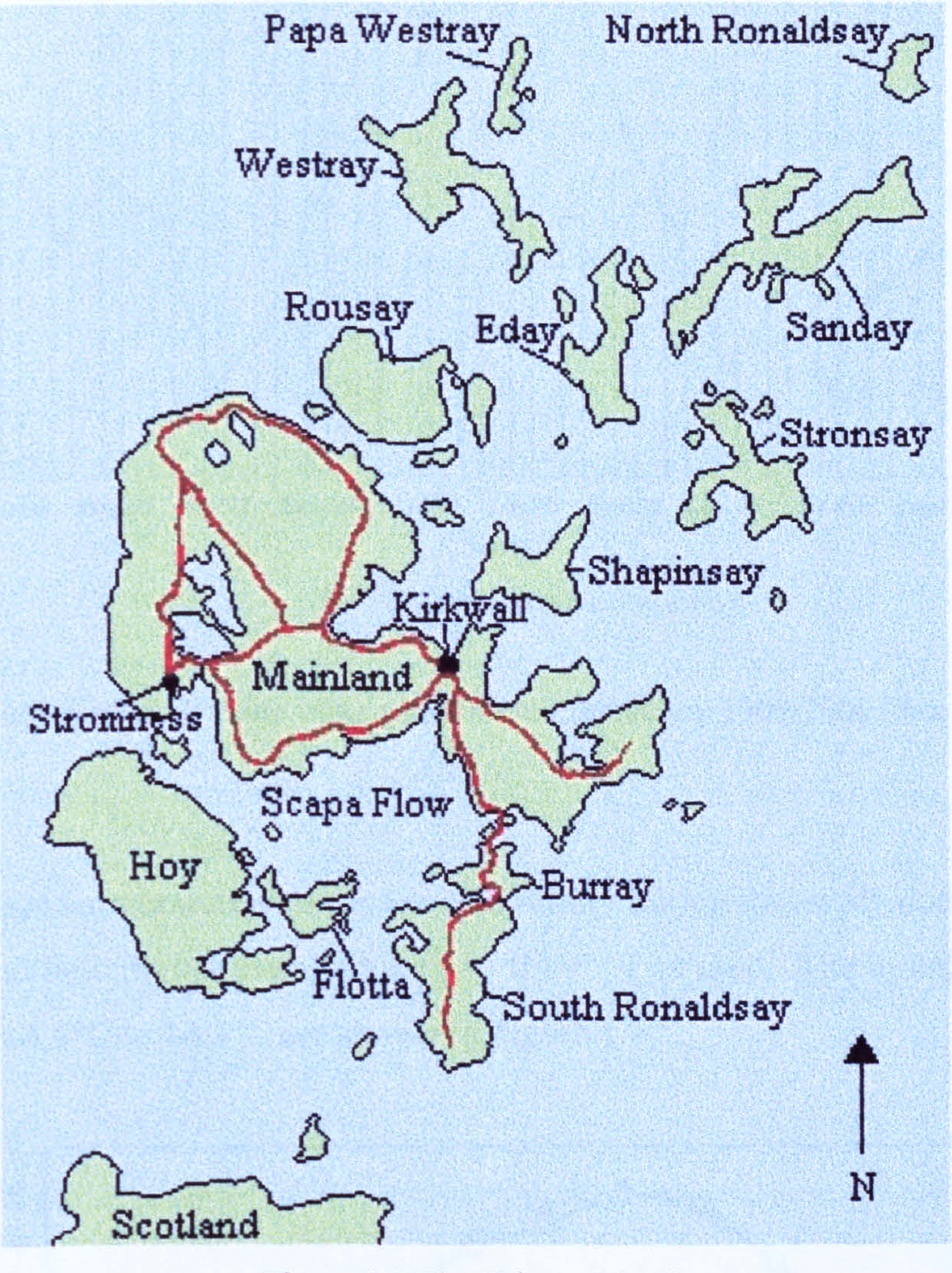


Figure 1.5 The Orkney Islands

The climate is temperate, and not as cold as might be expected for the latitudes involved, because of the influence of the North Atlantic Drift. Figure 1.6 shows the mean monthly rainfall and highest and lowest temperatures for Orkney between 1999-2000 (data from Met. Office). The mean annual temperature is 7.6°C, with a mean annual rainfall of 1009mm, comprising around 183 days of rain over 1mm. The highest temperatures correspond to July and August, which, along with June, correspond with the lowest rainfall. The lowest temperatures and highest rainfall correspond to the winter months.

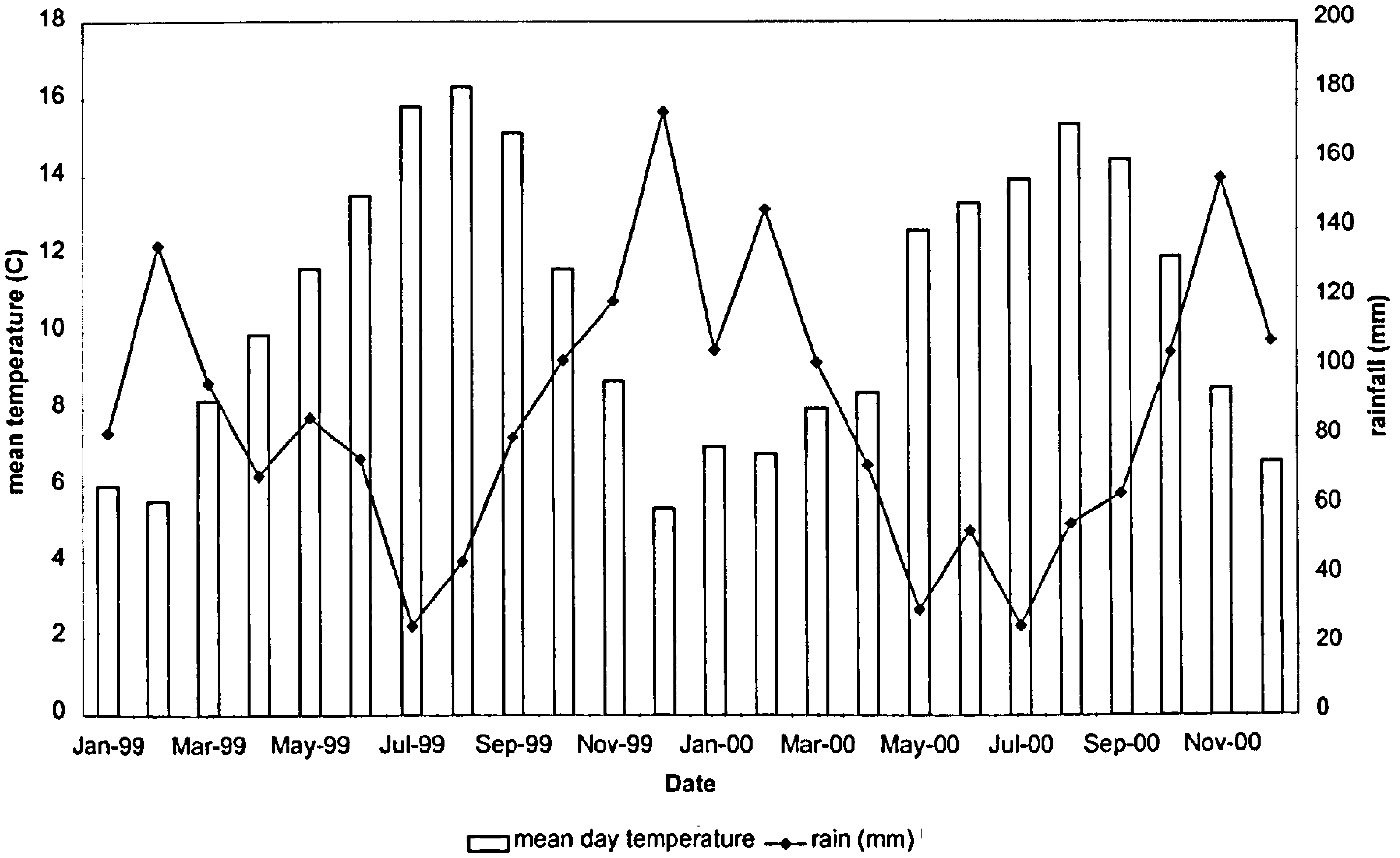


Figure 1.6 Mean monthly temperature and rainfall in Orkney 1999-2000 (data from Met. Office).

The sea surface temperature was measured monthly during this study during 1999 and 2000. A hand-held digital thermometer (+/- 0.1°C) was used. The monthly averages, ranging from 4.5°C to 14.3°C are shown in Figure 1.7.

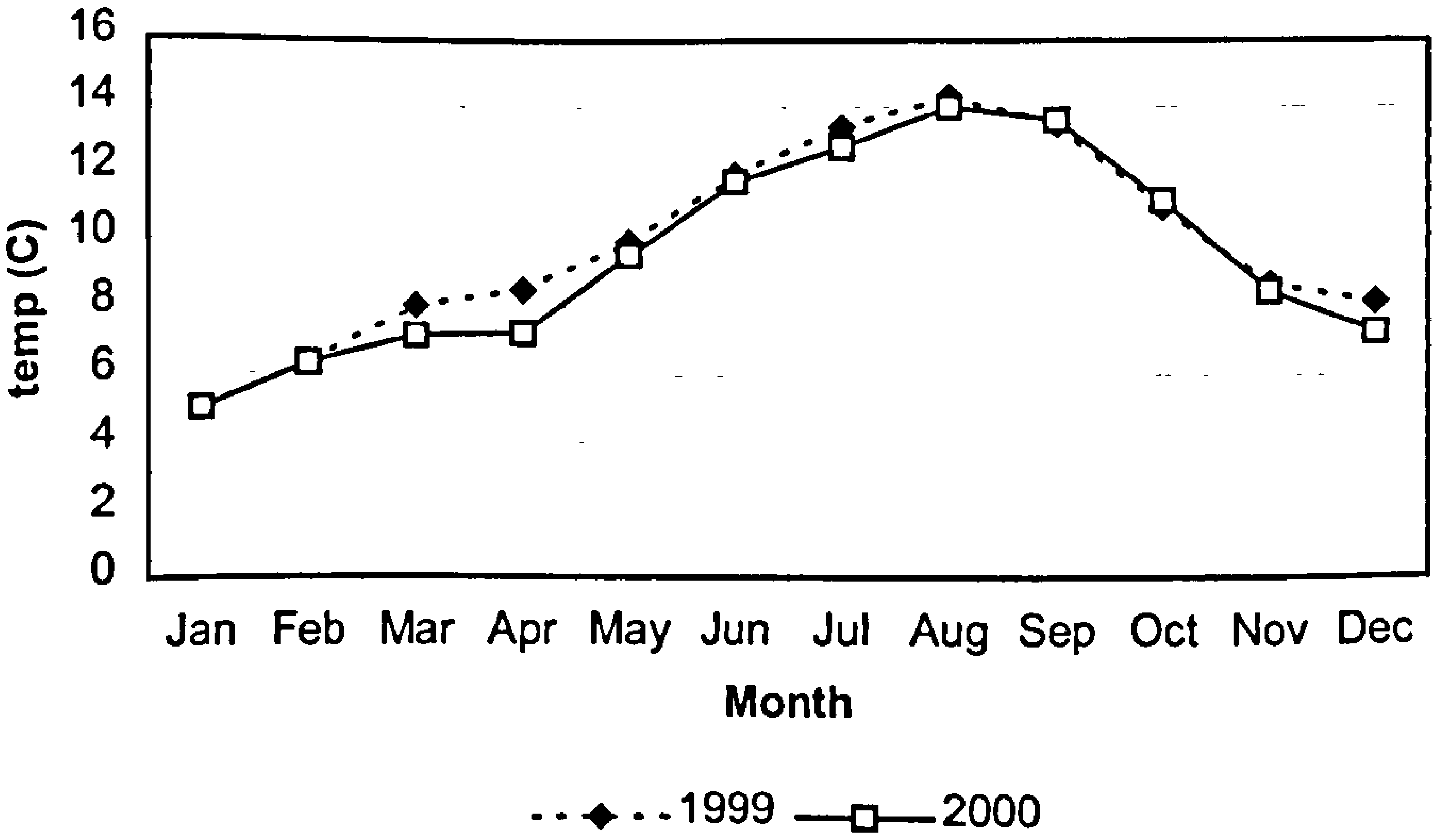


Figure 1.7 Average monthly sea surface temperature for 1999 and 2000.

As can be seen from the graph, the surface temperature follows a similar pattern for both years, of a low point at the start of the year, with a gradual increase to an August maximum, followed by a more rapid decrease to a winter minimum.

In general, it can be said that the climate is cool but mild, and lacking in extremes. The wind is a very significant part of the climate, with gales occurring on average 29 days per year (Jones, 1975).

The Orkney coastline extends over 800km. The islands rest on a narrow shelf, which falls steeply away to deeper waters to the east and west (57-73m), while the waters immediately surrounding the islands and skerries rarely exceed 36m (de Kluijver, 1993). Much of the coast is exposed and rocky, characterised in the sublittoral by the presence of *Laminaria* and providing good fishing grounds for fauna such as lobsters and velvet crabs. However, due to the configuration of the islands and the tides, a wide variety of habitats exist, some of which are more sheltered, such as the sandy bays to the north of Scapa Flow, or the maerl or *Posidonia* beds on the sheltered sides of holms and skerries.

The observed tidal pattern is a result of the interactions of two independent tidal systems - one in the North Atlantic and the other in the North Sea, which both rotate in an anticlockwise fashion, but with a time gap of several hours. This ensures that there is a net west to east flow of water through the Orkney Islands, which in some sounds can generate considerable tidal streams (Jones, 1975).

The islands are influenced by the North Atlantic Drift, which carries warm water northwards along the west coast of Britain. This helps to prevent extreme temperature fluctuations, which, together with the relatively damp atmosphere, allows the development of diverse littoral communities (Jones 1975). One of the most common of these communities is the kelp forest, typical of exposed, rocky shores and their immediate sublittoral zone. It is in these areas that velvet crabs are found in their highest abundance.

The velvet crab habitat is typified by the presence of *Laminaria digitata* as the main seaweed, on moderately exposed, rocky seabeds, subject to fairly strong tidal currents, such as in Hoy and Eynhallow Sounds. The dominant fauna found in these areas are the echinoderm *Echinus esculentus* and the topshell, *Gibbula cineraria* (Murray *et al*, 1999). Other crustacean species overlapping habitats with *Necora puber* include the European lobster, *Homarus gammarus* and the ubiquitous shore crab *Carcinus maenas* (although this species is found in greater abundance in more sandy areas). Undersized edible crabs, *Cancer pagurus*, are also found here. *Necora puber* is also found in and around the many wrecks lying on the bottom of Scapa Flow.

1.4 The Importance of Shellfish Fisheries in Orkney

The Orkney fishing sector accounts for an important source of employment, both full time and part time. Figure 1.8 shows the changes in registered employment in this sector since 1986. Data on employment is estimated on 31 December of each year by the fisheries officer in each Sea Fisheries District. Both full-time and part-time employment has experienced a small but steady decline since the early 1990s. However, this is mainly due to crewing changes in the whitefish fleet (Tallack, 1998). Before then, full time fishing was on the increase, whereas part timers were remaining relatively steady. This contrasts with historical data, which shows a general decrease in the fishing sector from the 1960s until the mid-1980s, which corresponds to the start of the velvet fishery and the opportunity for fishermen to practice their trade all year round (ICIT, 1999). The large changes between 1992 and 1994 do not correspond to real changes in the number of fishermen, but to changes in legislation and registering rules. From 1993, there was a requirement that all vessels of under 10m total length should be licensed. The effect of this was to bring in a significant number of vessels onto the register, which had previously had their landings grouped. This correspondingly had an effect on the number of fishermen employed in the sector. Although not possible to quantify exactly, the Scottish Office Sea Fisheries Statistics Tables (1995) estimates that nationally, some 1500 fishermen were included in the register for the first time, whereas some 300 left the industry in 1993. This must be taken into account when using these data for effort estimation (see Part 5). There have also been a number of changes throughout the years in measurements and legislation regarding vessel registration, which leads to similar effort estimation problems.

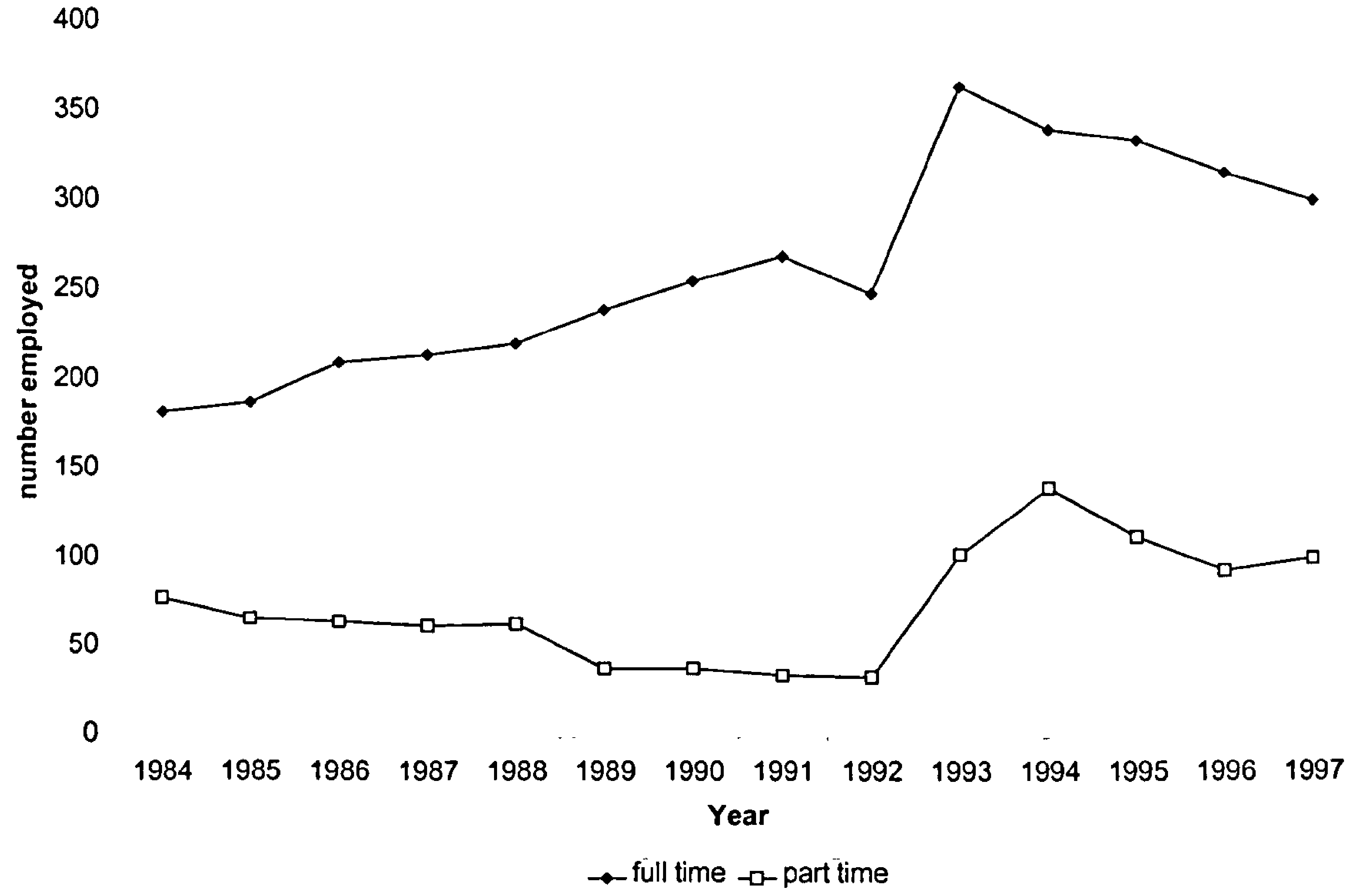


Figure 1.8 Fishing sector employment in Orkney (data from OIC, 1998).

Most fishermen given the choice would prefer to fish for velvet crabs as opposed to scallops (pers. comm. Alan Coghill, Orkney Fisherman's Association). This may be due to the high frequency of bans placed in local waters due to PSP, ASP and other toxins in the water column, as well as the general decline in local catches of scallops.

Figure 1.9 shows the relative importance of different species to the Orkney fleet. Whereas whitefish dominate, these are caught mainly offshore and do not form part of the inshore fishery. The European lobster is still the most important shellfish species in terms of economic revenue (11%), but is followed closely by the velvet crab (10%), king scallop (8%) and edible crab (7%).

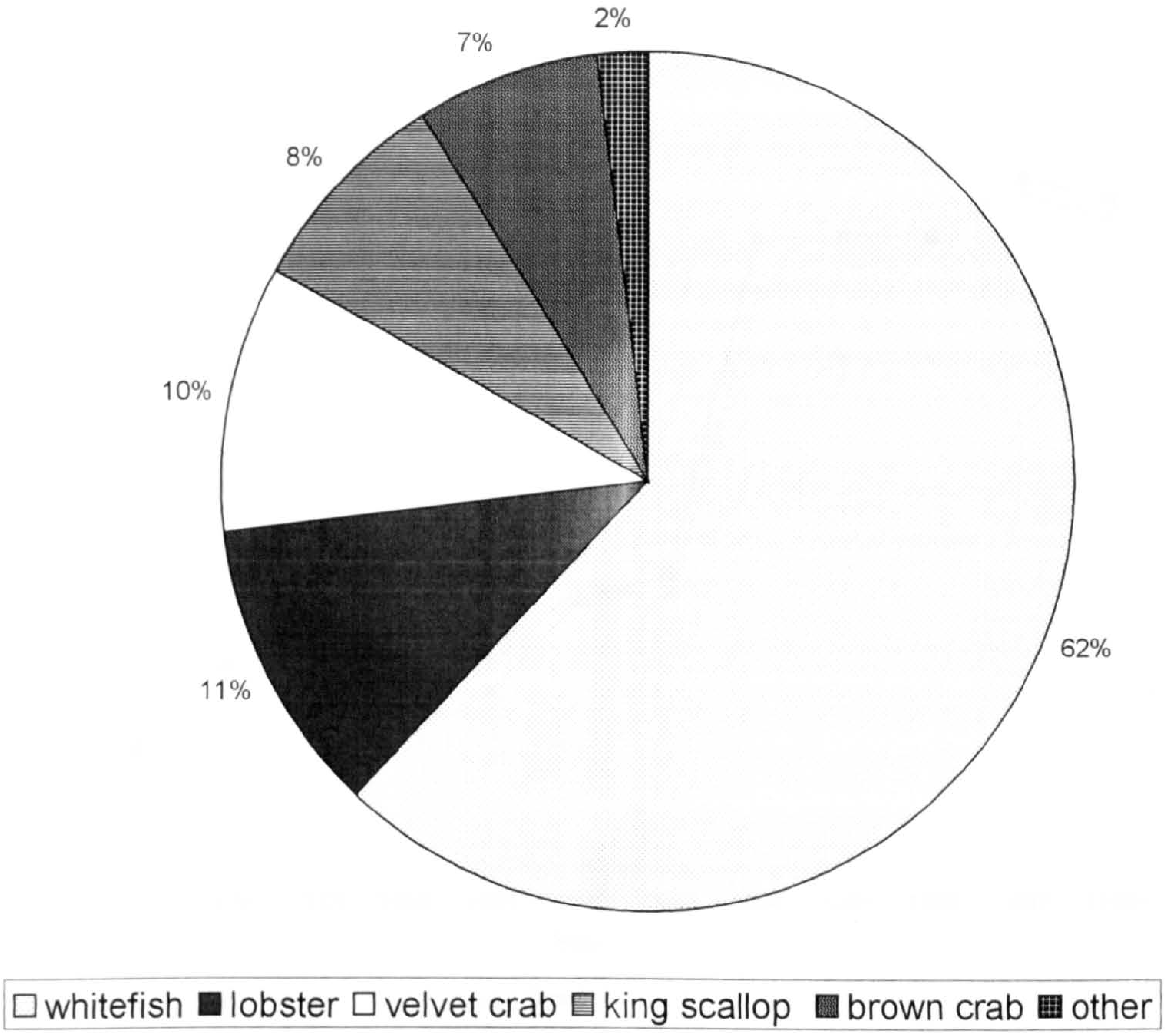


Figure 1.9 Relative importance (revenue) of species landed by the Orkney fleet, 1997 (data from OIC, 1998)

1.5 The Velvet Swimming Crab Fishery in Orkney

The development of the velvet swimming crab fishery in Orkney occurred recently. Velvet crabs were discarded as by-catch in the recent past and considered pests for stripping bait intended for lobsters. However, a foreign market for velvet crabs has developed due to overexploitation of Spanish stocks in the 1980s (Gonzalez-Gurriaran, 1981), which has led to an industry which now boasts a yearly income of over £1m (OIC Report, 1998). It has allowed fishermen to diversify from the seasonal Brown Crab (*Cancer pagurus)* and Lobster *(Homarus gammarus)* fisheries into a year round fishery which incorporates the velvet crab.

Figure 1.10 shows the yearly catch and total income from velvet crabs since the fishery began in the mid-1980s.

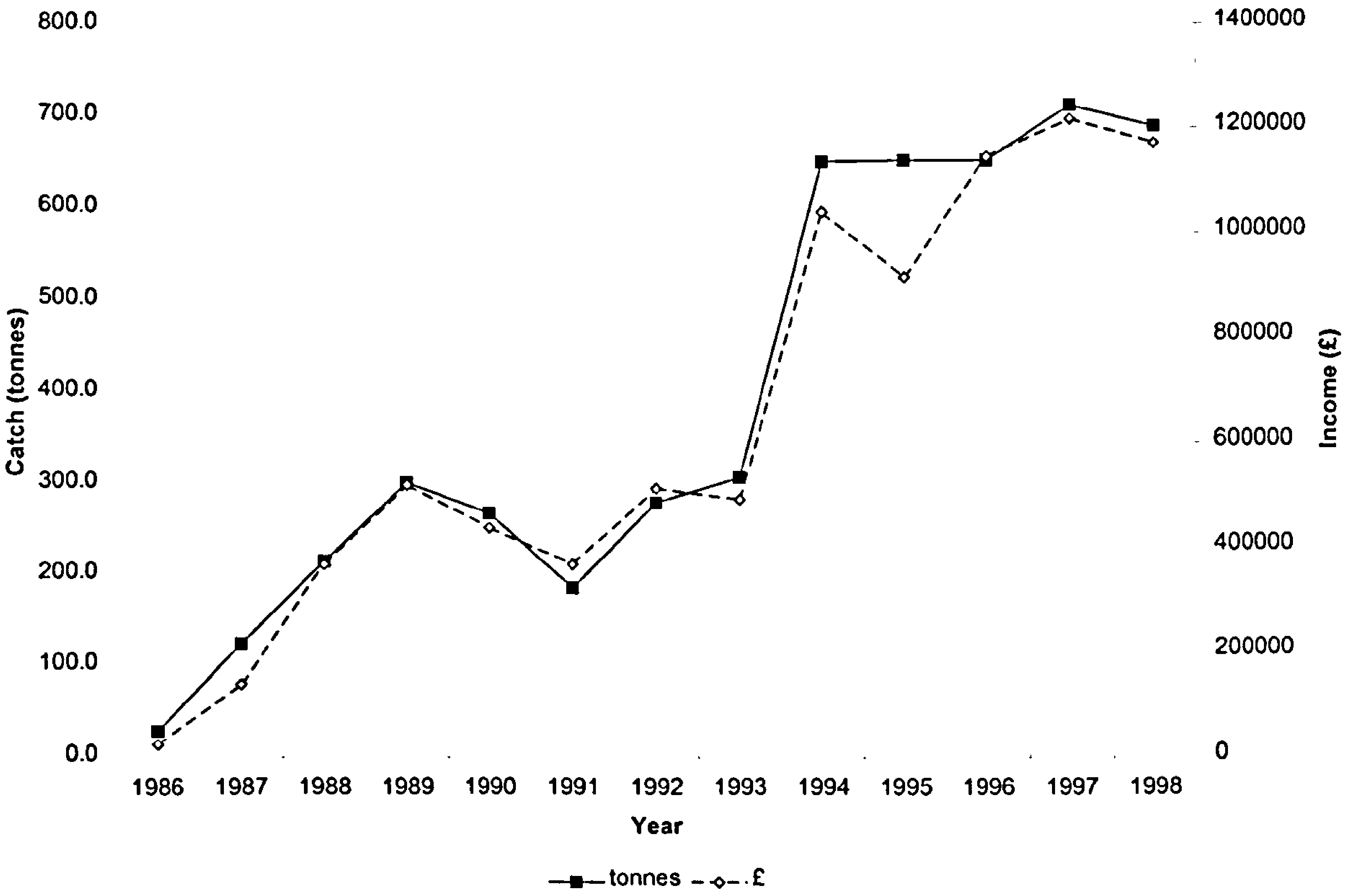


Fig. 1.10 Catch and income of velvet crabs in Orkney (Data from OIC, 1998)

There are seasonal fluctuations to the catch. Different areas are targeted throughout the season. The west coast fishery is generally early in the season, from March to July, whereas the northern isles fishery is most intense later on in the year and over Christmas.

Important landing ports include Stromness, Kirkwall and Westray. Merchants pack and sell the crabs mainly to Spanish companies who pick up their live cargo weekly and transport them to Europe, where they are marketed as luxury food items, especially in the weeks leading up to Christmas, the most lucrative period for velvet fishermen.

The crabs are divided in the packing companies into small (CW [carapace width] less than 75mm) and large (over 75mm CW). Towards the back end of the season, many velvets are boiled or frozen locally.

Occasionally, individuals of a much lighter colour are caught. These "red", or "blonde," crabs are not appreciated by the merchants, as they are noticeably lighter in weight than the normal crabs and appear to be more vulnerable during transport. It is has been postulated that they may constitute a separate stock, inhabiting deeper waters (Tallack, 1998) but there is no concrete evidence to support this as yet.

The method of fishing in Orkney is by the creel. Between 10-40 creels are laid on each backrope and laid in the fishing grounds. The bait, usually consisting of frozen horse mackerel or scad, is stripped by a combination of velvet crabs, edible crabs and lobsters, within two days (MacMullen, 1983).

The traditional Orkney creel was a wooden structure with a weighted base (18" by 20") and a single, hard eye. Mesh was usually made from sisal. In the 1960s, the double-eyed creel, which came from Shetland was adopted. This was slightly larger (19" by 27") and had a hinged door, which facilitated catch retrieval. The current creel (figure 1.11) is based on this design, but is now made of more durable materials – a plastic coated steel base and nylon mesh (stretched diameter ~4cm).

Figure 1.11 A double-eyed creel

Parlour creels, with an internal eye leading to a closed compartment are also frequently used and, to a lesser extent, more unwieldy triple-eyed creels are deployed.

The design of the eye varies depending on the target species, but the principle involves a tapering entrance, which facilitates entry but prevents exit. The mesh used in the construction of the eye tends to be smaller (2cm), whilst the diameter of the eye itself varies between 3-5 inches. Bucket creels (where the eye is a bottomless bucket in the top of the creel) based on the inkwell design are also sometimes used, but mainly for targeting lobsters and partans (brown crabs).

Velvet crabs are far less robust than common brown crabs or green crabs. Once they have been caught, they are held in floating cages or bags in tanks with seawater. The former method is preferred as the latter increases the occurrence of limb loss. The velvet crabs are then densely packed into 9kg crates, which are stacked in Vivier lorries where aerated seawater at 9-10°C is constantly pumped through the crates. Velvets are easily stressed by aerial exposure, hypoxia and high temperatures. Although the vivier system allows a degree of aeration, as the crabs are so tightly packed into the crates, which are in turn tightly packed, it is often the case that the inner core of crates stagnate and hypoxia results. Death often has a "snowball effect" on the surrounding individuals (Whyman et al, 1985). This means that the death of one individual causes the death of those adjacent to it, and so on. Stress due to aerial exposure is also size dependent, the larger individuals being the first to succumb, with the subsequent greater loss to the merchant.

The success of vivier transport is dependent on four factors: the quality of the velvets themselves, the quality of the holding water (in terms of aeration and temperature), the quality of the equipment and correct handling (Sea Fish Industry Authority, 1990).

One of the main companies which imports velvets from Orkney is Lurreitxaso S.A., based in Asturias, northern Spain. Lorries arrive on the Monday morning ferry from Scrabster and load up before taking the afternoon ferry back to the mainland, driving down to Poole via Glasgow and taking the ferry to Cherbourg, France. From there, they drive through France, across the border at the Pyrenese mountains and on to Oviedo. The whole journey takes between two and a half and three days, during which no further treatment is given to the crabs. Mortality on arrival varies between 15-20%.

1.6 Legislation

UK inshore creel vessels are required to hold Miscellaneous Shellfish Licences, but other than this, there are no restrictions on gear design, effort and allowable catch. The Sea Fisheries (Shellfish) Act 1967 is the main regulating tool regarding UK shellfish species. However, the only legal limitation on the velvet crab fishery is The Undersized Velvet Crabs Order 1989 (SI 1989 No.919), which implements a 65mm carapace width minimum landing size. Catches for scientific research are exempt from this order.

Whereas for other species such as edible crabs, a whole range of other limitations are also in place (e.g. the prohibition of landing soft shelled or ovigerous female edible crabs), similar provisions for velvet crabs do not exist. However, in Orkney, it is common practice to return soft and ovigerous crabs to the sea, as the merchants will not accept these. This is an example of a market-driven rather than a legally binding measure, which is followed by most operators in the area.

Aside from these limitations, a voluntary ban was put in place in Orkney waters over the summer months (1 June to 31 October) from 1993-1997. This was designed to ease the pressure on the stock during the moulting period. Warmer temperatures, causing higher mortality, and low prices, result in lower returns during this period, whilst reducing the remaining stock for colder month fishing. The ban did not prove successful and was lifted in the summer of 1998.

As the ban was purely voluntary, mixed levels of adherence meant that fishermen stood to lose their fishing grounds to those landing velvets throughout the summer. The ban was limited to Orkney, so it was possible for operators to land their catch in the rest of Scotland.

At present, a group representing the creel fishermen of Orkney is in the process of applying for a Regulating Order for its inshore waters. Regulating Orders are applied to defined areas, for specified shellfish species and for a defined period of time. They are aimed at local bodies, which have the objective of developing an efficient and sustainable shellfishery (ICIT, 1999). Restrictions may be applied to activities carried out in the area and tolls may also be imposed on these activities so long as this is done in an equitable manner and without discrimination. Any revenue from such a practice must be utilised in the improvement and cultivation of the specified fishery.

The proposal is for the Order to cover a six-mile limit around the Orkney Islands for an initial duration of 15 years. This would involve the installation of a permit scheme in order to regulate the fishermen operating in the area. A number of management tools are in the process of being debated, but perhaps the one most pertinent to the velvet crab fishery involves the limitation of the number of creels per vessel. It is envisaged that an independent management committee would liase with local scientific bodies including the Marine Laboratory (Aberdeen) and ICIT (International Centre for Island Technology – a part of Heriot-Watt University) to coordinate further research.

Section B: Previous Research and Literature Review

1.7 Previous Studies on the Velvet Swimming Crab

1.7.1 General

Necora puber (L.) is a true crab of the family Portunidae (swimming crabs). Portunids are rapidly moving marine crabs, which are able to swim, due to the propulsion caused by action of the last two podomeres, which are flattened into paddles. Of the seven portunid species occurring in the British Isles, it is the largest (Ingle, 1983). It has previously gone by a variety of names, including *Portunus puber* (L.) (Leach, 1814), *Macropipus puber* (L.) (Christiansen, 1969) and *Liocarcinus puber* (L.) (Ingle, 1980).

Its common name, the velvet swimming crab, is subject to local variations, known as the devil crab, lady crab or velvet fiddler crab, amongst others.

The velvet swimming crab is predominantly black, with short, light brown hairs covering the exoskeleton, giving it a characteristic "velvety" feel (Tallack, 1998). The adult has a carapace length of up to 65mm and carapace width of about 90mm although larger crabs have been recorded (MacMullen, 1983).

The dorsal surface of the carapace is flattened and the frontal margin has up to ten narrow unequal teeth of which the middle pair are the largest (Hayward and Ryland, 1990). The dactylopodite is provided with median and marginal ridges. The most distinguishing features of the crab are its eyes, which are bright red. There are also red, black and blue markings at the joints or on the legs and pincers (Hayward and Ryland, 1990) (see Figure 1.12).

Sex is distinguished by the shape of the abdomen. Males have a triangular abdomen, with the third, fourth and fifth segments fused. The female abdomen is large and rounded, with seven segments. Males have two pairs of pleopods, which are developed for copulation, whereas females have four pairs of pleopods lined with fine hairs, specialised for carrying eggs.

Figure 1.12 *Necora puber*, the velvet swimming crab

N. puber is widely distributed around NW European waters, from the Norwegian coast at 61°N (Christiansen, 1969) down to what was the Spanish Sahara, 24°N (Capart, 1951). In the Mediterranean, it is limited to Spanish, French and Adriatic coasts (Clark, 1986).

N. puber, unlike the other portunid species occurring in British waters, which prefer sand or gravel, is found on rocky substrates from the lower shore down to 70m (Hayward and Ryland, 1990). It also occurs in large numbers under mussel rafts in the rias of Galicia, NW Spain (Gonzalez-Gurriarán, 1981). This is due to the increased food supply and changes in the sediment arising from shell deposits (Romero *et al,* 1982). Individuals may also be found at greater depths, but those occurring deeper than 80m are typically bright orange in colour, with fair-coloured setae. It has been proposed that these "red velvets" may belong to a separate stock (MacMullen, 1983).

Early work on *Necora puber* focused on larval development (e.g. Lebour, 1928; Rice and Ingle, 1975b), feeding habits (Czepa, 1907; Kitching end Ebling, 1967), moulting (Drach, 1933), chemoreception (Laverack, 1963), cheliped abnormalities (Calman, 1913; Audigé, 1927 and Abeloos, 1932) and parasites (Bourdon, 1965).

Velvets are known to feed on a wide variety of substances, including polychaetes, gastropods, bivalves and barnacles (Choy, 1986b) as well as small crabs (Romero *et al*, 1982) and even juveniles of their own species (Choy, 1986b). Brown algae also form an important dietary resource (Norman and Jones, 1992). Generally, they are opportunistic omnivores, their food varying according to seasonal and local availability.

Food consumption has been found to vary according to moult stage and season (Freire and González-Gurriarán, 1995). There appears to be no feeding during the immediate premoult and postmoult stages, whilst feeding in the recent postmoult stage is greater than in the intermoult stage. The seasons of highest food consumption are autumn and winter.

Velvets are predated upon by the octopus *Octopus vulgaris*, and also possibly by cod, ray, large crustaceans and cuttlefish (MacMullen, 1983; Michael, 1987).

The behaviour of the velvet swimming crab is well-documented (Glass,1985; Smith, 1990; Choy, 1986b). *N. puber* is cryptic during the day and active at night. Males appear to be more active than females (Norman, 1989). Smith (1990) noted that *N. puber* reacted agonistically when they encountered one another, and observed that this was representative of the situation in the field. He postulated that this antisocial behaviour may be a mechanism of preventing spread of disease, or that large aggregations may attract predators.

Movement in the velvet swimming crab is in the typical sideways fashion. The velvet swimming crab is highly mobile (Bell, 1853) and probably shows little site attachment. Mark recapture trials have shown large changes in crab populations due to emigration (Norman, 1989). Sex based migrations are common in many decapods and may be related to the breeding cycle (Allen, 1966).

In recent years, mainly owing to the commercial interest in the species as the fishery has developed and declined, research has focused more on the population dynamics and life cycle in different locations (Gonzalez-Gurriarán, 1981, 1985a, 1985b; Choy, 1986b; Norman, 1989; Bakir, 1990; and Tallack, 1998).

1.7.2 Reproduction

The study of the reproduction of any organism can be divided into two parts. Firstly, there is the study of pairing and the various acts preceding copulation, copulation itself, and the following processes with respect to individuals. Secondly, there is the study of the reproductive cycle of the species as a whole.

Mating in the Brachyura is seasonal, and whilst the ultimate causes for this may lie in a number of ecological factors, the immediate cause is usually the intermittent presence of crabs which are in a condition to mate (Hartnoll, 1969). Two of the more important factors that regulate the ability to copulate are the maturity of the individual and its stage in the moult cycle.

There are a number of ways in which sexual maturity can be determined. Generally, previous studies have focused on physiological maturity as the size at which 50% of the population are sexually mature. Methods to measure this include examining males for presence of sperm in the vas deferens, and examining females for presence of sperm plugs, sperm in the spermathecae, ovary development and presence of eggs on the abdomen [Gonzalez-Gurriarán and Freire (1994); Choy, (1986b); Norman, (1989)]. Functional maturity may also be measured as the size at which changes in the relative growth rates of certain body parts become evident. Analysis of morphometric data has been carried out by Gonzalez-Gurriarán and Freire, (1994); Choy, (1986b); Norman, (1989); Bakir, (1990) and Wilhelm, (1995). Gonzalez-Gurriarán and Freire (1994) found that for males, there is a change in allometry of the length of the right (crusher) chela and the first pleopod, which correspond to sexual maturity. In females, the abdominal width was found to have two phases of growth.

The Spanish stock of velvet crabs reaches maturity after the first year (González-Gurriarán and Freire, 1994). The size of individuals at sexual maturity is an important factor as it may be used as a management tool to protect immature individuals until they have had a chance to produce at least one brood.

The growth of sexual characters is under hormonal control (Lockwood, 1968); the ovary produces a female hormone whilst a male hormone is produced by the androgenic gland - a group of cells lying along the vas deferens.

Maturity occurs at the pubertal moult (Teissier, 1960). At this moult, there is a discontinuity in the relationship between pre-ecdysis and post-ecdysis carapace width (CW). Maturity of *N. puber* can be determined both internally and externally.

The testes of the male are tubular and are found in the anterior part of the body cavity. These testes are composed of numerous densely packed tubules. The speramtozoa are developed here, giving the testes a white appearance when ripe. Mature males also display swollen vas deferentia, full of sperm. The vas deferentia open to the exterior at the tips of two small papillae on the coxae of the last walking legs. The first two swimmerets are modified as gonopods (this occurs at maturity), which act as intromittant organs for transfer of sperm to the female (Bakir, 1990).

Females show paired, tubular ovaries, which are large and orange when ripe. Short oviducts communicate with the exterior by short vaginae, the openings of which are on the sternum of the sixth thoracic somite (Bakir, 1990). Fertilised eggs are released from the vaginae and attach to four pairs of swimmerets by glue from the eggs themselves. Females may be carrying eggs, but maturity may also be determined by the presence of sperm plugs (Hartnoll, 1969), which keep the sperm from leaving the female, and by observation of the stage of development of the gonads.

Gonad development can be divided into four distinct stages (Gonzalez-Gurriarán, 1985a):

1. Undeveloped gonads. Inactive, white ovary.

2. Gonads partially developed, yellow-brown in colour. Ovocites not larger than 250μm.
3. Gonads well extended within the carapace. Compact ovary, dark violet or brown in colour. Ovocites less than 400μm.
4. Maturity. Ovary practically fills the body cavity, intensely violet or brown in colour, with large ovocites (more than 400μm in diameter).

According to Choy (1986b), females are able to copulate and spawn as soon as the pubertal moult is attained. However, in the case of males, it is possible that at least one post-pubertal moult is necessary in order for successful copulation as the male is always larger than the female it is paired with (Choy, 1986b).

The male is attracted to a pre-moult female by pheromones and also tactile stimuli (Eales, 1974; Dunham, 1988). Males display agonistic behaviour towards each other in the presence of sexually receptive females (Smith *et al*, 1994). Pairing occurs from 1-9 days before copulation, the males attending the females while they moult. In all observed cases [Gonzalez-Gurriarán, (1985a); Choy, (1986b); Norman and Jones, (1992)], the males were significantly larger then the females; this may be related to his dominant role in the pair.

Copulation takes place while the female is still soft. The male grips the female with his walking legs and chelipeds, and inserts the first pair of pleopods into the vulva of the female. The pair remain in the copulatory position for 4-20 hours. The male will attend the female for up to two days after copulation has taken place (Gonzalez-Gurriarán, 1985a).

The pattern of behaviour of courtship and mating outlined above may have considerable survivorship value. By the male attending the female both before and after copulation, a number of potential problems are avoided. As a crab is extremely vulnerable during the moult process, it tends to conceal itself at this time. This would make it difficult for a mate to find it. However, if it moulted in the open, it would be even more vulnerable to predation. By pairing before ecdysis, not only is the presence of the male assured while the female is still soft, but the hard male may also offer protection and even assist in the moulting (Hartnoll, 1969).

After copulation, the female gonads begin to develop. The eggs are not fertilised until spawning takes place (the sperm is stored by the female and its loss is prevented by formation of sperm plugs). After only one impregnation, females can spawn several times and may even moult between spawnings (Gonzalez-Gurriarán, 1985a). Spawning appears to occur over a period of 4-5 days.

The period of incubation of the eggs varies according to temperature (Gonzalez-Gurriarán, 1985a). At 18°C, the mean length of incubation was 36 days, whilst at 12-13°C, it took 48 days. As the eggs develop, they increase in size due to osmotic uptake of water. After about 25 days, when the eggs are 390-400µm in diameter, the eye spots become visible. After 35 days, the pigmentation of the larvae is almost complete. Hatching takes about 40 hours from when the first larvae are clearly visible to the hatching of the last egg.

Fecundity in *Necora puber* has been examined by Choy (1986b, 1988), González-Gurriarán (1981) and Norman and Jones (1992) and found to be directly related to the size of the female. It was found that there was significant egg loss during development (14% for small females, 18.5% for large females [Norman and Jones, 1992]) and that females suffering limb loss had significantly lower broods than those which did not. There was considerable geographical variation in fecundity for different stocks.

No reproductive cycle has been observed concerning males. However, females show a distinct cycling pattern to their reproductive stages, as can be seen by the yearly variation in the number of ovigerous females sampled in field studies [(González-Gurriarán, (1985a); Glass, (1985)] and the stages of gonadal development of these females. This cycle can be related to the growth cycle. González-Gurriarán (1985a) found two distinct peaks of female maturity, in January and March, due to the fact that most females in the study area could have two successive spawnings. At Plymouth, a peak of ovigerous females was observed in spring (Lebour, 1928), whereas in Cotentin (west coast of Channel) the time of female maturity was spread over a period from March to August. (Martin, 1980).

1.7.3 Larval Development

Since Lebour's (1928) study of decapod larvae, much other work has been carried out on decapod larvae, but until recently, this work has focused mainly on *Carcinus maenas* (e.g. Williams, 1968; Dawirs, 1980, 1983, 1984; Rice and Ingle, 1975a). Rice and Ingle (1975b) have described the stages in larval development of *N. puber*, and Mene *et al.* (1991) have examined the effects of temperature and salinity on larval development. Harms and Seeger (1989) studied the development and survival of the larvae in relation to different food regimes in the laboratory, whilst Bigot (1979) and Martin (1980) carried out studies into larvae obtained from the natural environment. Larval studies have also been carried out in Galicia (Mene, 1987) and Swansea (Choy, 1991).

The main conclusions of these studies refer to the developmental stages of the larvae and the factors affecting these. It appears that the larvae of *N. puber* hatch at the zoeal stage and go through a total of 5 zoeal stages, then a megalopa stage, which settles and undergoes metamorphosis into the first crab instar. The main factors affecting larval survival are temperature, predation and food limitations (Thorson, 1950). The quantity and quality of food will affect the developmental time (Roberts, 1974) and thus sub-optimal levels will increase the development time and hence the risk of mortality from starvation or predation (Harms and Seeger, 1989).

Decapod larvae are generally thought to be carnivores, and attempts to rear them have usually involved the use of *Artemia* as prey (Rice and Ingle, 1975b; Harms and Seeger, 1989; Choy, 1991 and Mene, 1991). Most attempts have been successful, although Harms and Seeger (1989) were unable to rear *N. puber* larvae to first crab instar under any conditions when they looked at different algal and *Artemia* diets for a number of crab species. This was perhaps due to insufficient prey density, as suggested by Choy (1991) who found that a diet of mixed algae and *Artemia* or a commercial product gave the best survival rates. He suggested that the shape of the algae was an important factor in it being an appropriate food or not.

Some species are thought to hatch as prezoea, which then undergo a moult to zoea 1 within a short period (Roesijadi, 1976, Bigford, 1979, Campbell and Fielder, 1987). However, it is possible that this prezoeal stage may only occur in sub-optimal conditions. Wear (1967) suggested that hatching occurs due to an increase in larval size after uptake of water during embryonic development. Thus, in conditions of sub-optimal salinity, the rate of water uptake may increase and lead to premature hatching at the pre-zoeal stage. Pre-zoeal stages have been observed in *Portunus pelagicus, P. sanguinolentus* (Campbell and Fielder, 1987), and Lebour (1928) describes this stage occurring in *N. puber* and goes further by stating that all British crabs hatch from the egg as a prezoea. Harms and Seeger (1989) noted that 31% of larvae developing to megalop stage also went through a sixth zoeal stage. However, this may be an artefact caused by the rearing conditions, rather than a true representation of the natural larval cycle, as this stage has not been observed in any other study carried out on *N. puber* larvae.

Mene *et al.* (1991) found that the duration of each stage of zoeal development was quite similar, but that the megalopa stage was generally twice as long as each zoeal stage. They also found a sharp drop in survival between zoea V and megalop stage. Stage duration varied according to temperature. At the conditions most approximating those in this study (15°C and 34‰), individuals took on average 45-54 days to develop from hatching to first crab instar, spending 12-17 days at the megalopa stage. These individuals were reared on *Artemia* alone.

Occurrence of larvae in the natural environment has been monitored in the North Sea through the Continuous Plankton Records (Rees, 1955). Choy (1991) carried out a survey to determine the temporal distribution of *N. puber* larvae in the Irish Sea and in Swansea Bay, and found the larvae to appear in the water column in April, some two months later than in southern England, and to remain in the water until October-November, also slightly later than more southerly waters.

The larvae of *N. puber* have been described in detail by Williamson, (1911), Lebour (1928), Rice and Ingle (1975b), Clark (1984) and Mene (1987). Figure 1.13 shows the characteristic traits of each stage, and these are summarised briefly below:

The prezoea is only about 1.76mm in total length, and exists for a few hours after hatching (Lebour, 1928). It lacks the dorsal spines of later stages.

The zoea of *N. puber* are clearly recognisable as they are larger and have longer, straighter spines on the carapace, losing the lateral spines on the telson in later stages. Zoea I measures around 2.24mm from the tip of the dorsal spine to the tip of the rostral spine, whereas this length is increased to 4mm by stage V (Lebour, 1928). When zoea V is ready to cast its skin, the dorsal spine becomes hollow and the remains of the living tissue contained in it descends and is seen as a red knob at the base of the spine. In the megalopa, this remains as a slight prominence.

The megalopa is small and lacks a dorsal spine (Rice and Ingle, 1975). It is a green colour and has a carapace length of around 1.28mm.

1.7.4 Juveniles

Juvenile velvet swimming crabs are thought to occupy the littoral zone, all year round, with greater abundance in the warmer months (Tallack, 1998). Little work has been carried out on juveniles to date due to their apparent lack of abundance. Choy (1988) found a distinct juvenile class size of 5-10mm and another at 35-40mm by overturning stones and boulders at low spring tide in Swansea Bay. He suggested offshore migration occurred as the animals grew. Bakir (1990) suggests that it is not migration that is the cause of so few juveniles being found in deep water, but their reluctance to enter pots, perhaps signifying different feeding habits.

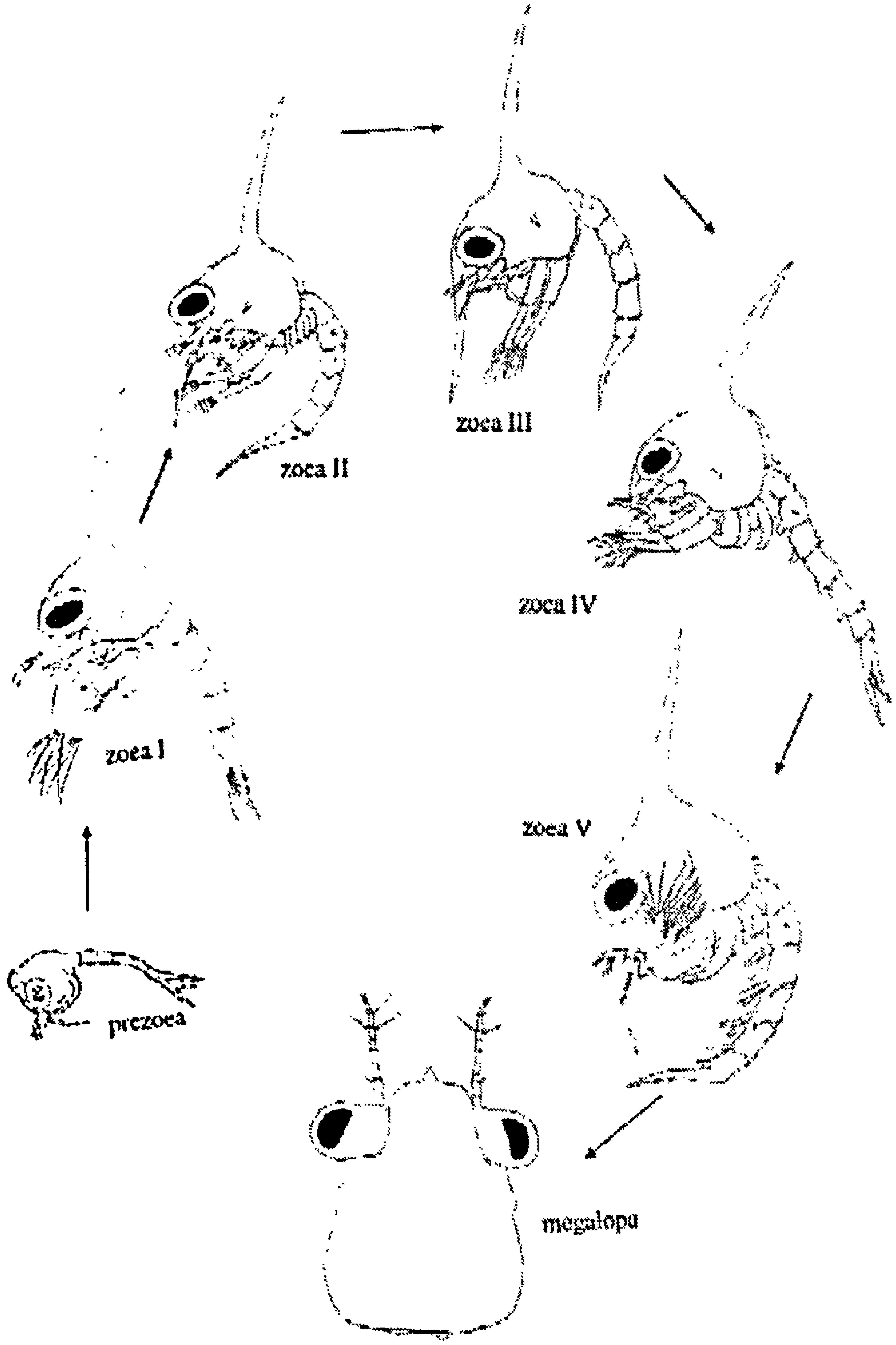


Figure 1.13 The larval cycle of *Necora puber* (pictures from Rice and Ingle, 1975 and Lebour, 1928)

1.7.5 Growth

Growth in crustaceans takes three forms. Firstly, there is a change in overall size over a period of time, producing a growth curve, which generally shows a reduction in growth rate as the individual ages. Secondly, many crabs exhibit relative growth, where certain parts of the body may grow at a different rate to other parts, thus changing the shape of the animal. This is known as allometric growth. The sexual organs of juvenile crabs, which are small, undergo positive allometric growth so that at the onset of puberty, they have attained the relative proportions that are necessary for their adult functions. Finally, there is also growth in the form of regeneration of lost appendages.

Growth in size in velvet swimming crabs is discontinuous, in the form of a succession of moults (ecdyses) separated by intermoults (Hartnoll, 1982). Some increase in size, by stretching of the integument, has been demonstrated between moults in the decapod shrimp *Crangon crangon* and several species of mysids (Mauchline, 1973), but this is limited. The process of moulting does not allow ageing by use of annual growth rings in persistent skeletal material.

The growth factor is the percentage by which the post-moult exceeds the pre-moult length (Mauchline, 1976, 1977). This is variable both within and between species, but generally highest during the early stages of a species. The mean growth factor of larval decapods is as high as 22.3% (Rice, 1968), but may vary between 3-44% (Hartnoll, 1965).

There are a number of factors, both intrinsic and extrinsic, which affect the growth of an individual during the moult stage. Whereas in species like *Carcinus maenas* (Crothers, 1967) and *Panulirus longipes* (Chittleborough, 1975) sex does not appear to affect adult moult increment, there are numerous examples where the female increment is significantly smaller- *Homarus gammarus* (Ennis, 1972), *Cancer pagurus* (Bennett, 1974a) and *Cancer magister* (Butler, 1961). Some studies indicate that *N. puber* also falls into this category (González-Gurriarán, 1985b, Choy, 1986b, Norman, 1989, Bakir, 1990). There is only one clear example where the females show a larger increment than the male, namely in *Callinectes sapidus* (Tagatz, 1968).

It is to be expected that most species follow the former pattern as the female must divert more energy to reproduction, and therefore less to growth.

The frequency of moulting also changes as individuals age. Generally, this will decrease, as moulting is a hazardous period and the crab is at its most vulnerable to predation at this stage, so once sexual maturity has been attained, it is advantageous to reduce the number of further moults. However, it is not necessarily beneficial to suppress moulting altogether- the exoskeleton is subject to wear and tear; joints may become inhibited by particles getting stuck, and the amount of epifauna on the carapace may limit the crab, so most crabs undergo moulting to some extent once maturity has been attained (Warner, 1977). For those species in which terminal anecdyis (moult inhibition) occurs, the life of the crab is limited once the final moult has occurred.

Autotomy is the voluntary shedding of limbs, either as a response to injury or as a means of escape. This is achieved by co-operation between mechanical and neurological processes cutting off all vital supplies to the limb to be sacrificed, and forming a plug over the wound (McVean and Findlay, 1976). The loss of body fluids is prevented by an internal partition, which remains behind as a seal over the stump. This is quickly supplemented by clotted blood, which accumulates to form a scab. Autotomised limbs can only be reformed by moulting, and the process of autotomy stimulates the onset of the moult, although the growth increment may be reduced as energy is diverted form overall growth to replace the lost limb. Where the major cheliped is lost, the velvet crab will generally switch at the next moult so the minor cheliped will develop into the major cheliped and the autotomised major cheliped will grow as the minor. The significance of this is probably to do with the importance of the major cheliped in feeding. This process results in "left handed" crabs.

The moult cycle itself is a continuous process and is probably largely under hormonal control, modified via the central nervous system according to both internal and external environmental conditions (Warner, 1977). Ecdysis, the shedding of the old exoskeleton, can be divided into two phases:

1. Passive: water uptake commences and a split develops along the epimeral line of each branchiostegite posterior to anterior, and between the back of the carapace and the first abdominal segment. The back of the old carapace begins to rise, exposing the new carapace underneath, which has a wrinkled appearance.

2. Active: this begins once the carapace has been raised to an angle of about 30°. Contractions of muscles at the base of the legs loosen the limbs, which are slowly withdrawn from the old skeleton.

Various studies have been conducted to determine the life span and maximum size attained by *N. puber*. The results vary according to the geographical location of the site sampled. According to Gonzalez-Gurriarán (1981, 1985b) the velvet crab in Galician waters reaches a maximum size of 101-112mm CW for males and 89.3mm for females and has a life span of 4 years. Choy (1986b) identifies a maximum size of 78-85mm for males and 68-73mm for females with terminal ecdysis occurring after 5.5 years, although Bakir (1990) disagrees and finds no evidence of terminal ecdysis in Irish waters- crabs growing to a CW of 91-96mm for males and 90-92mm for females, showing a much smaller difference in size due to sex than those crabs studied in the other areas. According to Bakir (1990), the growth rate in females slows down after the first year and a half of life, corresponding to the time of the first brood. This would appear logical as energy reserves are diverted from growth to reproductive effort. However, it is data from the other areas, and not his that would point to this conclusion.

1.7.6 Studies Regarding Fishing and Effort

Previous studies into decapod crustacean fishing methods include comparisons of the Scottish creel and the inkwell pot (Thomas, 1954 and Shelton and Hall, 1981/2), the efficiency of parlour pots (Lovewell *et al.* 1979) and the effects of soak time on *Cancer pagurus* and *Homarus gammarus* catches (Bennett, 1974b). Miller (1990) has reviewed the effectiveness of crab and lobster traps. Other studies have examined the effects of hunger, relatedness and bait damage on a variety of marine crustacea (Moore and Howarth, 1996). Different baits have been studied in relation to *Cancer* *pagurus* (Chapman and Smith, 1974) and various studies into the chemical basis of bait attractiveness (Løkkeborg and Johannessen, 1992; Mackie,1973; Mackie and Shelton,1972) have also been carried out.

The only study that has examined the methods of catching velvet crabs is that of González Escalante and González-Gurriarán (1984), in which the effects of different baits on the catch were studied. Sardines were found to be the best bait, although there was no significant difference in catches using sardines, horse mackerel and bogue. Mussels were found not to be as effective as bait. Soak times were investigated in relation to escape gaps, with the conclusion that these gaps were inefficient at allowing undersized crabs to escape if the soak time was short (2-4 hours).

1.8 Methods Used in Previous Research

A range of methods has been used to carry out the various studies on the vital parameters of *Necora puber* in different areas. Whereas the main objective of most studies has been to determine the reproductive cycle and growth parameters of the stock in question, and in some cases, to provide a degree of stock assessment, the procedures have varied.

Size at sexual maturity was determined by gonadal studies by González-Gurriarán (1985a). These involved a general description of the ovaries and testes, which were divided into a series of stages depending on their development. The stages were identifiable by their colour, size and other parameters. Choy (1986b), Norman (1989) and Bakir (1990) also carried out gonadal studies, each with slight variations in the number and description of stages involved. Bakir (1990) went further and produced a detailed analysis of the microscopic structure of the gonads. Choy (1986b) also used morphometric analysis to determine a point of sexual maturity, based on work carried out by Warner (1977) and Hartnoll (1982). Morphometric differences related to the onset of sexual maturity were noticed in *Necora puber* by Drach (1933). Norman (1989) also carried out these studies, and later, González-Gurriarán and Freire (1994) carried out a comprehensive study into the relative growth of appendages and abdominal segments using multivariate analysis and bivariate regression methods to compare one- and two- phase growth models.

Studies of fecundity generally involve counting a small proportion of eggs and working out the total by weight or volume ratios. Differences arise in the methods used to count the eggs. González-Gurriarán (1985a) hardened the eggs with formalin, after which they were washed and dried. Choy (1985) suggested a method to remove eggs from the pleopods using a hypochlorite solution. Norman (1989) freeze-dried and desiccated the eggs before weighing the egg mass. The weight of the pleopods was deducted after this. Bakir (1990) also dried and weighed the eggs. In a preliminary study of the Orkney stock, Tallack (1998) examined the eggs soon after the females were obtained, using wet weight.

Growth studies have attempted to identify the growth parameters from the von Bertalanffy (1934, 1938) growth equation:

$$\mathbf{L(t) = L\infty * [\ 1 - exp\ (\ \text{-}K * (\ t - t_0))]}\ldots\ldots\ldots\ldots\ldots\ldots\ldots[1]$$

Where: L(t) is the length at age t

L∞ is the asymptotic length

K is the growth constant, the rate at which L∞ is reached

t_0 is the point in time where the fish has zero length

González-Gurriarán (1985b) used Ford-Walford (Ford, 1933; Walford, 1946) plots to determine L∞, K and t_0, from animals reared under laboratory conditions. The plot follows the equation:

$$\mathbf{L\ (t+\Delta t)\ = a + b * L\ (t)}\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots[2]$$

Where **a** and **b** are the intercept and slope of the straight line respectively. If Δt is 1 year (as would be the case with annually moulting species) then:

$$\mathbf{L\infty = a/1\text{-}b}$$

$$\mathbf{K = \text{-}ln\ (b)}$$

He felt that his estimate of L∞ from this method was too high so, while the rigor of this may be questionable, he used the Pauly (1980) approximation:

$$L\infty = L\ max / 0.95$$

He incorporated this value into the growth curve for the Spanish stock. Other studies have focused on length-frequency analysis in order to determine modal points for use with either Ford-Walford or Gulland and Holt plots. Choy (1986b), Norman (1989) and Bakir (1990) all used probability paper techniques to determine the modal sizes, as explained in Cassie (1954). Using probability paper involves a degree of subjectivity in the identification of modal points. A method which lessens the degree of subjectivity, but is nonetheless similar, is the Bhattacharya (1967) method. This method consists of splitting a composite distribution into its separate normal distributions by means of a log transformation into a straight line, assuming that the initial left-hand curve of the composite distribution is the uncontaminated slope of the first cohort. The effectiveness of both probability paper and Bhattacharya analysis depends on the extent to which the modal sizes are merged in the composite distribution.

Choy (1986b) and Norman (1989) used the Gulland and Holt (1959) plot to give estimates of L∞ and K. This follows the equation:

$$\Delta L / \Delta t = K * L\infty - K * L(t)(mean) \ldots\ldots\ldots\ldots\ldots\ldots\ldots [3]$$

Where L(t)(mean) is the mean length of L(t) and L(t+1)

If this is plotted with L(t)(mean) as the independent variable, and $\Delta L/\Delta t$ as the dependent variable, the resultant linear regression can be used to determine K and L∞, where the line follows the equation $y = a + bx$, (**a** being the intercept and **b** the slope).

$$K = -b$$

$$L\infty = -a/b$$

Norman (1989) also used the computer programme, ELEFAN, which directly analyses a time series of length-frequency data. He found a variation of 3mm between the ELEFAN and the probability paper estimates of $L\infty$, and some variation of K in females. Further variation was found when he used reared individuals to estimate K and $L\infty$.

Bakir (1990) used the Ford-Walford plot to determine $L\infty$ and K, but was not confident of the results, preferring to use the Pauly (1980) expression of $L\infty$ in subsequent analysis. However, he maintained his K and t_0 values from the Ford-Walford analysis.

As Bakir (1990) was investigating an unfished stock, he assumed total mortality (Z) was equal to natural mortality (M). He used the Pauly M formula (Pauly, 1980), relating mortality to $L\infty$, K and average water temperature. However, there is debate as to whether this equation is suitable for crustacean species (Pauly, 1984, Sparre and Venema, 1992). Choy (1986b) also used this method to determine M.

Direct measurements of M are difficult to obtain due to the many factors causing it, e.g. predation, disease, and old age. Most methods are rough estimates. Beverton and Holt (1959) noticed that there was a general relationship between M and K. The higher the K value, the higher the corresponding M value, and vice versa. They found a general M/K relationship of 1.5-2.5.

According to Alagaraja (1984), mortality is related to longevity. He defined the natural life span as the age at which 99% of a cohort was dead due to natural causes only (i.e. Z=M). Hence the approximation:

$$\mathbf{M1\% = -ln\ (0.01)\ /\ Tm}$$

Where M1% = natural mortality corresponding to 1% survival
Tm = longevity (years)

When González-Gurriarán (1985b) carried out yield per recruit analysis on the Spanish stock, he took a range of estimated values for M, from 0.2-0.6, thus exploring a series of possible situations. He estimated total mortality (Z) by use of the exponential decay model (Gulland, 1971; Beverton and Holt, 1957):

$$Nt = N_0 \cdot e^{-Zt} \dots\dots\dots\dots\dots\dots [4]$$

Where Nt are the numbers remaining at time t (in this case one year)

N_0 are the original numbers.

Choy (1986b) determined Z using length-converted catch curves. These are plots of the logarithms of numbers caught against age, or in some cases, size. In the case of crustacean fisheries, length converted catch curves are used, in which length is converted to age using the equation:

$$t(L) = to - 1/K * \ln (1- L/L\infty) \dots\dots\dots\dots [5]$$

The main slope of the catch curve is used to determine Z. The initial points are discarded as they refer to sizes not fully exploited, and the final points, too close to $L\infty$ are also discarded. From the straight line regression of the points used:

$$Z = -b$$

Where **b** is the slope of the regression (y = a + bx). The catch curve can also be used to determine the selectivity of the catch gear, by examining the initial points of under-exploited sizes. If the regression line used for mortality determination is extended backwards, a comparison can be made of what was caught and what should have been caught.

Some studies have attempted to examine distribution and abundance of velvet crabs. Population density in terms of crabs per square metre has been estimated using trawl data (Gonzalez-Gurriarán, 1985b), divers (Bakir, 1990) and collection by hand (Choy, 1986b). Bakir (1990) also carried out a tagging experiment, by which 800 tagged animals were released in a number of areas. He used claw and suture tags, recapturing 18 of the released animals, all within the same area of release. A tagging programme is currently underway in Millport, Scotland (pers. comm. Combes, Millport Marine Lab.).

1.9 Gaps in Knowledge Identified by Previous Studies

Little work has been carried out on *Necora puber* compared to other commercially important crustaceans such as lobsters, edible crabs and the portunid blue crab, *Callinectes sapidus*. Until recently, the only systematic study on a natural population of *N. puber* was the work carried out by González-Gurriarán in Spain (1981, 1985a, 1985b). Since then, stocks have been studied in Plymouth (Norman, 1989), Dalkey (Bakir, 1990) and Swansea (Choy, 1986b). These have highlighted the fact that there is considerable variation in the timing and length of some of the vital processes in understanding a population, such as size at sexual maturity, the duration of the moulting and mating period, growth rates and maximum size reached. It is therefore essential to determine these parameters for the Orkney stock as a baseline from which to carry out further research and make decisions regarding the management of the fishery. This should include some work on the larval stages and especially on the juveniles, which appear to have been largely neglected until now. Little is known about the movements of the adults in comparison to that of lobsters and other crab species.

There is a degree of variation depending on the methodology used to carry out analyses, especially in the area of population dynamics. Presentation of fixed, precise figures assigned to parameters such as $L\infty$ and K can be misleading and should be viewed with caution, not only because they vary according to the method, but because the methodology itself is built upon assumptions that may not necessarily hold true.

The growth parameters $L\infty$ and K are important figures in crustacean stock assessment, as they are used in population dynamics and various stock assessment models. For this reason, the methods used to obtain these figures must come under careful scrutiny. The studies that have depended upon laboratory growth figures must take into account the different conditions between the laboratory tanks and the open sea. But more importantly, those studies which have relied upon modal point analysis from length-frequency data must recognise the drawbacks and subjectivity involved in such analysis. The validity of such methods must be placed under rigorous examination. At the same time, investigations should be carried out into developing new methods that are less subjective and depend less on fisheries data, which in itself is selective, due to the gears involved.

In terms of the fishery, despite the vast amount of literature discussing the effectiveness of different fishing practices (bait, soak time, mesh size) on edible crabs and lobsters, only one study has focused on velvet crabs to date, and questions must be asked about the methods used to catch velvet crabs in Orkney.

1.10 Aims of Current Study

The general objective of this study is to examine the life cycle of the Orkney stock of the velvet swimming crab, paying particular attention to those factors that might influence the fishing industry. A review of the current state of the fishery and its management is also included as a primary objective.

From the general objective and the questions arising from 1.9, a series of aims was elaborated (see Introduction, Section B), bearing in mind the evidence for geographical variation in many aspects that had previously been studied in other areas. From these aims, specific questions were formed. These are summarised below:

Part 1: Background

1. What is the importance of *Necora puber* and other portunids in worldwide fisheries?
2. What is the importance of *Necora puber* to the Orkney Isles?
3. What knowledge of the Orkney stock can be obtained from studies of other stocks?
4. What are the gaps in our knowledge of the Orkney stock?
5. How may these gaps be addressed?

Part 2: Reproduction

1. At what size is sexual maturity attained?
2. When does mating occur, and is there a size relationship within a pair?
3. What is the brood size?
4. Is the brood size affected by the size of the female, limb loss?
5. Is there egg loss during development?
6. What are the stages (and duration) of egg development?
7. How often does reproduction occur, and what is the timing?
8. Can fecundity be used to estimate preliminary mortality (Z) figures?

Part 3A: Larvae

1. Is there a prezoeal stage for *Necora puber?*
2. Can the prezoeal stage be described?
3. What is the development time through each stage in the laboratory?
4. What is the mortality through each stage in the laboratory?
5. Is larval rearing on a large scale feasible?
6. Are larvae comparable in morphology with those from other stocks?
7. When are larvae present in the water column?

Part 3B: Juveniles

1. Where are juvenile *Necora puber* found in Orkney?
2. Can a measure of abundance be obtained?
3. Which is the best method of obtaining juveniles?
4. To what extent are juveniles morphologically similar to adults?
5. When does settlement occur?
6. Is the sex ratio 1:1?
7. How fast do they grow?
8. When do they reach sexual maturity?
9. When do they reach MLS (minimum landing size)?
10. How often do they moult?
11. What are the moult increments?

12. Can growth curves for the entire population be constructed from juvenile data?

Part 4: Population dynamics

1. What is the relationship between CW, CL and weight?
2. Does the sex ratio change over time, and if so, why?
3. How often and when do adults moult?
4. How long does the moult process take?
5. Is tagging an effective method to measure growth/movement?
6. What are the von Bertalanffy growth parameters (L_∞ and K) for the stock?
7. What are the advantages/limitations of the methods used?
8. Are there any differences between males and females?
9. What are the values for Z, M and F?
10. Can the population structure be modelled?
11. How do the population dynamics compare with other areas?

Part 5A: Baiting practice

1. Is there a difference between fresh, frozen and salted bait?
2. Does soak time affect catch?
3. What are the reasons for creels not fishing?
4. Do lobsters and crabs interfere with one another in terms of catch?

Part 5B: The state of the fishery

1. Does the mean size of individuals caught change over time?
2. What is the selectivity of the fishing gear used?
3. Can we observe changes in catch and effort over the years?
4. Is it possible to carry out size-cohort analysis on the stock?
5. Can yield per recruit analysis be used as a tool for predicting results of changing the MLS?

Part 5C: Market considerations

1. What is the monthly catch of velvet crabs in Orkney, per port?
2. To what extent is mortality at the packing stage important?
3. Does the quality of the catch change throughout the year?
4. How much do discards affect the industry?
5. What is the price fluctuation throughout the year, at first sale and at the marketplace?

Section C: Study Area

1.11 Main Fishing Zone

The methodology for each part of this study is laid out in detail at the beginning of each relevant section. Many of the analyses carried out involved data collected from a two-year sampling programme, which took place aboard the vessels Double Twos, a catamaran modified to perform the operations of a creel boat and Velvet Crab, a small, part time creel boat. Both vessels are based in the harbour of Tingwall (Figure 1.14). Fishing was carried out mainly up Eynhallow Sound and in the Westray Firth, to the north of the island of Rousay, but focused between the harbour of Tingwall and the island of Eynhallow, on both sides of the Sound. There were a number of reasons for choosing this particular area. Firstly, it is easily accessible from Stromness by road, and is an area of intense fishing, so availability of boats is not a problem. Secondly, its position allows for fishing at least some parts of the Sound all year round, with the weather only rarely preventing this.

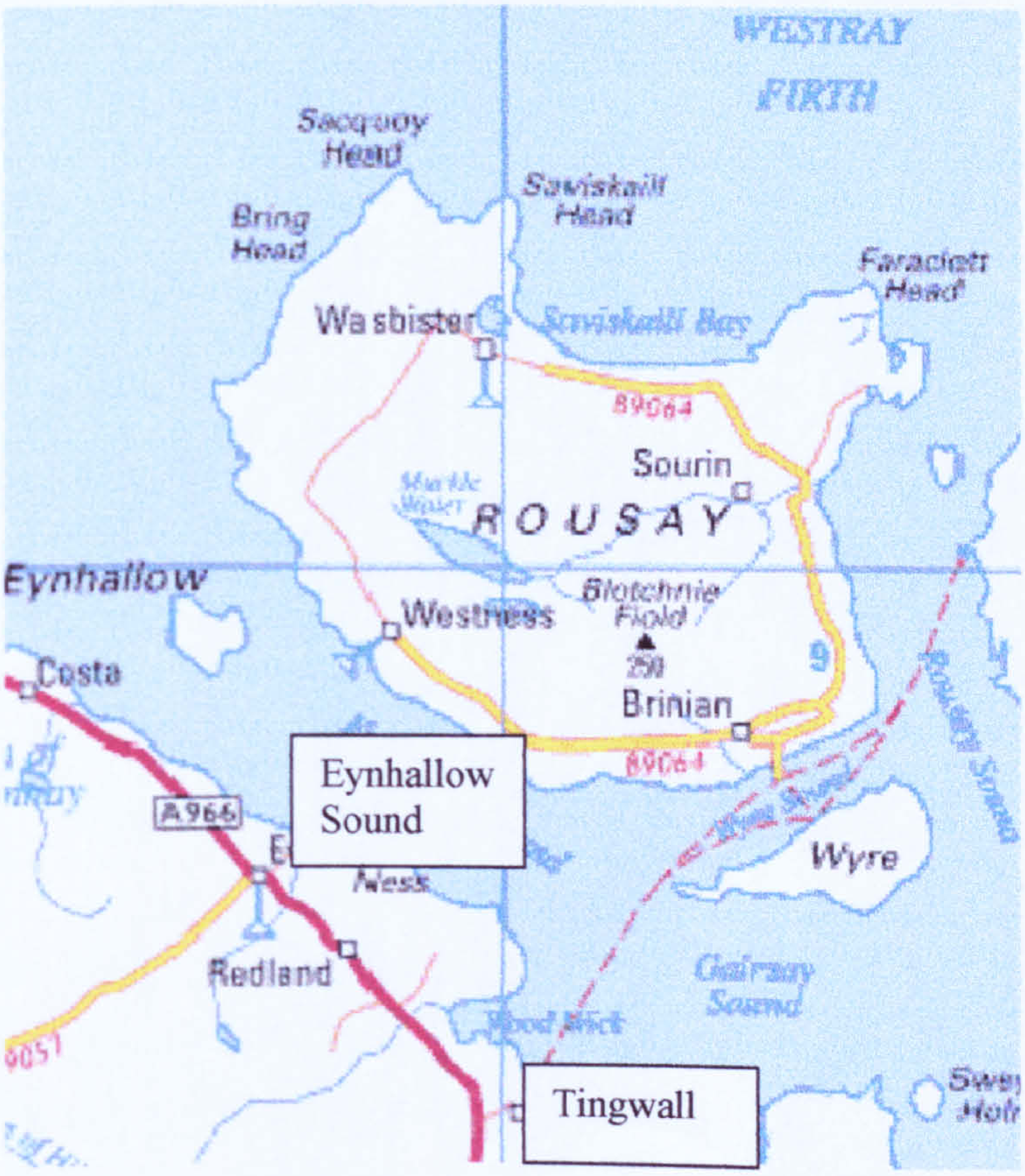


Figure 1.14 Tingwall and Eynhallow Sound (from www.multimaps.com)

Rousay's west coast is very exposed to wave action, although the majority of shores within Eynhallow, and Rousay Sounds are moderately exposed, being of gently-sloping broken bedrock and stable boulders. The shores are dominated by fucoid algae, with the kelp *Laminaria digitata* in the sublittoral fringe (Murray *et al.* 1999).

Eynhallow Sound (Figure 1.15) is characterised by tide-swept bedrock platforms. In the centre of Eynhallow Sound, the tide-swept bedrock below the kelp forest has a dense faunal turf, dominated by the soft coral *Alcyonium digitatum* and the bushy bryozoans *Securiflustra securifrons* and *Flustra foliacea* (Murray *et al.* 1999). To the south-east of the small island of Eynhallow, there is a large expanse of medium and fine sand with various bivalves and areas of eelgrass *Zostera marina*.

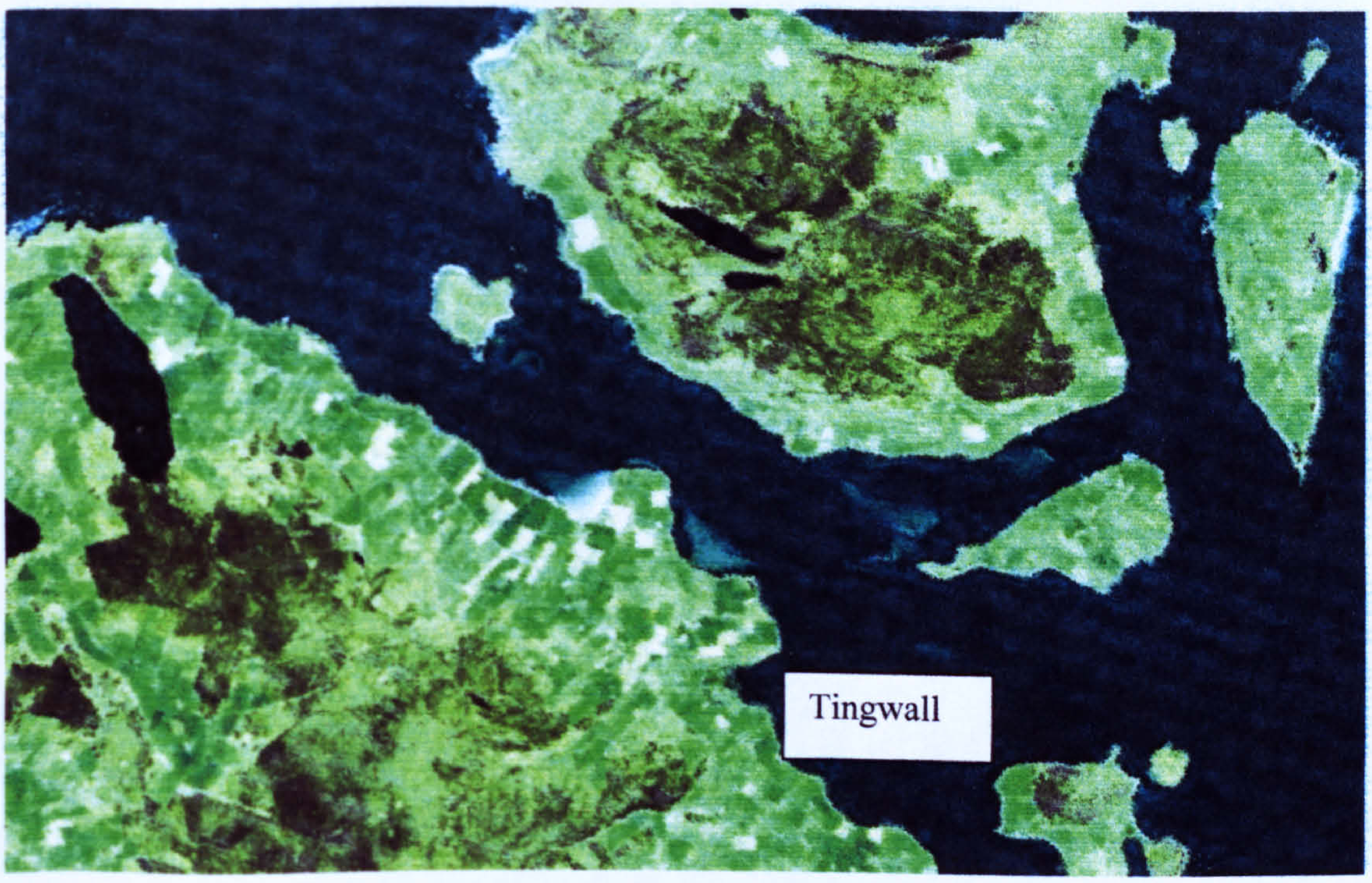


Figure 1.15 Satellite photograph of Eynhallow Sound showing position of Tingwall harbour (from The Times Window on the UK CD-ROM)

The area is intensely fished, with boats tending to concentrate on the waters hugging the shoreline on both sides of the Sound and around the island of Eynhallow itself, as well as further offshore and to the north of Rousay.

1.14 Bait Experiments

The bait and fishing experiment described in Section 5A were carried out in Auckwall Bay, also known as Wass Wick (Figure 1.16).

Figure 1.16 Wass Wick: location of gear experiments (from www.multimaps.com).

The exact positions of each location are summarised in Table 1.3. The seabed in this area is similar to that of most of the coastline of Eynhallow Sound – rocky with wrack and laminarians, and some sandy areas characterised by the presence of green crabs (*Carcinus maenas*) and spider crabs (*Hyas araneus*).

Equipment	**North position**	**West position**
Selectivity creels	59° 04.95	003° 01.54
Bait effectiveness	59° 04.95	003° 01.30
Soak time	59° 05.07	003° 01.66

Table 1.3 Position of gear experiments

PART 2: REPRODUCTION

2.1 Aims

The aims of this section are to determine certain aspects relating to the reproductive capability of the Orkney stock, after previous studies have shown how there is much geographical variability in some essential parameters which are used in fisheries management (refer to Section 1.8).

Estimates of size at the onset of sexual maturity are among the most important information regarding commercially exploited biological populations. The onset of sexual maturity can vary considerably between individuals and populations, so an estimate of the size at which 50% of a population is mature is often required (Fonteles-Filho, 1989). The first aim of this section is to estimate the size of both males and females at the point of sexual maturity, in both a physiological and functional sense, as this is the basic parameter in the establishment of minimum landing sizes (MLS).

Estimation of sexual maturity may be carried out by microscopic or macroscopic examination of the gonadal stages for both males and females, taking into account that for parts of the year, the ovaries are undeveloped (Choy, 1988). Another method is to examine the changes in growth of various parts of the body, as carried out by Drach (1933), Choy (1988), Norman (1989), and González-Gurriarán and Freire (1994). These studies found that changes in allometry attributable to puberty occurred in the fourth and sixth abdominal segments for females, and in the height and length of the crusher chela for males. One disadvantage of this method is that it identifies a minimum size of maturity, and does not necessarily reflect the size at which significant reproductive output is achieved (Somerton, 1980).

As stated in Section 1.7.2, the male tends to be significantly larger than the female in a mating pair. It is important to determine the extent to which this is true in the local population, and the amount of this difference, as this may have long-term implications on the population structure if fishing legislation is based mainly on a blanket MLS.

The fecundity of females is a very important aspect of the reproductive biology of a species, as it gives information on the total fecundity of that species or population. It is the aim of this section to also examine the fecundity of the local population and some of the aspects (including size, limb loss and time of year) which may affect this, as well as to compare it with that of females in other areas.

Once the fecundity pattern for the population has been established, it is then important to determine how fast the eggs develop, how long they spend at each stage and when this occurs throughout the year. This section also examines egg size at each developmental stage, the duration of the incubation period as a whole, and the duration of each individual stage of development.

The reproductive cycle in general may be established in terms of the most important aspects relating to this: the mating period, the incubation period and the hatching period. This information may prove vital when examining fluctuations in catch rate and the possibility of introducing closed seasons. The final aim of this section is to determine the reproductive cycle of the population as a whole over the two-year study period, in order to determine exactly how many generations are spawned in a year, and to discover when this occurs and over how long a period of time.

The questions asked in this section are summarised below:

1. At what size is sexual maturity attained?
2. When does mating occur, and is there a size relationship within a pair?
3. What is the fecundity?
4. Is fecundity affected by the size of the female, limb loss?
5. Is there egg loss during development?
6. What are the stages (and duration) of egg development?
7. How often does reproduction occur, and what is the timing?
8. Can fecundity be used to estimate initial mortality (Z) figures?

2.2 Methods and Materials

2.2.1 Sexual maturity

González-Gurriarán (1985a) recommends a combination of internal and external methods of determining the size at sexual maturity. In this study, both gonadal examination and relative growth of body parts was used.

Over the study period, some 400 crabs of all sizes were caught from the main sampling area and through shore searches (Dataset 7, Appendix A). These were taken back to the laboratory, sexed and measured (CW was used as the independent variable). If caught during the reproductive period (between October and June), females were examined for presence of eggs, sperm plugs and the ovary condition. The maturity index used for ovarian examination was that according to González-Gurriarán (1985a). The testes of the male crabs were examined for maturity. The crabs were grouped into 2mm size classes and separated by sex. The percentage of sexually mature crabs for each size class was plotted against CW. A selection ogive was fitted to the data points using regression analysis of the variable section of the graph (Figure 2.1). This gave estimates of the size for males and females at which 25%, 50% and 75% of the population are sexually mature.

In order to obtain a functional index of sexual maturity, 173 females and 272 males of all sizes were obtained from the main study area and shore searches from January 1999 until December 2000. The CW, sex and gonad maturity of each crab were determined. The length and height of the crusher chela and the basal width of the fourth and sixth abdominal segments were also measured (Dataset 7, Appendix A).

The data was plotted separately for each sex as a bivariate scatterplot. For each sex, trend-lines were constructed for those individuals known to be sexually mature, and for those known to be sexually immature. In the cases where discontinuities occurred, this was assigned as the mean point of sexual maturity. In those cases where a change in the slope of the relationship occurred, the trend-lines were extended to the point where they intersected, assigned as the mean point of sexual maturity.

2.2.2 Mating

Throughout the study period, all mating pairs caught in creels in all sampling expeditions were recorded in terms of the CW of both partners, as well as their location and date of capture (Dataset 10, Appendix A).

2.2.3 Fecundity and egg development

Around 10 berried (ovigerous) crabs were collected during each outing of the general sampling period (Dataset 1, Appendix A) and taken to the laboratory for immediate analysis of fecundity. The egg mass was cut from the endopods and weighed to the nearest 0.001g. A small sample of eggs was removed and weighed separately. The number of eggs was then counted under a binocular microscope (100x). The mass of one egg was thus obtained and from that, the number of eggs in the egg mass was calculated. This was carried out three times for each individual in order to account for experimental error. Each female was also measured for CW, weight and limb loss, to be used in further analysis (Dataset 8, Appendix A).

The eggs were also examined for their developmental stage and size. Eggs were staged according to the description in Table 2.1, adapted from Norman (1989).

Stage	Description
1	Newly spawned, full of yolk, lacking cleavage
2	Few large, or many small cells visible
3	Eyespots first visible
4	Chromatophores and eyespots well developed; obvious heartbeat

Table 2.1 Stages in egg development (Norman, 1989)

Three eggs from each ovigerous female were chosen at random and staged. Three measurements of diameter were taken at perpendicular angles of each egg in order to give a mean diameter (in latter stages, the eggs are less spherical and more elliptical).

In addition to this, one female laid her eggs whilst in the laboratory. She was examined each week and a sample of her eggs measured for mean diameter, long diameter, and stage. Although laboratory conditions were not equal to conditions at sea (mainly in terms of temperature), this served as a guide to egg development (Dataset 9, Appendix A).

2.2.4 Reproductive cycle

During each outing of the main sampling period, all berried females out of the first 100 crabs caught were recorded along with their CW and limb loss, to give a measure of the periodicity and temporal distribution of this part of the reproductive cycle (Dataset 1, Appendix A).

2.2.5 Estimation of mortality

The exponential decay model described in Section 1.8 (Baranov, 1918; Beverton and Holt, 1957) was used to give initial estimates of Z. The mean fecundity and number of spawnings in a lifetime were used to determine the total number of eggs released during the lifetime of an individual. A steady state population was assumed, whereby each female gave rise to two viable offspring (one of each sex) in her lifetime. It was assumed that only two offspring reached the first crab instar, after which there was no mortality until they had successfully reproduced.

2.3 Results

2.3.1 Sexual Maturity

Figure 2.1 shows the results of physiological maturity examinations for males and females. In total, 176 males and 130 females were measured, but only a small number of these fell into the critical size categories (see Table 2.2).

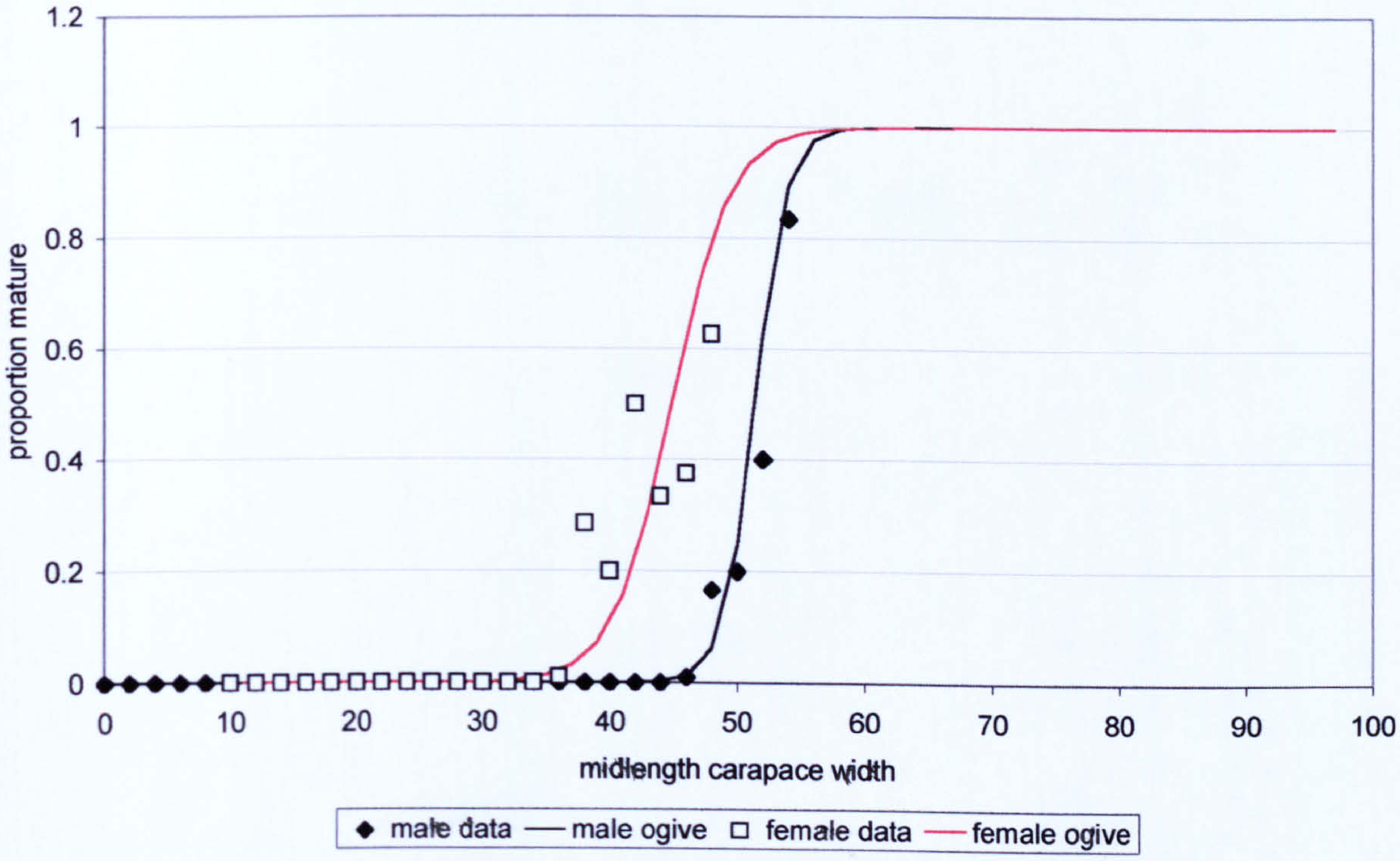


Figure 2.1 Proportion of individuals with sexually mature reproductive systems at each size

From the graph, with the confidence that all females under 36 mm CW are immature, and all those over 50mm CW are mature, the consequent selection ogive joining these points gives an approximate 50% maturity for females of around 44.9mm CW (L25% = 42.3mm, L75% = 47.3mm). In the same way, all males under 45mm CW are immature and all those above 55mm CW are mature, giving a curve with a 50% maturity size of around 52.4mm CW (L25% = 51.0mm, L75% = 53.7mm). According to the graph, maturity for both males and females occurs over a narrow size range of at most 10mm. This probably coincides with a single moult, with the variation displayed being a simple variation of size distribution around a mean.

Size (CW) mm	No. males	No. mature	No. females	No. mature
37	3	0	2	0
39	1	0	5	2
41	5	0	5	1
43	1	0	2	1
45	4	0	2	1
47	4	0	3	2
49	6	1	4	3
51	5	1	5	5
53	5	2	7	7
55	6	5	10	10
57	16	16	11	11
59	11	11	10	10
61	8	8	7	7

Table 2.2 Individuals and number mature, sampled at each size class for gonad maturity

The following figures show the results of the morphometric measurements carried out on males and females in order to determine a physiological size for puberty. In all the graphs, black points refer to males, whereas the unfilled squares refer to females. Figure 2.2 shows the relationship between carapace width and the length of the major (cutter) chela; Figure 2.3 shows the relationship between carapace width and the height of the major chela; Figure 2.4 shows the relationship of carapace width and the width of the fourth abdominal segment; and Figure 2.5 shows the relationship between carapace width and the width of the sixth abdominal segment.

Appendix B summarises the regression results and analysis of the degree of allometry of the variables measured to determine sexual maturity.

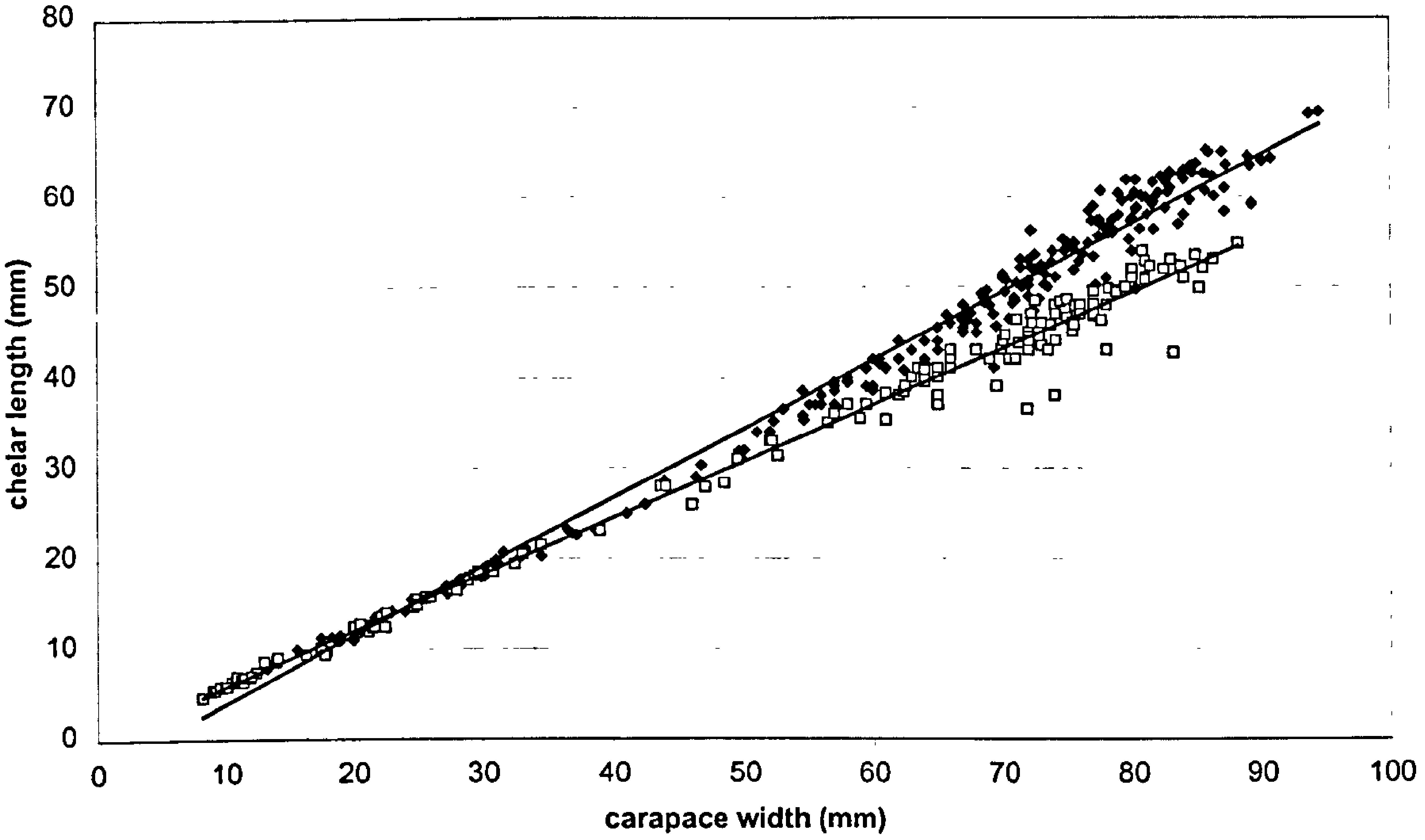


Figure 2.2 Length of major chela in relation to carapace width (filled points = males; unfilled points = females)

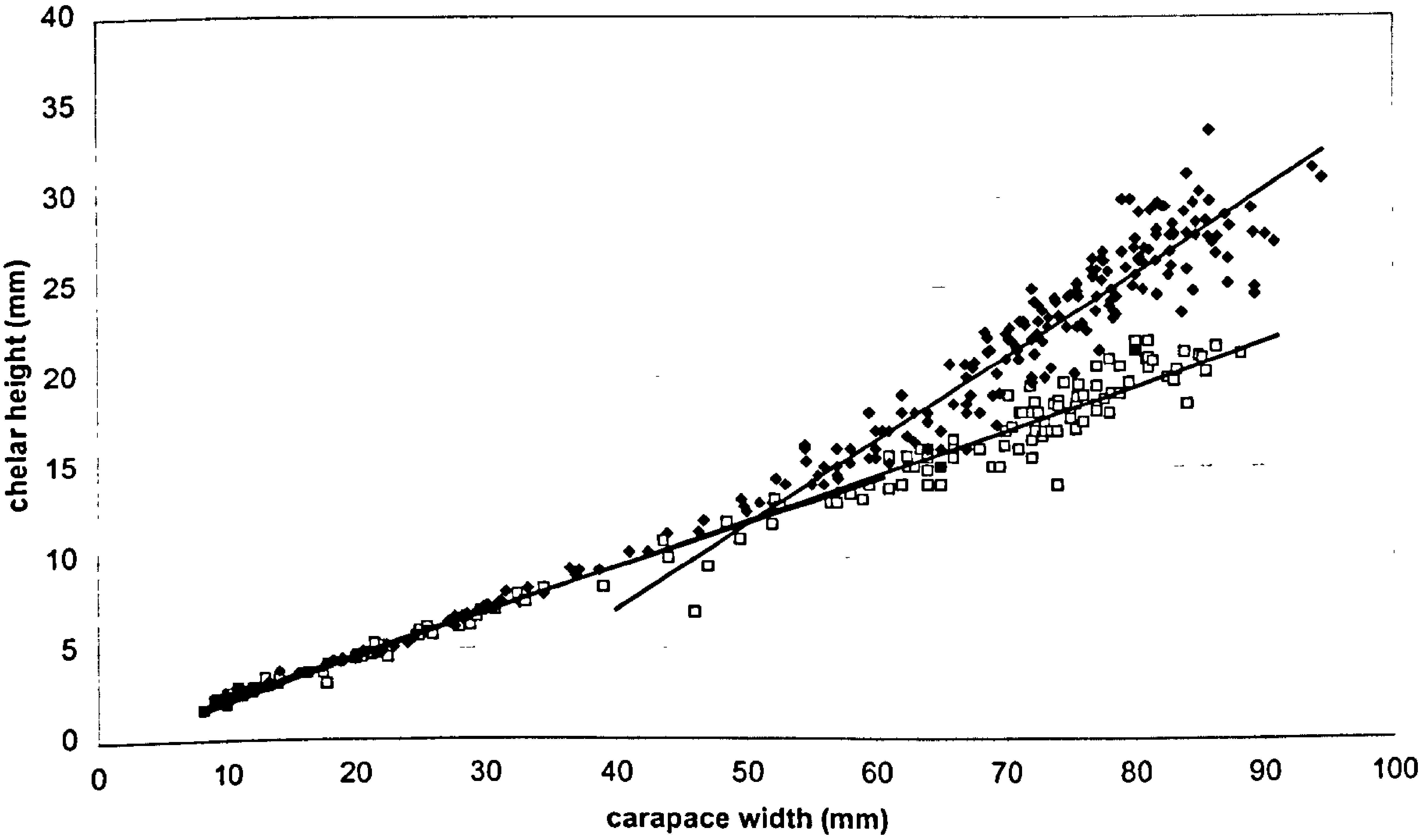


Figure 2.3 Height of major chela in relation to carapace width (filled points = males; unfilled points = females)

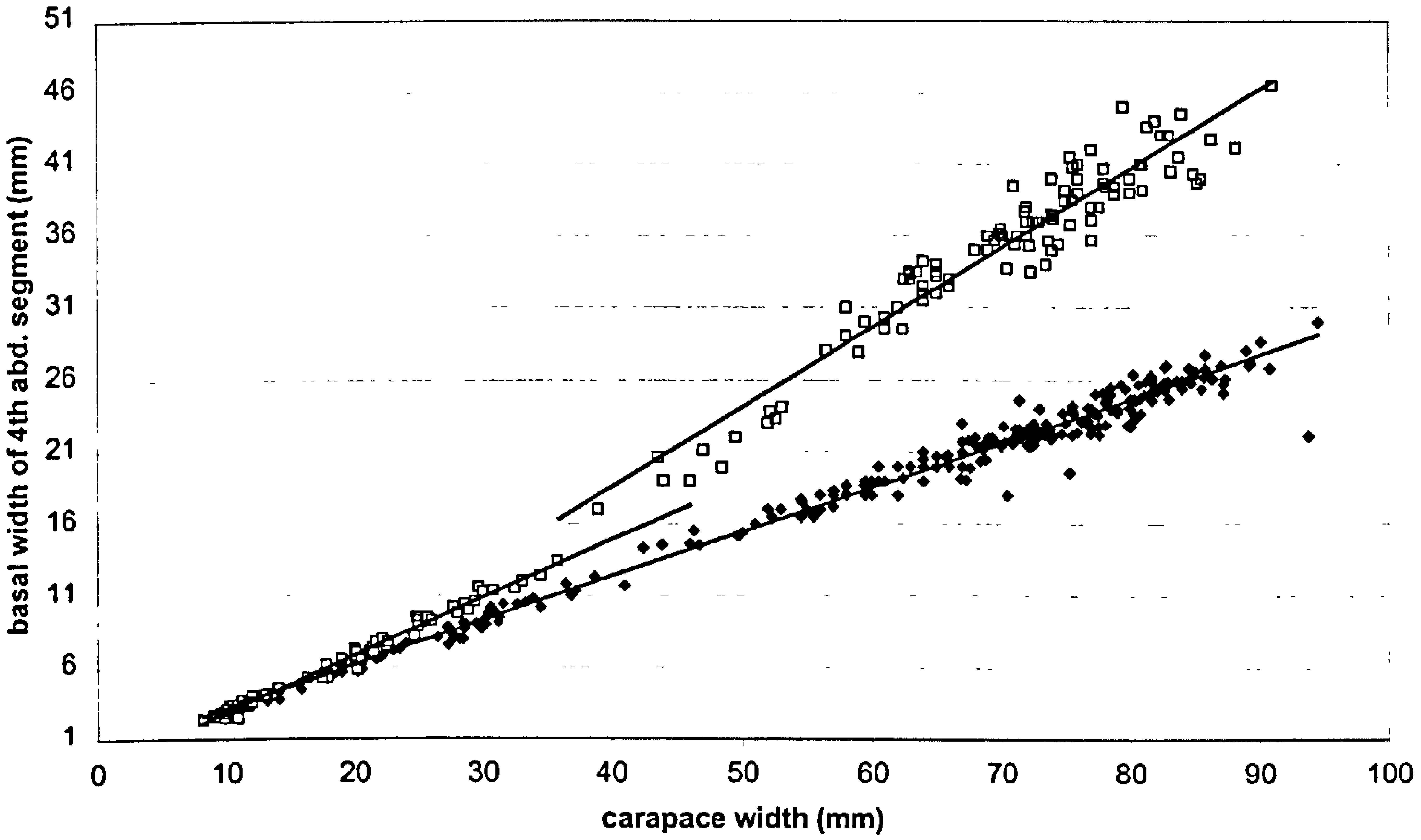


Figure 2.4 Relationship between carapace width and basal width of fourth abdominal segment (filled points = males; unfilled points = females)

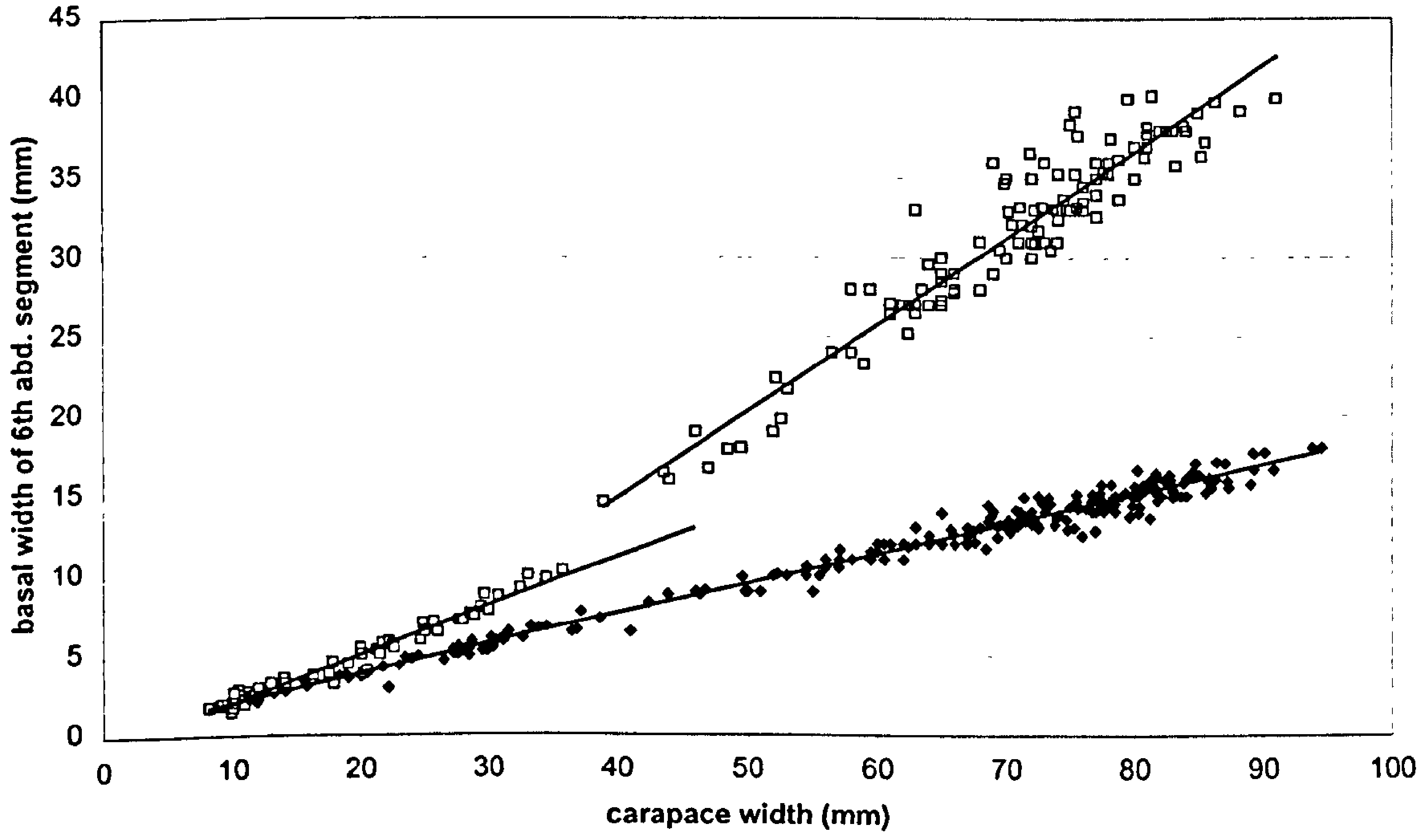


Figure 2.5 Relationship between carapace width and basal width of sixth abdominal segment (filled points = males; unfilled points = females)

Figures 2.2 and 2.3 suggest that the major chela grows at a faster rate for males than for females overall. There is no clearly visible discontinuity or change in growth rate in terms of the length of the chela for either males or females. However, there is a marked increase in the growth rate in terms of the height of the chela in males. This occurs at a carapace width of around 51mm. There is no corresponding change for females. The increase in chelar height with increasing carapace width is isometric for females and juvenile males, showing positive allometry in adult males.

Figures 2.4 and 2.5 show that abdominal growth in segments four and six are isometric for males, showing no discontinuity. There is positive allometric growth in both segments for juvenile and adult females, although the extent of the allometry increases once the pubertal moult has been attained, where there is also a discontinuity. This occurs around a carapace width of 38-40mm.

2.3.2 Mating

Due to the small numbers of mating pairs that were found during the study period, not much information can be gathered about the duration of the mating act or the length of time a mating pair remains together. Table 2.3 shows the date, location and size of each individual for all mating pairs found:

Date	Location	Male CW (mm)	Female CW (mm)	Difference
13 Sept 99	Tingwall	70	61	9
22 Sept 99	Tingwall	65	58	7
22 Sept 99	Tingwall	65	59	6
13 Sept 00	Aikerness	73	63	10
13 Sept 00	Aikerness	75	64	11
13 Sept 00	Aikerness	67	60	7
13 Sept 00	Aikerness	72	65	7

Table 2.3 Date, location and size of mating pairs

Although only a few mating pairs were recorded, some observations can be made. Firstly, for both years, all the pairs were found in the month of September, indicating a very discrete mating season, corresponding to this month. Secondly, all males were consistently larger than their female counterparts (by a value of between 7-11mm CW). The difference in size between the male and female may also be significant. Referring to Figure 2.1, the size difference at puberty is of around 7mm, so it is possible that this difference is continued throughout life, with individuals only being able to mate with those of their same age. The reasons for this may be purely geometrical and related to the mechanics of the process of copulation.

2.3.3 Fecundity

Figure 2.6 shows the relationship between brood size and carapace width for all individuals measured, regardless of egg stage or limb loss. The highest egg number was 278 000 (cw: 81mm) and the lowest was 5000 (cw: 76mm).

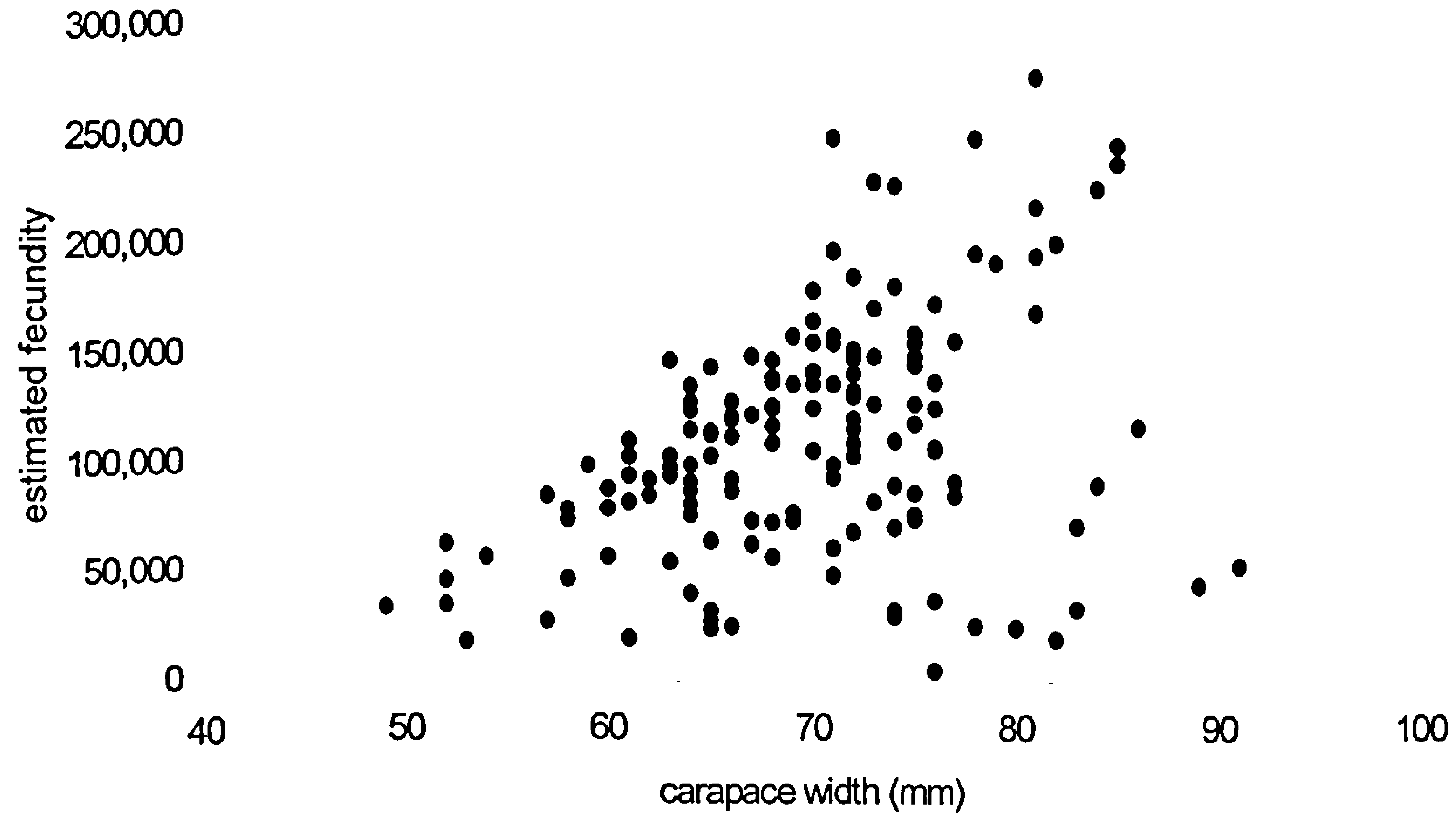


Figure 2.6 Egg number and carapace width

The size of females examined ranged between 50 and 89 mm CW. From the graph it can be seen that, although there is a general positive correlation between carapace width of the individual and the brood size there is also much variability. This variability appears to increase with increasing carapace width. There were a significant number of large females with very small egg masses, corresponding to the points on the lower right hand side of the graph. The reasons behind such small numbers of eggs in these females were not known, but may be stress-related.

In order to determine whether the stage of development may account for some of the variability shown in Figure 2.6, and also whether limb loss may have an effect, the size-fecundity relationship was broken down for individuals at each stage, omitting any individuals experiencing limb loss. The results of this graph are shown in Figure 2.7.

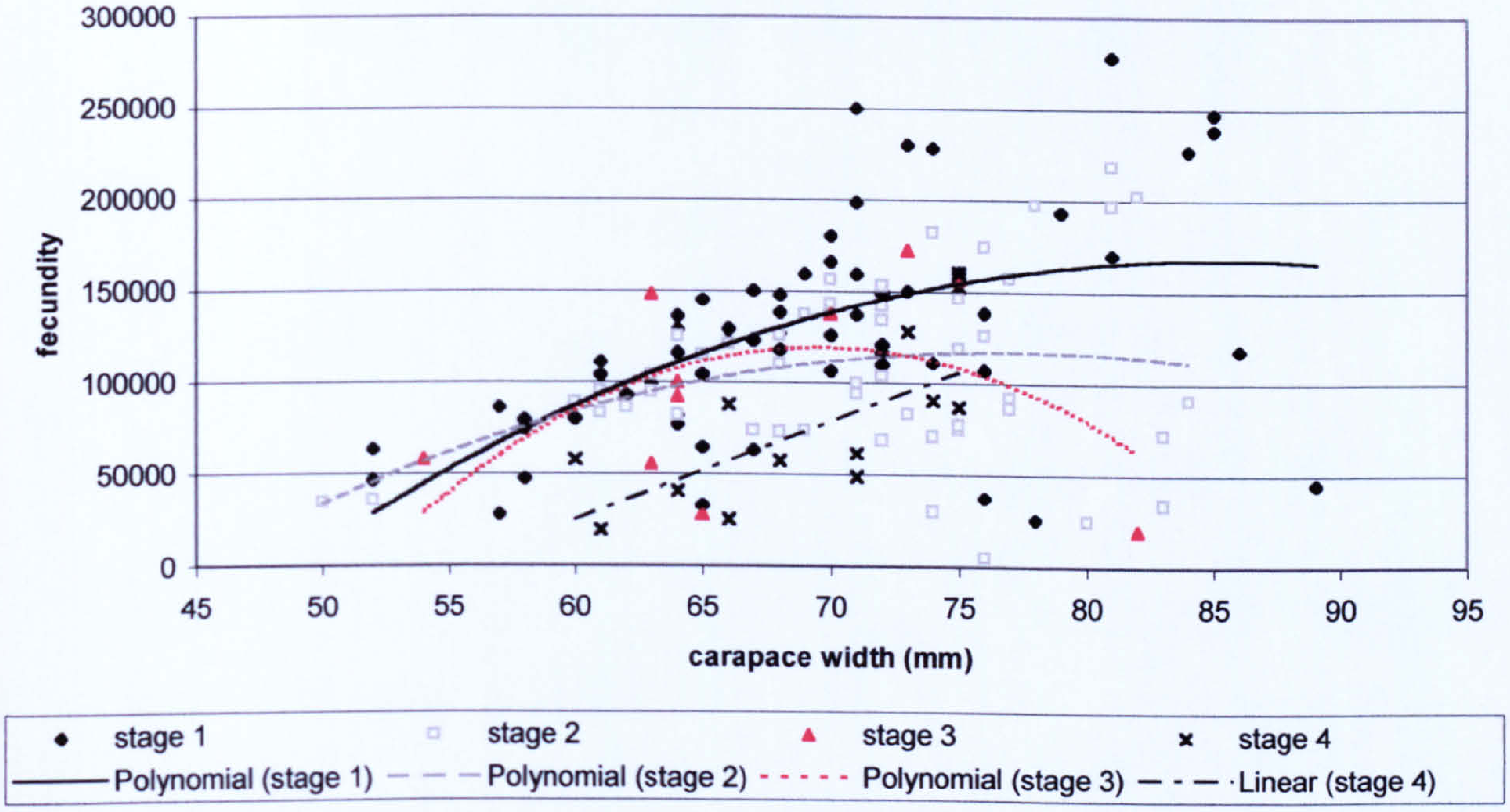


Figure 2.7 Fecundity related to development stage of egg, showing trend-lines for each stage.

The graph shows some evidence of a decrease in the number of eggs at later stages in comparison to that of early stages at each size class. There is still, however, much variation in fecundity at different sizes for each egg stage. Thus, although egg loss does occur throughout the incubation period, this alone is not responsible for the range of fecundities found. The mean brood sizes corresponding to each egg stage were plotted on Figure 2.8.

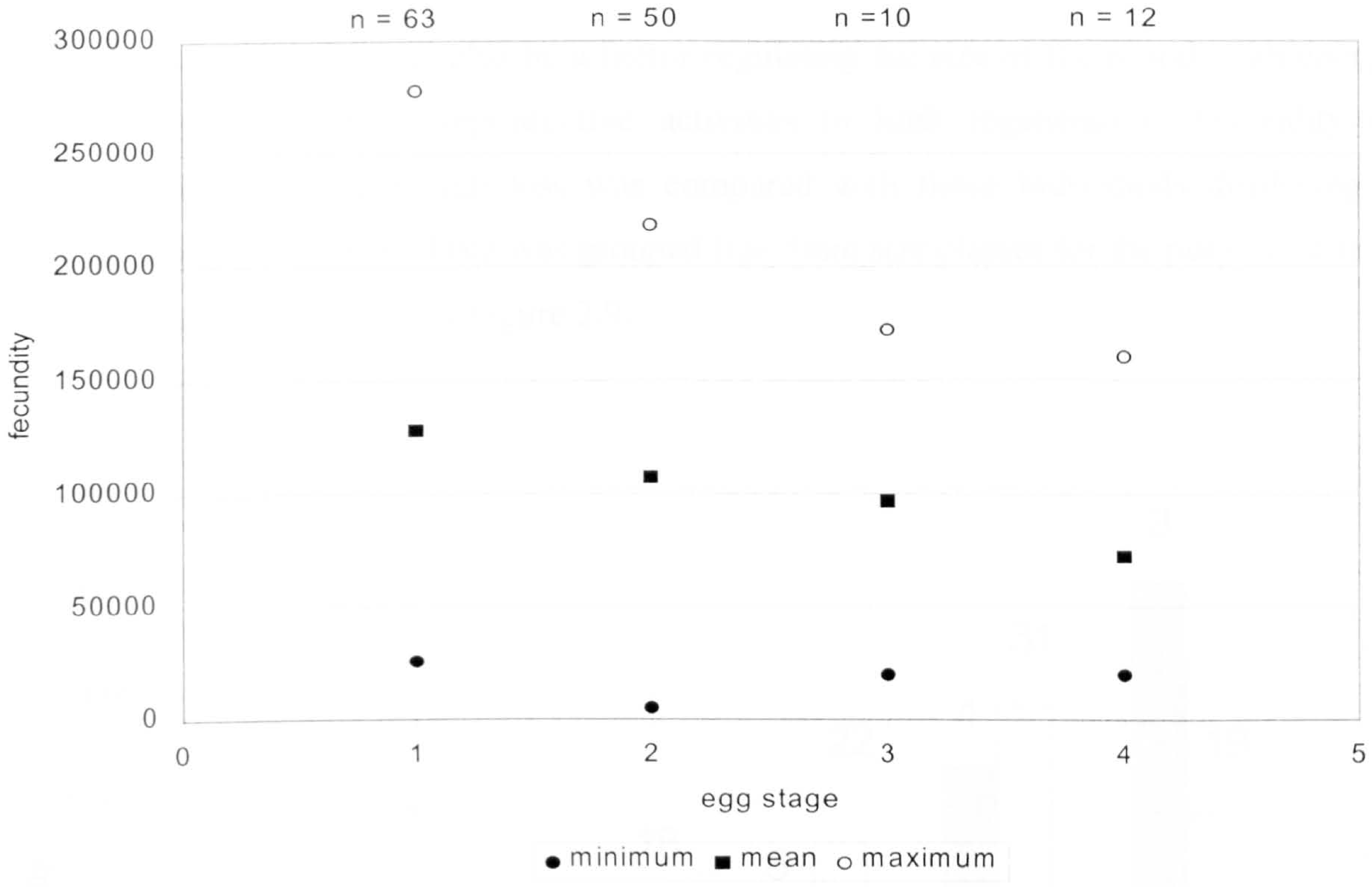


Figure 2.8 Mean fecundity at different stages of egg development

The graph above takes no account of the sizes of individuals involved, but does show a clear decrease in egg number with stage, from 128,000 eggs at stage 1 to only 72,000 at the fourth stage. One way ANOVA was carried out on the fecundity measurements, showing this difference to be significant:

Anova: Single Factor

Groups	*Count*	*Sum*	*Average*	*Variance*
1	63	8057765	127901	3.32E+09
2	50	5356850	107137	2.35E+09
3	10	966500	96650	3.03E+09
4	12	866600	72216.67	1.69E+09

Variance	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	3.83E+10	3	1.28E+10	4.568264	0.00446	2.673744
Within Groups	3.66E+11	131	2.8E+09			
Total	4.05E+11	134				

The loss of limbs may also be a factor regulating the size of the brood, with energy being diverted from reproductive activities to limb regeneration. Fecundity of individuals showing limb loss was compared with those individuals displaying a complete set of limb. Data was grouped into 5mm size classes for the purpose of this. The results are shown in Figure 2.9.

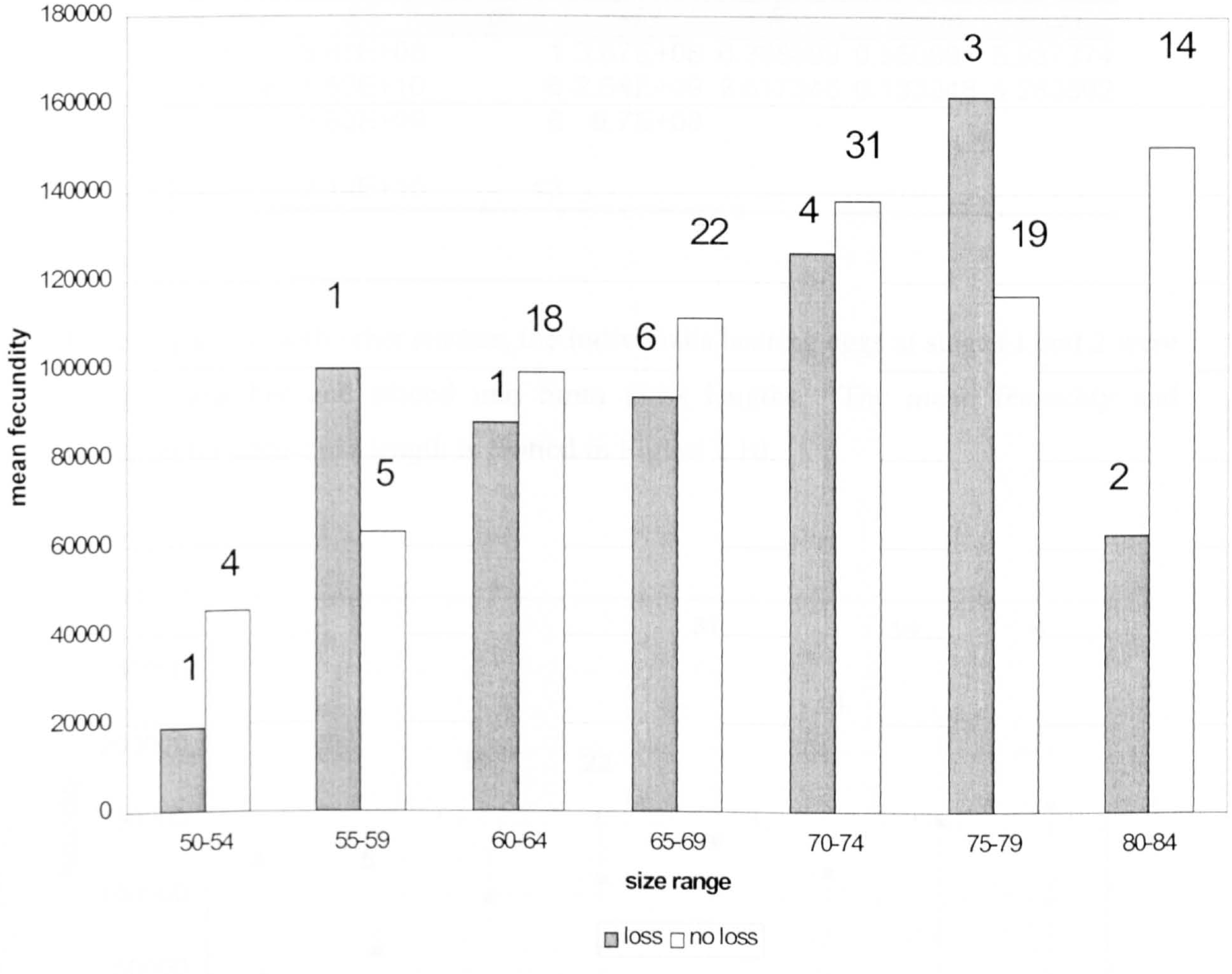


Figure 2.9 Comparison of fecundity between individuals showing limb loss and those with a complete set of limbs. Numbers above columns refer to sample size.

15 ovigerous females experiencing limb loss were found. Of those found, the extent of limb loss varied from one limb to five. The means for the limb-loss classes are therefore made up of fewer (and in some cases one) individuals. Although in all size classes except two, fecundity was higher for those animals not showing limb loss, a two-way ANOVA test showed there to be no significance in these differences:

ANOVA

Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Rows	3.87E+08	1	3.87E+08	0.398809	0.550991	5.987374
Columns	1.52E+10	6	2.54E+09	2.617345	0.133348	4.283862
Error	5.82E+09	6	9.7E+08			
Total	2.14E+10	13				

For comparison with other studies, the individuals bearing eggs at stages 1 and 2 were grouped together and placed into 5mm class lengths. The mean fecundity and variation for each class length is plotted in Figure 2.10.

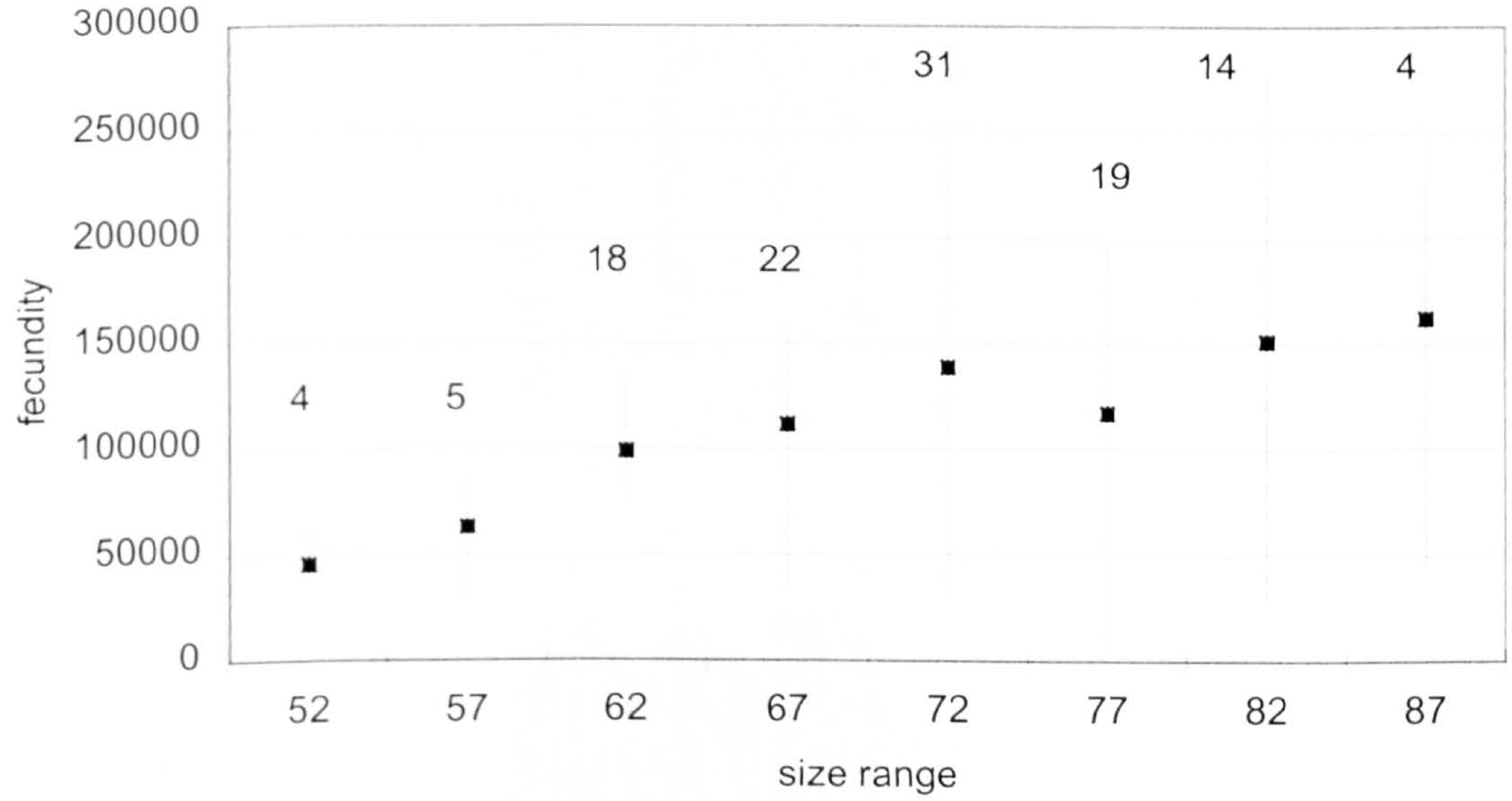
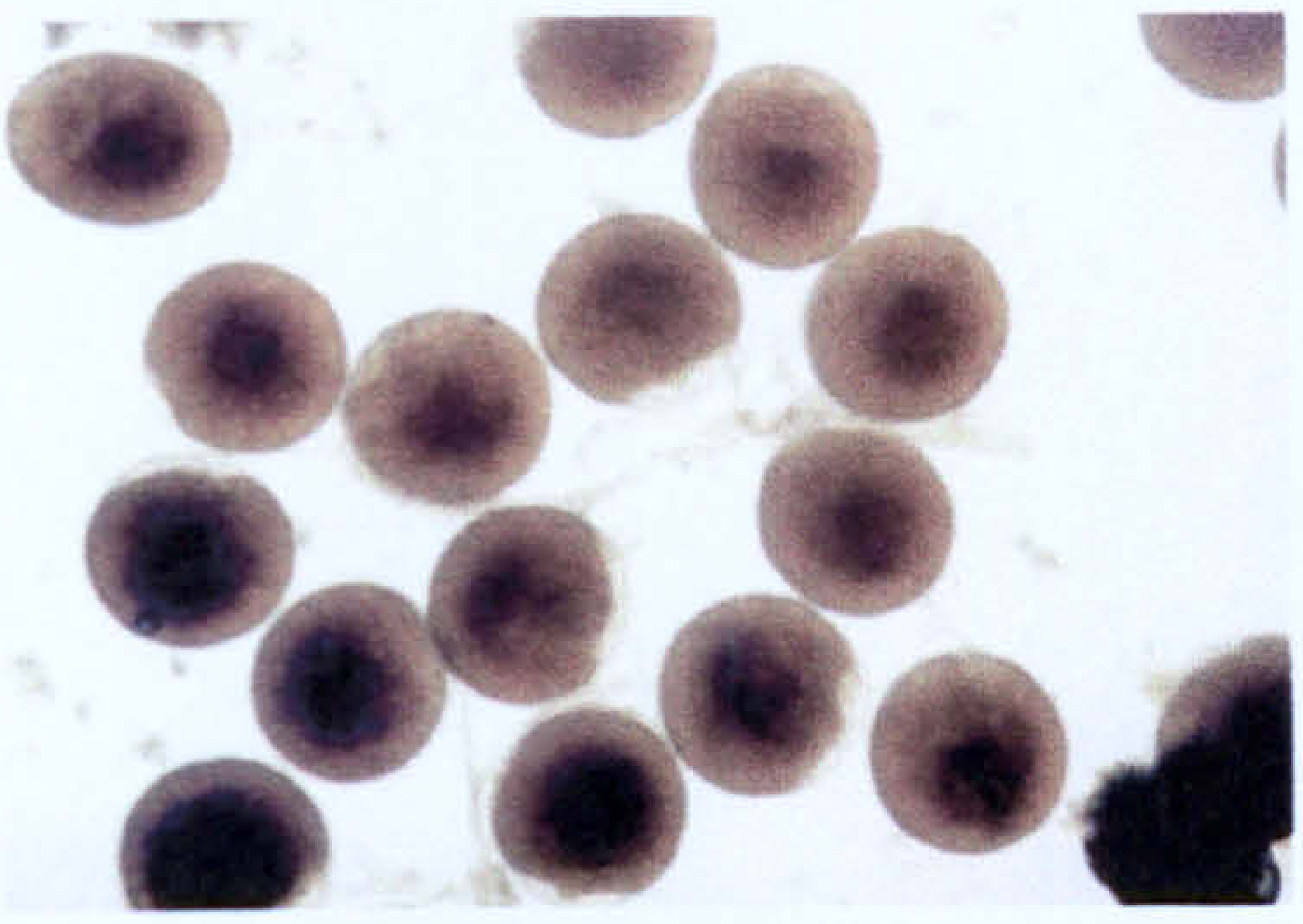


Figure 2.10 Mean fecundity and range (shown by vertical lines) for early (stages 1 and 2) egg development in different size ranges. Numbers above each column refer to sample size.

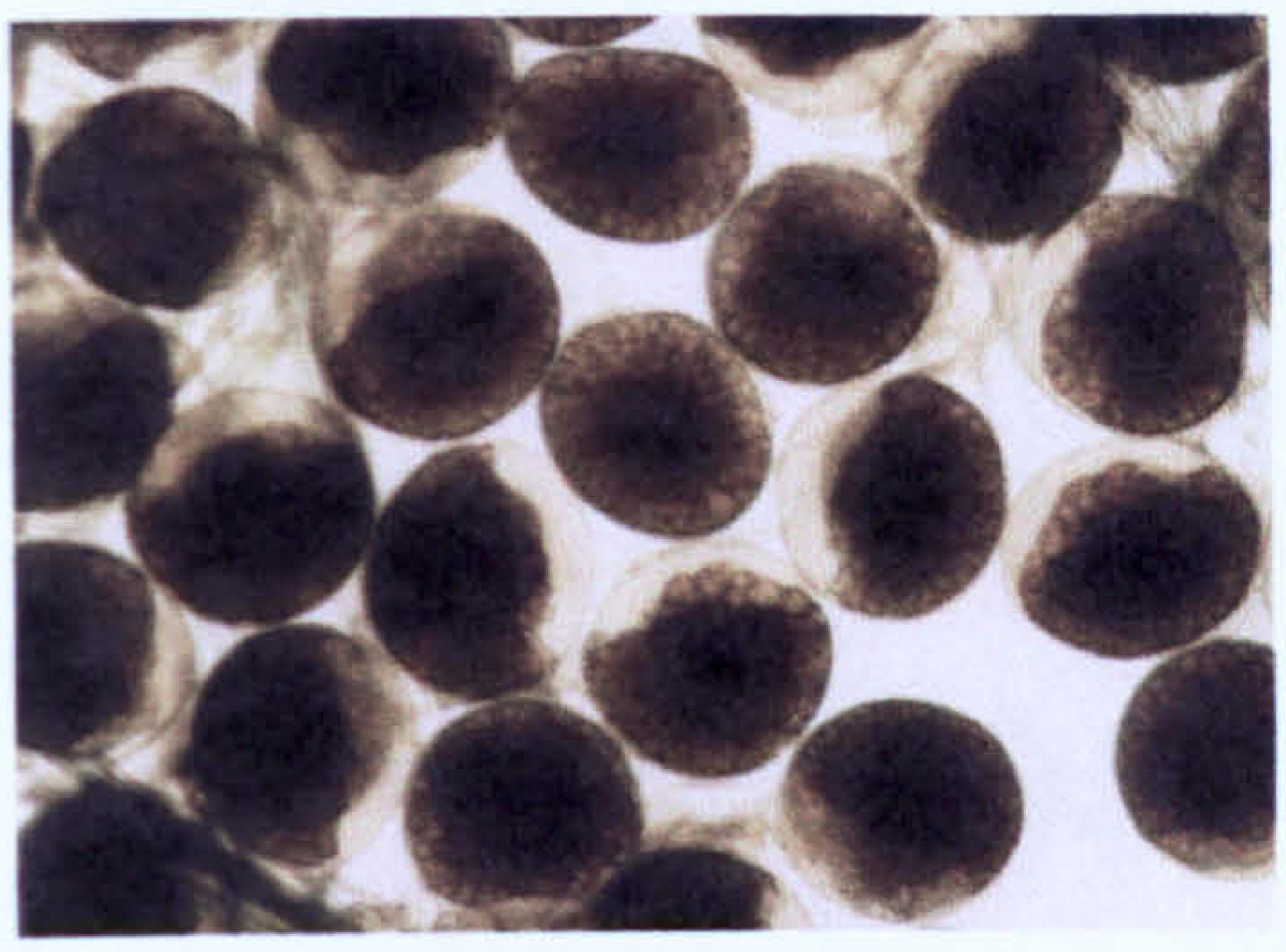
Figure 2.10 shows a similar pattern to Figure 2.6. There is an overall trend tending towards an increase in fecundity with size, but the variation in fecundity is very large and also increases with increasing size of the individuals. There appears to be a tendency for the mean fecundity to increase faster at smaller sizes, and to level off once the animals reach larger sizes of over 80mm CW.

2.3.4 Egg Development

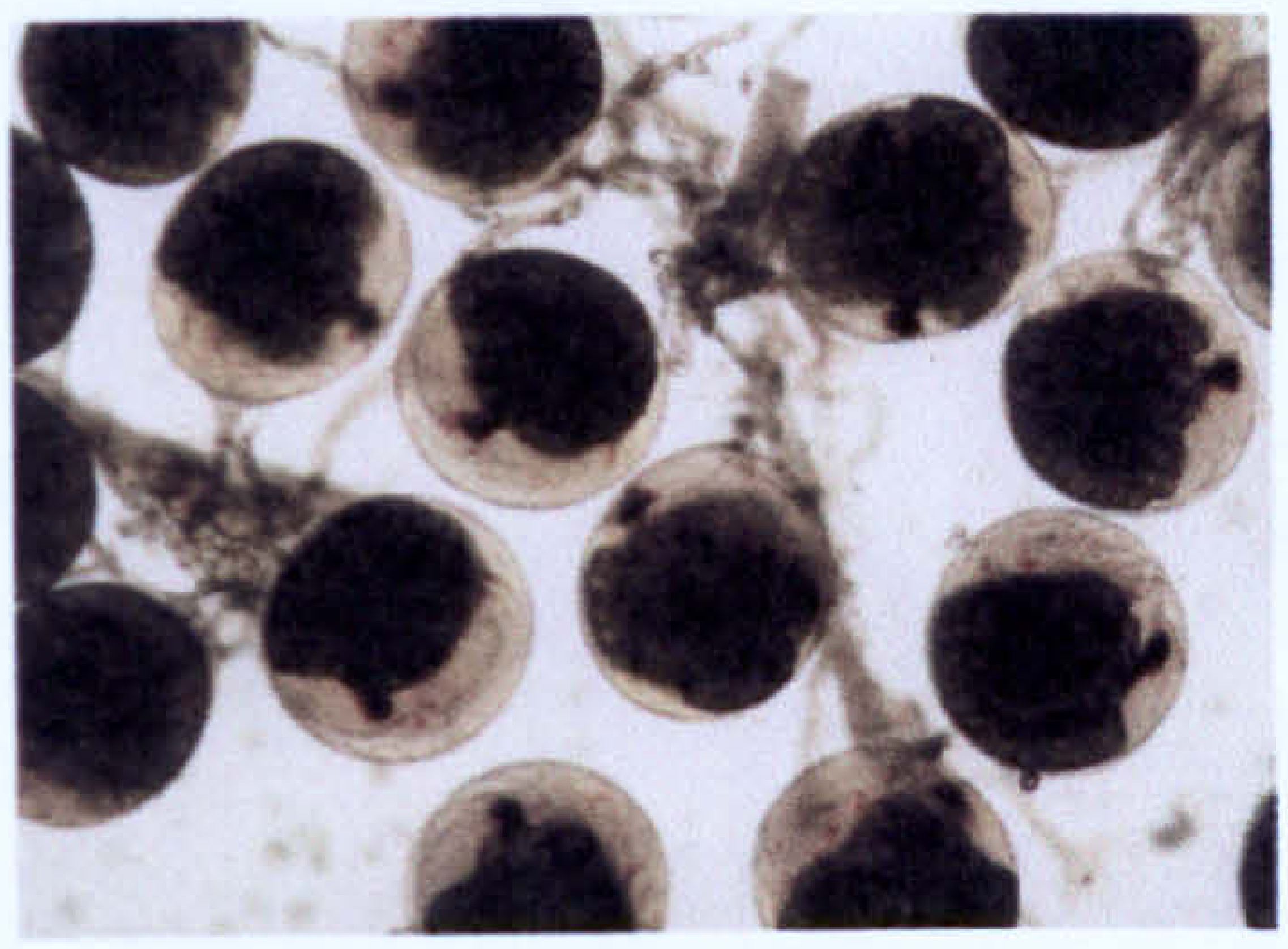
Plate 2.1 shows the characteristics of the eggs of *Necora puber* at each stage of development. Referring to Table 2.1, it can be seen how there is a progression from the yolk-filled egg of stage 1 to a ball of cells in stage 2. The eyespots are visible by stage 3, and by the final stage, the chromatophores are very clear, and in live samples, it is possible to make out the heartbeat of the unhatched larva within the egg.



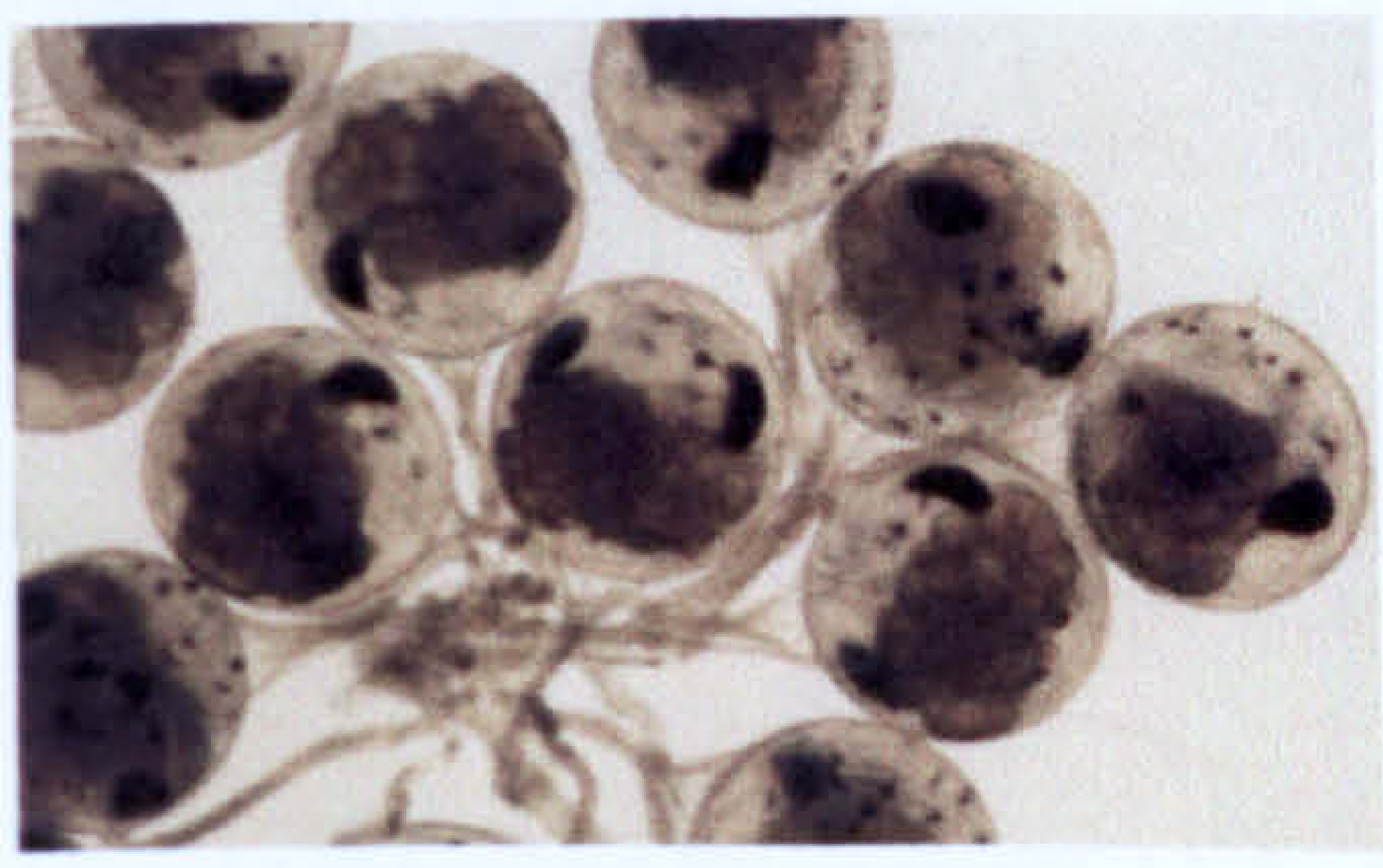
a.stage I



b. stage II



c. stage III



d. stage IV

Plate 2.1a-d Characteristics of egg stages of *Necora puber* (not to scale)

Figure 2.11 shows the increase in mean diameter of the eggs as they develop.

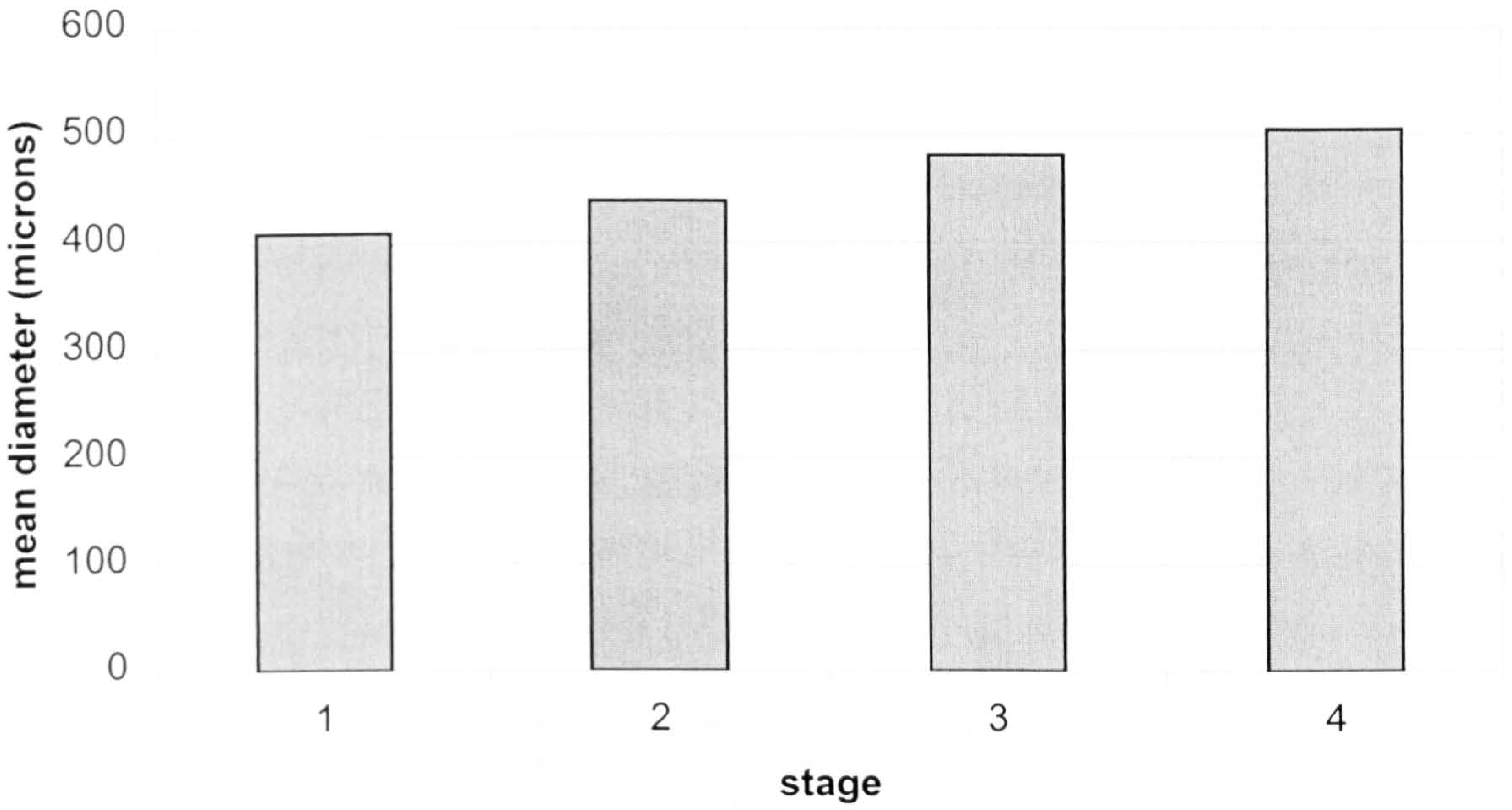


Figure 2.11 Egg growth during development

It can be seen from the graph that the mean diameter of the egg increases from when it is spawned at stage 1 (409μm) to when it hatches at stage 4 (505μm). The increase in size and volume from one stage to the next is fairly constant throughout development, with no obvious discontinuities.

One female (CW: 57, no limb loss) who spawned whilst in the holding tank was kept for observation of the development of her eggs. Her eggs were checked daily for their developmental stage. The results of this are shown in Figure 2.12.

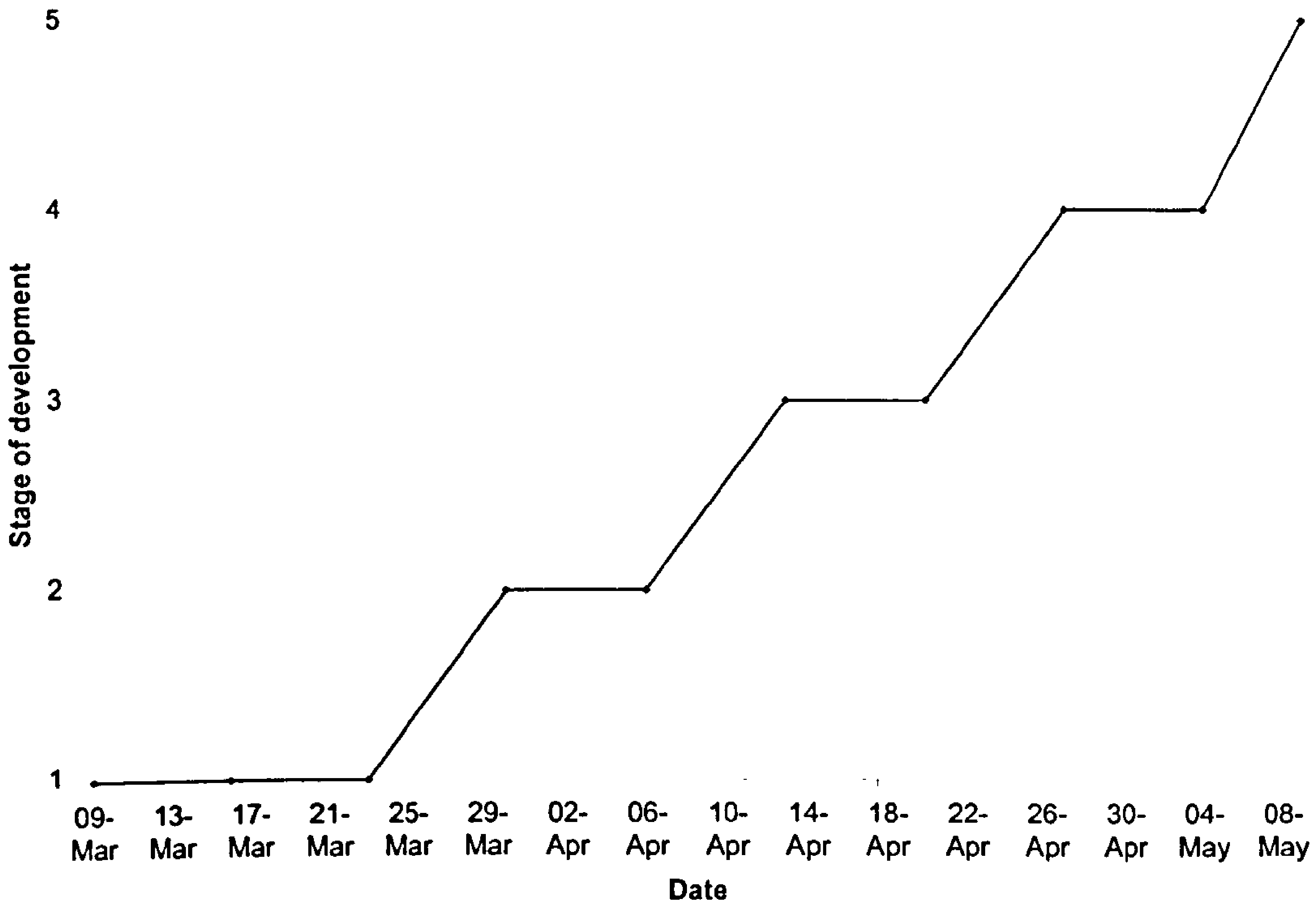


Figure 2.12 Development of eggs on laboratory female (stage 5 = hatching)

The entire process of development, from spawning to hatching, took place over 60 days. Stage 1 had the longest duration, of 24 days. Stages 2 and 3 lasted around 2 weeks each whilst stage 4 was completed in 8 days, after which the eggs hatched, at night and over a period of only a few hours. However, as the temperature of the tank water was 12°C, a few degrees warmer than that of her natural environment, this can only be used as a guide, and is not translatable into the field unless it is in terms of the relative length of time each stage lasts.

2.3.5 Reproductive Cycle

There was no change in the reproductive condition of males throughout the study period. Once males reach maturity, their gonads appear to be ready for mating at all times. All the adult males examined displayed ripe gonads, regardless of the time of year. With females however, this is not the case. Ovaries go through a cycle from when the eggs begin to develop, to when they are spawned, whereupon the ovary is spent and development of new eggs begins. Observing the periodicity and abundance of ovigerous females shows the frequency of the reproductive cycle over the study period.

The results of the two-year monthly survey carried out in this study are shown on the graph (Figure 2.13) below. The graph shows ovigerous females as a percentage of total females caught during the general sampling programme (Dataset 1, Appendix A). Table 2.4 shows the numbers of females caught at each date.

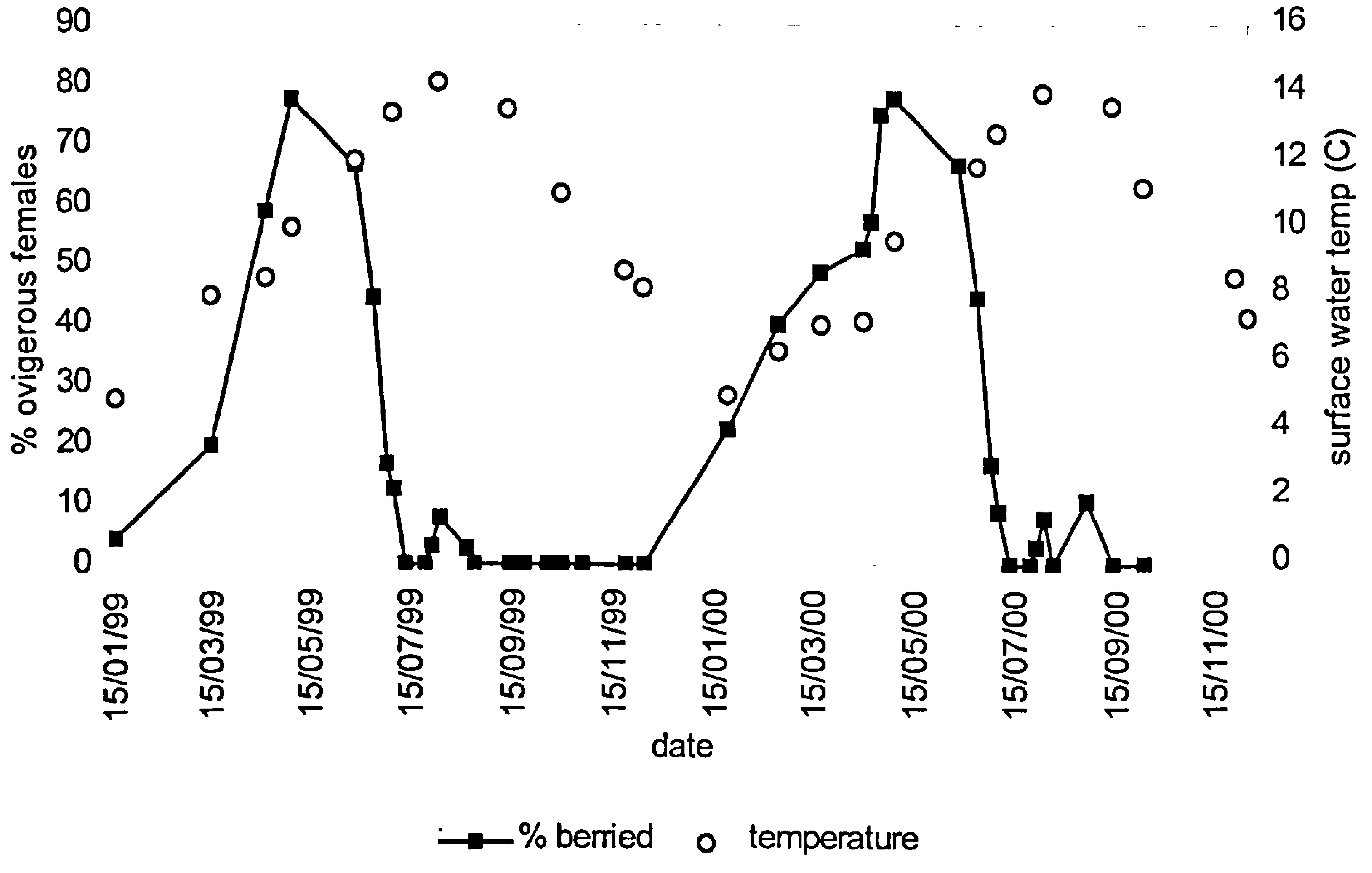


Figure 2.13 Occurrence of ovigerous females during main sampling programme

As can be seen from the graph, there is only one peak in the female reproductive cycle, corresponding to the beginning of May. The late spring and short Orkney summer suggest that berried females will appear in the catch later than in southern UK and Spain, and that favourable conditions last only long enough to produce one batch of larvae each year. Another aspect of the graph is the difference between the reproductive period of 1999 and that of 2000. The former year shows a later start and a more peaked season, whereas in 2000, significant numbers of ovigerous females were found earlier, although the main spawning period occurred at the same time in both years, around mid-March. This may be temperature related. The temperature plot on the same figure shows that the increasing occurrence of ovigerous females coincides with the start of the warming period of the waters. Egg release appears to occur just before the maximum temperature is reached, possibly to ensure the most favourable conditions for the development of the larvae. At this time, the zooplankton bloom is generally occurring, so there is higher food availability than at other times of year, as well as higher temperatures.

date	berried	tot. females	Date	berried	tot. female
15/01/99	3	63	23/01/00	27	121
15/03/99	3	15	23/02/00	20	50
18/04/99	13	22	20/03/00	18	37
04/05/99	7	9	15/04/00	10	19
12/06/99	2	3	20/04/00	12	21
23/06/99	8	18	26/04/00	21	28
01/07/99	2	12	04/05/00	7	9
05/07/99	7	56	12/06/00	2	3
12/07/99	0	31	23/06/00	8	18
24/07/99	0	22	01/07/00	2	12
28/07/99	2	69	05/07/00	5	57
02/08/99	1	13	12/07/00	0	31
18/08/99	1	39	24/07/00	0	22
23/08/99	0	7	28/07/00	2	69
13/09/99	0	22	02/08/00	1	13
22/09/99	0	5	07/08/00	0	20
06/10/99	0	30	28/08/00	2	19
15/10/99	0	66	13/09/00	0	14
27/10/99	0	44	02/10/00	0	13
22/11/99	0	68	27/11/00	0	110
03/12/99	0	60	05/12/00	0	66

Table 2.4 Number of berried females and total females obtained at each date, used for figures 2.13-14.

Although the tank female data is simply a guide as to the duration of each egg stage, data gathered during the general sampling programme allowed for a study of the relative proportion of ovigerous females carrying eggs at each stage throughout the two-year study period. This is shown in Figure 2.14 below. It can be seen from the graph that there is only one period of egg development per year.

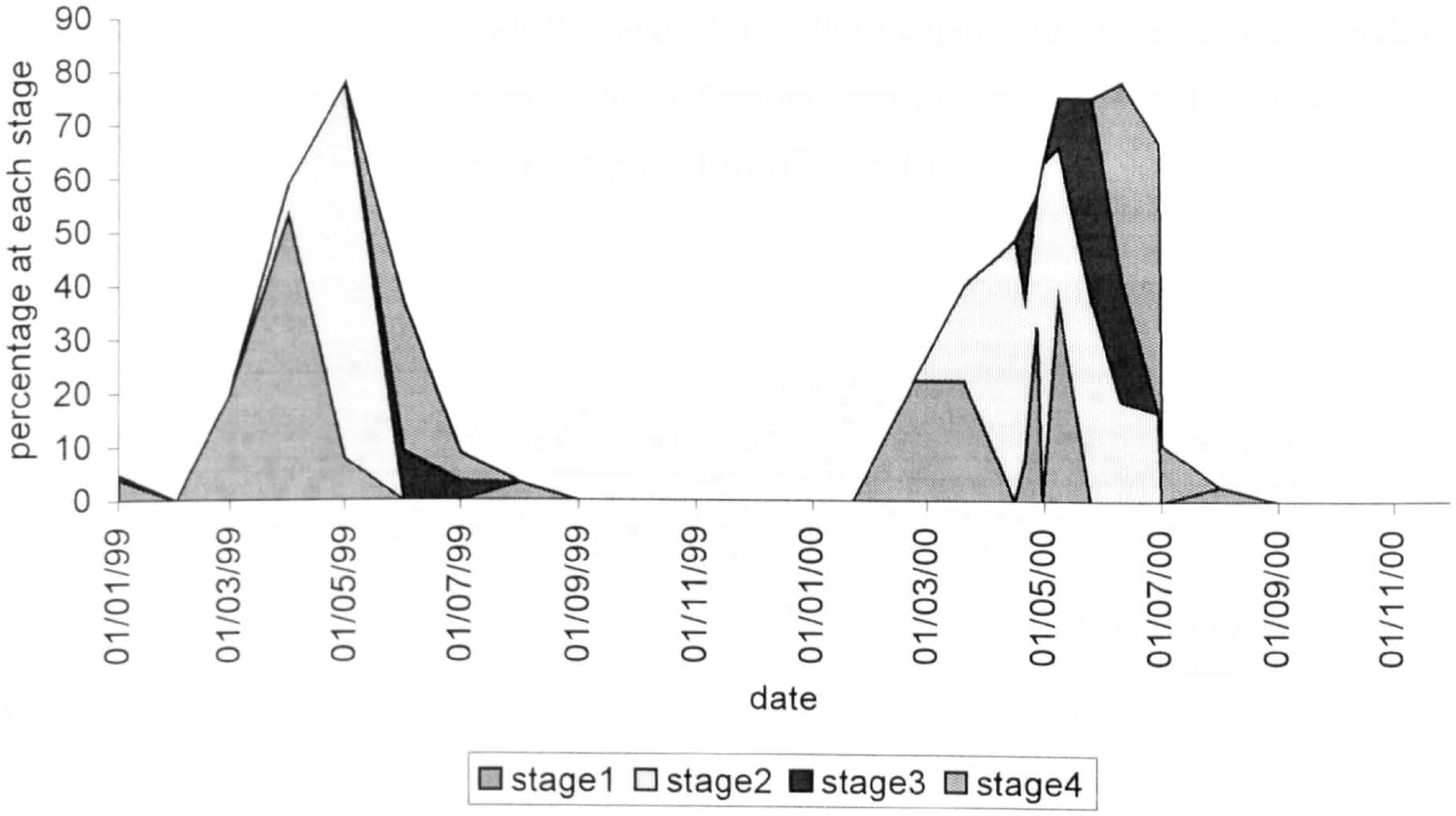


Figure 2.14 Proportion of eggs at each stage of development as a percentage of all females captured during general sampling programme (Dataset 1, Appendix A)

The graph shows the percentage of berried females found at each egg stage, and must be analysed in conjunction with Figure 2.13. Thus, the percentage values for stage 1 eggs at the end of the summer correspond to a small number of females, who appear to spawn their eggs almost immediately after release of the previous batch. The main spawning season however, occurs in the first months of the year (February and March). There is no indication that eggs spawned earlier than this develop further, as stage 2 eggs are not generally found on females until mid-March. The first egg stage would therefore appear to last some 6-8 weeks, followed by the shorter second stage, with a duration of 3-4 weeks, a similar but slightly shorter third stage, and the final, fourth stage, lasting around 4 weeks. Most eggs hatched around the end of June and early July. This gives a total development time of 16-20 weeks, at least twice as long as that displayed by the female in the tank (Figure 2.12).

It was postulated that size of the individual may have some influence on the spawning time. Carapace width was plotted against month of capture for all ovigerous females between the months of January and September over the two-year study period. The results of this are shown on the graph below (Figure 2.15):

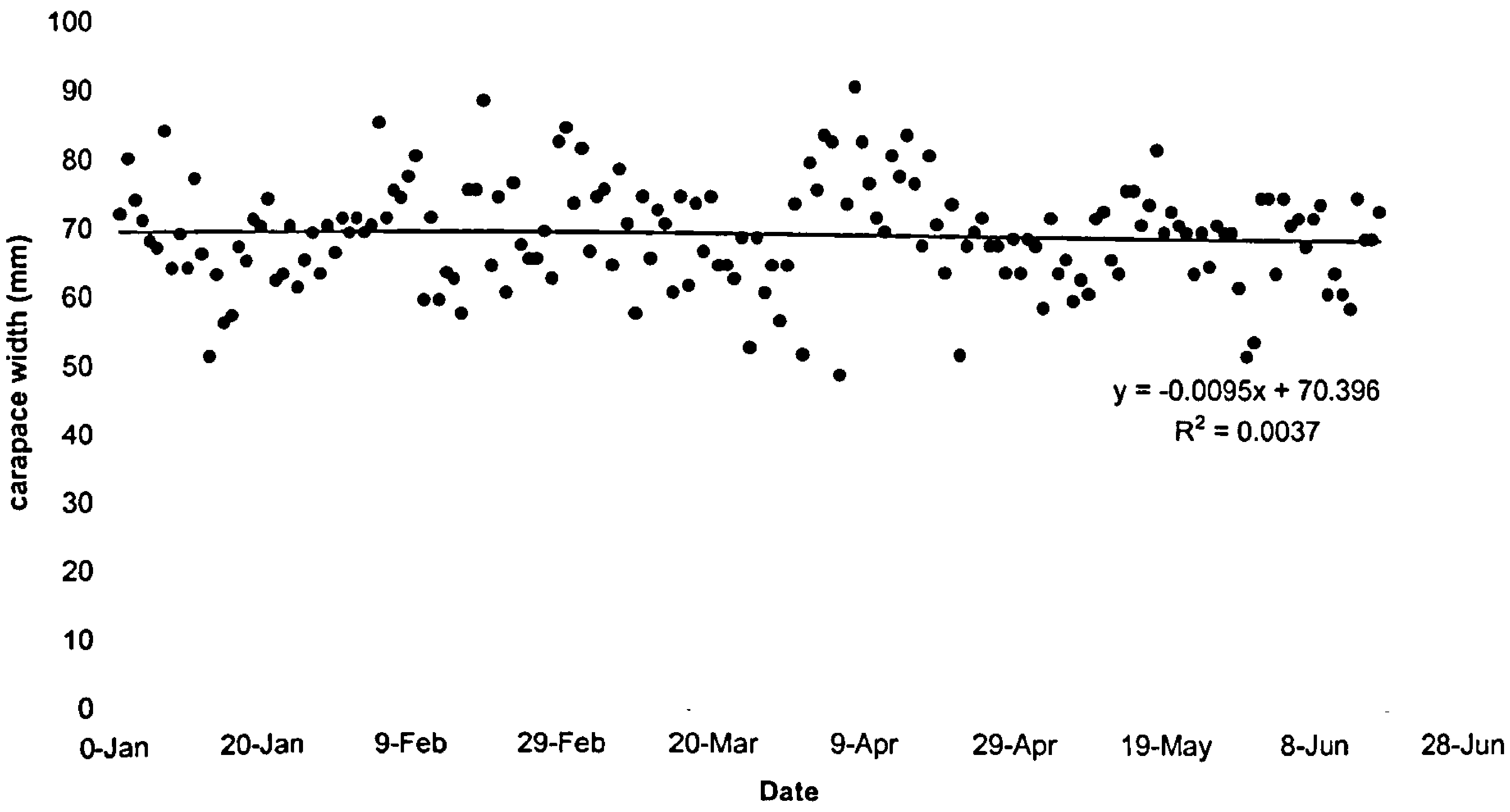


Figure 2.15 Size and month of capture of ovigerous females

Although it might appear that there is some pattern showing fluctuations in the sizes of ovigerous females, this is likely to be an artefact from sampling. The ovigerous period lasts throughout the spring, so there is no basis for the cycling in sizes suggested by the figure. The reason for such a pattern probably lies in the fact that, over this period, various bays and areas were sampled. The size composition of the catch can vary greatly from one area to another, probably due to factors such as habitat and food availability.

2.3.6 Estimation of total mortality

An preliminary estimate (independent from fisheries data) of natural mortality may be obtained from the fecundity data, making certain assumptions. The mean fecundity for the stock is 112,000 eggs. In a stable population, throughout the lifetime of a female, she produces two offspring (one male and one female) who are reproductively successful. Assuming (from Part 4) that the female undergoes 5 spawnings in her lifetime, this is a total 560,000 eggs, 2 of which are eventually successful. Mortality can be estimated by using the exponential decay model (Baranov, 1918; Beverton and Holt, 1957), outlined in Section 1.7.

If maturity occurs at three years (as suggested by data in Part 3, Section B), the mortality of the stock was calculated for a number of possible lifespans, always assuming 112,000 eggs per year as the mean fecundity. The initial total number of eggs was plotted on a logarithmic scale against the final total of 2, at the end of each lifespan. Figure 2.16 shows the results of this:

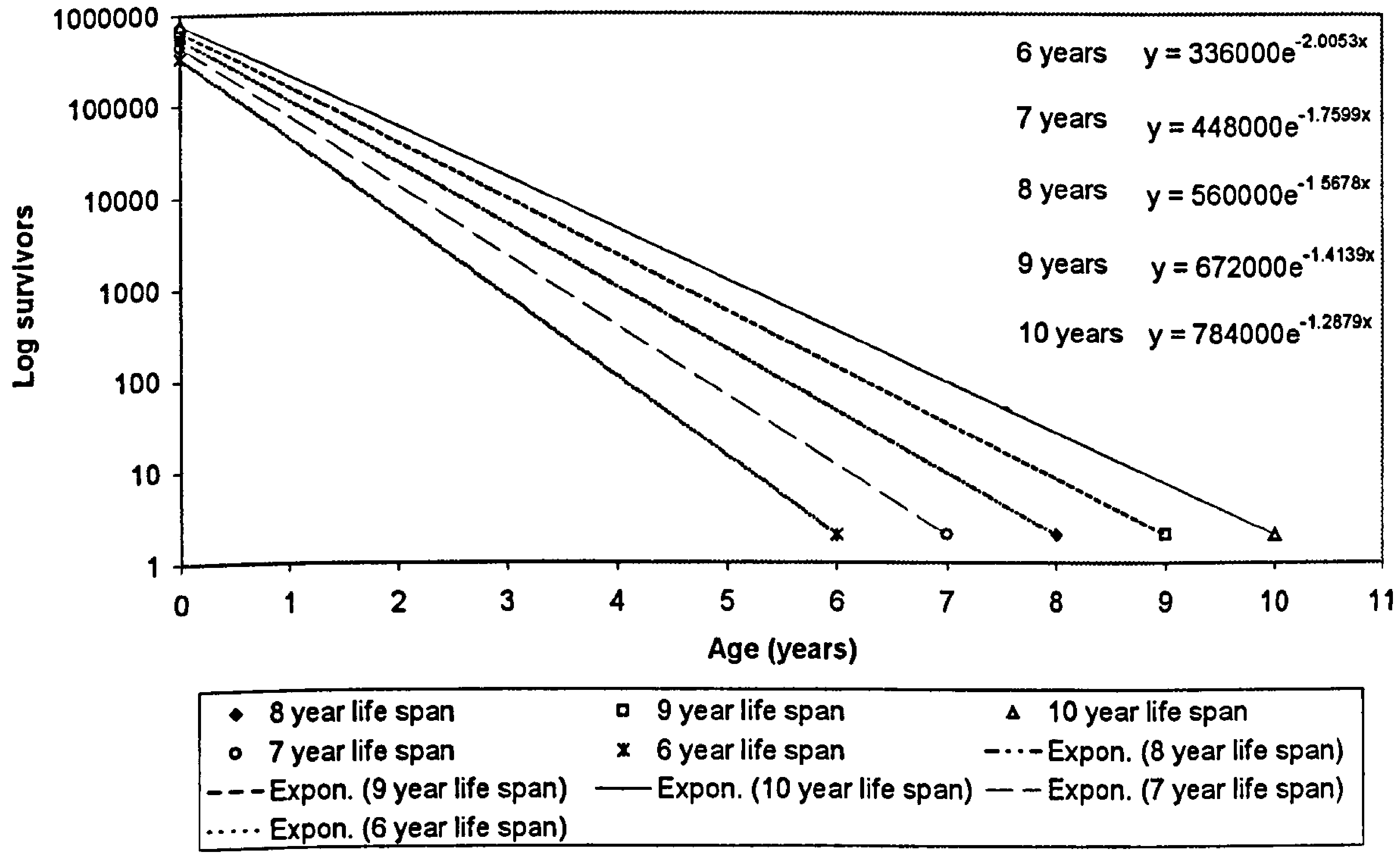


Figure 2.16 Estimated natural mortality from fecundity according to various lifespans. Lines refer to exponential regression on different lifespans.

The values given range between Z = 1.29-2. As this particular model does not take fishing into account, the total mortality (Z) is the same value as natural mortality (M). The values are very high, but they assume a constant mortality rate from hatching through the whole life cycle. The larval mortality analysis carried out in Part 3 proves this to be untrue, as larval mortality is several orders of magnitude higher than this. Juvenile mortality is probably also quite high. In fisheries research, Z is generally calculated from the recruitment size, so the values obtained here give some idea of the maximum possible value in further analysis.

2.4 Discussion

Sexual maturity can be defined as the moment when copulation and fertilisation are both feasible (González-Gurriarán, 1985a). This is an important consideration, as it implies that the male must also be capable of holding the female during the pre-copulatory embrace and copulate successfully (González-Gurriarán and Freire, 1994; Hartnoll, 1969). The examination of gonads may not be entirely accurate, as the gonads develop after copulation has taken place so, as suggested by González-Gurriarán (1985a), the best estimates of sexual maturity should involve a combination of external and internal examinations. Another problem which should be addressed is the different criteria used in various gonadal studies. Bakir (1990) identifies seven ovarian stages, whilst Choy (1986b) and Norman (1989) use only five stages. This study followed the system set out by González-Gurriarán (1985a), which consisted of only four stages for females, whilst for males, a simple division of ripe/unripe was used.

The value of precise figures relating to sizes of sexual maturity, using either morphometric measurements or gonad analysis, should be viewed with caution. Table 2.4 summarises some measurements carried out on *N. puber* in other studies. There is, in most cases, a large difference between sizes depending on the method used. In any case, the size at puberty may vary from year to year due to environmental conditions affecting growth. The important conclusions to be made from such analyses lie in establishing a range of sizes over which the process of becoming sexually mature occur, and to ensure that this is taken into account when using such information in the management of the fishery.

The Orkney data indicates a number of important points. The first of these is that females become sexually mature at a smaller size than males. This was compared with data from other studies. Table 2.5 shows the size at sexual maturity for male and female velvet crabs using different methods in different areas. In all cases, the female appears to mature at a smaller size than the male. In some cases, the difference is of only 0.5mm, but in most cases, there is a large difference of a few millimetres between the sexes. The sizes are generally in the same range for each area, although the Spanish stock seems to mature at a larger size than those stocks around the UK, possibly due to faster growth rates in warmer waters.

Location	Method	Male	Female
Orkney (current study)	Allometric	51	38-40
Orkney (current study)	Gonad obs.	51	43
Wales	Allometric	42	38
Wales	Gonad obs.	54	37.5
Ireland	Gonad obs.	50	49.5
Plymouth	Allometric	46.5	40.5
Plymouth	Gonad obs	48.5	48
France	Allometric	No data	40-46
Galicia	Allometric	53.3	52.3
Galicia	Gonad obs	54.7	49.8

Table 2.5 Size at sexual maturity for velvet crabs according to present and other studies (Bakir (Ireland), 1990; Choy (Wales), 1988; Drach (France), 1933; González-Gurriarán (Galicia), 1994; Norman (Plymouth), 1989). Gonad observations refer to the size at which the probability of maturity is 0.5

In Galicia, sexual maturity occurs at one year (González-Gurriarán, 1985a). Bakir (1990) suggests that this is also the case in Ireland, although he provides no evidence to back up his statement. It is likely that in Orkney, sexual maturity does not occur until later in the life, due to the harsher environmental conditions (see Chapter 3, Section B).

There is a reproductive advantage in the male being as large as possible. Firstly, this gives him a courtship advantage over smaller males and secondly, in view of the evidence that females will only mate with males larger than themselves, the larger the male, the bigger the selection of potential mates will be. The increase in chelar size for males has been attributed to a number of reasons, including courtship displays, territorial defence and combat, and possibly as an aid in copulation (Hartnoll, 1974; 1985). The female, however, must divert resources from growth into the production of eggs, which may explain a slower growth rate than for males. The discontinuity in abdomen size for females may be explained by the necessity of having a suitable brood chamber in which to rear her eggs (Hartnoll, 1974).

The Orkney data for females correlate closely with the size of the smallest ovigerous females found during the study period so, in accordance with Norman (1989) and González-Gurriarán (1994), females appear to be able to copulate and spawn successfully once the pubertal moult is reached, not needing a further moult, which is the case with some other brachyuran species such as *Ovalipes catharus* (Davidson and Marsden, 1987).

Another point, which stands out from all the data in Table 2.5, including that obtained in Orkney, is that the size at onset of sexual maturity for males and females is well below the UK minimum landing size of 65mm. The result of this is that all individuals of both sexes are given at least one chance of successful procreation before it is legal for them to be removed from the population.

It is also apparent from the data collected during this study that the onset of sexual maturity occurs over a relatively narrow band of sizes. This is the case for both males and females. This suggests that puberty is a well-defined process, acting almost in the fashion of a switch, and occurs over just one moult. Hence, any variation in size at maturity is simply a result of the natural size variation of individuals at that age, and that all individuals reaching the age of approximately one year, undergo a pubertal moult, after which they are fully capable of successful reproduction.

The information obtained on mating pairs was sparse, mainly due to behavioural reasons. The actual process of copulation was not observed during this study, but has been described in detail by González-Gurriarán, (1985a). However, paired couples were observed. Mating occurs while the female is still soft, after having cast her shell. Couples pair up some days before female ecdysis occurs, and the male stays with the female for some time after the act of copulation. As this occurs at a vulnerable time for the female, it is logical to assume that the individuals seek some sheltered and protected place in order to carry out this process. They are unlikely to be foraging for food at this time, so are not usually found in creels, and therefore were a rarity during the study period. Other studies relying on pot captures for data found the same problem (e.g. Bakir, 1990), whereas in samples obtained by trawling, mating pairs were found more frequently (e.g. González-Gurriarán, 1985a). Trawling was initially considered for this study, at least as a supplement to creel data, but was discarded due to the unsuitability of the substrate.

Those mated pairs which were obtained, consistently displayed a larger male (some 6-11mm larger than the female) with a female who had already undergone the moult process several days earlier as determined by the state of the shell, which in all cases was soft but hardening. The reason for this size difference may lie in the dominance of the male (Glass, 1985; Smith, 1990). This would suggest that defence from conspecifics is a significant element in mating behaviour (Norman, 1989). As mating requires females to be in a soft-shelled state, the mating cycle follows the female moulting cycle, which occurs once a year in Orkney, towards the end of the summer (August-September).

It is possible that there is an element of geometry in determining the size relationship between males and females in a mating pair. This may have a large role in limiting females to having larger mates of at least a certain size. From the information obtained in this study, where differences in size ranged from 6-11mm, this may suggest that the shape and size of the individual places an upper limit on the male, too. However, this is not supported by Norman (1989) who found a mean difference of 16mm between males and females with a range from –2-36mm, out of 41 mating pairs. González-Gurriarán (1985a) found a mean size difference of 16mm with a range from 0-36mm, in 20 mating pairs.

The fecundity of *Necora puber* showed the same trend in Orkney as in all other study sites: that there was a positive relationship between increasing size and greater fecundity, although there was much variation, especially at larger sizes.

However, whereas previous studies have assumed an exponential increase of fecundity with size [González-Gurriarán (1985a), Choy (1986b), Norman (1989) and Bakir (1990)], the current study found that a more suitable line to describe the fecundity of velvet crabs in Orkney is a line which shows a gradual slowing of the increase in egg number after a certain size is reached. This implies that there is a maximum egg number for the species, attained at a certain size, after which fecundity either remains constant or may even decrease. Cushing (1975) claims that growth is an agent of fecundity, i.e. that animals grow large in order to be able to produce more eggs and stabilise the stocks. This may be true up to a certain size, beyond which the maintenance of such a large body may take up energy, which would otherwise be diverted to reproduction, thus causing a decrease in fecundity after this point.

The table below shows the largest number of eggs found in each study, and the size of the female carrying this brood.

Location	Latitude	Largest brood	CW female	Largest female
Galicia	42.31 N	448 786	89mm	89mm
Plymouth	50.23 N	366 000	81.7mm	81.7mm
South Wales	51.35 N	262 000	62mm	71.5mm
Dalkey	53.17 N	746 334	72mm	?
Orkney	59.04 N	278 000	81mm	89mm

Table 2.6 Largest broods found on animals in different study areas (Norman, 1989; Choy, 1988; González-Gurriarán, 1985a; Bakir, 1990; and current study)

It can be seen from the table that the maximum fecundity observed in Orkney is in the same order of magnitude as for the other areas, and in the case of South Wales, is actually slightly higher. The results from Dalkey are anomalously high and are, therefore, somewhat surprising. It is interesting to note that for neither Orkney, South Wales, nor Dalkey, do the highest fecundity results correspond to the largest animal. This may either be a reflection of the increased variability in fecundity with larger animals, or an indication that fecundity starts to level off after a certain size is attained.

Table 2.6 also shows the latitudes of the different studies carried out. If the Dalkey results are set aside, there is a large difference shown by the females in Spain with respect to the UK stocks. In general, fecundity of temperate water crabs is smaller and the egg size larger than that of their warmer water confamilials of comparable size (Sastry, 1983). Within Portunidae, the warm water crabs *Callinectes, Scylla,* *Portunus* and *Ovalipes* all carry 1-2 million eggs per brood. Colder water *Carcinus, Liocarcinus* and *Necora* all carry less than half of that. It is possible that this assumption also holds true for separate stocks within the same species; in which case, the differences between Spain and the UK are to be expected. This plasticity has been observed in other decapod crustaceans such as *Nephrops norvegicus* (Thomas, 1964) and *Heterozius rotundifrons* (Jones, 1978). It would appear that in the case of *N. puber,* fecundity decreases as latitude increases. Otherwise, the differences may be due to experimental factors, and the different methods used to determine fecundity, or the manner in which the females were kept prior to measurement.

Egg loss occurred during development at all stages. This could be as a result of a number of factors, including both physical factors such as abrasion, and physiological factors such as unsuitable oxygenation. Ovigerous females were observed fanning their abdomens in the tank. This behaviour became more frequent if the water was not well aerated, so is probably a response to lack of oxygen reaching all the eggs. Females were also noticed preening their egg mass and removing (presumably) unviable eggs from the mass. There is also an inherent mortality associated with development (Jewett *et al.*, 1985). Balasundaram and Pandian (1982) studied egg loss in the prawn *Macrobrachium nobilii,* concluding that this occurred as a result of space limitations as the eggs increased in size and abrasion during ventilatory movements of the female. They found a significant loss of eggs in the first two days following spawning. This may be related to attachment difficulty, in which case the same could possibly be applied to *Necora puber.* They also studied egg loss in a number of decapod crustacean species, concluding that the method of incubation is also a determining factor in the amount of egg loss, with a pouch being the most effective, followed by a marsupium, and direct attachment of eggs to appendages being the method entailing highest egg loss.

At the time of mating, the ovaries are unripe. Maturation takes place over a series of months, and the eggs are fertilised upon spawning (González-Gurriarán, 1985a). The presence of sperm plugs helps to retain the sperm throughout the ovary maturation period. In some areas, females are capable of multiple spawnings in one year, without moulting, which implies resistant sperm able to survive several months inside the female before fertilisation (González-Gurriarán, 1985a; Norman, 1989). The time from mating to spawning was approximately 5 months in Orkney, if mating was considered to take place in August-September, and the main spawning period around February. This is consistent with the upper time limit suggested by González-Gurriarán, (1985a), who observed a gonadal development of between 75-162 days in Spain, at a water temperature of 15°C. The water temperature in Orkney only reaches 12°C in the surface waters in summer. Maturation occurs over the autumn and winter, at bottom temperatures of around 6°C.

The female that spawned in the tank previously buried herself in the sandy area. She remained buried in sand over a period of several days, and throughout her ovigerous stage, she was often observed in this condition. If this behaviour, also observed by González-Gurriarán, (1985a), is carried out to aid the adhesive process of the eggs onto the abdomen, this may suggest some form of migration off the rocky habitat usually occupied by *Necora puber* and onto softer substrate during this period. This may help to explain why the sex ratio of the catch is skewed towards males during the period when females are in an ovigerous state (see Part 4).

The initial egg diameter was 409μm. The eggs increase in size over the period of development, due to water uptake by osmosis (Davis, 1968; Wear, 1974). At the same time, they become less spherical and more elliptical in shape. The mean size of those eggs ready to hatch was 505μm, compared with 460μm (González-Gurriarán, 1985a) and 420μm (Zoriquiey-Alvarez, 1968) for animals in Spain, and 440μm, measured in Plymouth by Lebour (1928). The egg size was therefore more consistent with those found in Dalkey, Ireland (Bakir, 1990) of 375-575μm, and in Swansea, of 360-550μm (Choy, 1986b), and larger than those found in other studies. This may be due to environmental conditions (Sastry, 1983).

The development of the eggs is temperature related (Norman, 1989). The eggs laid by the laboratory female hatched after 60 days, at a temperature of 12°C, whereas the development time in the sea (with a bottom temperature of around 6°C) took 16-20 weeks, at least twice as long as in the tanks. The summer brood in Spain at 18°C took 36 days, whereas the winter brood at 12-13°C took 48 days (González-Gurriarán, 1985a). Choy (1986b), Norman (1989) and Bakir (1990) also found temperature dependence in egg development for the stocks in their study areas. Initial development of the eggs is very slow, but the rate of development increases with time, possibly due to the corresponding increase in water temperature with the onset of spring.

Decapod crustaceans around the world generally display one of two methods of breeding (Sastry, 1983). The tropical crab, *Callinectes danae* reproduces continuously throughout the year (Costa *et al.,* 1998), as do most tropical and subtropical brachyurans. This continuous cycle is contrasted with the restricted breeding system, generally correlated with some favourable environmental conditions (Sastry, 1983), that typifies temperate species.

In terms of *Necora puber*, no reproductive cycle was observed concerning males. Their gonads appeared to be mature all year round, although it is unlikely that they are able to copulate whilst soft. However, females show a distinct cycling pattern to their reproductive stages, as can be seen by the yearly variation in the number of ovigerous females sampled in field studies (Gonzalez-Gurriarán, 1985a; Glass, 1985) and the stages of gonadal development of these females. This cycle can be related to the growth cycle. Gonzalez-Gurriarán (1985a) found two distinct peaks of female maturity, in January and March, due to the fact that most females in the study area could have two successive spawnings. At Plymouth, a peak of ovigerous females was observed in spring (Lebour, 1928), whereas in Cotentin (France) the time of female maturity was spread over a period from March to August. In Orkney, females have a distinct seasonal breeding pattern, with spawning occurring in winter, and eggs being carried until their release in June-July. Throughout this period, the proportion of females in the catch is significantly low, and may be due to a combination of migration to softer substrates for better egg attachment, and the fact that females tend to have a smaller appetite when ovigerous (González-Gurriarán, 1985a) so are less likely to enter creels. Egg development is very slow at first, and it is not until the spring that there is a noticeable abundance of later staged eggs on female abdomens. There was no significant difference in the sizes of ovigerous females found at different times of year, and it would appear that a very high proportion of the female population becomes ovigerous each year. The eggs are all released over a period of a few hours, generally at night (pers. obs.). The larval life stage is discussed in Part 3, Section A.

The implications of the reproductive capability of the stock on the management of the fishery are several-fold. Firstly, the MLS of 65mm is well above the size at which sexual maturity is attained, for both males and females. Mating occurs when the female is soft and therefore vulnerable. However, as she is protected by the male at this point, and does not enter creels, she is not susceptible to fishing effort whilst she mates. In the same sense, if spawning does take place off the usual fishing grounds, on a softer substrate, then again, there is little threat from the fishery at this stage. However, identification of the location of the substrate used for this would be advisable, as it is possible that other activities may disturb this process. As ovigerous females are less likely to enter creels, this reduces the fishing pressure on them automatically. The practice in Orkney of returning those ovigerous females which do enter the creels reinforces this, although it is not known whether the stress of the capture, handling and return to the sea has a negative effect in itself on the viability of the brood. As the animals are of low value individually, scrubbing of the egg mass, which was a regular occurrence in lobster fisheries, does not occur. The end result of this is that females are under less fishing pressure than males for much of the year – the 4-5 months in which they are ovigerous, and the period during which they are soft and mating. This differential pressure on the sexes may have long-term effects on the reproduction of the stock, however, if fewer larger males remain to mate with the large females, thus reducing the overall egg production.

PART 3: LARVAE AND JUVENILES

Section A: Larvae

3.1 Aims

Section 1.7.3 summarised the main work carried out to date on the larval stages of *Necora puber* and the conclusions of these studies. Geographical variablility (through the effects of temperature and salinity) affects the time period and length of development of larvae of different stocks, and may also affect size attained at each developmental stage.

The aims of this section are to identify the length of time spent at each of the five larval stages and one megalopa stage of the velvet swimming crab, *Necora puber* under conditions most approximating the natural conditions of the waters surrounding the Orkney Islands, UK. It is also the intention to estimate mortality at each stage. These data will be correlated with data from plankton trawls carried out in the field and will also serve as a baseline for the consideration of larval rearing of this species on a large scale. In addition to this, morphometric measurements will be carried out on each stage of larval and megalopa development for comparison with the work carried out in Spain by Mene (1987).

These aims are summarised in the questions below:

1. Is there a prezoeal stage for *Necora puber?*
2. Can the prezoeal stage be described?
3. What is the development time through each stage in the laboratory?
4. What is the mortality through each stage in the laboratory?
5. Is larval rearing on a large scale feasible?
6. Are larvae comparable in morphology with those from other stocks?
7. When are larvae present in the water column?

3.2 Methods and Materials

Larval rearing work was carried out at the Orkney Water Test Centre (OWTC) on the island of Flotta, from 30/6/00 to 31/7/00. All seawater used in these methods is treated in the following way:

Seawater is pumped from 2m below the surface in Scapa Flow to a 20,000 litre holding tank which continuously overflows to waste. Three settlement tanks placed 9m above ground level are used as buffers for fluctuating demand and as direct supplies of raw seawater to the laboratory and hatchery.

In the first stage of treatment, the water is sand filtered to 10μm and then passed through nominal 1μm polypropylene cartridge fiters. The system filters around 5000 litres per hour. The filtered water is then passed through a titanium plate heat exchanger to a degasser, which removes excess dissolved nitrogen, and finally to a storage tank.

When the water from the tank is used in the hatchery, it is passed through a nominal 1μm filter and UV light. The hatchery operates a ring system through which the water circulates before returning to the storage tank. The water passes through the polishing filter and UV light every 15 minutes.

The broodstock, collected from Eynhallow Sound, was kept in 100 litre capacity tanks, half filled with treated seawater (TSW), which was changed every other day. Berried females with eggs at an advanced stage of development were chosen, and they were not fed. Prior to changing the water, the containers were checked for presence of larvae by use of a 212μm sieve.

The larvae were placed into 50 litre vats at varying densities in a recirculating system ensuring constant water flow (see Figure 3.1).

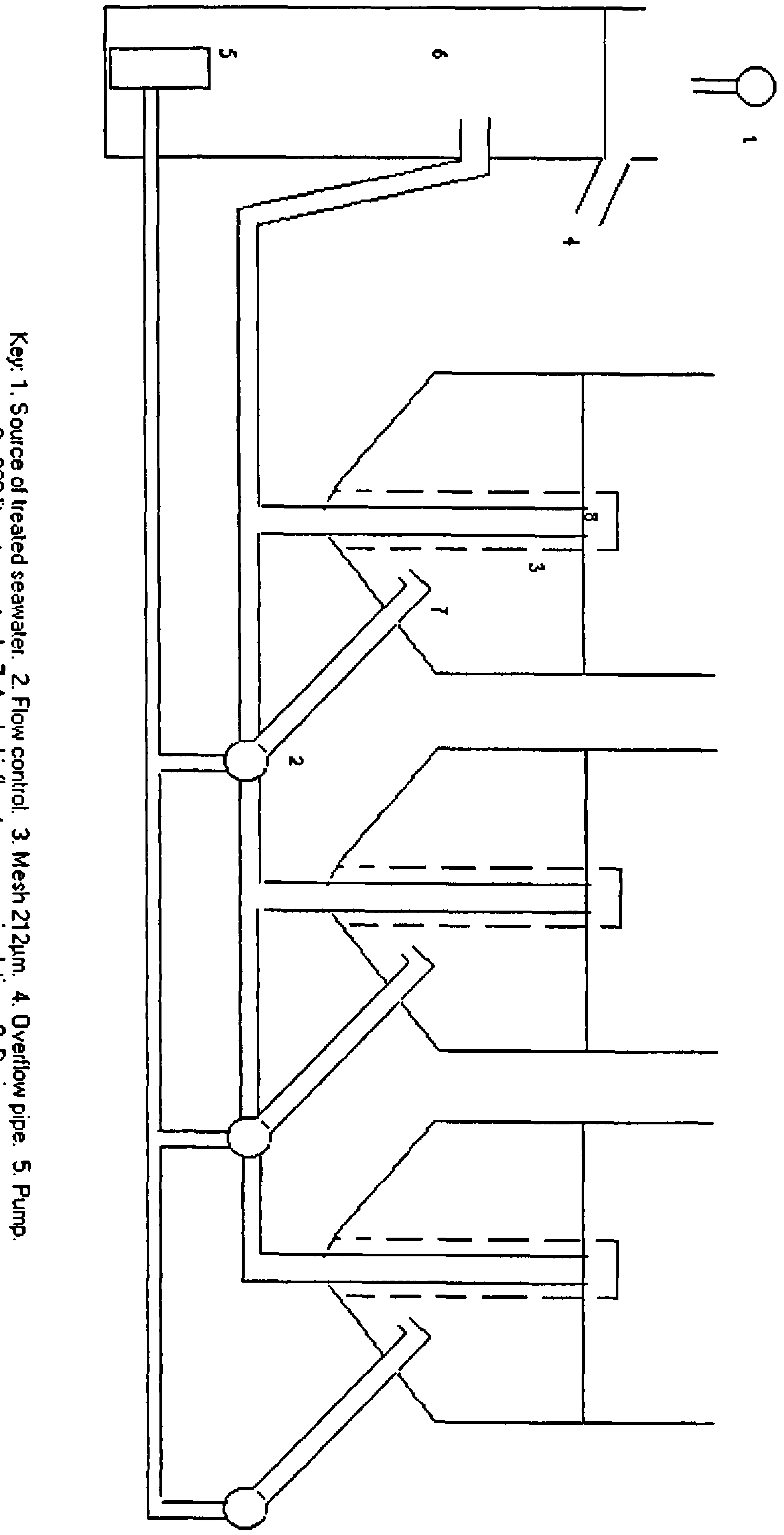


Figure.3.1 Schematic of larval rearing system used on Flotta

A reserve container of 200 litres of TSW, from which the vats were filled, was flushed through with new TSW every other day. The larvae were placed under a constant source of light, which closely approximated natural conditions at this time of year. Feeding took place every other day after the system had been flushed through. Larvae were fed on a mixed diet of *Artemia* and algae. Larval stages I-III were fed on freshly hatched *Artemia* at a prey density of around 6 individuals per ml, whilst the later stages were fed on 6-day old *Artmeia* at the same density. Algal feed in the form of a Tahitian strain of *Isochrysis galbana*, a single-celled, motile yellow flagellate, was added at 100 000 cells per ml. The temperature was maintained at a constant 17.5°C, a few degrees higher than the natural waters due to the treatment processes undertaken.

Every other day, prior to feeding, 3x100ml samples were taken from each vat after vigorous mixing of the water to ensure random distribution of the larvae within. These samples were used to determine the population size of the larvae in the vats. Those larvae observed were preserved with a few drops of 20% formalin solution and checked under a microscope for their developmental stage. The following characteristics, illustrated in Figure 3.2, were also measured for comparison with work carried out on *N. puber* larvae elsewhere.

10 measurements were carried out on each aspect at each stage and the mean of these measurements was used for further work. All the data recorded from the larval rearing experiments is presented in Dataset 4 (Appendix A).

Larval mortality rates were assessed by using the exponential decay model (Baranov, 1918; Beverton and Holt, 1957) used in Part 2. These were compared with estimated mortality rates in the wild.

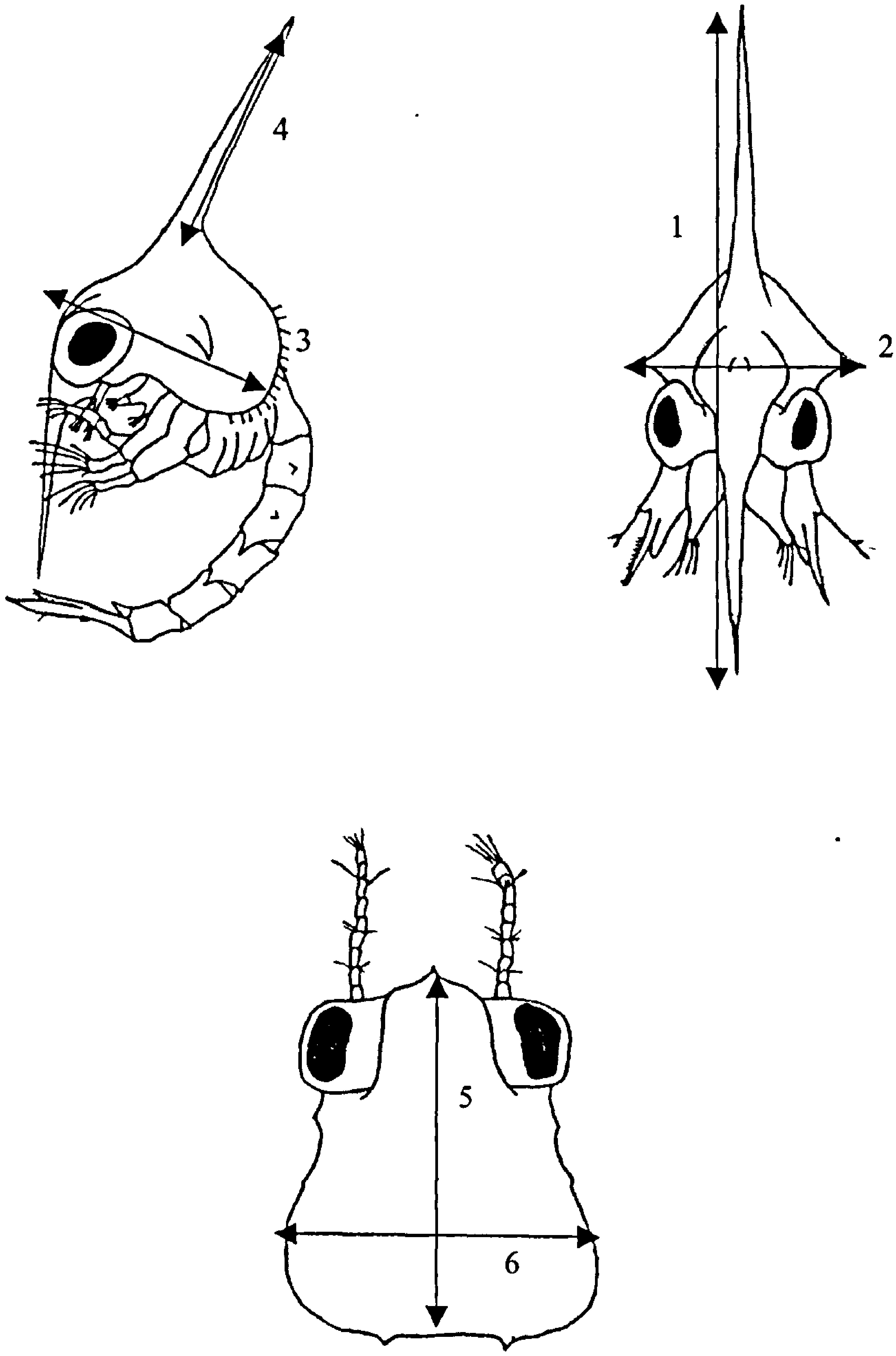


Figure 3.2 Measurements taken from larvae during rearing experiments (Diagrams adapted from Mene, 1987). Key below.

1. Length from apex of dorsal spine and that of rostral spine
2. Carapace width, taken between the apices of the lateral spines
3. Carapace length
4. Length of dorsal spine
5. Carapace length of megalopa
6. Carapace width of megalopa

The occurrence of *N puber* larvae in Eynhallow Sound was assessed by carrying out monthly (from September to May) and weekly (from June to August) plankton hauls from a fishing vessel. A standard haul lasted 5 minutes, using a 30cm diameter 200μm mesh net. The net was towed just below the surface of the water, not exceeding a depth of 1m. The contents of each tow were emptied into a glass jar and fixed using a few drops of 5% phenoxy-ethanol solution. The container was then taken back to the laboratory for observation. The number of *Necora puber* larvae was counted and for each larva, the stage of development was noted (Dataset 3, Appendix A).

3.3 Results

3.3.1 Occurrence and description of the prezoeal stage

As the larvae generally hatch at night, it was usually a number of hours before access could be had to them, so the probability of catching the prezoeal stage was very slight. However, in one broodstock container, two crabs that had not been acclimatised to the higher temperature of the hatchery died. The remaining female had eggs, which hatched and subsequently died still at the prezoeal stage, possibly due to contamination from the two dead adults.

In order to determine whether the larvae would have hatched as prezoea regardless, or whether the stress induced by the presence of two dead adults had caused premature hatching, a tank was set up at the main laboratory of ICIT, which could be checked at more regular intervals. The first female to hatch her eggs did so within 8 hours of being checked, at which point 99% of the larvae were at the zoea I stage, whilst the remaining 1% were indeed present as prezoeae. This indicates that prezoeal hatching does take place, but that well within 8 hours, there is a moult to the zoeal stage.

Figure 3.3 shows the general features of the prezoeal stage. The prezoea is around 1.5mm in total length. Carapace length ranges between 0.58-0.64 mm (mean: 0.605; n=10). The prezoea is enveloped by the prezoeal cuticle, under which are visible the dorsal and rostral spines. The dorsal spine is especially noticeable as a protrusion under the cuticle on the dorsal surface. Apart from this, the carapace is devoid of any spines or processes.

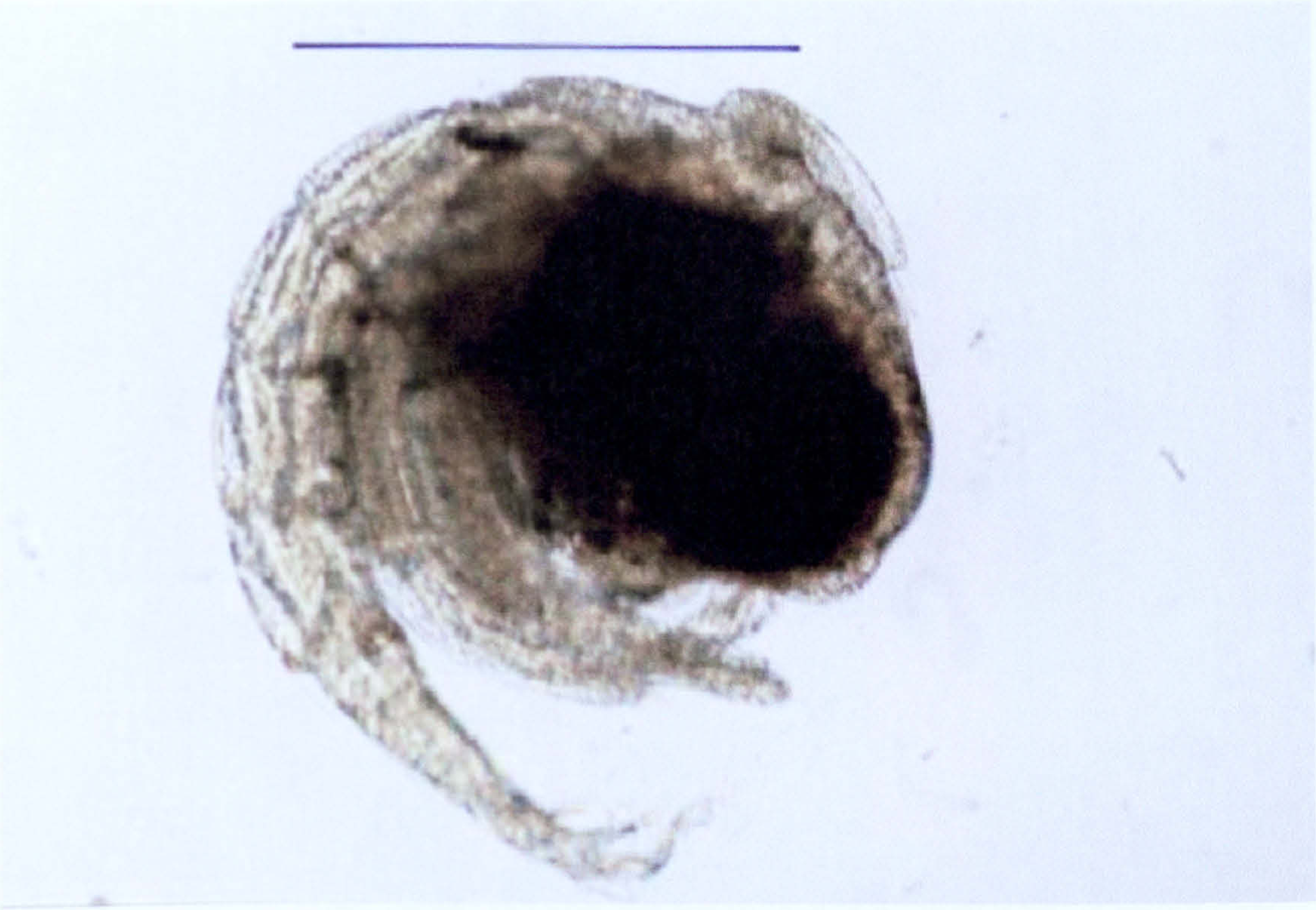


Figure 3.3 Photograph of the prezoeal stage of *Necora puber* (scale: bar = 500μm)

The telson is shown in Figure 3.4. There are 7 spines present on each side of the telson. The seventh spine is the shortest and is devoid of setae, as with most prezoeae from the division Brachyrhynchia (Ingle, 1992). Of the remaining spines, only the third spine displays setae: along both margins and from base to tip. In the enlargement section of the photograph shown, the fourth spine extends through the prezoeal cuticle.

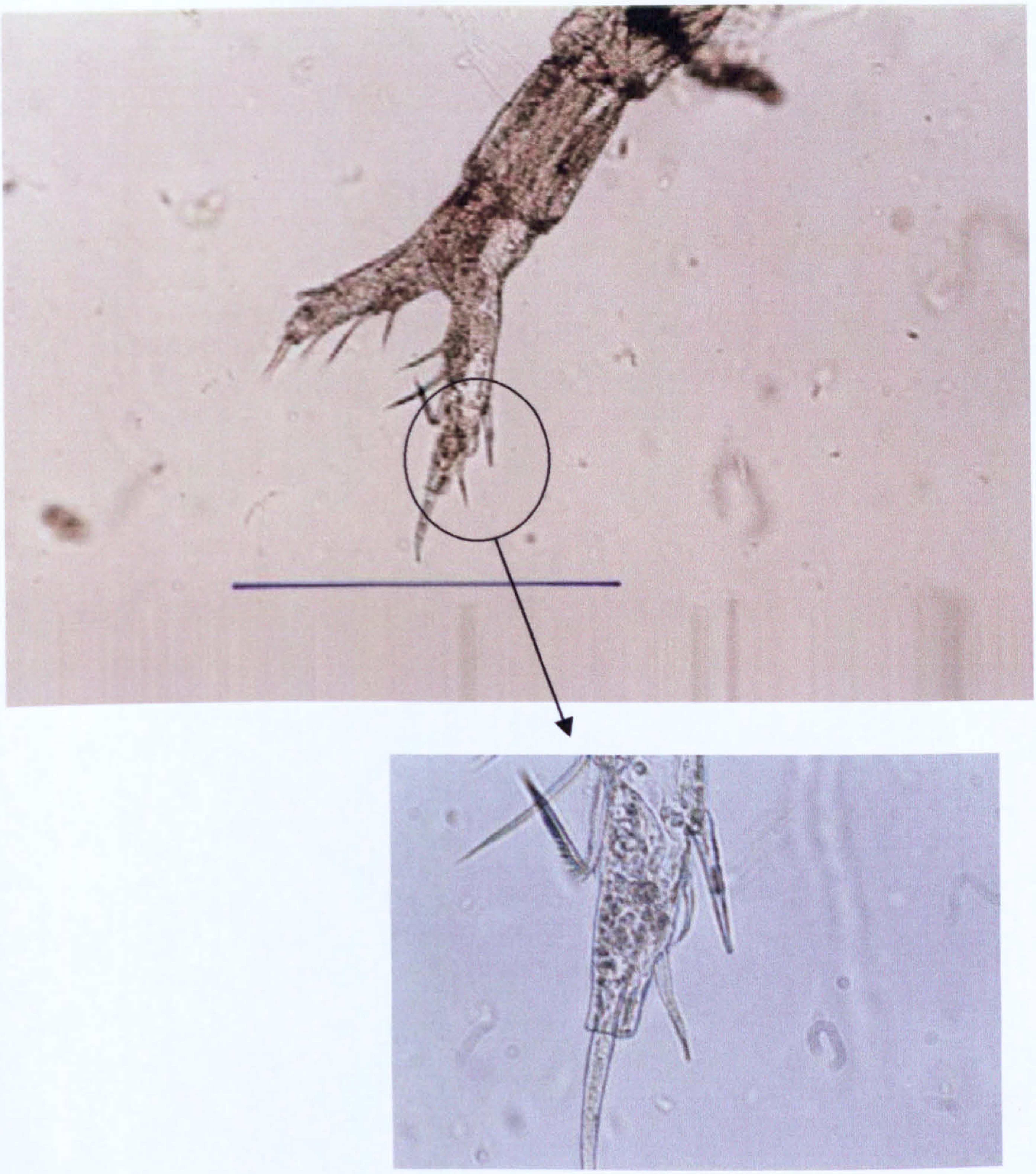


Figure 3.4 Telson of prezoea and enlargement of fourth spine of same (scale: bar = 500μm)

The prezoeal stage was observed to swim in a different fashion to the zoeal stage larvae. Swimming was in a jerking manner consistent with observations made by Hong (1988) on prezoeal stages of other species, which were described as swimming "to the surface by jerking the body backwards using the antennular, antennal and telson processes."

3.3.2 Larval Development

Figure 3.5 shows the percentage of surviving larvae at each stage of development throughout the period of study, using data from batch 2, the only batch to complete the entire developmental process from hatching to first crab instar.

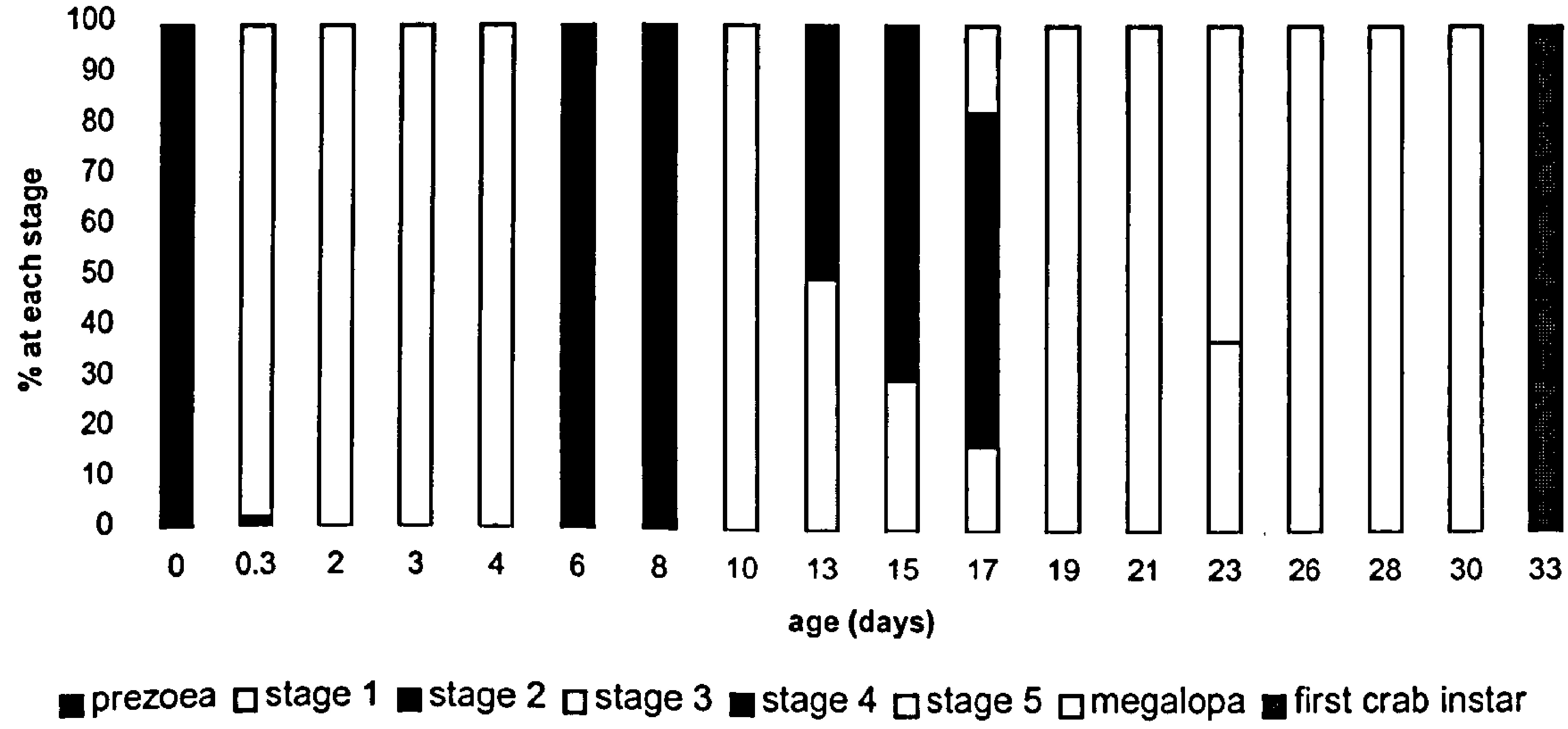


Figure 3.5 Development of velvet crab larvae under laboratory conditions.

As can be seen from the graph, the entire developmental process took 33 days. However, the time spent at each stage was not distributed evenly. The prezoeal stage lasted only a matter of hours – within 8 hours of hatching, 99% of prezoea had undergone the moult to first zoeal stage. The first zoeal stage had a duration of 4-6 days, as did the second stage. The third stage showed more variation in its length depending on the individual, lasting from 3-8 days, with the fourth and fifth stages both lasting another 4-6 days. The megalopa stage was the most time consuming – individuals spending around 10-11 days at this stage, before undergoing the final moult to first crab instar.

The synchronicity of development becomes less evident throughout the process. Bearing in mind the small genetic variability between the larvae (which were all reared from the same female), and the identical conditions in which all were reared, close synchronicity between moults was expected. Although this was certainly the case for the prezoeal and early larval stages, by stages 3 and 4, there was up to a few days difference in the time of moulting. This was especially true for day 17, where stages 3, 4 and 5 were all present in the larvae.

3.3.3 Survival

Figure 3.6 shows the number of surviving individuals over time, expressed as fractions of a year. A power cut to the system on the second day led to the pumps acting as siphons and removing most of the water in the 50-litre vats. As a result of this, the initial mortality of the population was extremely high.

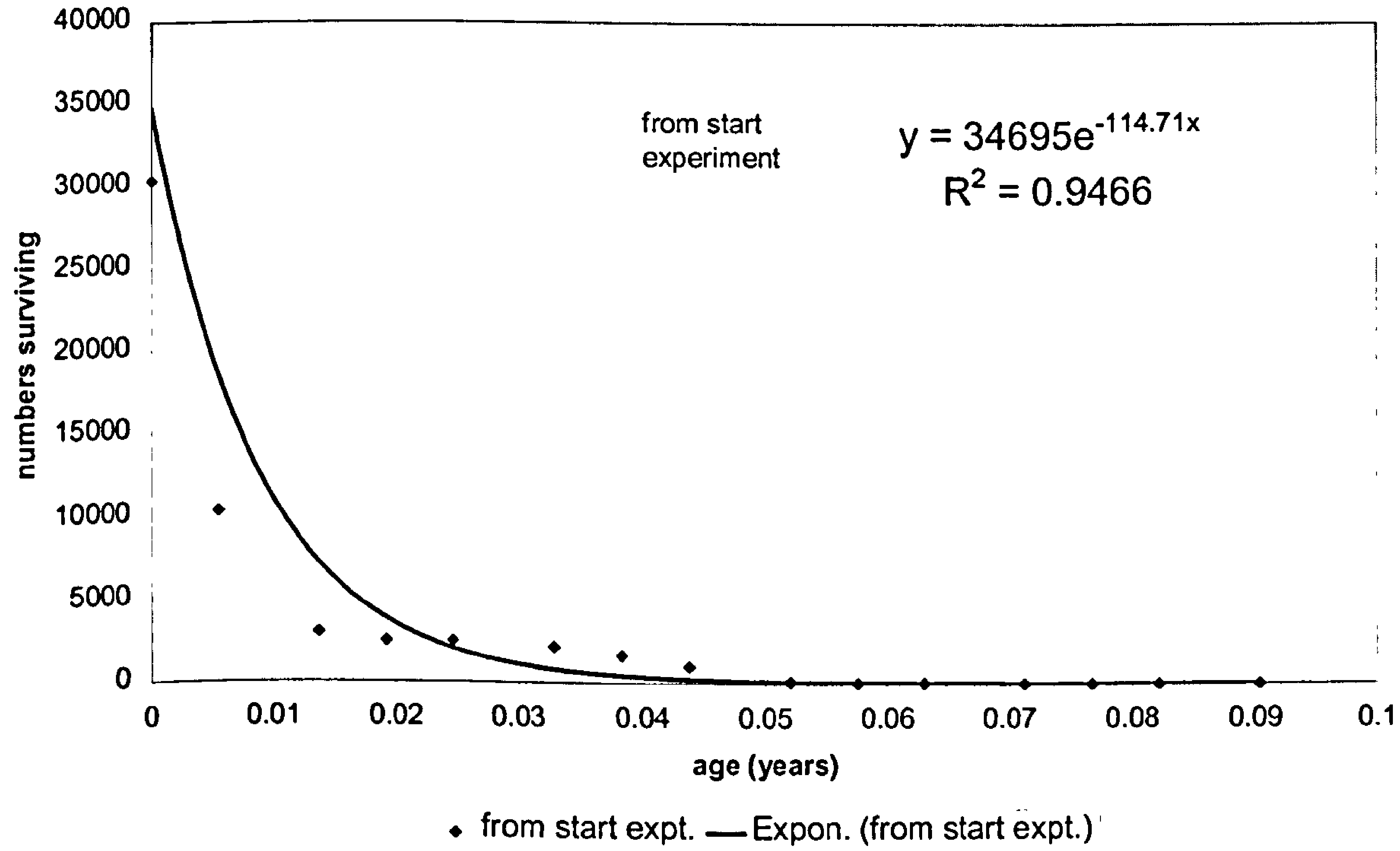


Figure 3.6 Number of larvae surviving over time.

From the equation given of the exponential decay in the graph, Z can be calculated as:

Z = -b

Where b is taken from the equation of the curve: $y = a^{bx}$

The value for Z obtained from this is 114.7. However, the mortality was not constant over the entire developmental period. Z values were calculated for each stage of development and plotted on figure 3.7, below:

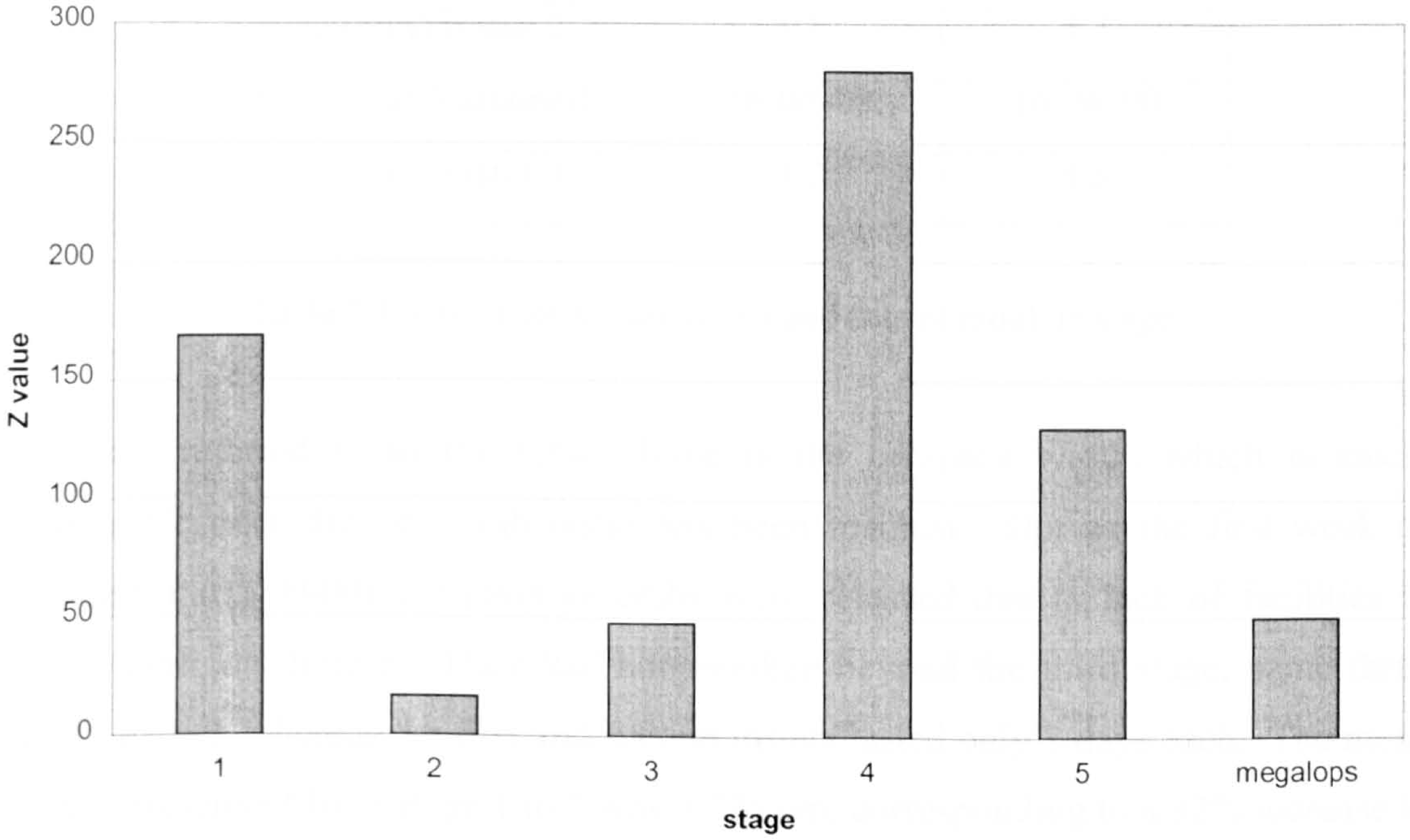


Figure 3.7 Mortality values (Z) calculated from each stage of larval development

Part of the huge mortality rate in zoeal stage 1 can be attributed to the malfunction of the pumps. However, the reasons for the remaining differences cannot be attributed to any one factor with certainty. It appears that there is a vast difference in mortality at different larval stages, with the fourth zoeal stage being the most vulnerable. Whether this is due to the conditions in the rearing tanks at that time, or to an inherent vulnerability at this stage, is not clear, but after this stage, the mortality rate is halved and then decreases yet again. From a total of around 30,000 larvae, two juvenile crabs were obtained, after 33 days.

The two juvenile crabs were maintained in individual compartments within a 5-litre plastic container, supplied with fresh seawater at ambient temperature daily, and with an air supply. They were fed every other day with crushed frozen krill, and observed for development. Table 3.1 shows their development:

Crab Number	**1**	**2**
Date instar 1 attained	31-07-00	31-07-00
Size (mm) instar 1	2.45	2.4
Date instar 2 attained	07-08-00	07-08-00
Size (mm) instar 2	3.1	3.3
Date instar 3 attained	16-08-00	16-08-00
Size (mm) instar 3	4.2	4.8

Table 3.1 Size of early crab instars and date of moult to stage.

The size referred to in the table above is the carapace width, which is easily measurable once the first crab instar has been reached. During the first week of September (05-09-00) the juvenile crabs were released due to lack of facilities to retain them any longer. They had not moulted beyond the third stage, some three weeks earlier, whereas the first and second instars lasted only 7 days each. The mean growth increment from stage 1 to 2 was 0.775mm, corresponding to a 32% increase in size. The mean growth increment from stage 2 to 3 was 1.3mm, corresponding to a 40% increase in size.

3.3.4 Morphometric measurements

Table 3.2 below shows the mean sizes of the various measurements taken at each different stage. As it was necessary to kill specimens before accurate measurements could be carried out, the smaller numbers of individuals at latter stages of development meant that sometimes, the desired number of 10 separate measurements was not possible to attain. The numbers in brackets show the number of measurements taken in order to obtain the mean. The range of sizes is also given underneath the first figure.

Variable	1	2	3	4	5	6
Stage 1 (27)	2.058	0.853	0.716	0.9		
Range	1.9-2.35	0.7-0.95	0.65-0.75	0.75-1.05		
Stage 2 (10)	2.535	0.858	0.828	1.052		
Range	2.45-2.65	0.8-0.92	0.8-0.875	1-1.09		
Stage 3 (10)	3.14	1.115	0.995	1.374		
Range	2.8-3.6	1-1.2	0.95-1.1	1.1-1.6		
Stage 4 (10)	3.757	1.2	1.2	1.745		
Range	3.375-4.03	1.2	1.125-1.275	1.6-1.87		
Stage 5 (5)	4.53	1.55	1.496	2.075		
Range	4.4-4.75	1.52-1.58	1.4-1.55	1.925-2.175		
Megalopa (2)					1.963	1.463
Range					1.9-2.025	1.45-1.475

Table 3.2 Morphometric measurements of *Necora puber* larval stages. (1= length from tip of dorsal spine to tip of rostral spine. 2= carapace width. 3= carapace length. 4= length of dorsal spine. 5= carapace length of megalopa . 6= carapace width of megalopa. All measurements are in mm. See Figure 3.1 for further details). Sample number in parenthesis.

The relationship between total length (as measured from the tip of the dorsal spine to the tip of the rostral spine) and carapace width for each stage is summarised in Figure 3.8.

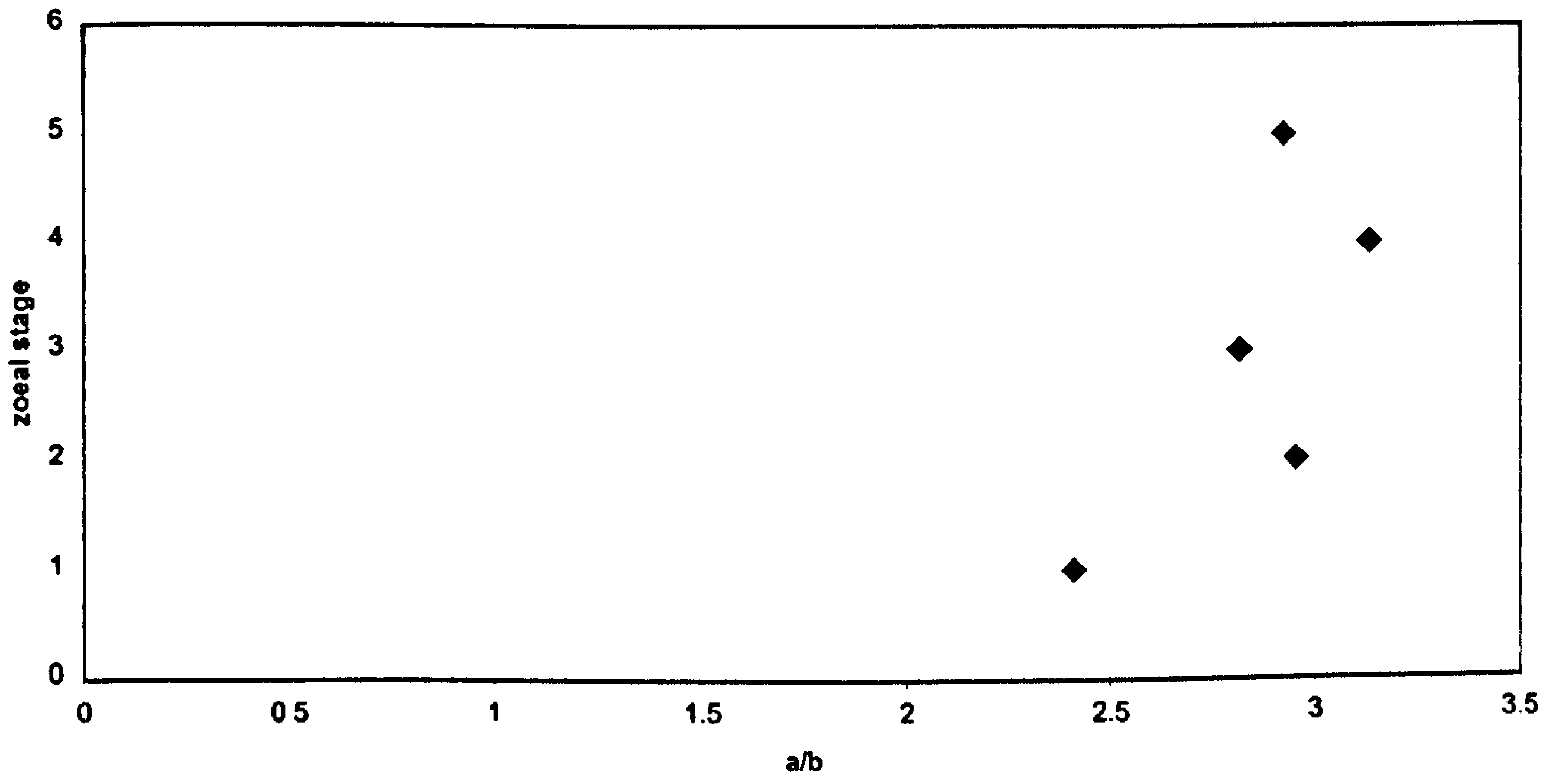


Figure 3.8 Length-width (a/b) relationship of larval stages of *Necora puber*

It can be observed that there is a general pattern that remains relatively constant throughout growth with a length-width ratio of between 2 and 3. The first stage has the lowest ratio where the total length is smaller in proportion to the carapace width in comparison with the other stages. However, overall, the increase in size in development does not affect the proportions of the larvae.

3.3.5 Plankton Trawls

The plankton trawls were not particularly successful either in numbers of individuals caught or in being able to obtain specimens from each developmental stage. The results of the trawls are shown in Figure 3.9.

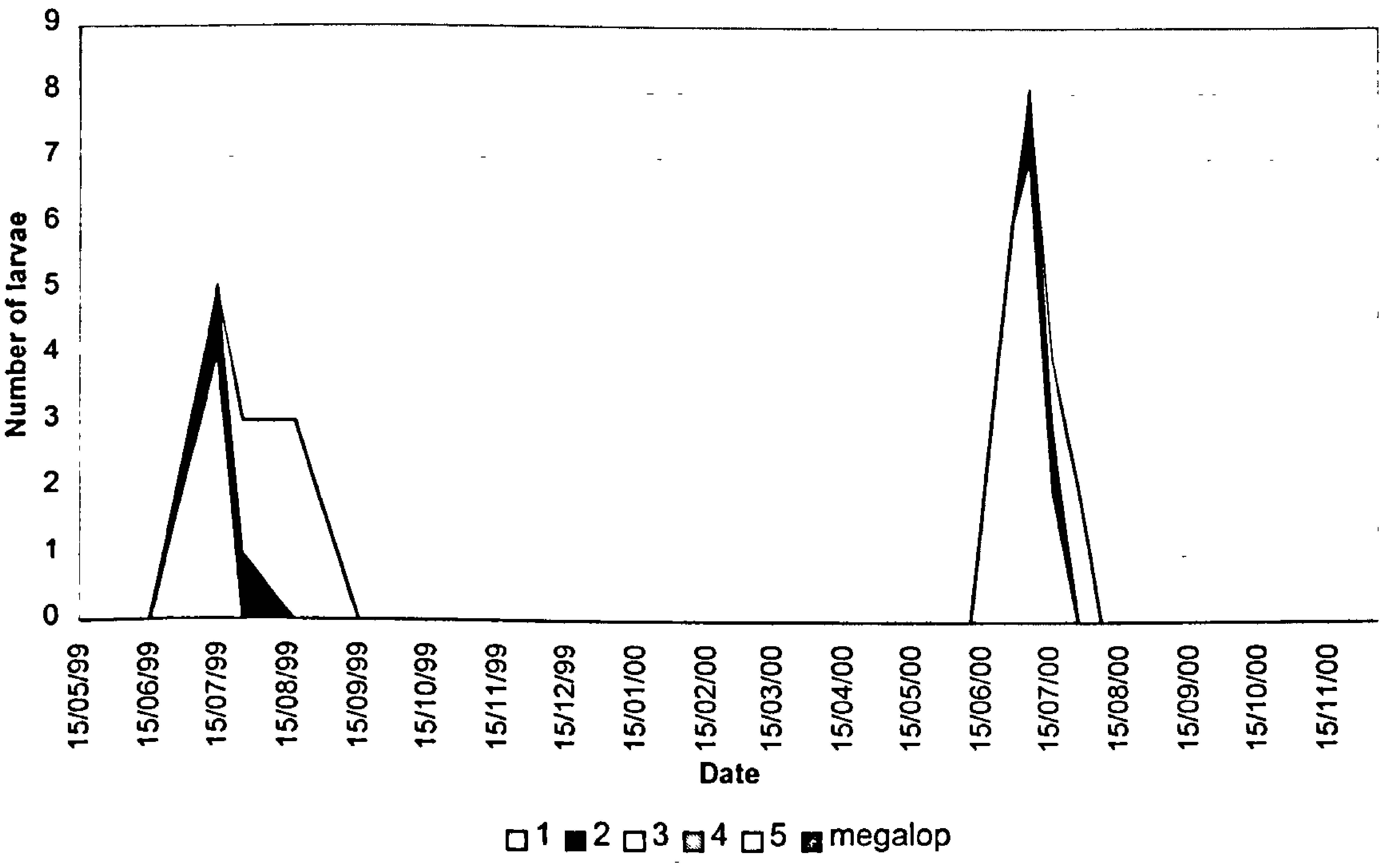


Figure 3.9 Results of plankton trawls in Eynhallow Sound: number of larvae at each stage.

The first point to notice is that very few individuals were caught. However, those that were obtained point to a larval period spanning the months of June and July. The reasons for the low numbers caught could be many. It is possible that the larvae prefer slightly deeper water than the surface and immediate waters sampled. It is also possible that larvae are found clustered in certain areas, and that the area sampled was simply an area of low larval density. There may also have been problems with the experimental method – it may be that a 5-minute tow is not long enough to obtain significant data.

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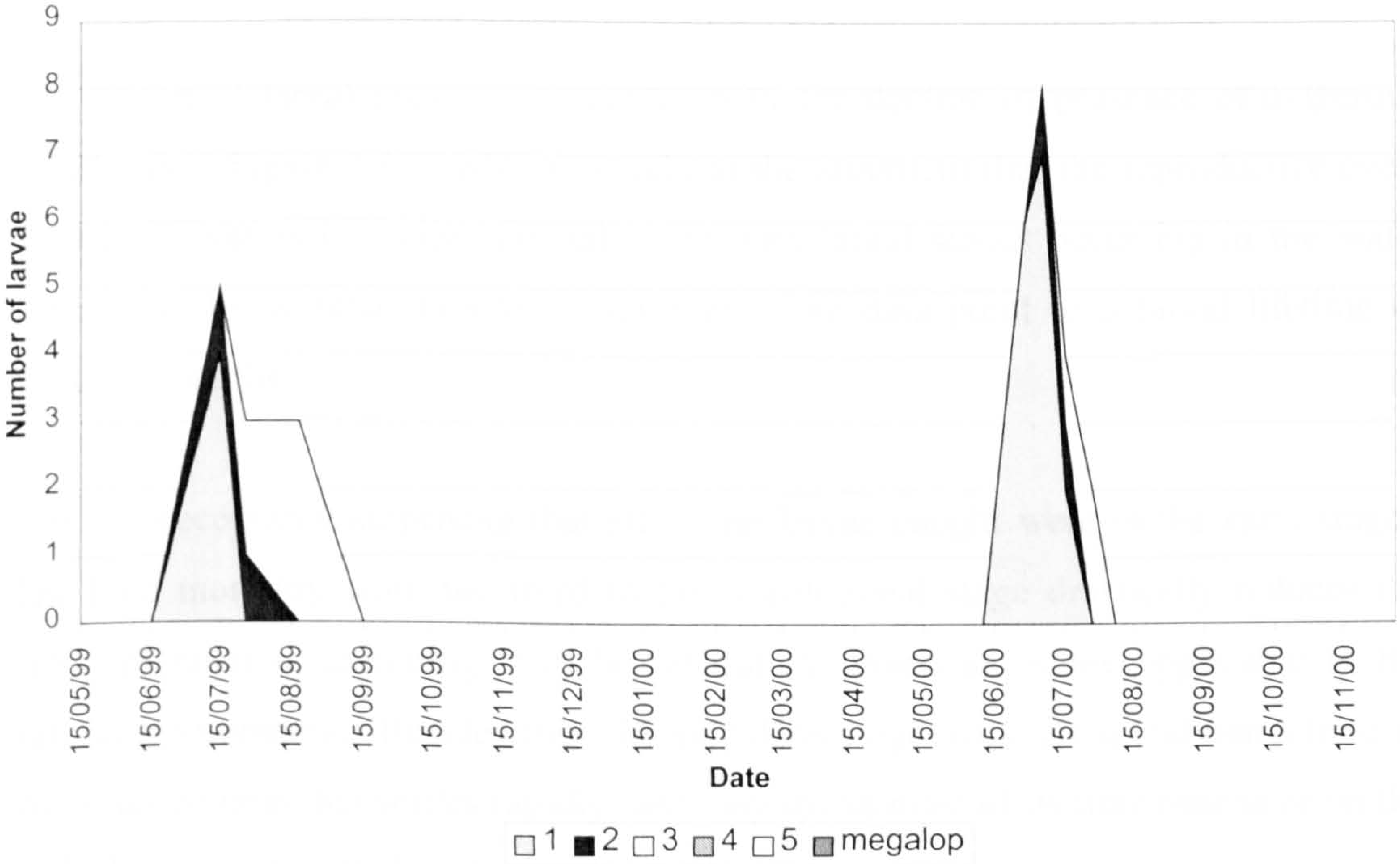

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As the net diameter (30 cm), speed (1 knot) and the length of the tow (5 minutes) are known, it is possible to work out the distance travelled during the tow and the volume of water sampled, assuming that there was no water movement during this period. The equation used for this is:

$$\text{Volume} = (\text{speed} / \text{time}) \times \pi r^2$$
$$= 32\text{m}^3$$

This implies larval densities of 0.156-0.25 larvae per cubic metre of water during peak periods.

The timing of larval presence coincides with the decline of presence of ovigerous females (see Figure 2.13), adding weight to the argument that the reproductive cycle in Orkney waters is a clear annual cycle with larval stages occurring in the water column in the warmer months of summer. The data point to a larval lifetime of around 3 months.

It is not necessarily surprising that all of the larvae caught were in the early stages. The high mortality from the third to the fourth zoeal stage drastically reduces the larval population, assuming that the laboratory observations are applicable to the natural environment. Besides this, the megalops stage does not spend much time in the water column, but settles rapidly, and may spend most of its time near to or on the seabed seeking a suitable substrate for settlement.

Larval mortality in the wild can be estimated according to a number of assumptions. The average fecundity of *Necora puber* is 112,000 eggs (see Part 2). Theoretically, in order to maintain a stable population, each female should produce one male and one female reproductively capable offspring, over her entire life. It was assumed that a female could spawn five times in her life (assuming yearly spawning and five years life-span after sexual maturity). Assuming also that there is no mortality between reaching the crab 1 instar and sexual maturity, this implies the production of 2/5 larvae per year. Figure 3.10 shows the mortality of larvae, taking the development times as 33 days (for comparison with the laboratory study), 60 days and 90 days, using 112,000 as the initial number of larvae produced, and 0.4 as the final number obtained:

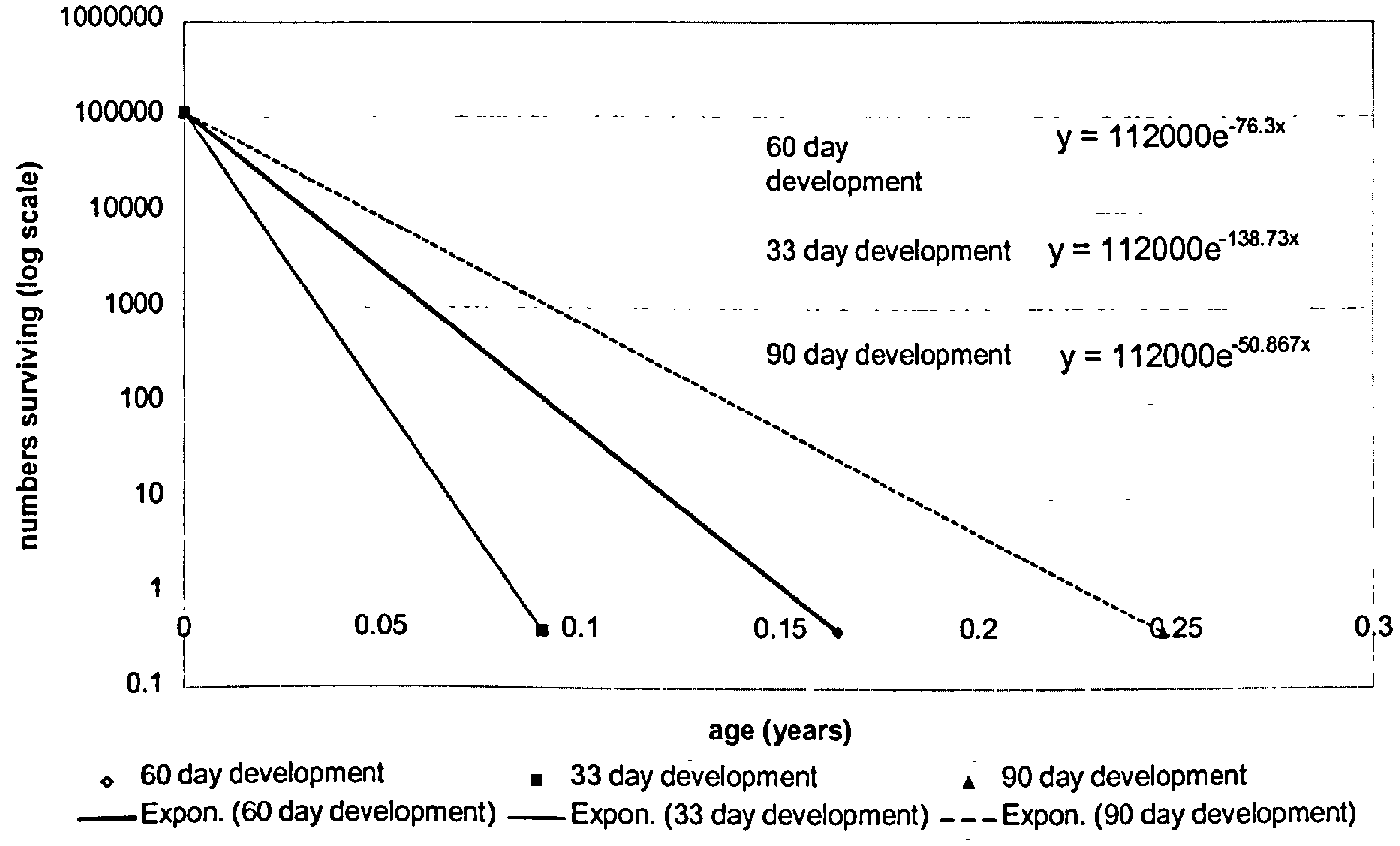


Figure 3.10 Estimated larval mortality in the wild, at three development times, plotted on logarithmic scale. Lines refer to exponential regressions on theoretical development times.

From the graph it can be seen that there are huge mortalities involved in larval development. The total mortality rate for a development time of 33 days is comparable with that experienced in the laboratory. The more realistic natural development times of 60 and 90 days express a much lower mortality rate than the laboratory experiments. In order for laboratory rearing of larvae to be successful, mortality rate should be considerably lower than that expressed in this laboratory study and in the wild. Ideally, conditions in the laboratory should be such that mimic the wild, so that mortality should reflect conditions in the wild after the effect of predation has been removed. However, in batch rearing this may not be possible, as cannibalism is a possibility at high densities (Mene, *et al.*, 1991).

3.4 Discussion

The occurrence of the prezoeal stage, observed on two separate occasions during the larval rearing experiments, adds fuel to the ongoing argument as to whether this stage is a naturally occurring part of many decapod life cycles, or whether it is an artefact caused by sub-optimal rearing conditions (e.g. Churchill, 1942; Mir, 1961; Webber and Wear, 1981; and others).

Prezoea are not observed in the plankton, and they are rarely observed in the laboratory, as their duration is so short. In the case of the velvet swimming crab, the stage appears to last less than 2 hours. Prezoeas were first described in detail by Faxon (1880), and Lebour (1928) gave a detailed account of the prezoea for several species, including *Necora puber*. An increasing number of prezoeal stages have been described in recent years, for species such as the deep sea spider crab, *Anamathia rissoana* (Guerao and Abello, 1996), and *Portunus pelagicus* and *P. sanguinolentus sanguinolentus* (Campbell and Fielder, 1987). However, the authors of this last study remain sceptical as to whether these forms are naturally occurring. They suggest that for *P. s. sanguinolentus* at least, suboptimal rearing conditions are implicated in the presence of this stage.

Hong (1988) reviews the prezoeal stage in various species and states that the prezoeal stage can be separated from the first zoeal stage, not only by its morphology, but also by its behaviour. The prezoea swims in a jerking motion using the antennular, antennal and telson processes, as opposed to the continuous perpendicular swimming motion of the first zoeal stage, which uses the maxillepedal setae and the telson. This difference in behaviour was observed in the live prezoea found during this experiment.

Once the first zoeal stage has been attained, there is agreement that there are five zoeal stages, followed by a megalopa stage, which settles and metamorphoses into the first crab instar. Various larval rearing experiments have been carried out on *Necora puber* (Lebour, 1928; Choy, 1991; Mene, 1987; Mene *et al.*, 1991). The length of development is related to the water temperature. In those places where there were two spawning periods per year, the winter batch would take up to four times longer to develop than the summer batch (Choy, 1989). The results of the current study cannot be applied directly to the natural waters, because it was not possible to keep the temperature of the tank water the same as that in the sea. Choy (1991) found that larvae reared in South Wales at 12°C took over 60 days to complete their development, whereas development at 18°C only took 40 days. The larvae in the current study had attained first crab instar by day 33 (at 17.5°C). This may be due to other conditions being more favourable (e.g. dietary), but it is also possible that the Orkney stock is adapted to cold water and is therefore able to develop at a more rapid pace than its warmer water counterparts under similar conditions.

Temperature and salinity experiments carried out by Mene (1991) achieved similar results to the current study, with larval development time at a temperature of 20°C and a salinity of 30 being a mean 28.6 days. The fastest growing larvae were those reared at 25°C and a salinity of 35, completing development in 28 days.

In the natural environment, the temperatures are much lower and therefore the duration of the larval stage is correspondingly longer. Martin (1980) researched the presence of *Necora puber* (referred to as *Macropipus puber*) larvae in the English Channel and found the highest abundance of Zoea I in May-June and of megalops in September. This would give a development time of around three months.

The present study found limited larvae in the water column, being restricted by time and gear constraints. However, zoea I stages appeared in June and July, and zoea III stages were observed in September. Hence, the first three stages alone may last over two months. The total development time is probably longer than that observed by Martin (1980) due to the colder environment of Orkney waters. The larvae also appear in the water column later in the year compared with the English Channel, probably also for environmental reasons. Drake *et al.* (1998) studied the seasonal and tidal patterns of decapod crustacean larvae in the Bay of Cadiz (SW Spain). They found indications of diel migration in *Liocarcinus* species (which include *Necora puber*), as larval presence was significantly higher at night. They also postulated the possibility of an export of early larval stages out to sea for further development, as an explanation for large numbers of zoea I stages with respect to latter stages being found in the bay. Martin (1980) also found some spatial heterogeneity with respect to the larval stages, as well as a large difference between the abundance of zoeae and that of megalopas. Latter larval stages were not found in this study, possibly simply due to sampling error, but the absence of megalopa was to be expected, as this stage settles and spends some time on the bottom before undergoing metamorphosis.

The increasing variation in time spent at each larval stage may have a number of impacts in later analysis of growth and moulting. Potentially, the larvae in these experiments had the same access to food, were kept in the same conditions and came from the same genetic stock. If these developmental differences are inherent at such an early stage, they may increase in later stages as young and adult crabs, making determination of age by size a more complicated process with a wider range of sizes corresponding to similar ages. However, it is interesting to note that, although these differences did arise during larval development, those individuals reaching the first crab instar did moult from zoea 5 to megalopa and then onto the crab stage, all at the same time. It is possible therefore, that the individuals moulting out of time with these larvae were in some way defective and would not have reached the crab stage at all.

It was observed in the laboratory that the megalopa spent only 2-3 days floating in the water column, before settling on the bottom of the tanks, displaying their limbs and moving around the bottom in crablike fashion. In both cases where metamorphosis occurred, it took place under the airstones in the container, and overnight. The reasons for this are probably for protection at this vulnerable stage. The size of the megalopa (CW = 1.463mm) was comparable with that in other studies: 1.4mm CW (Mene, 1987).

The change in mortality rates at each stage may reflect changes in the natural environment if these changes are inherent in the species, such as moulting difficulties. However, the conditions in the laboratory, with high food density and high larval density contrast with those in the open sea, where larval density is lower and there is threat of predation. The megalopa stage may be particularly vulnerable for this reason, as it settles and searches for a suitable substrate before undergoing metamorphosis.

According to Brook's Law (Fowler, 1909), "during early growth, each stage increases at each moult by a fixed percentage of its length, which (percentage) is approximately constant for species and sex." Table 3.3 shows the growth factor at each developmental stage for this study, using carapace length as the basis for measurement:

Stage	Growth factor
I-II	1.156
II-III	1.202
III-IV	1.206
IV-V	1.247

Table 3.3 Growth factor at different larval stages.

These figures fit with the general pattern observed by Brooks (1886) of a typical growth factor of 1.25 for decapod crustaceans. Later studies have shown there to be much more variability. Rice (1968) studied the early growth of 47 species, finding a growth factor of between 1.05 and 2.7 (average: 1.29). Rice suggested that this constant could only exist if all biological variations could be taken into account. As this is not so, because the water temperature changes over time, as do light and food conditions, then the exponential growth curve will display irregularities. The growth factor is probably slightly different between stocks in different areas (Table 3.4, showing the relative larval sizes between Orkney and Spain indicates this).

The overall morphological measurements carried out on the larval stages of *Necora puber* did not differ greatly from those carried out on the Spanish stock. Table 3.4 summarises the total lengths of larvae at each stage from the two areas:

Stage	Orkney	Spain	Spain (growth factor)
Zoea I	2.058	2.02	
Zoea II	2.535	2.38	1.18
Zoea III	3.14	3.10	1.3
Zoea IV	3.757	3.90	1.26
Zoea V	4.53	4.55	1.17

Table 3.4 Comparison of mean total lengths (in mm) of larval stages from Orkney and Spain (Mene, 1987).

Although the larvae from Orkney are slightly larger to begin with, stages 4 and 5 are larger in Spain. However, all the Orkney measurements fall within the range of measurements for Spain, with the exception of the second zoeal stage, whose Orkney mean length is outside the range for the Spanish larvae (2.25-2.50). The overall growth rate is slightly higher in Spain, possibly due to higher temperatures and better food availability.

However, certain differences do arise between studies in different areas, possibly due to rearing conditions or natural conditions. Bigot (1979) found that larvae collected from the sea were significantly larger than those measured both in the current study and in Mene's study (1987). Mene suggested that the reason for this was that rearing conditions were never optimum for larval growth. It is also possible that only the largest larvae survive in the natural environment, whereas greater laboratory survival of smaller larvae will distort the mean sizes compared to those surviving in the wild.

The survival rate of the larvae in the current experiment was extremely low, due to a number of factors. Other studies have reared larvae individually or in low numbers (Choy, 1991; Mene *et al.*, 1991). However, one of the aims of this study was to examine the feasibility of mass production. This entailed risks, as was demonstrated during the first massive loss of larvae, when the pumps ceased to work, and acted as siphons, removing a huge proportion of the larvae from the vats over the first two days of the experiment. Cannibalistic tendencies (Choy, 1991) in latter stages combined with the huge mortalities involved made the vats unviable, so the few remaining larvae were transferred to smaller, 5-litre containers, and the water changes carried out manually. This proved labour intensive and time consuming, and potentially expensive. The end result of two juvenile crabs from a batch of 30,000 is not promising.

Necora puber larvae have some potential advantages when considering mass rearing. They reach commercial size after 4 years, in comparison with the lobster, which takes 5-6 years and at present, is released into the wild as a stage XII juvenile, with comparatively low survival prospects. *Necora puber* could be released into the wild after a much shorter period, which could be determined by a preliminary survey on survival of early crabs instars. Alternatively, a system which eliminates the release process altogether; rearing the crabs to commercial size then selling them, could be contemplated, using large nursery areas for adult crabs.

However, the main considerations of such an enterprise must be whether it is needed at all, and whether it would be economically viable. Part 5 of this thesis deals with the fishery and carries out stock assessment, answering the first question. As to whether the enterprise would be economically viable, it must be taken into account that although growth is fast, the actual value per weight in comparison with the lobster is very low. In order to obtain a sustainable hatchery, the survival rate must be improved on drastically. The average price of a velvet crab of a size around the MLS, weighing about 75g, at £1.20 per kilo, is only 10p. Even if the hatchery were set up for selling only at Christmas time, the value would only be double. The alternative of rearing the crabs until they are much larger (>75mm), and therefore of double value, implies keeping them for another year at least. The economics are very clear. In order for such as enterprise to make money, the total costs must be below 10p for every crab surviving to adulthood. Taking into account the larval feed itself, which in this experiment cost £40, plus running and labour costs, it is apparent that at present, commercial rearing to market size is not an option.

The other option would be to have a hatchery as part of the strategic management plan of the local fishery, within an area restricted by a regulating order (such as that currently under proposal for Orkney). In this case, mass rearing for release into the wild at an early stage, using subsidies and levies from the stakeholders involved in the industry, may be viable. However, in order for this to work, it should previously be determined whether juvenile survival is the limiting factor in the fishery.

Section B: Juveniles

3.5 Aims

For the purpose of this study, a juvenile velvet crab is defined as any crab smaller than the size at which sexual maturity is obtained. Little work has been carried out to date on juvenile velvets. The reason for this may well be the difficulty of obtaining specimens. Juveniles appear to occupy an "awkward" habitat, the first few metres of water on a moderately exposed rocky shore, characterised by *Laminaria* and sometimes extending up into the *Fucus* zone (Tallack, 1998). They are therefore only exposed at very low spring tides, but are too shallow for effective diving and other hand collection techniques. Whereas brown crab juveniles were found extensively on all rocky shores at low tides, juvenile velvets were much scarcer, probably due to the fact that only the upper part of their distribution was being sampled.

The specific questions asked during this part of the study are summarised below:

1. Where are juvenile *Necora puber* found in Orkney?
2. Can a measure of abundance be obtained?
3. Which is the best method of obtaining juveniles?
4. To what extent are juveniles morphologically similar to adults?
5. When does settlement occur?
6. Is the sex ratio 1:1?
7. How fast do they grow?
8. When do they reach sexual maturity?
9. When do they reach MLS?
10. How often do they moult?
11. What are the moult increments?
12. Can growth curves for the entire population be constructed from juvenile data?

3.6 Methods and Materials

Shore searches were carried out at low water spring tides in a number of exposed and semi-exposed rocky shores on Mainland Orkney. Once juvenile velvets were found (on the Scapa Flow facing shore of Inner Holm, Stromness and on a number of beaches around Eynhallow Sound), periodical searches were carried out monthly (see Figure 3.11).

Initially, a number of methods were used in the attempt to obtain juveniles. Bottle traps were used on Skaill Beach and Warebeth Beach, both close to Stromness. Snorkelling was undertaken in Aikerness Beach and Waulkmill Bay. Five creels were covered in small mesh (1cm) and used in the general fishing ground, whilst ten small creels (40cm x 30cm x 20cm high with a mesh size of 1cm) were constructed and set in locations such as Skaill Bay, Inner and Outer Holms of Stromness and Aikerness. None of these methods were successful in obtaining juvenile velvet crabs. The only successful method involved turning over rocks and stones at low spring tides in the *Laminaria* zone.

All velvets observed during the spring-tide shore searches, regardless of size, were recorded (Dataset 2, Appendix A). These were taken back to the laboratory and used for measurements of sexual maturity (see Section 2.3.1). Their carapace width was measured, and they were sexed, before being placed in tanks (60cm x 30cm x 30cm) with 50 litres of raw seawater where they were fed on frozen krill and observed for moulting.

The sexing of small juveniles is not easy, as the difference in abdominal width between the sexes is not apparent at this early stage. In order to determine the sex of an individual, it was necessary to gently lift the abdomen with forceps and observe the structures underneath. Males display two pairs of uniramous, rod-like pleopods, which function together as reproductive tools to pump sperm into the females. Females have biramous, setose pleopods on the second-fifth segments. These are modified for carrying eggs. Both sets of structures are apparent from a very small size, long before sexual maturity is attained. However, the practice of lifting the abdomen was found to greatly increase subsequent mortality, and was therefore discontinued. Where sex was not readily identifiable after this, a question mark was inserted into the sex column of the datasheet (Dataset 2, Appendix A).

A measure of the relative abundance of crabs was obtained by dividing the numbers caught by the time and number of people involved in the search (these were normally carried out by 2 people, for one hour prior to and one hour after low tide).

Once juvenile velvet crabs were located (on three main beaches), these beaches were sampled monthly. The data were organised into 2mm size classes from which modal points were determined. Gulland and Holt plots were used to estimate K and $L\infty$, and these figures were incorporated into the von Bertalanffy growth equation to produce initial estimates of the growth curves pertaining to the Orkney stock.

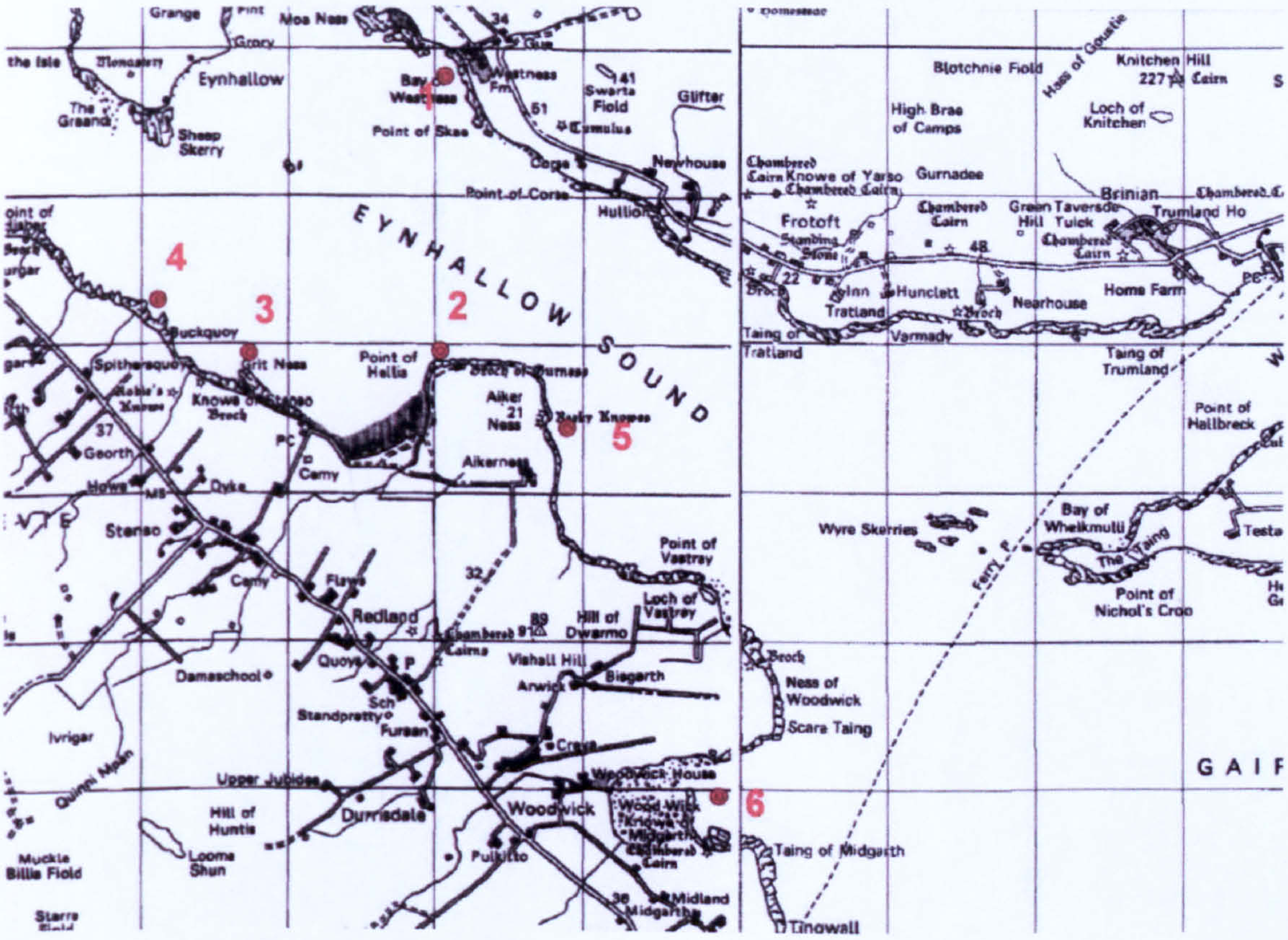
The juvenile crabs obtained during the larval rearing experiments were maintained in tanks for observation, as stated in Section 3.3.3. In addition to this, throughout the duration of the study, some individuals were brought back to the laboratory and placed in tanks in order to directly measure their size increment after moulting. The number of individuals was limited due to tank availability and size. One tank (80cm x 40cm) was filled with 8 litres of seawater. This was used for one individual at a time. The seawater was changed regularly and the crab fed with creel bait or frozen krill, depending on availability. Another tank (120cm x 40 cm) was filled with 20 litres of seawater and used for three or four individuals at any one time. Both tanks were fitted with air supplies and filters, but neither tank was temperature or light control.

The moult increments were used to obtain information on the growth factor of the stock, and how this changes with size. From this, moult sizes were estimated. Using this information combined with the growth curves from the von Bertalanffy growth equation, and estimating moult times, a stepwise growth pattern for the stock was created.

3.7 Results

3.7.1 Distribution

Figure 3.11 shows a map of the sites sampled around Eynhallow Sound. The table beneath the map summarises the locations, the range of tidal heights during which surveys took place, and a measure of the relative densities of juveniles where these were found.



Station	Name	Tidal height above CD	Velvets present	Mean No/hour/person
1	Westness	0.3-0.4	Y	13
2	Gurness	0.1-0.3	Y	6
3	Gritness	0.1-0.3	Y	9
4	Buckquoy	0.4	N	-
5	Aikerness	0.4	N	-
6	Woodwick	0.4	N	-

Figure 3.11 Map of Eynhallow Sound and beaches surveyed for juvenile *Necora puber*.

They displayed a patchy distribution, which made estimates of abundance difficult. Where they were found, it was under large rocks and boulders at low spring tides (0.5m or lower). This coincided with the *Laminaria* zone, but within this area, juveniles seemed to prefer areas with a combination of rocks and sand, in which they were sometimes buried. They were never found in areas of black, anoxic sediment. A good indicator of possible presence of juvenile velvet crabs in a particular area was the breadcrumb sponge, *Halichondria panicea* (Hazlehurst, 2001).

There was some overlapping with juvenile *Cancer pagurus* and *Carcinus maenas*, the former of which was around ten times more abundant. This may indicate that the habitat for juvenile velvet crabs extends below the low water mark. A detailed account of the ecology of juvenile *Necora puber* is given in a concurrent study by Hazlehurst (2001).

Some measure of the relative abundance of individuals can be estimated from the numbers obtained during the sampling outings. Juvenile velvet crabs were most abundant on the Westness shore, where an average 13 individuals were found per person per hour, compared with Gurness beach, where only 6 individuals were found per person per hour. This may partly be due to the relative sampling difficulty at Gurness. This beach is made up of large boulders and a heavy seaweed cover, which required more effort to overturn and reach the areas potentially inhabited by velvet crabs. As well as this, there appeared to be less potential sites for velvet crabs at Gurness with respect to Westness. Gritness beach was more comparable to Westness beach in terms of the structure of the shore and the number of potential areas for velvet crabs to occupy.

3.7.2 Morphology

Figure 3.12 shows a second instar crab, reared from the larval experiments discussed in the previous section.

Figure 3.12 Second instar crab reared in laboratory (scale: carapace width = 3.3mm)

The juvenile in the figure above does not display red eyes, the flattened last pair of pereiopods, or the velvety texture; the main external characteristics of velvet crabs. In addition to this, the eyes are proportionally much larger than in the adult, and situated in a peripheral location in comparison with the adult, where the eyes are in a frontal position. This may well have implications in terms of survival. Whereas in the adult, frontal vision is preferred, as it makes locating prey or other food sources easier, the more peripheral location of the juvenile eyes in the early stages may enable it to detect and thus avoid potential predators more effectively. The chelae are differentiated into a cutter and a crusher, but it would appear that the other characteristics typical of velvet crabs appear in individuals as they grow.

Once the crabs reach a size of around 30mm, the characteristics ("velvety" feel and red eyes) are present. There is some variation in the colouring at this stage, but this is also evident among the adults. However, Hazlehurst (2001) noticed three distinct morphs at the smaller juvenile stage (around 10 mm). These varied in terms of colouring and patterns on the carapace. She suggested this may have the function of camouflage, and may thus depend on the nature of the substrate.

3.7.3 Sex Ratio

The numbers of juveniles of each sex at each beach during different sampling times are shown in Table 3.5

Location	date	male	Female	Unknown
Westness	23+24-May	36	31	19
Gritness	02-Jun	3	7	20
Gurness	03-Jun	2	0	18
Westness	24-Jun	13	6	18
Gurness	25-Jun	4	1	16
Westness	26-Jun	14	12	19
Gritness	23-Jul	24	16	9
Gurness	24-Jul	14	6	7
Westness	25-Jul	63	32	26
Remaining		60	50	19

Table 3.5 Numbers of juvenile velvet crabs of each sex found on the shore

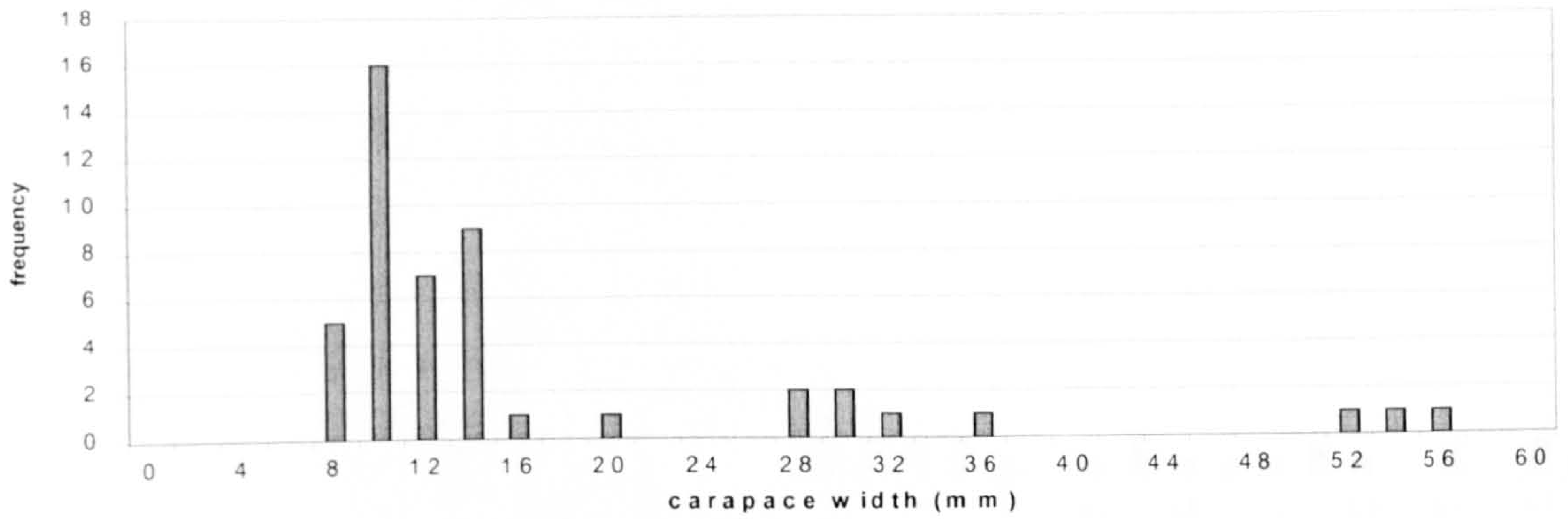
A chi-square test showed there to be a significant difference between the numbers of males and females obtained (p=0.001 at 9 d.f.). However, there are also a large number of individuals whose sex is unknown due to their size. These generally refer to those individuals below 12mm, after which sex can be easily distinguished from the shape of the abdomen.

3.7.4 Size Distribution

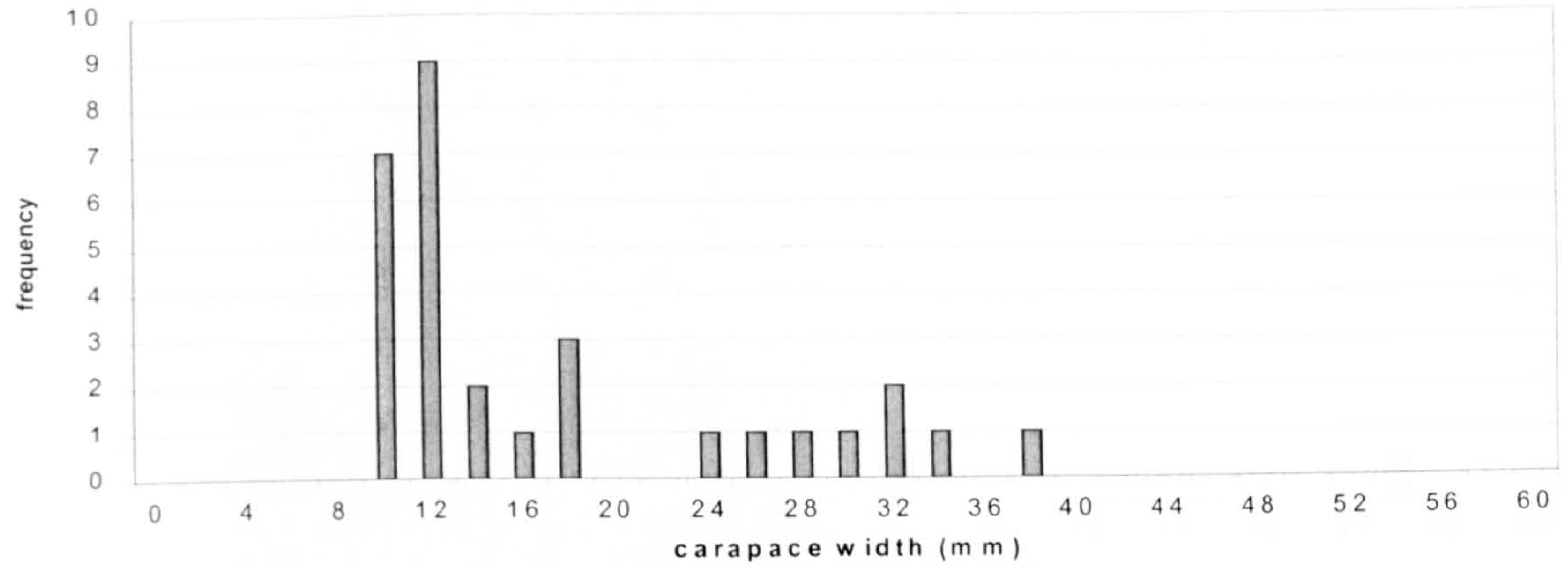
Figures 3.13-15 show the size-frequency distribution for juveniles on two Mainland beaches (Gritness and Gurness) and one Rousay beach (Westness). Individuals were grouped into 2mm size groups.

At this stage, the samples were not separated into the sexes. The graphs show the size distribution of individuals at each beach from May to July 2001.

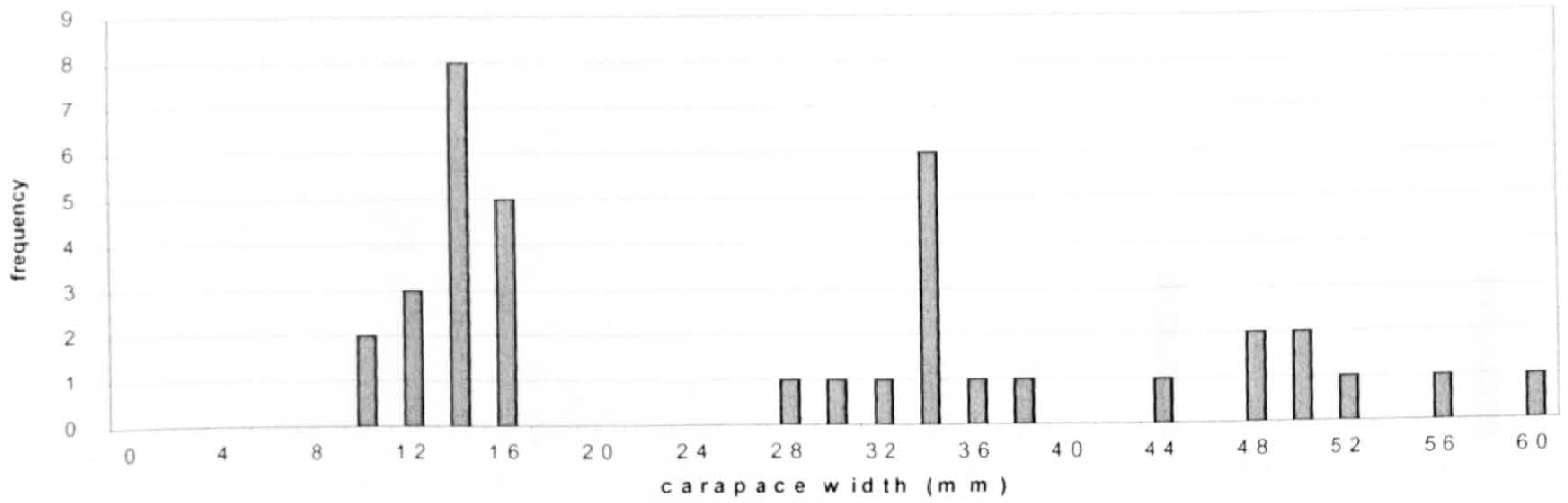
Gritness, 3-4 May 2001



Gritness, 2 June 2001



Gritness, 24 June 2001



Gritness 23 July 2001

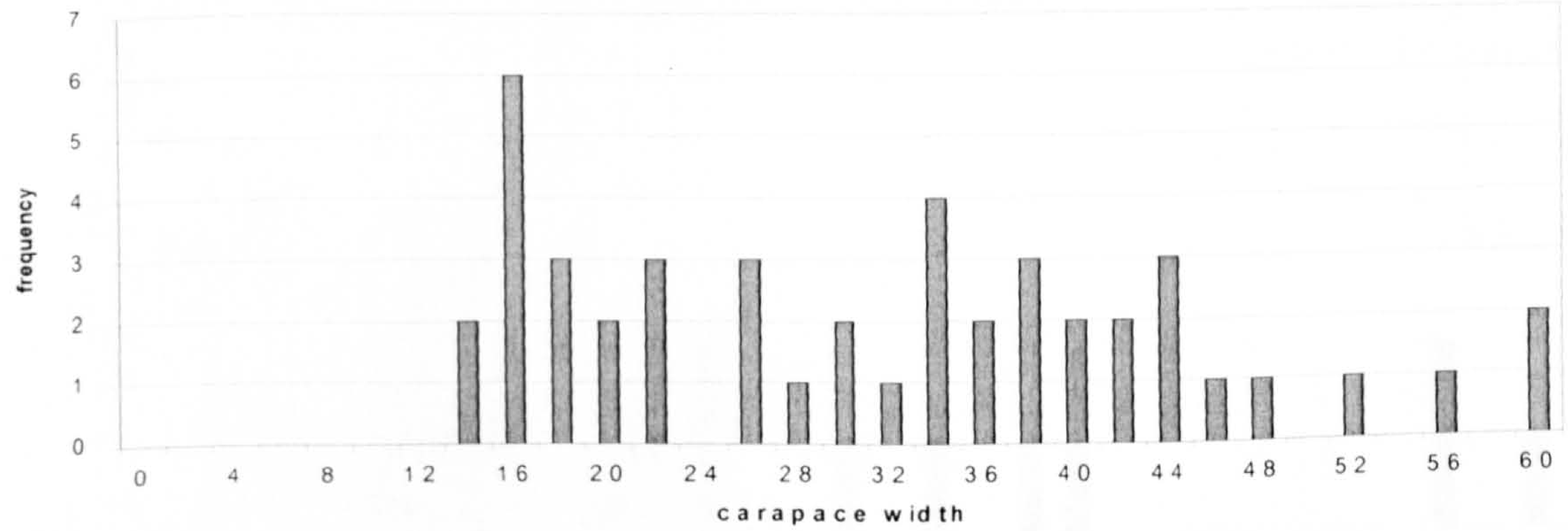


Figure 3.13 Size distribution from Gritness beach

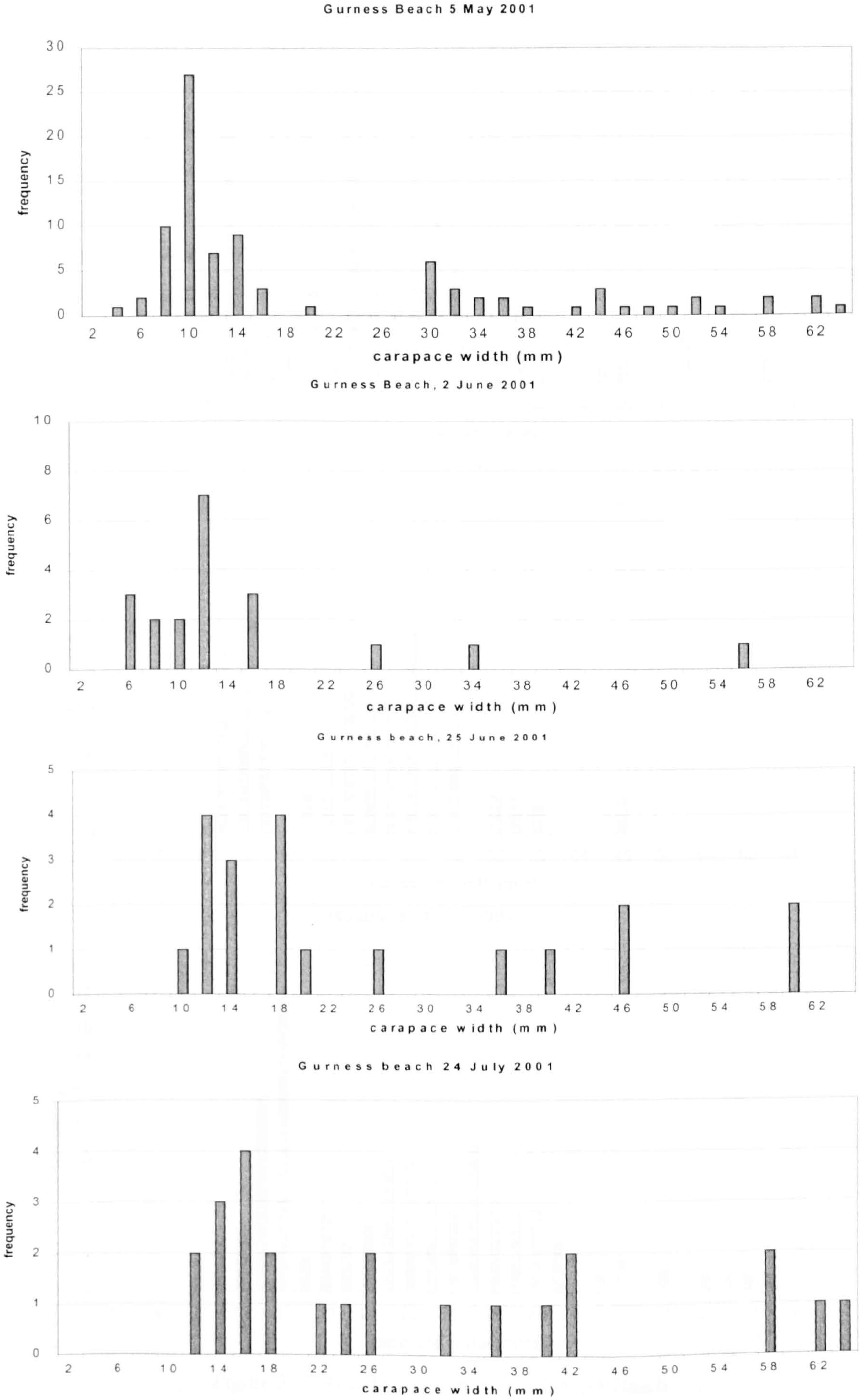
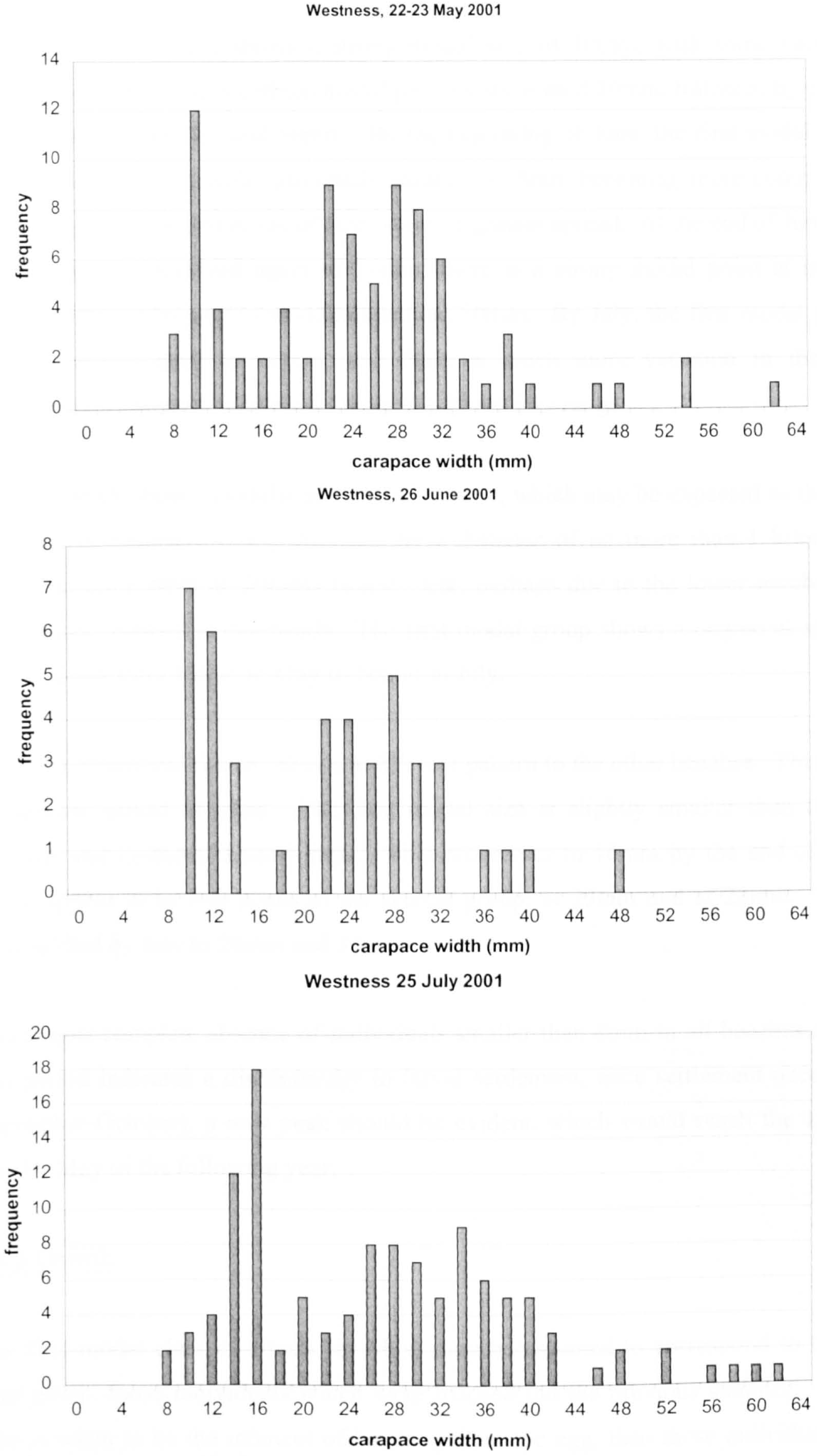


Figure 3.14 Size distribution from Gurness beach


Westness, 22-23 May 2001

Westness, 26 June 2001

Westness 25 July 2001

Figure 3.15 Size distribution from Westness Beach

Gritness beach in May shows a strong modal size of 10mm, with some variation around this point. A less defined modal peak exists around 30mm, followed by a third group of individuals around 50mm. By the beginning of June, the first modal point has moved to 12mm, with individuals around 16-18mm becoming more common in the sample. The second group of sizes shows a greater spread. At the end of June, the first group has increased again to 14mm, there is a strong modal point at around 34mm, followed by some individuals around 50mm. By July, the first modal group has progressed again to 16mm, and there is much more variation in the size distribution, with more individuals in the 40-50mm size range.

Gurness beach shows a similar pattern to Gritness, which may be expected as the two beaches are separated along the coast by a distance of no more than 1 kilometre. However, the pattern at Gurness is less clear, perhaps due to the lower numbers of individuals obtained at this beach. The first modal group shows a degree of spread, but increases from 10mm in May to 16mm in July.

Westness beach, on Rousay, shows a different pattern to the other beaches. There is a far greater spread of sizes. The first modal size is slightly smaller than that of Gurness and Gritness; around 9mm. This progresses to 16mm by the end of July. There appear to be two peaks in the second group: at 23mm and at 28mm. These have shifted by July to 28mm and 34mm.

The almost complete absence of individuals smaller than 8mm in all beaches during this period indicates a discontinuity in larval settlement; once settlement occurs (in September-October), a new peak should be evident, which would reach the 10 mm size by May of the following year.

3.7.5 Growth

The first modal class of 10mm (in May) may be assumed to correspond to the 0+ year group: those individuals which were hatched out the previous summer. If age zero is taken to be the moment of hatching from the egg, then these individuals are around 9-10 months (0.75-0.83 years) old (if age zero is taken to be settlement, then they are 2-3 months younger). This can give a preliminary estimate of the range within which K lies, if there is a confident estimate of L∞. From the Powell-Wetherall plots in section 4, L∞ is known to lie between 95-103mm. Substituting these values in the von Bertalanffy growth equation gives K values ranging between 0.2 and 0.3.

The modal size of the first cohort changes through the months, indicating a period of moulting. The mean size of the first cohort by the end of June, as determined using Bhattacharya's (1967) method of modal analysis, is around 15 mm. At this point, these individuals are one year old. The second modal peak was estimated to be around 35 mm, and the third identifiable modal point was 51 mm. The distribution of sizes around the modal point may be a cause for concern when analysing adult growth patterns. Whereas the first cohort is clear to identify, with a standard deviation of 1.9, there is more variation in the successive cohorts, to such an extent that later cohorts may be extremely difficult to identify using modal analysis.

Assuming that these modal groups are separated in age by one year respectively (given that reproduction occurs on a yearly cycle), a preliminary measure of growth can be obtained using the Gulland and Holt plot (Figure 3.16):

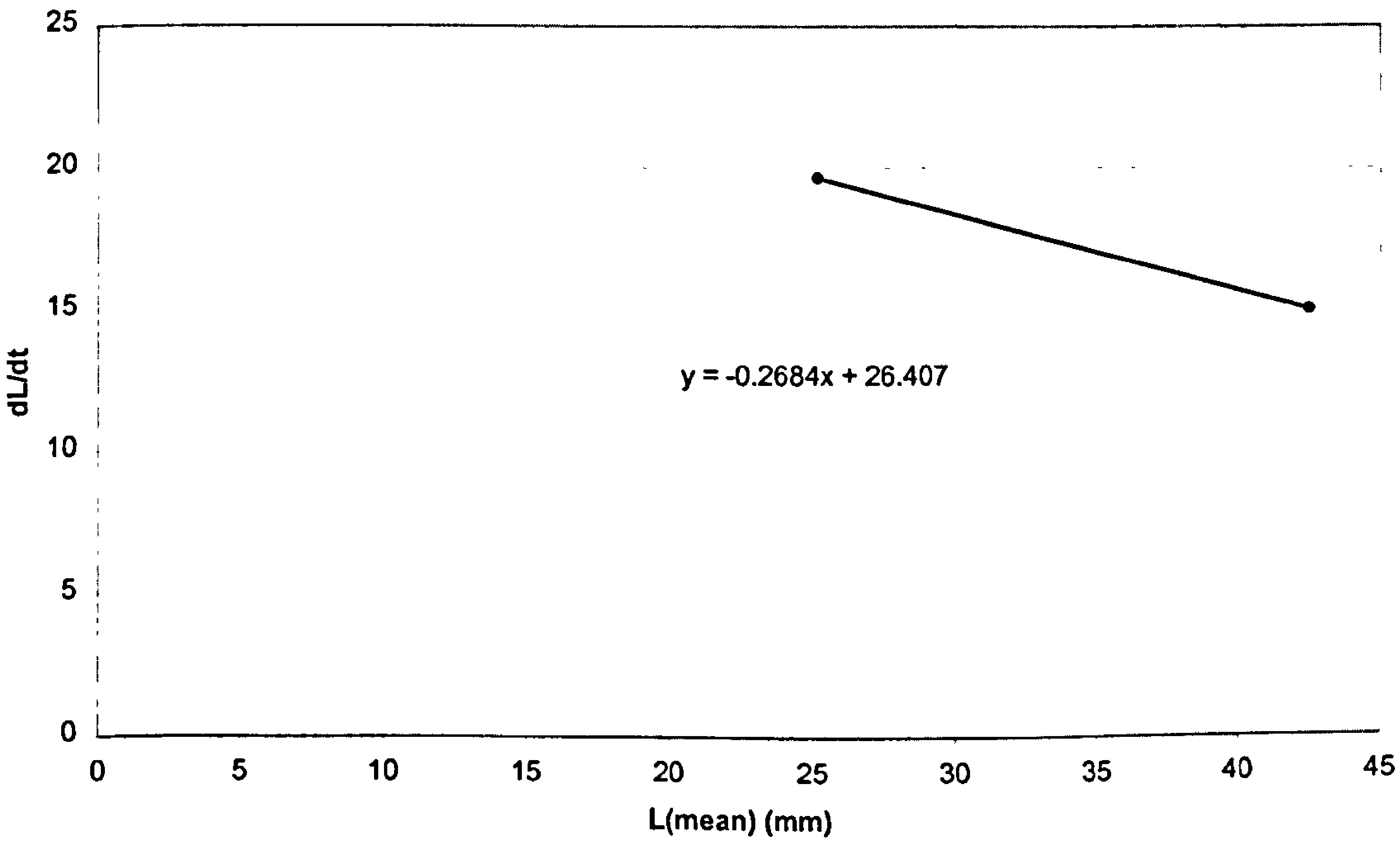


Figure 3.16 Gulland and Holt plot for early growth of *Necora puber*.

From the plot, $L\infty$ and K were calculated according to the formulae below:

$$K = -b = 0.268$$

$$L\infty = -a/b = 98.4$$

As a comparison, the Ford-Walford method was also carried out on the same data to obtain estimates of K and $L\infty$. These were found to be in the same of the estimates using the Gulland and Holt plots ($K = 0.28$, $L\infty = 98.4$mm).

However, both methods were found to be highly sensitive to small changes in the modal size classes. A change of 0.5mm in the third cohort, to 50.5 mm caused a change in $L\infty$ to 108 mm and a slightly smaller change of K to 0.236. This demonstrates the sensitivity of the models to such a fundamental step as the determination of modal points. As most methods used imply some degree of subjectivity, this shows the limitations of such analysis.

A problem involved in this use of juveniles is that evidence from other studies (González-Gurriarán, 1985b; Choy, 1986b; Norman, 1989; Bakir, 1990) points to female growth slowing in relation to that of males, once sexual maturity is reached. If this is the case in the Orkney stock, it will not be detected by this method. However, as seen later (Part 4), the estimated difference between adult males and females is so small in comparison with other stocks, that it may be worth sacrificing this difference in order to obtain a better overall growth pattern using juvenile data.

The value t_0 can be calculated by rearranging the von Bertalanffy growth equation to give:

$$\mathbf{t_0 = t + (1/K) \ln [(L\infty - Lt)/L\infty]}$$

Hence, if size at a given age is known, estimation of t_0 can be carried out. Table 3.6 shows the results of this, using a variety of size-at-age data:

age	size	To
1	15.4	0.364925
2	34.5	0.389099
3	52	0.194995
0.75	10	0.350116
0.833333	12	0.34806
0.916667	14	0.344005
1	16	0.337853

mean value for to: 0.345009

Table 3.6 Calculation of t_0

An alternative is to force the growth curve to pass through a point at which there is confidence in the data. In this case, there a carapace width of around 15mm at an age of one year was assumed. This removes anomalies in lower ages, which may not conform to the von Bertlanffy growth pattern.

Taking 15.35 mm as the modal size of individuals at one year from hatching, growth curves were constructed using the von Bertalanffy growth equations, for a range of L∞ and K values:

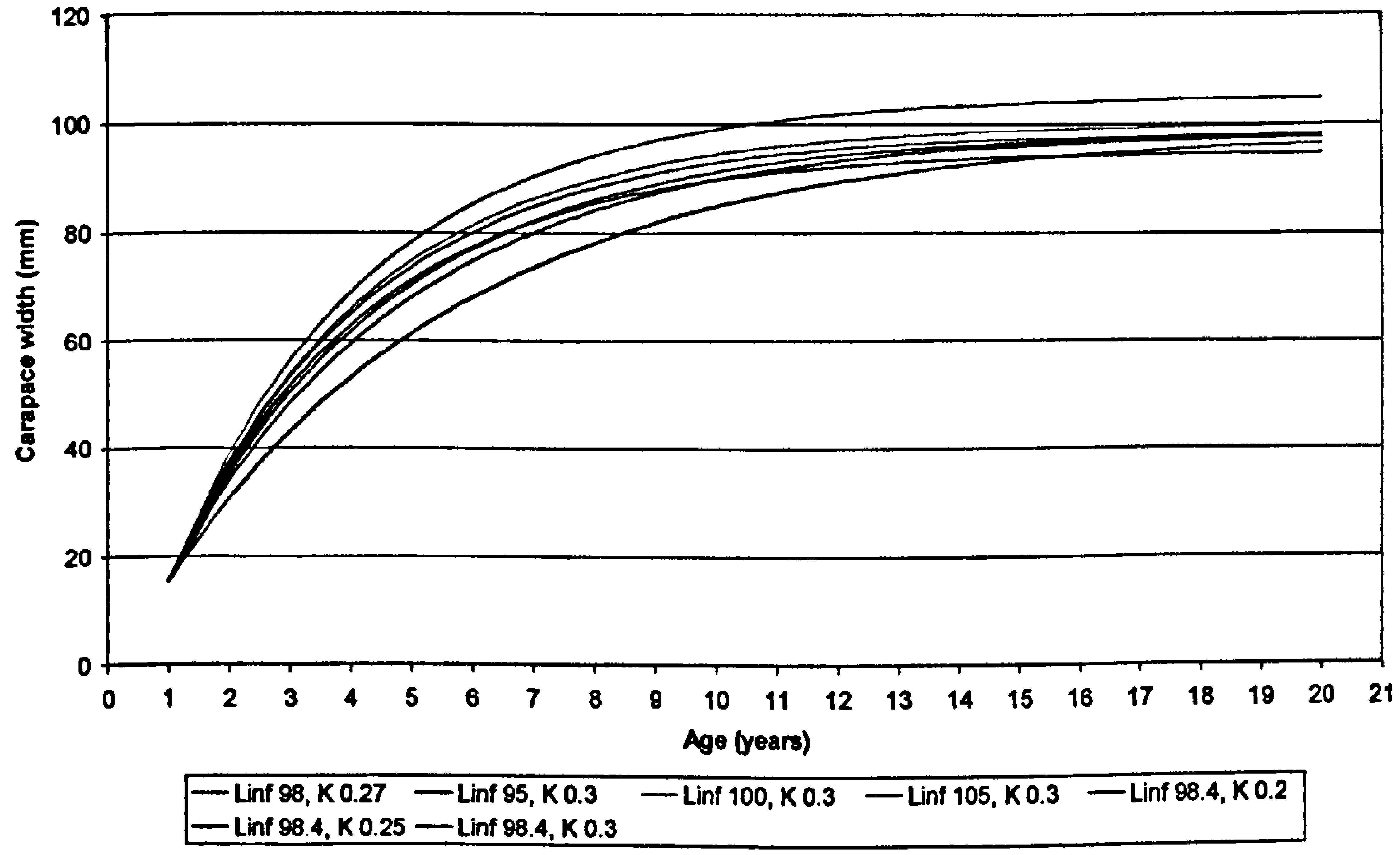


Figure 3.17 Growth curves for *Necora puber* based on parameters estimated from juvenile growth data.

The curves would suggest an age at sexual maturity of around 3 years (slightly earlier for females), with the MLS of 65 mm being attained at 4 years. The life-span is around 10 years, if it is assumed that few individuals attain sizes greater than 90 mm.

3.7.6 Moulting

During the study period, recently moulted (soft) juveniles were found and recorded (Dataset 2, Appendix A). Table 3.7 summarises this.

Number	**Date**	**Location**	**Sex**	**CW**	**comments**
1	02/06/01	Gritness	F	17.5	
2	02/06/01	Gritness	?	16.5	
3	03/06/01	Gurness	?	15.7	
4	03/06/01	Gurness	?	10.7	
5	03/06/01	Gurness	?	15	
6	03/06/01	Gurness	?	11.7	
7	24/06/01	Gritness	F	29.2	
8	24/06/01	Gritness	?	12.2	
9	25/06/01	Gurness	?	39.4	
10	26/06/01	Westness	F	30.8	
11	26/06/01	Westness	F	27.5	
12	26/06/01	Westness	F	34.8	
13	26/06/01	Westness	?	21.6	moulting
14	26/06/01	Westness	?	9.8	
15	26/06/01	Westness	F	22.3	
16	26/06/01	Westness	F	20.6	
17	23/07/01	Gritness	F	37.8	
18	23/07/01	Gritness	F	44.5	
19	23/07/01	Gritness	M	21.9	
20	23/07/01	Gritness	M	50.8	
21	23/07/01	Gritness	M	55.8	
22	23/07/01	Gritness	M	65	
23	23/07/01	Gritness	M	72.3	
24	24/07/01	Gurness	M	74.6	
25	25/07/01	Westness	F	33.5	
26	25/07/01	Westness	F	39.2	
27	25/07/01	Westness	F	39.9	
28	25/07/01	Westness	M	18.9	
29	25/07/01	Westness	M	27.7	
30	25/07/01	Westness	M	34.9	
31	25/07/01	Westness	M	37.8	
32	25/07/01	Westness	M	38	
33	25/07/01	Westness	M	44.4	
34	25/07/01	Westness	M	47.5	
35	25/07/01	Westness	M	58.2	
36	25/07/01	Westness	M	65.4	

Table 3.7 Occurrence of recently moulted juveniles during shore searches.

No soft crabs were found in April or May of 2001. There were no soft crabs amongst those juveniles found in the winter of 1999-2000 around the Holms of Stromness. This coincides with Norman (1989) who found that juvenile moulting was minimal from January-June. From the table, it can be seen that all sizes of juveniles are represented. It is not possible to say whether there is a delay in moulting relating to one or other of the sexes.

Analysis of the length-frequency graphs (figures 3.13-15) showed there to be no significant differences between males and females in terms of modal sizes. The graphs show a progression of modal size in the first cohort from 10 mm to 12 mm then to 15 mm between May and late June/July. There is also a progression of animals around the mid-30 mm CW to mid-40 mm in late June.

Some individuals moulted whilst in tanks in laboratory conditions. Although the environmental conditions were different to those in the sea, the moult increments were documented in Dataset 11 (Appendix A). Table 3.8 summarises these results.

sex	Cw before	cw after	Date	Next	Date	next	date
f	34	41	05/11/99				
f	39	43	31/12/99				
f	18.8	21.4	15/06/00				
f	55	59	02/10/00	been in tank 2 months			
m	34	40	01/07/99	56	99-09-30		
m	38	46	08/07/99	55	21/10/99		
m	51	57	10/07/99				
m	60	70	30/09/99				
m	19.4	21.7	16/06/00				
m	24.2	26.5	17/06/00				
m	28.5	32.5	24/07/00				
?	Megalops	2.45	31/07/00	3.1	07/08/00	4.2	16/08/00
?	Megalops	2.4	31/07/00	3.3	07/08/00	4.8	16/08/00
?	8	10.5	29/05/00				
f	25.4	32.7	16/06/01				
m	60.2	66.8	25/07/01	found at Westness beside moult			

Table 3.8 Laboratory moults of *Necora puber*.

Although there appear to be multiple moulting events in immature crabs, these may not necessarily occur at evenly spaced periods. It would seem that in the earlier stages (first and second crab instar), the juveniles moult after only seven days. After this however, the intermoult period seems to increase. The larger male (initial CW: 38mm) spends almost 3 months at the next stage (46mm), before moulting to a size of 55mm, at which point it was sexually mature and did not moult again for the remainder of the time spent in captivity.

The growth factor for each moult was calculated by dividing the post-moult carapace width by the pre-moult carapace width. The growth factor was found to be between 1.1-1.45. The growth factor was plotted against pre-moult carapace width as the independent variable, in order to determine whether a pattern emerged relating growth factor to size. This is shown in Figure 3.18.

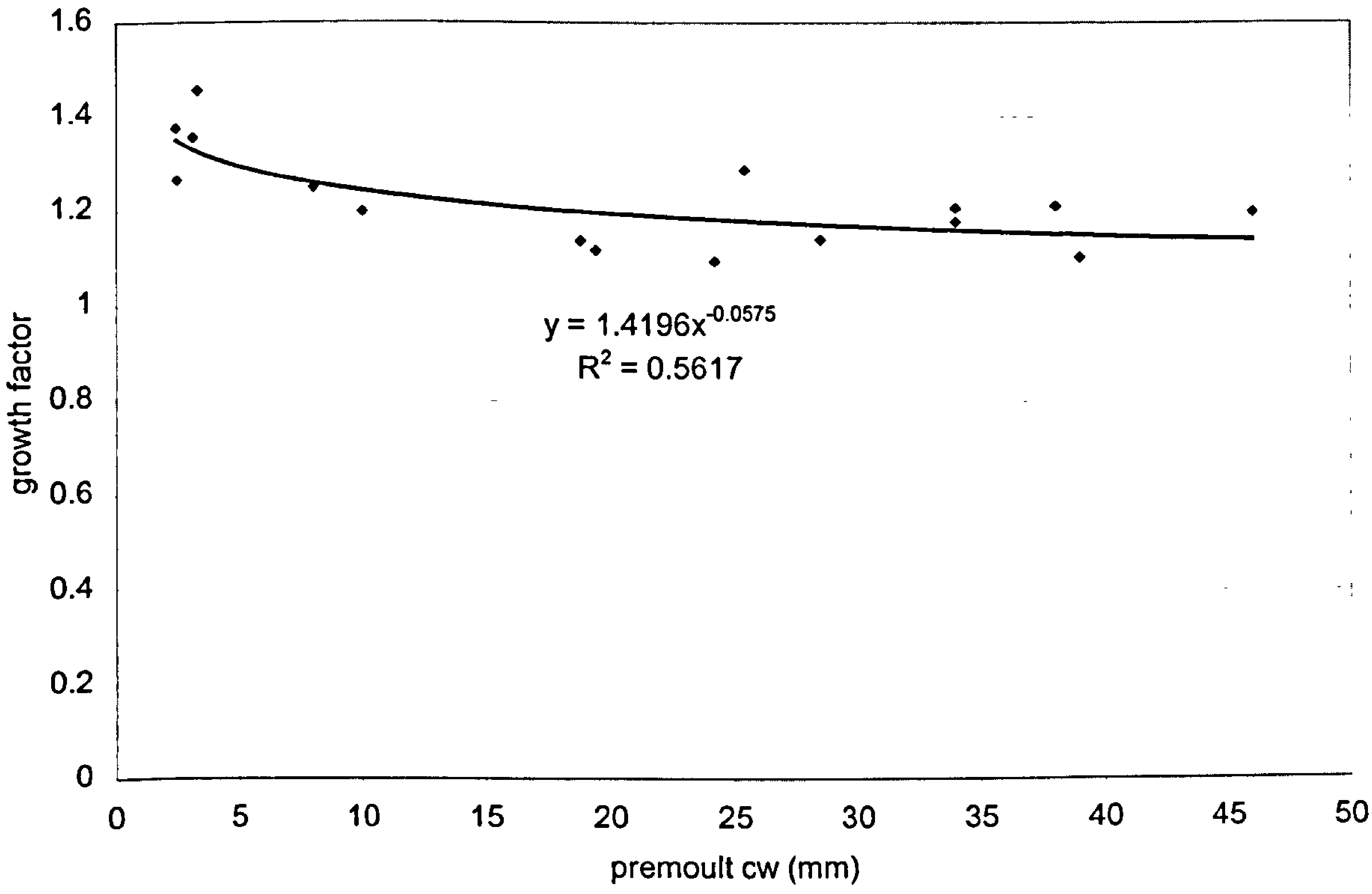


Figure 3.18 Growth factor related to size of individual.

The growth factor appears to change, decreasing as the animal gets larger. Smaller animals increase in size by a factor of over 1.4, whereas growth in adults is less than 1.2. The growth factor can be used to predict successive moult increments. This is shown on Table 3.9, where constant growth factors of 1.18, 1.2, 1.3 and 1.4 are used, as well as the variable growth factor described by the equation in Figure 3.18 (referred to in the Table as "growth model").

	Growth Factor				Growth model
Instar	**1.3**	**1.4**	**1.2**	**1.18**	**1.4196x^-0.0575**
1	2.45	2.4	2.4	2.4	2.45
2	3.1	3.36	2.88	2.832	3.303353
3	4.2	4.704	3.456	3.34176	4.378054
4	5.46	6.5856	4.1472	3.943277	5.709176
5	7.098	9.21984	4.97664	4.653067	7.332236
6	9.2274	12.90778	5.971968	5.490619	9.282209
7	11.99562	18.07089	7.166362	6.47893	11.59251
8	15.59431	25.29924	8.599634	7.645137	14.29398
9	20.2726	35.41894	10.31956	9.021262	17.41397
10	26.35438	49.58651	12.38347	10.64509	20.9755
11	34.26069	69.42112	14.86017	12.56121	24.99653
12	44.5389	97.18956	17.8322	14.82222	29.48952
13	57.90057		21.39864	17.49022	34.46099
14	75.27074		25.67837	20.63846	39.91144
15	97.85196		30.81404	24.35339	45.83532
16			36.97685	28.73699	52.22125
17			44.37222	33.90965	59.05233
18			53.24667	40.01339	66.30662
19			63.896	47.2158	73.9577
20			76.6752	55.71465	81.97526
21			92.01024	65.74328	90.32585

Table 3.9 Moult sizes at different growth factors (numbers in red refer to approximate pubertal moults)

The table above is simply a guideline to help understand the potential number of moults required for an individual to reach a certain size. Although it is clear from Figure 3.18 that the growth factor does not remain constant throughout the life of an individual, a range of constant factors were chosen, which fell in the range of factors displayed by the moulting individuals reared in the laboratory. In comparison with the moults predicted by the equation (the last column in Table 3.9), a constant growth factor of 1.4 is too high to be maintained throughout the life of an individual. Until the first year (15mm), the growth factor is comparable to 1.3, after which it decreases to around 1.2, and further decreases at higher sizes. The results suggest that a one-year old individual of around 15mm is at the eighth instar, with a further 3-5 moult to the second year, a further 2-3 moults to achieve sexual maturity in the third year, and yearly moults thereafter.

The moult sizes calculated from analysis of moult data from individuals reared in captivity were compared with the peaks shown in the size-frequency distributions of the shore surveys (Figures 3.13-15). The resultant premoult-postmoult size relationships are shown in Figure 3.19.

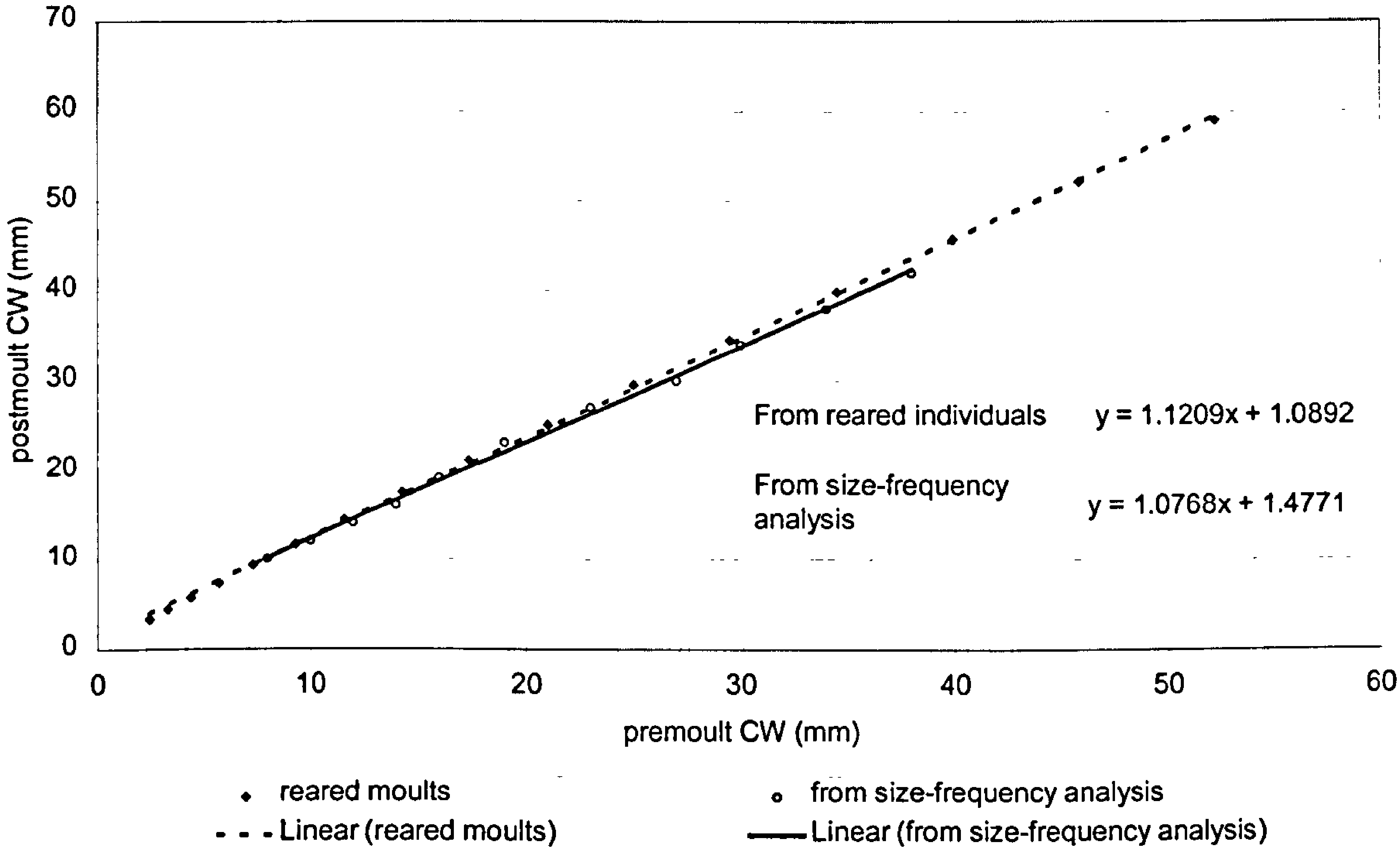


Figure 3.19 Comparison of premoult-postmoult sizes using reared animals and identification of modal sizes in shore surveys.

A t-test showed the difference between the two lines not to be significant at the 95% level. This indicates that the moult increments under laboratory conditions are comparable to those in the wild. It also indicates that a variety of moult stages are present at the same time for juveniles, and that the variation in the size-frequency distributions is due to this rather than differences in growth rates.

3.7.7 A stepwise growth curve

The data from the equation-derived moult increments can be compared with the size-at-age equation obtained from the von Bertalanffy growth curve constructed in figure 3.17. This is shown in table 3.10.

From moult increment equation		**From von Bertalanffy functions**	
Instar	**Size (mm)**	**Age**	**Size (mm)**
1	2.45	2-3 months	2.45
2	3.3		
3	4.4		
4	5.7		
5	7.3		
6	9.3		
7	11.6		
8	14.3	1 year	15.4
9	17.4		
10	21.0		
11	25.0		
12	29.4		
13	34.5	2 years	35
14	40.0		
15	45.9		
16	52.2	3 years	50
17	59.0	4 years	61
18	66.3	5 years	70
19	74.0	6 years	76
20	82.0	7 years	81
21	90.3	8 years	85
22	98.2	9 years	89

Table 3.10 Moult frequency and growth data compounded.

From this table, and using field and laboratory evidence of moulting frequency, a discontinuous growth curve may be constructed, depicting the growth of *Necora puber* over the whole life cycle. This is shown in figure 3.20 below:

Figure 3.20 Stepwise growth curve for *Necora puber*

The discontinuous curve above is a better approximation of the life pattern of *Necora puber* than the continuous growth curve described by the von Bertalanffy equation. However, the variation in sizes shown in the size-frequency graphs (Figures 3.13-15) suggest that there is a considerable amount of variation in the length of time spent at each moult size, so this graph should be considered as an average pattern of growth for the stock. In addition to this, some of the early moults were estimated, as further work into moulting frequency at these sizes must be carried out.

3.8 Discussion

Initially, juvenile *Necora puber* were hard to find, and this was due to a number of reasons. Firstly, previous descriptions of the habitat occupied by juveniles (lower shore, under rocks in the *Laminaria* zone) were vague. Most of the shore around Mainland Orkney fits this description, and therefore, much time was spent investigating various beaches. Some of these were apparently devoid of velvet crab presence, others yielded small numbers of juveniles (such as Skaill and Inner and Outer Holms around Stromness), and others were richer beaches such as Gritness, Gurness and Westness, all around Eynhallow Sound.

The cryptic behaviour of the juveniles made them hard to find when carrying out shore searches. These searches, which were the most successful of the methods attempted to find juveniles, were limited by two important factors. The first of these factors was time: the *Laminaria* zone was only partially uncovered by the tide, and even this was only for a couple of hours at low water springs. Due to their cryptic behaviour, they were only found under rocks and stones. Searches were limited to those rocks and stones which could be moved or overturned.

It is probable that only part of the habitat occupied by juvenile velvet crabs was sampled during these shore searches, and that the distribution extends into the sublittoral and possibly into adult grounds. However, as yet, it has not been possible to test this, as a suitable and standardised trapping method has not been designed. The bottle traps and miniature creels used in this study were unsuccessful, although small green crabs (*Carcinus maenas*) were caught in them. At present, a study at ICIT is continuing this work, attempting to devise a trap that implies equal catchability for all sizes of juveniles. Tank tests are currently underway (pers. comm., Hazlehurst, ICIT), but the main problem is devising a system which prevents escape of small individuals whist allowing entry of larger individuals. A compartmentalised system may be the best design. Further studies must also be carried out as to the best way to stimulate a juvenile velvet crab to enter such a trap, and whether it will do so seeking food or shelter.

All monthly samples from the three main beaches surveyed showed three progressively smaller peaks in their size-distribution using large (5mm) size cohorts. These were also evident using 2mm size cohorts in some beaches, particularly Gritness. The clearest mode was present in all beaches and progressed from 10mm in May to 12mm at the start of June and 14mm by the end of June. The modal size was slightly smaller in Westness. As discussed in part 2, the velvet crab stock in Orkney has a yearly reproductive cycle, with the main hatching period in June, and settlement occurring between August-September, at which point, the first crab instar is around 2.4 mm in width. This cohort therefore corresponds to those individuals settling in the previous year. Following from this, the subsequent modal points refer to cohorts settling in previous years. This implies that sexual maturity (around 45mm for females and 52mm for males) does not occur until the third year, in direct contrast with studies in other areas, where sexual maturity is attained at one year (González-Gurriarán, 1985a; Gonzáez-Gurriarán and Freire, 1994; Norman, 1989; Choy, 1986b). The reason for this is probably geographical.

The implications on this are varied. From the pre-pubertal estimates of $L\infty$ and K, it was seen that although $L\infty$ lay in a similar range to that of other stocks, K was significantly lower, giving a life-span of around 10 years. This is discussed in more detail in section 4, but the reality is that instead of a short lived, fast growing animal, reaching sexual maturity in one year, the Orkney stock is long lived, slow growing and does not become sexually mature until later in life.

The variation in sizes found could be attributed not so much to variation within a moult stage (i.e. variation around K), but to the variability in the length of time spent at different moult stages. This time appears to be highly flexible, so that, at any given point in time, individuals are found at a number of moult stages. The expected pattern would be one of a clear progression of a cohort, with modal sizes dropping out of the distribution as the entire cohort completes the moult, with a degree of synchronicity as to when this occurred. However, although this is largely the case in the first cohort (with the presence of some individuals which appear to be a stage or two behind and a few which appear to be slightly ahead of the majority), the pattern is not so clear later on. This is especially the case at Westness beach, where a wide range of moult stages is present. This implies that that some individuals progress through the moults at a much higher pace than others. The reason for this may lie in the patchiness of food distribution. The consequences may be felt in larger sizes, when attempting to use length-frequency analysis to determine modal sizes.

The moult data indicates that, on average, there are 7 moults in the first year, 5 moults in the second year and 2-3 moults in the third year, after which sexual maturity occurs and moulting is annual (see Part 4). This implies a lower moult frequency than in other study areas. In Wales, *Necora puber* undergoes 12 moults in the first year, followed by 3 in the second and yearly after that (Choy, 1986b). In Galicia, the stock shows a similar pattern to Wales, with 12 moults in the first year, 2 in the second and yearly moults after this (González-Gurriarán, 1985b). Both Choy (1986b) and Norman (1989) suggest a quiescent period in the winter months during which no signs of moulting activity are observed. Circumstantial evidence points to this also being the case in Orkney. If moulting is limited by temperature, the quiescent period is likely to be longer in Orkney waters than in the warmer waters of the southern UK and Spain. This may partly explain why the moult frequency in Orkney is lower with respect to other areas.

The use of juvenile stages alone to determine the life parameters of the stock are, initially, promising, but must be compared with further methods including the adult population in Part 4. However, there is potential for fisheries-independent estimation of $L\infty$ and K, and the possibility of determining natural mortality, M (which is equal to pre-fishery total mortality, Z). This could be carried out if a standardised method of obtaining velvet crabs was developed, which implied the same likelihood of capture regardless of the size of the individual. At present, this is not the case, but the aforementioned trapping studies may make this a possibility in the near future.

PART 4: GROWTH AND POPULATION DYNAMICS

4.1 Aims

This section aims to obtain data on the size frequency, life expectancy, mortality, sex ratio, growth, L∞ (asymptotic length) and K (the rate at which L∞ is attained) of the velvet swimming crab, in order to obtain a fuller picture of the stock to enable possible future management and technical decisions to be taken with the fullest scientific knowledge. The size range caught in pots over the study period was also examined, and biometric analysis was carried out using carapace width (CW), carapace length (CL) and weight as measurements of size.

According to Fisher (1930), for random mating populations, the evolutionary stable sex ratio is 1:1. This assumes that the creation of individual progeny of either sex is equally resource-costly. However, a large number of surveys on different decapod species have shown skewed sex ratios, although the method of capture is crucial in these studies. Where this is the case then it may generally be assumed that sampling is selective, or that there is segregation of the sexes. However, it is also possible that there may be differential mortality influencing the ratio obtained. The operational sex ratio (Emlen and Oring, 1977) of crab populations is often heavily male biased, and previous studies have shown the velvet swimming crab to be no exception (Wilber, 1986; Choy, 1986b; Smith, 1990; Tallack, 1998). The sex ratio of the catch may change spatially and temporally. These changes must be identified and explained in terms of whether they accurately reflect the population or whether the fishery is selective towards one or other of the sexes. If the latter is true, this has implications for the management and sustainability of the fishery as a whole.

Knowing the age structure of wild populations is fundamental for effective fisheries management. Age determination of fish species has traditionally been carried out using hard parts, which produce a characteristic marker related to time in some way e.g. otoliths, scales or spines (e.g. Secor *et al.*, 1995). As increase in size in decapod crustaceans occurs only during times of moult, all external evidence of age or previous size is removed. This leads to a stepwise growth pattern, which does not allow for the direct estimation of age related to size. Attempts to find some permanent feature of decapods that is retained throughout life and that may give a direct measurement of age have so far been unsuccessful (Conan, 1978). Yano and Kobayashi (1969) investigated the possibility of using the number of lamellae in cuticles to determine age, with only relative success, although recent research into the use of lipofuscin has given encouraging results (Ju *et al.*, 1999; Medina *et al.*, 2000). Lipofuscin originates within secondary lysosomes as a result of cell metabolism, and may be extracted and quantified by a number of methods. Although encouraging, these methods are still at an experimental stage. As a result of this, crab growth studies have relied on a number of indirect methods, some of which are outlined below.

One of these methods is by field observation of crabs in the process of moulting, so that the newly moulted crab is found next to its old shell. In this case, both the new and the old exoskeletons may be measured, thus obtaining the size increment. The drawback of this method is the low chance of finding a significant number of crabs in this state. Another method involves tagging a series of animals that have been previously measured and releasing them back into the wild. Assuming that the tag is retained through the moult, on recapture, a further measurement will give the change in size over that period of time from release to recapture.

Tagging experiments have been carried out with crustacea for the last few decades. In the 1960s *Cancer* were tagged to determine growth and mortality of crabs, as well as getting some feel for movement (Mason, 1965). There are a number of types of tag, depending on the objective of the experiment, but in order to observe growth patterns, the tag must be retained after moulting. The suture tag was developed by Butler (1957). This tag is inserted into the base of the abdomen, along the split where moulting occurs. It is thus retained throughout the moult process. Tags have also been devised for the study of juvenile and immature animals, where size is an important issue. For a study of juvenile *Portunus trituberculatus*, coded microwire tags were successfully inserted into the base of the fifth pereiopod (Okamoto, 1999).

Tagging studies involve a series of assumptions. Firstly, preliminary studies must be carried out as to whether the tags themselves cause mortality among the target individuals. Although this can be tested simply under laboratory conditions, this does not allow for the possibility of tags increasing mortality by indirect means, for example, by making individuals more visible to predators. In the same way, tag retention must be ascertained: what percentage of tags are lost, and over what period of time? This may also be different under laboratory conditions from those in the wild.

Tagging studies generally involve the release of large numbers of individuals into an area, and the results often depend on the methods of recapture and on the collaboration of other persons not directly involved in the study. A tagging project must therefore be well publicised locally, and may involve some incentive for returns of tagged individuals.

Observing the moult process in tanks has the advantage that close monitoring is very easy, and a large number of animals can be observed if the facilities are large enough. However, this has the disadvantage that it is very difficult to reproduce the exact conditions that the animals would experience in the wild, so readings taken from laboratory tank experiments should be used with caution. Laboratory moults were analysed in Section 3B.

The final method used for inferring age from size is by use of size frequency data collected by measuring the sizes of a large number of individuals of the stock. This method was pioneered by Petersen (1891), for finfish, but is now mainly used for crustaceans and other animals where direct measurement of age is not possible. Computer programmes such as ELEFAN (Pauly, 1987) have been devised in order to overcome some of the subjectivity involved in identifying cohorts from sometimes almost indistinguishable groupings of size classes.

In addition to defining the growth and mortality parameters, this section also aims to determine the moult cycle itself. Questions to be addressed in this section include defining the moult period and identifying differences that may occur between the sexes. The length of the moult period has direct effects on the fishery, as soft crabs are voluntarily discarded in Orkney because they are not accepted by the merchants, due to their vulnerability to mortality.

Insofar as mortality is concerned, the fisheries biologist has two main jobs:

1. To estimate total mortality (Z)
2. To split Z into estimates of fishing mortality (F) and natural mortality (M)

The importance of these parameters is apparent when undertaking stock assessment studies, as growth and mortality together with recruitment form the basic building blocks from which an overall picture of the stock dynamics can be obtained.

The questions dealt with in this section are outlined below:

1. What is the relationship between CW, CL and weight?
2. Does the sex ratio change over time, and if so, why?
3. How often and when do adults moult?
4. How long does the moult process take?
5. Is tagging an effective method to measure growth/movement?
6. What are the von Bertalanffy growth parameters (L_∞ and K) for the stock?
7. What are the advantages/limitations of the methods used?
8. Are there any differences between males and females?
9. What are the values for Z, M and F?
10. Can the population structure be modelled?
11. How do the population dynamics compare with other areas?

4.2 Methods and Materials

4.2.1 General Measurements and Sex Ratio

These were carried out during the main sampling programme of this study (Dataset 1, Appendix A). This was carried out monthly from September to April and weekly where possible in the remaining months over a two-year period from January 1999-December 2000.

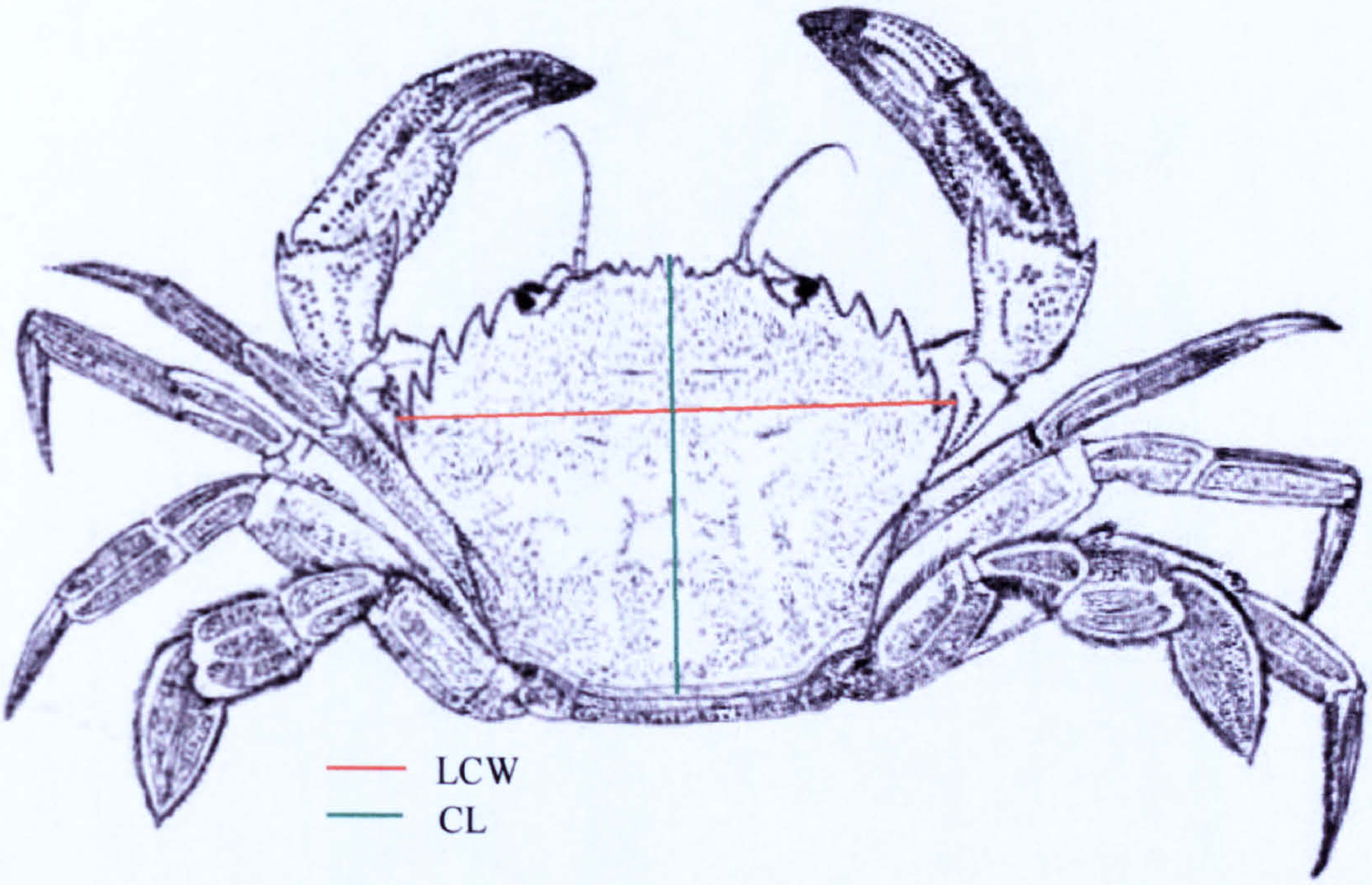


Figure 4.1 Measurements made on velvet crabs

Section 1.11 and Figure 1.14 show the main sampling area: Eynhallow Sound. On each of sampling survey, the first 100 velvet crabs caught were measured for the following attributes: sex, carapace width (CW) and carapace length (Figure 4.1). Sex was determined by the shape of the abdomen. Males have small, white, triangular abdomens, whereas the female abdomen is broader and darker. Carapace width was measured as the distance between the fifth anteriolateral spines. [Presence of eggs, limb loss and moult stage were also recorded for other studies]. Surface water temperature, weather and general area sampled were also recorded. From each survey, a small number of individuals of both sexes were taken back to the laboratory survey, a small number of individuals of both sexes were taken back to the laboratory and weighed. Crabs were blotted dry and left out of water for ten minutes before weighing on a top balance to 0.1g. In addition to this, the sex ratio of a box of velvet crabs selected at random in the OFS (Orkney Fisherman's Society) factory was determined (Dataset 5, Appendix A).

4.2.2 Moult Stage and Periodicity

Individuals caught during the general sampling programme were examined for their moult stage. For simplification, crabs were described as simply soft or hard, depending on the state of the carapace (Dataset 1, Appendix A). Any crab that would be rejected by the fishermen was considered soft.

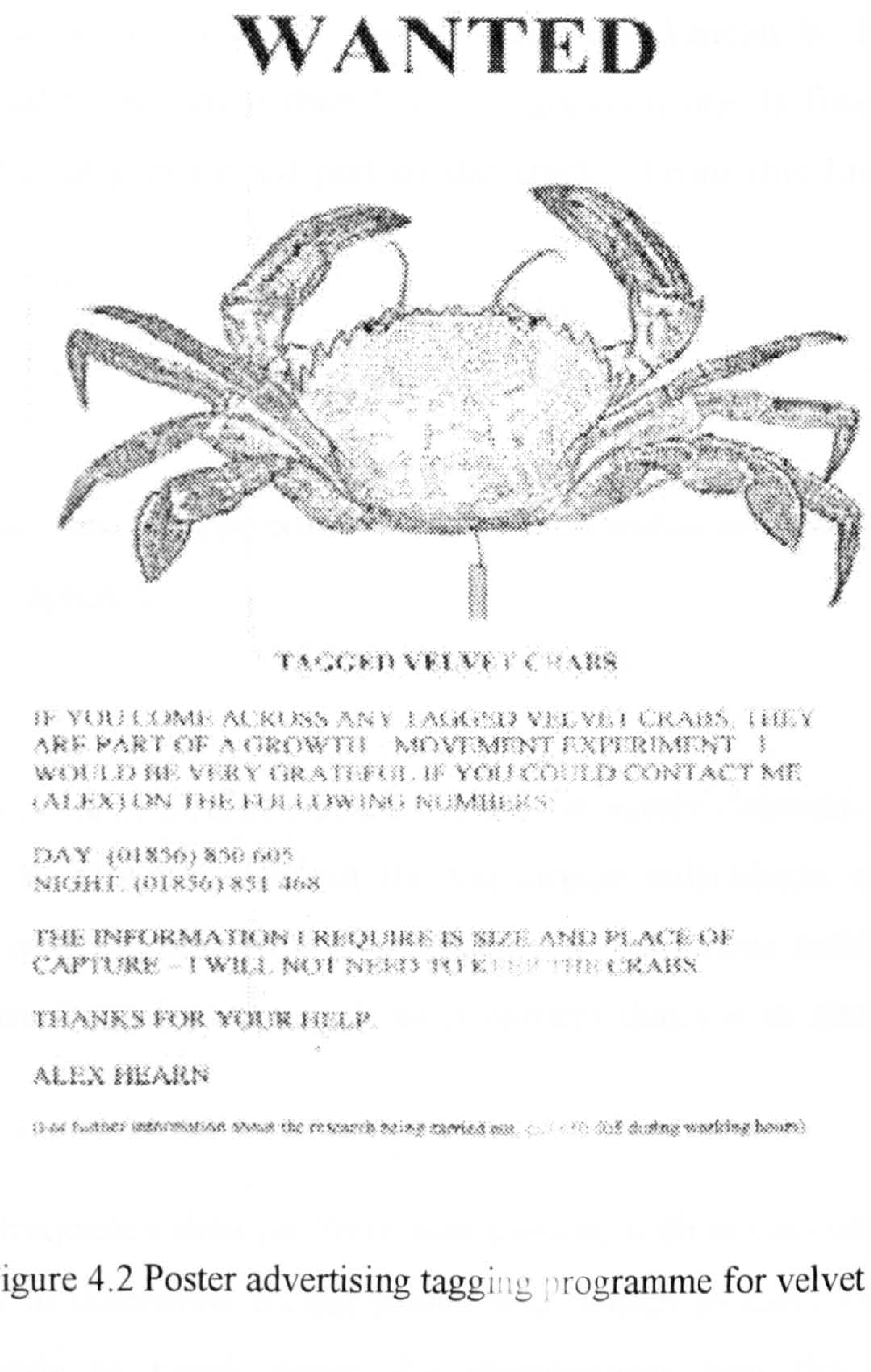
For the purposes of laboratory studies, the stages in the moult cycle described by Norman (1989) as adapted from Drach (1939) and Warner (1977), was used:

1. Soft: no calcification of new exoskeleton.
2. Early papershell: thin, flexible exoskeleton, easily depressed when touched. Light brown chelae are first to harden.
3. Late papershell: hard exoskeleton except branchiostegite region, which is still compressible. Chelae still light brown.
4. Intermoult: totally hard exoskeleton with dark chelae.
5. Late intermoult: completely hard exoskeleton, chelar teeth may be well worn, epifaunal growth common.

Where possible, recently moulted individuals were kept in tanks for observation of the duration of each stage in the moult process (Dataset 11, Appendix A). They were kept in individual 20 litre tanks with air supplies and fed on frozen krill daily. The seawater was changed every other day, but temperature was not controlled, and generally reached around 16°C (as this occurred over the summer).

4.2.3 Tagging

One thousand velvets were tagged (FT-94 suture tags from Floytag Ltd. USA) and released in the main fishing area (see Figure 1.14), once having recorded their sex, size, and limb loss. The tags were inserted into the base of the abdomen along the splitting line of moulting, so that they would be retained during the moult process. Local fishermen were requested to hand in any tagged individuals caught in creels (Figure 4.2).



WANTED

TAGGED VELVET CRABS

IF YOU COME ACROSS ANY TAGGED VELVET CRABS, THEY ARE PART OF A GROWTH MOVEMENT EXPERIMENT. I WOULD BE VERY GRATEFUL IF YOU COULD CONTACT ME (ALEX) ON THE FOLLOWING NUMBERS:

DAY (01856) 850 605
NIGHT (01856) 851 468

THE INFORMATION I REQUIRE IS SIZE AND PLACE OF CAPTURE - I WILL NOT NEED TO KEEP THE CRABS.

THANKS FOR YOUR HELP

ALEX HEARN

(For further information about the research being carried out, [illegible] during working hours)

Figure 4.2 Poster advertising tagging programme for velvet crabs.

Recapture data was to be used to observe movements as well as possible growth increments and may also be used to give an indication of fishing effort. Tagging began in 1999 and continued through May 2000 (Dataset 12, Appendix A).

4.2.4 Size-Frequency Data

The sampling programme described in Section 4.2.1 included the measurement of the CW for all individuals of both sexes. Initially, for each year, all data was combined and sorted into 2mm size groups for each sex. Powell-Wetherall plots were constructed for each year and each sex, in order to give initial estimates of L∞ and Z/K.

This is done by plotting (Lmean – L') against L', where L' is a series of lower size limits of fish fully vulnerable to fishing gear, and Lmean is the mean length of individuals equal to or longer than L'. A regression line is fitted through the data representing the fully exploited part of the stock. From this line, the following is calculated:

$$L\infty = -(a/b)$$

$$Z/K = -(1+b)/b$$

Pauly (1980) devised an approximation to give an initial estimate of L∞ based on the largest animal captured:

$$L\infty = Lmax / 0.95$$

For comparison, this was also carried out on the yearly datasets. The equation was then modified so that the mean of the ten largest individuals was used instead of Lmax. This removes some of the randomness in using one individual to determine L∞. This method can be unrealistic as it ensures that L∞ is always larger than the largest animal.

Monthly size-frequency data (in 2mm size classes, with sexes separate) for each year was then used to determine modal points with which to carry out growth analysis. Various methods to break down the distributions into the component curves corresponding to individual cohorts were explored. The probability paper method (Cassie, 1954), which was used in similar studies by Choy (1986b), Norman (1989) and Bakir (1990) was found to be highly subjective and not suitable for confident analysis of the samples obtained in this study. Bhattacharya analysis removes some of this subjectivity, and was therefore carried out for each sample in order to break down the distribution into its modal points.

This is a graphical method for separating a length-frequency distribution into a series of normal distributions. It works on the basis of approximating the assumed normal curve of a length-frequency distribution as a parabola, which is then converted into a straight line (Sparre and Venema, 1992) of the form:

$$\mathbf{dt\ (lnN) = a + b\ (L)}$$

where dt (lnN) is the difference between the natural logarithms of the number in one length class and the number in the preceding class. The straight line crosses the length axis at the point which is the mean (and the mode) of the length-frequency distribution, i.e. the normal distribution has a mean of (-a/b) and a standard deviation of $\sqrt{(-dL/b)}$, where dL is the length class interval.

dt(lnN) is graphed against L, and a straight line is fitted through the initial points which appear linear – "uncontaminated" points which belong to only one cohort. Using linear regression, the numbers of individuals in the first cohort are estimated. This leaves a remainder, which make up the uncontaminated section of the new next cohort and so on.

The modal sizes were combined with moult data to form a Gulland and Holt plot (Gulland, 1983), providing estimates of $L\infty$ and K. From these, it is possible to construct growth curves for the stock, using the von Bertlanffy (1938) growth equation (equation 1, p44)

If estimates are to be made about a population from a sample, then it must be assumed that the sample is representative of that population, in terms of both sex and individual sizes. On the one hand, this method assumes that all sizes of both sexes have equal catchability, in other words, that they are all equally likely to enter a creel.

This may not necessarily be the case, as is discussed at the end of this section. Gear selectivity experiments were carried out and have been discussed in section 1.14.

ELEFAN (electronic length frequency analysis) is a computer programme which separates normally distributed components of a distribution, identifies the growth parameters and generates growth curves (Pauly and David, 1981). It also incorporates a seasonally oscillating growth function, C, essentially a sin wave, based on the time of year when growth is slowest (WP), which can be modified in terms of intensity. ELEFAN was used by Norman (1989) and Choy (1986b) in their studies and gave results which were comparable to those obtained from other methods. In this study, ELEFAN came as part of the FiSAT (FAO-ICLARM Stock Assessment Tools) package (Gayanilo *et al*, 1997). The recommended approach in this package is to use a Powell-Wetherall plot to obtain a value for $L\infty$, followed by a scan of K-values, which gives the optimum K values fitting the data. There is also an automatic search routine which allows simultaneous variation of all four parameters.

4.2.5 Mortality

There are three kinds of mortality that must be identified: natural mortality (M), and fishing mortality (F), which make up total mortality (Z). An initial estimate of Z was obtained from the Powell-Wetherall plots described in 4.2.5. Values for K obtained from previous work were inserted in the Z/K ratio given by these plots to give initial values for Z.

Length converted catch curves were used to identify Z. The model used here consists of a basic plot of the natural logarithm of the numbers of fish caught at different age intervals against their corresponding age group (as outlined in King, 1995).

$$\mathbf{Ln[F/dt] = constant - Zt}$$

Where F = frequency in a length group

t = relative age = $(-1/K)\ln[1-L_t/L_\infty)$

dt = age at L_2 – age at L_1

ln(F/dt) is plotted against mean age t. A regression line is then fitted which excludes the following:

1. The initial ascending points, which correspond to sizes that are not fully recruited.
2. Data points from very small samples.
3. Data points close to $L\infty$

Z is estimated from the slope of the regression line (Z = -b), assuming the following to be true:

1. Z is the same in all age groups used in the plot.
2. All age groups used in the plot were recruited with the same abundance.
3. All age groups used in the plot are equally vulnerable to the sampling gear.

Although the Pauly M equation (Pauly, 1980) was used in studies by Bakir (1990) and Choy (1986b) in order to give an estimate of natural mortality, because this is an empirically derived equation based on observations of finfish species, it was decided that the use of this equation for crustaceans could not be justified. However, simply for comparison with these studies, this approach was tested in the present study.

For the purposes of using M in later prediction models, three methods of estimating M were used. All methods outlined below are approximations rather than rigorous equations. The first of these methods is that oultined by Alagaraja (1984) which relates M to longevity:

$$\mathbf{M1\% = -ln(0.01)/Tm}$$

Where Tm is the longevity.

The second method was that proposed by Rikhter *et al.* (1977), which correlates M with the age of massive maturation (Tm50%):

$$\mathbf{M = 1.521 / (Tm50\%^{0.720}) - 0.155}$$

The final method was Pauly's (1980) M equation, which was derived empirically from a large number of fish species, and relates M to physical factors such as temperature:

$$\mathbf{LnM = -0.0152 - 0.279*lnL\infty + 0.6543*lnK + 0.463*lnT}$$

Fishing mortality (F) was estimated by subtracting M from Z. All these methods assume a constant parameter throughout the life of a cohort and between cohorts.

4.2.6 Simulations

In order to model the populations and understand the size-distributions which were being obtained during the sampling programme, two simulations were constructed, based on different methods of growth.

The first simulation consisted of growing a population of velvet crab through 8 years, using K and L∞ values obtained from juvenile growth data (Section 3B) and with a mean starting size of 15.35mm at one year (with a 10% variation around the mean). Using the von Bertalanffy growth equation, mean sizes for subsequent years were calculated. 1000 individuals were grown on in this way, using a normal distribution of 10% around the K value. A size-frequency chart was constructed from this. Different values for natural mortality were then added, and finally, fishing mortality was added to those individuals above the MLS.

The second simulation relied on growth increments per moult rather than a yearly growth increment. Using moult increment data and growth parameters obtained from work carried out in Section 3B, 1000 individuals were grown from an initial size of 10mm. Each individual was given a random value, 10% around a normal distribution of K, and grown to the next moult using the following equation:

$$\mathbf{L_{t+m} = L\infty - (L\infty - L_t) * exp(-K * \Delta t)}$$

Where L_{t+m} = carapace width after moult

L_t = carapace width at time t

Δt = time spent between moults expressed as part of a year.

Δt was calculated using the following equation:

$$\mathbf{\Delta t = \ln (L\infty - L_t) / (L\infty - L_{t+m}) / K}$$

The individuals were grown through all the moult sizes and size-frequency graphs were constructed. These were further modified by adding a mortality component, which could be varied. Depending on the time of year, more or less weight could be given to show the expected population structure present in the wild. This method aimed mainly to show the progression of juvenile stages through the year, as yearly moult should ensure equal representation of all adult stages (once mortality has been taken into account).

4.3 Results

4.3.1 General measurements

CL was plotted against CW for males and females on the graph below (Figure 4.3).

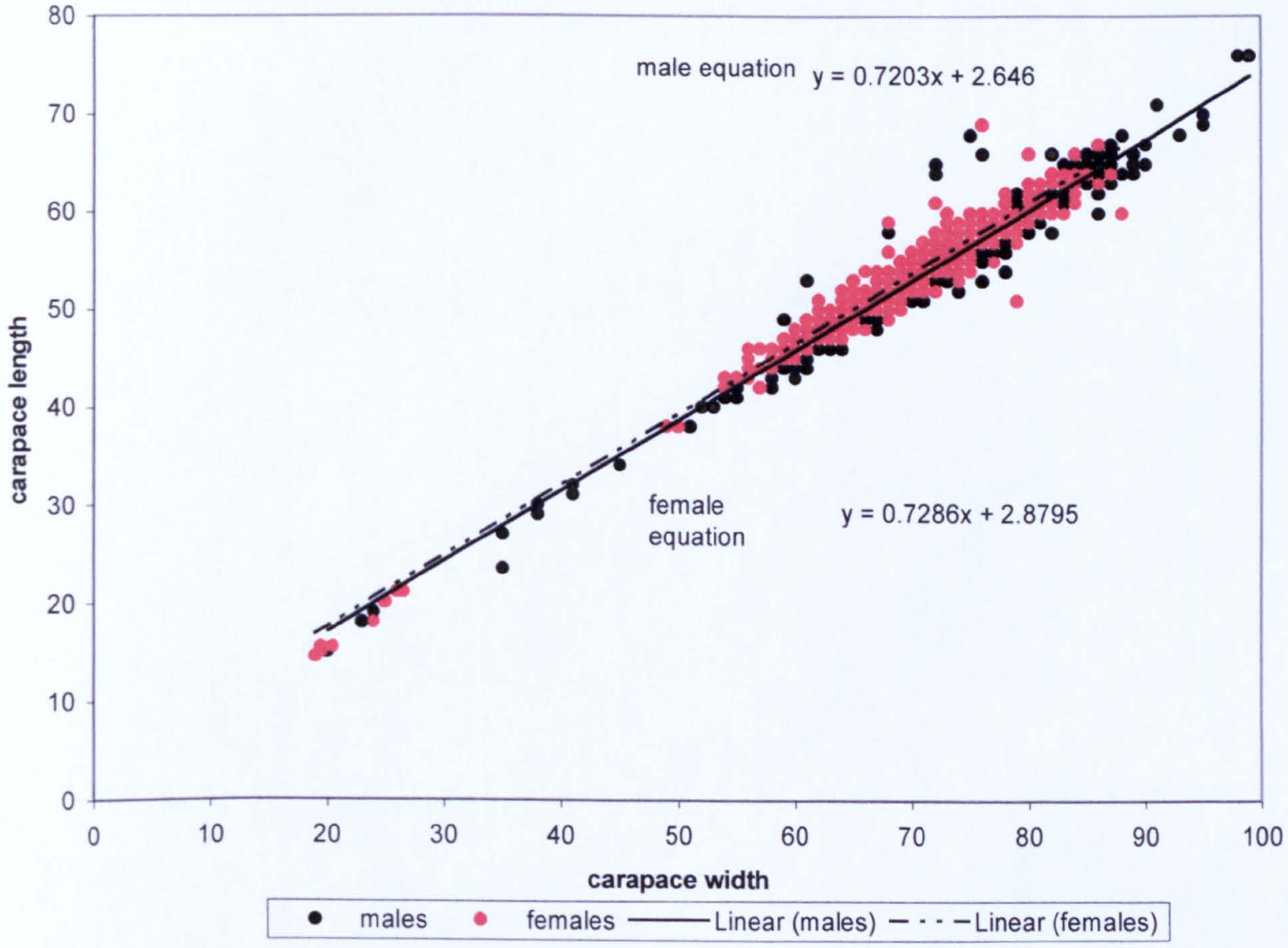


Figure 4.3 Relationship between CW and CL for velvet crabs (n= 1071 males; 629 females)

There is a strong linear relationship between increase in carapace length and corresponding increase in carapace width. The strong positive correlation between the two variables is shown by the r-square values (0.9534 and 0.9448 for males and females respectively). Two further points may be observed regarding carapace length and width. Firstly, there is no apparent discontinuity in either males or females around the point of sexual maturity. This implies that the carapace is not affected by the processes occurring at puberty. Secondly, the regression lines for males and females are virtually identical, indicating that the carapace increases in size in a uniform fashion regardless of the age or sex of the individual, and plays no part in secondary sexual characteristics.

The CW–weight relationship of males and females is shown on Figure 4.4. The basic form of the length-weight relationship is given as:

$$\mathbf{W = qL^b}$$

Where W= weight
L= length
q= constant
b= constant (usually around 3)

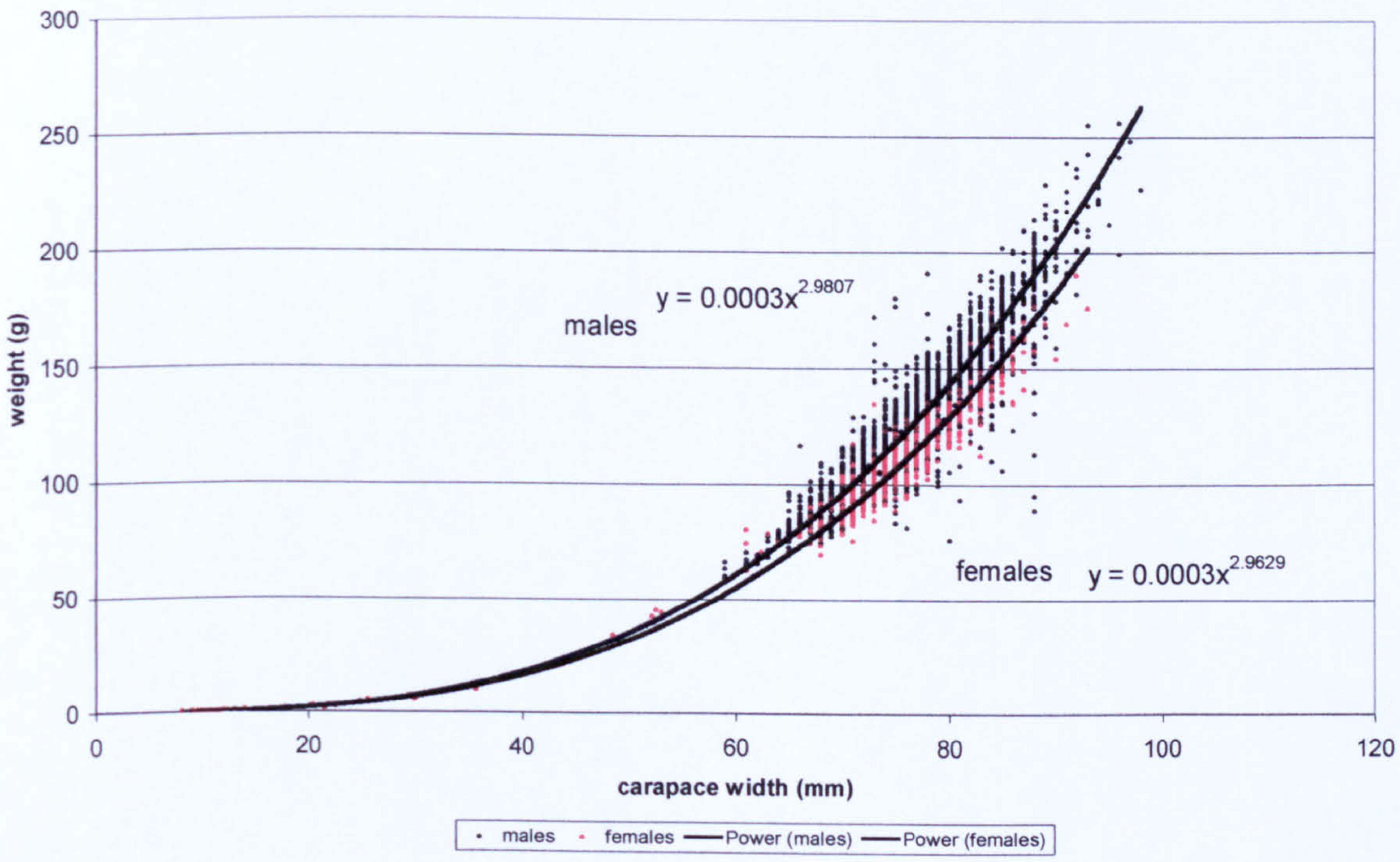


Figure 4.4 Length-weight relationship for velvet crabs (n= 2661 males; 809 females)

Unlike the CW-CL relationship, the change in weight with increasing size of an individual does show a difference depending on sex. This difference is virtually non-existent at smaller sizes, but becomes apparent at around 50mm CW. This corresponds to the general size at onset of puberty and is probably mainly due to the increased growth in the chelae experienced by males. Females do not display positive allometric growth in their chelae so their weight does not increase at such a high rate as in males.

4.3.2 Sex Ratio

Figure 4.5 shows the sex ratio of catch samples (Dataset 1, Appendix A) throughout the year. The overall sex ratio calculated using all catch individuals taken throughout the 2-year study period was 1.86:1 in favour of males. However, this was subject to large temporal variations, as shown below:

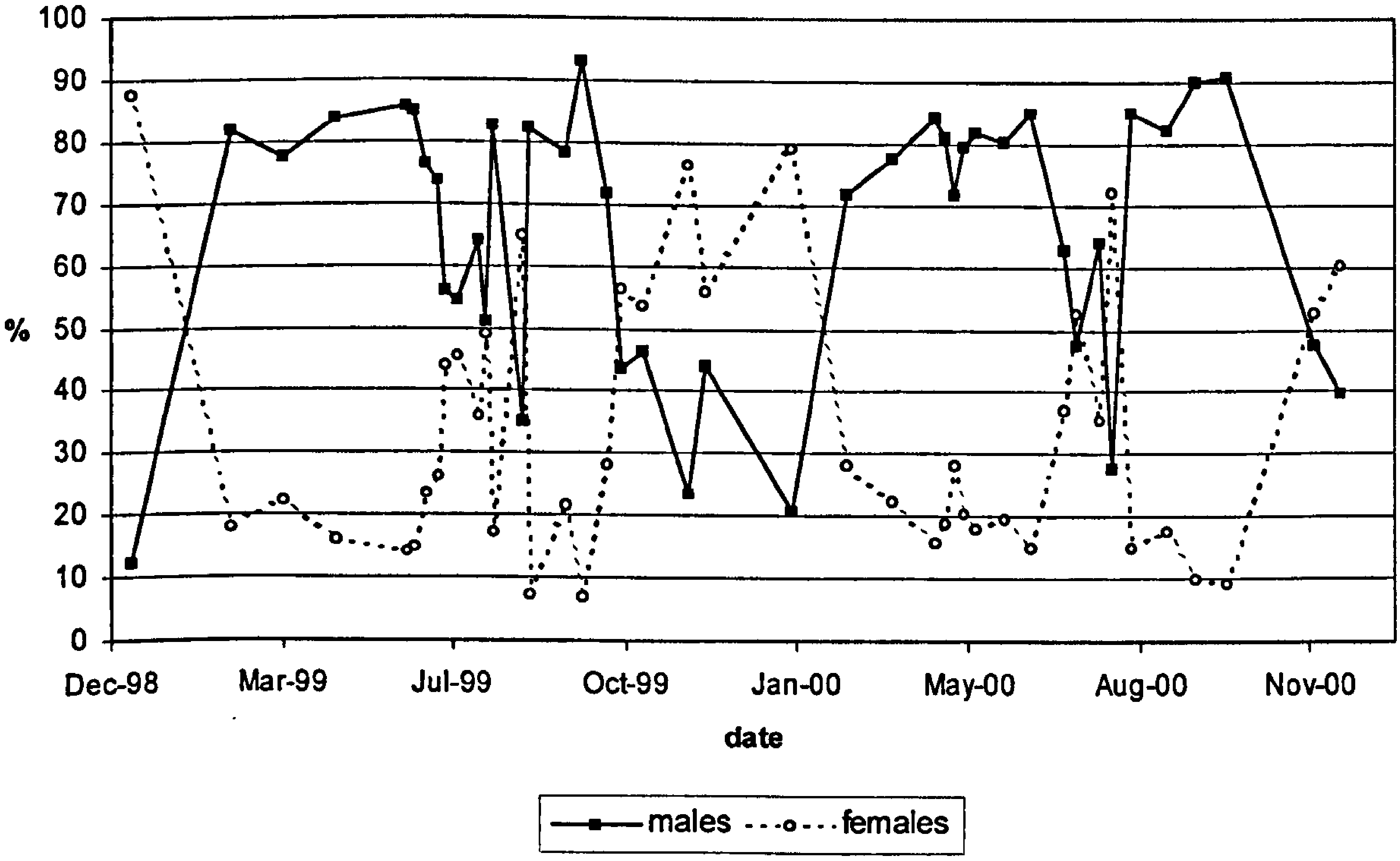


Figure 4.5 Sex ratio of catch samples during study period 1999-2000.

The patterns for both years are virtually identical. At the start of the calendar year, 80-90% of the catch is female. This ratio changes drastically within a few weeks, so that by February, over 70% of the catch is made up of males. Males dominate the catch with similar percentages until July, when the ratio becomes more equal, and females gain a slight advantage towards the end of July or middle of August (depending on the year). From the end of August to October, the males dominate once more, sometimes making up over 90% of the catch. From the end of October to January, the proportion of males falls once more whilst females make up 60-80% of the catch.

The sex ratio for those animals measured at the market (Dataset 5, Appendix A) was also graphed for comparison. Whereas the catch data took into account all individuals caught, and took place in mostly the same area (Eynhallow Sound), market data only involved measuring animals of a marketable size and state, thus not including berried, undersized or soft crabs. In addition to this, the random selection of boxes meant that individuals from all over Orkney were measured, thus not being confined to one local area. The overall sex ratio favoured males with a ratio of 1.59:1. Figure 4.6 shows the results of monthly measurements:

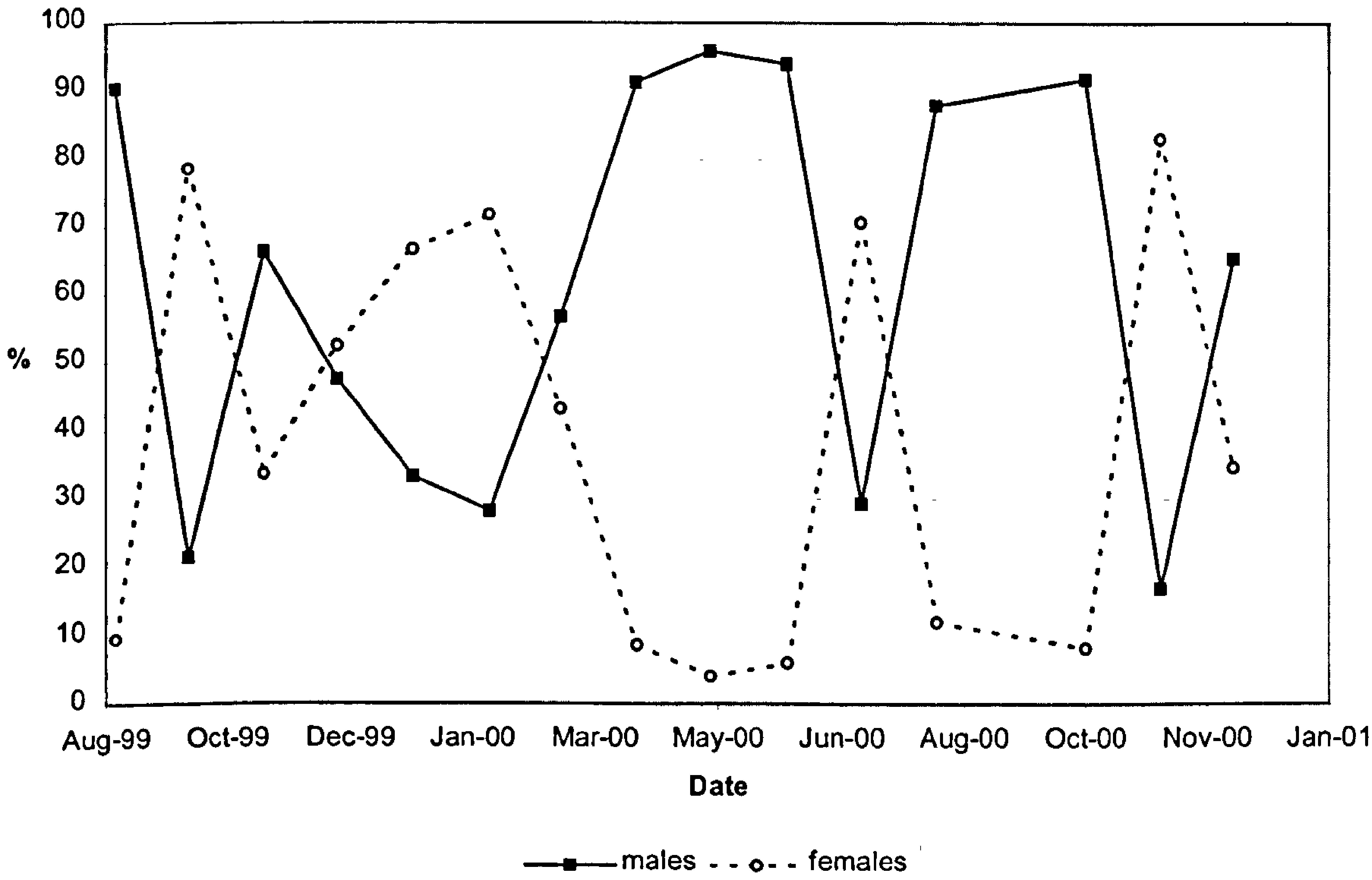


Figure 4.6 Sex ratio of market samples 1999-2000.

Being monthly samples, the pattern observed here is not as detailed as that shown in the previous graph of catch samples. However, some aspects of the graph correspond quite closely to those of the previous graph. There is a large majority of males (over 90% in April, May and June) in the first half of the year, followed by a brief inverse with females making up 70% in July. Males return to dominate from August to October (no measurements were taken in September because OFS closed for the month due to poor catches and low prices). For the remaining months, there appears no clear pattern, except an increase in the proportion of females between November 1999 and January 2000.

Also interesting to note is that only 4 of the 15 samples showed sex ratios that were similar (between 40-60% males and females). This was also the case with the catch data, out of which only 8 from 43 samples showed similar sex ratios.

Because undersized, berried and soft crabs had been removed from the samples before measuring, it was felt that a statistical comparison between catch and market data would not be valid. The main trends are apparent from the graphs alone.

4.3.3 Moulting and the moult cycle

The occurrence of soft crabs in the catch throughout the period of study is shown in Figure 4.7, below.

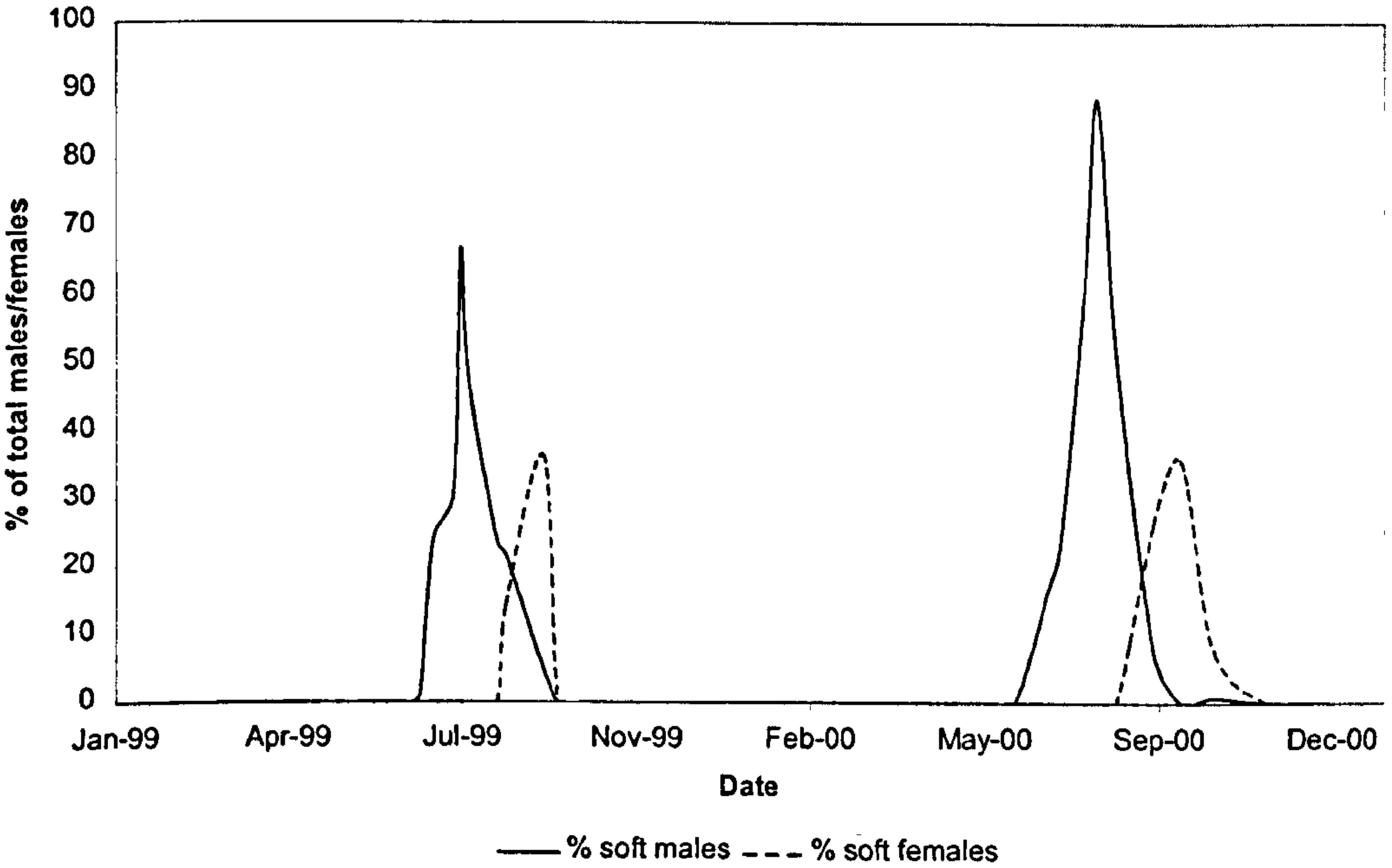


Figure 4.7 Occurrence of soft crabs as a percentage of catch

The very sharp and clear peaks occurring over the months of July-September in each year indicate that the moult process is an annual process restricted to a narrow time period. The data gathered in the two years is very similar, both in terms of the shape of the graphs and in terms of the percentages involved. The male appears to moult first, and a much higher percentage of soft males are found in the catch with respect to females (up to a maximum of 89% in July 2000). Throughout August, the amount of soft males declines. A second, smaller peak occurs in the middle of August, caused by the increasing number of soft females. However, there are far fewer soft females caught in comparison to males, and whereas the peak for females is not until mid-September, by this time most of the catch is made up of males (see Section 4.3.2).

Using the methodology laid out in Section 4.2.2, those recently moulted individuals in the laboratory tanks were examined for the state of their carapace, from the moment of moulting until they were considered suitable for landing (i.e. no longer soft). The results of this are shown in Figure 4.8:

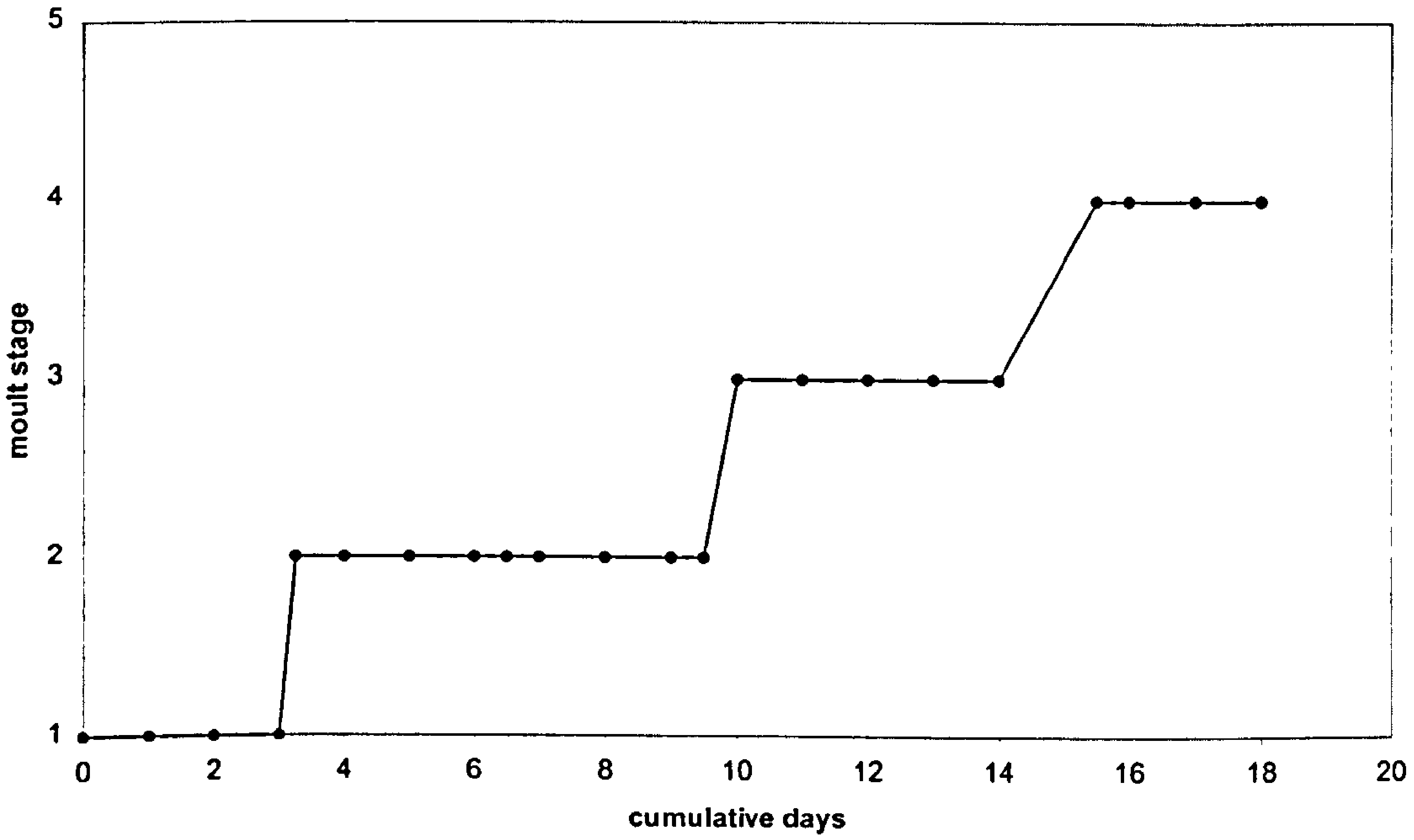


Figure 4.8 Length of moult stages (mean from n=4)

Key: 1= soft; 2= early papershell; 3= late papershell; 4= intermoult.

It must be taken into account that the divisions used here are subjective, so may vary depending on the person involved. Also, it was only possible to follow the progress of 4 individuals, so these results are not necessarily representative of the population as a whole. Finally, as the observations took place in tanks where the temperature was some degrees warmer than the natural environment, and where other factors (such as light and food) did not correspond to conditions in the wild either, this may also produce errors if applied strictly to the local stock.

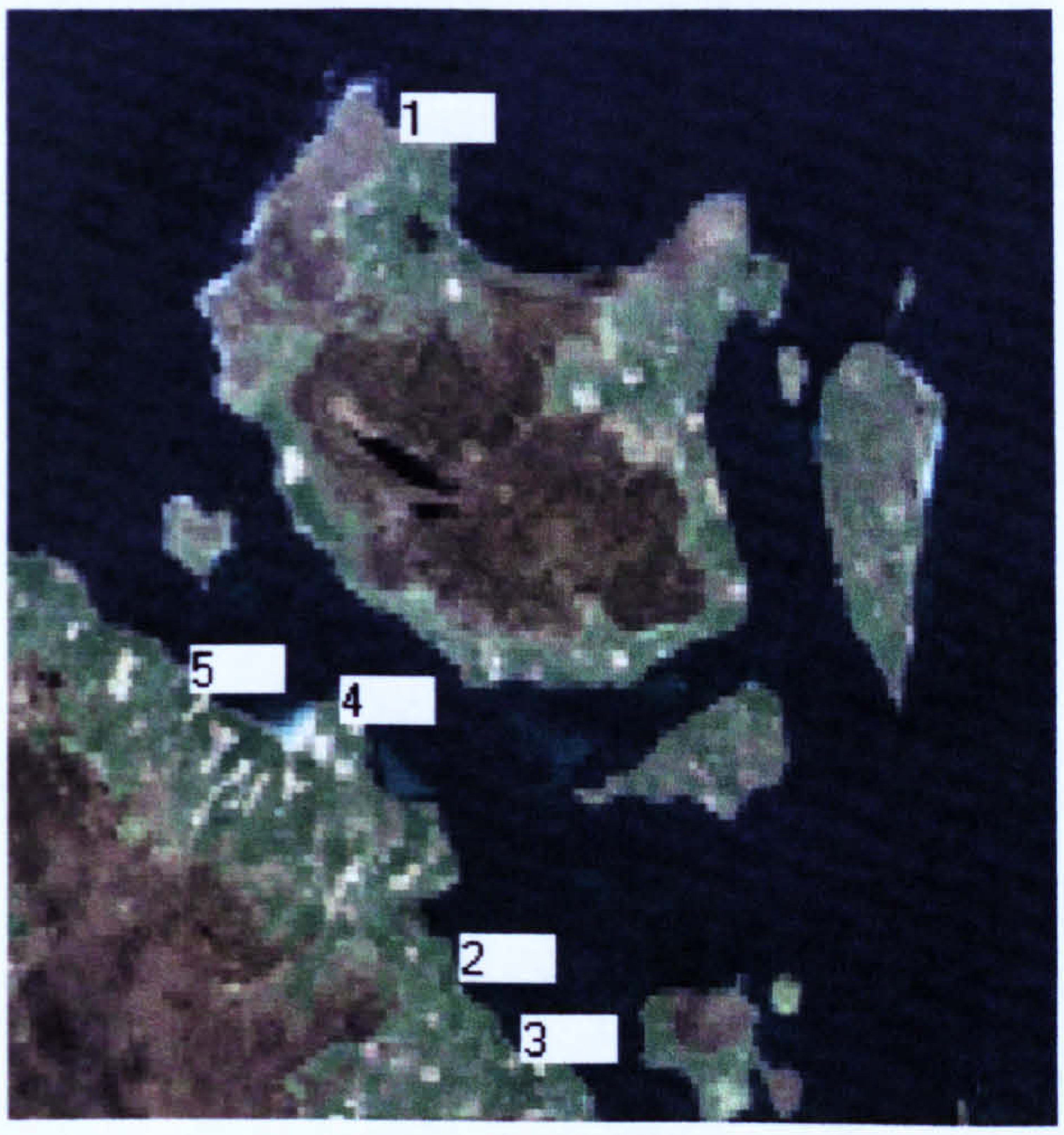
However, as a guide, it can be said that at least 15 days are required under laboratory conditions in order for an individual to moult and harden to the stage where it will no longer be discarded after being caught. This period is probably extended for the natural waters of Orkney, which are cooler than those in the laboratory.

The carapace appears to harden inwards from the outer layer. Thus, in only a few days, the early papershell stage is achieved, this being an initial hard "skin" on the carapace. Once this has begun, the hard layer gets progressively thicker, going through the subjective early and late papershell stages, until the hardening process is complete and the animal can be said to be at the intermoult stage.

4.3.4 Tagging Results

Preliminary studies carried out on tagged individuals under aquarium conditions found the tagging mortality to be around 30%. Tag retention was very dependent on the angle at which the tag was inserted into the base of the abdomen.

Figure 4.9 shows a map of the area in which tagging release took place. There were five release sites: North of Rousay, Tingwall Harbour, North of Evie, Broch of Gurness and Wass Wick. The table beneath the map gives the exact locations of the release sites and the tag numbers for individuals released at each site.



Number	Name	North	West	Tags
1	North Rousay	59°12.00	3°03.51	1-50
2	Tingwall	59°05.40	3°02.73	51-175, 243-275, 356-775
3	North Evie	59°07.50	3°06.40	176-242
4	Gurness	59°07.45	3°04.45	277-355
5	Wass Wick	59°04.95	3°01.30	776-980

Figure 4.9 Release sites for tagged animals. Table refers to station numbers in map. (Map reproduced from The Times – Window on the World CD-ROM)

The results from the tagging programme were inconclusive as only 4 individuals were recaptured, from 1000 released. None of these individuals had completed a moult, so no information on growth could be obtained. Table 4.1 summarises the data from the recaptured individuals:

Tag No	Sex	CW	release	site	Recapture	Site
452	M	80	27-10-99	Tingwall	23-02-00	Tingwall
468	M	66	27-10-99	Tingwall	31-12-99	Tingwall
693	F	70	29-10-99	Auckwall	08-11-99	Auckwall
875	M	64	22-04-00	Auckwall	27-07-00	Auckwall

Table 4.1 Information on recaptured tagged crabs.

With such a small number of recaptures, the only observation that can be made is that none of the recaptured animals seem to have moved from the bay in which they were released. Whether this is anecdotal or represents some territorial behaviour in the velvet crab is not clear at present, but further research may determine this.

4.3.5 Using single samples for initial estimates of L∞

Figures 4.10-13 show the total length frequency distributions for males and females in 1999 and 2000.

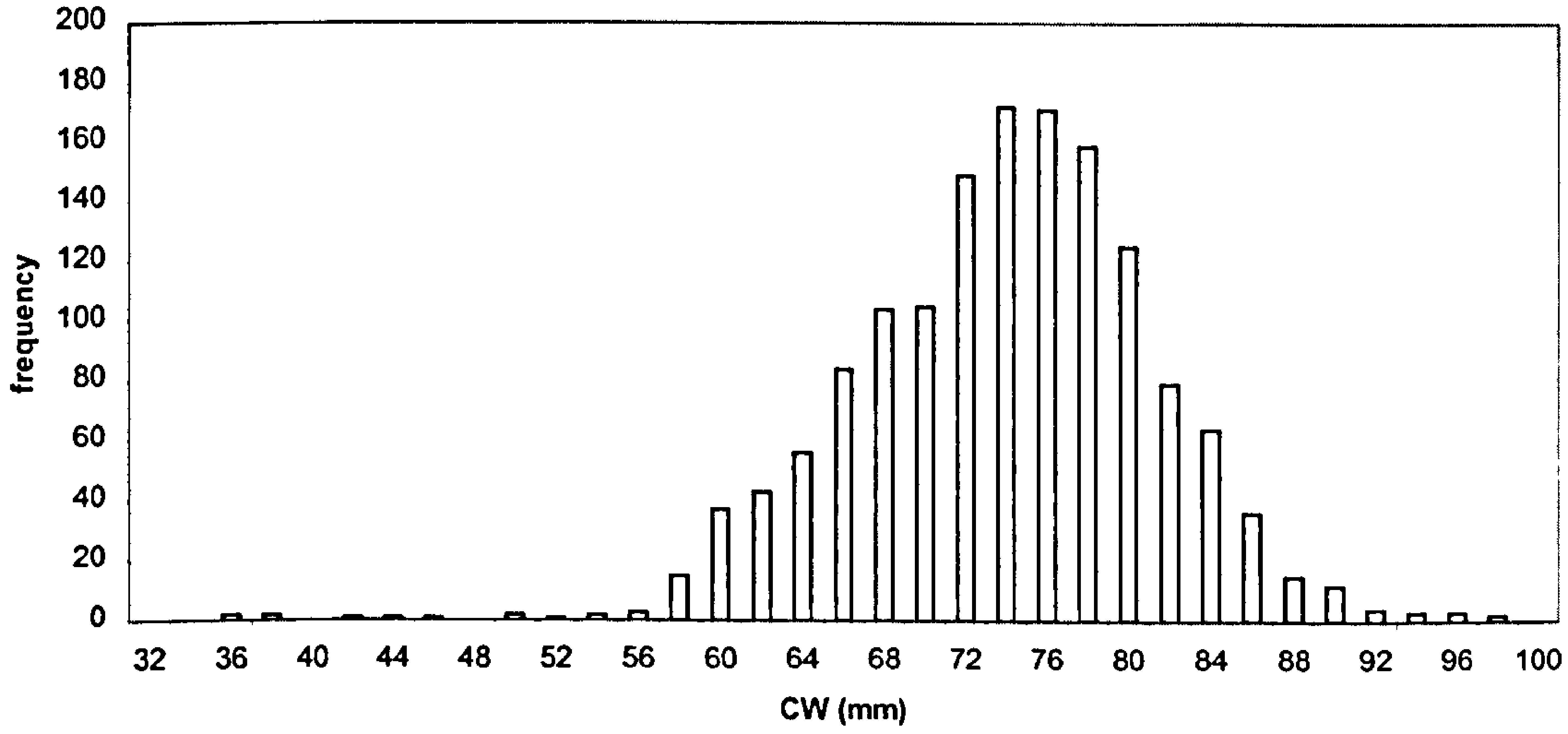


Figure 4.10 Length-frequency distribution for males in 1999

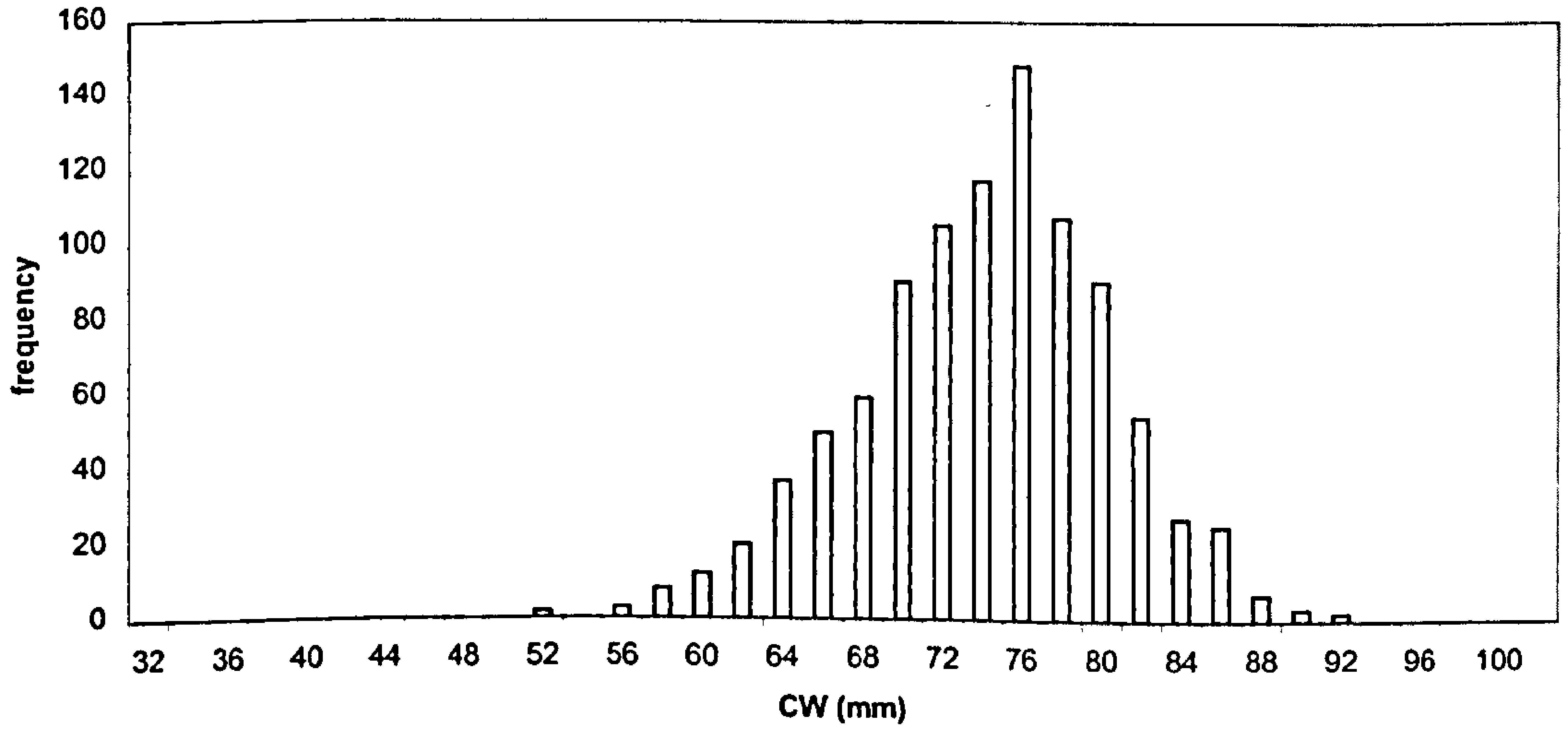


Figure 4.11 Length-frequency distribution for females in 1999

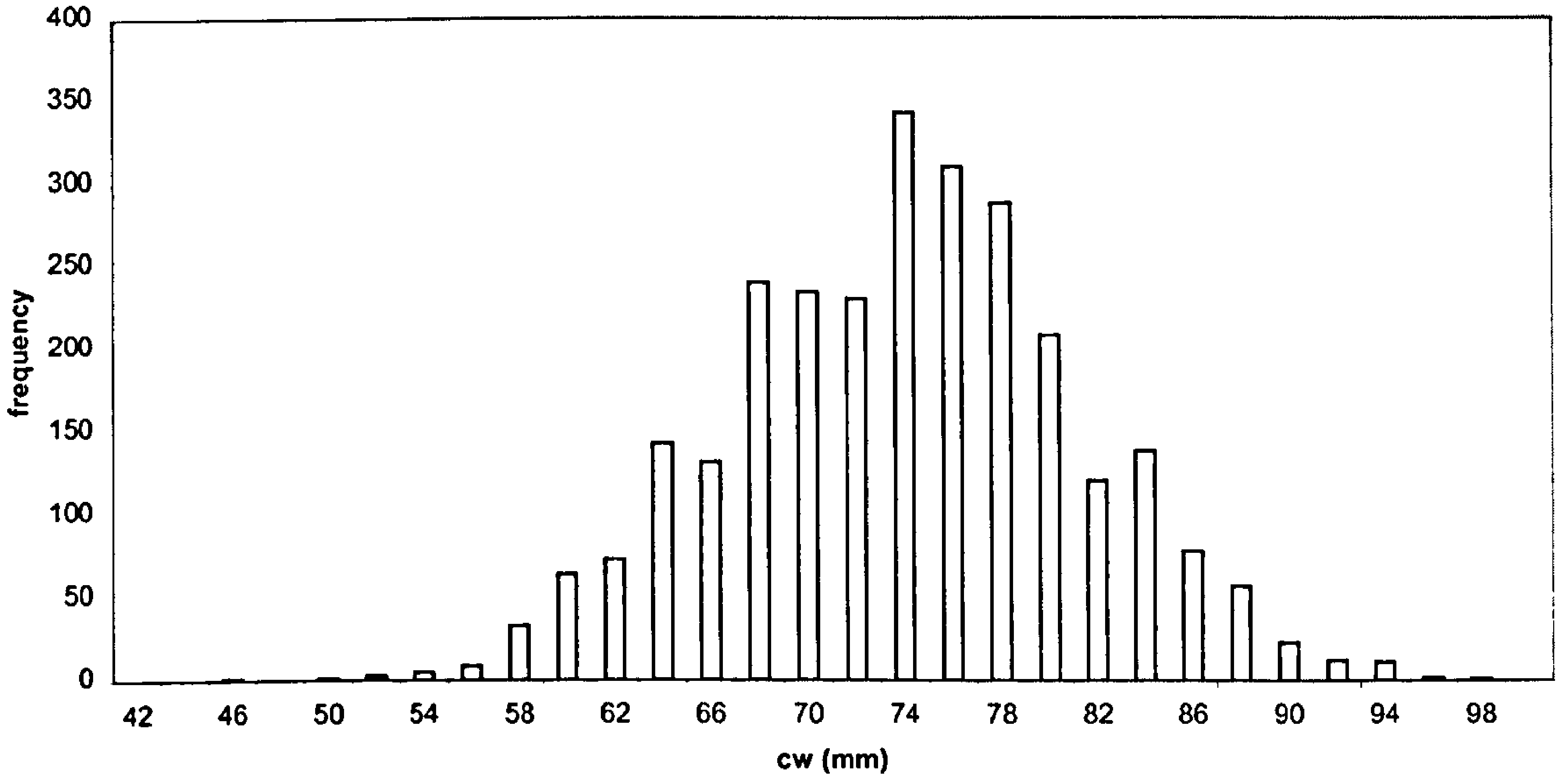


Figure 4.12 Length-frequency distribution of males 2000

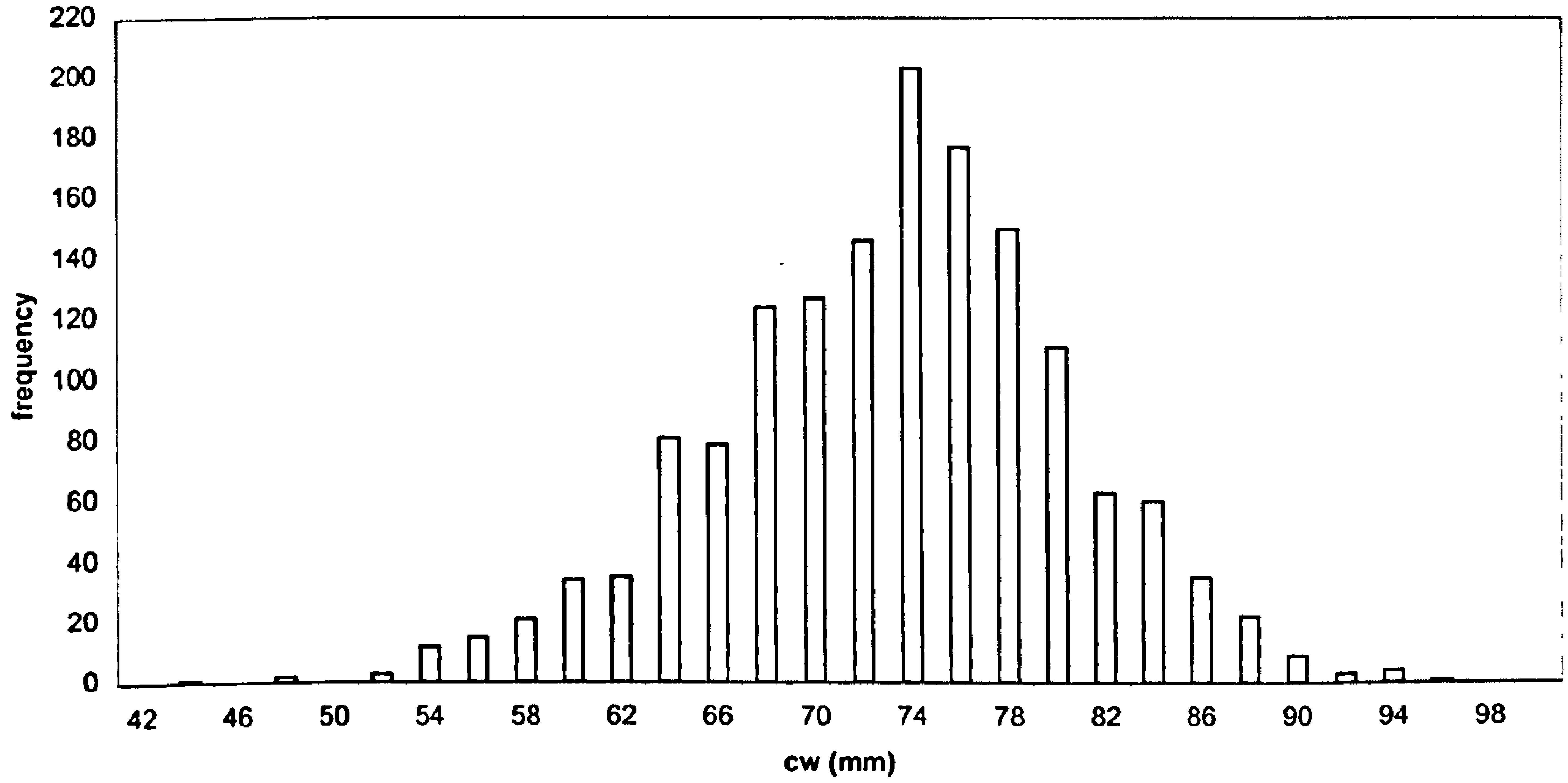


Figure 4.13 Length-frequency distribution of females 2000

The range of sizes of individuals caught during the study period (using creels) is from 36-98mm for males and 52-92mm for females in 1999 and from 46-98mm for males and 44-96mm for females in 2000. The mean size of individuals is similar for both sexes in both years: 73.88mm and 72.14mm for males and females respectively in 1999; and 73.99mm and 73.26mm for males and females respectively in 2000.

These distributions were used to elaborate a Powell-Wetherall plot, which gives an estimate of L∞ and Z/K.

The Powell-Wetherall plots for males and females in 1999 and 2000 respectively, are shown below:

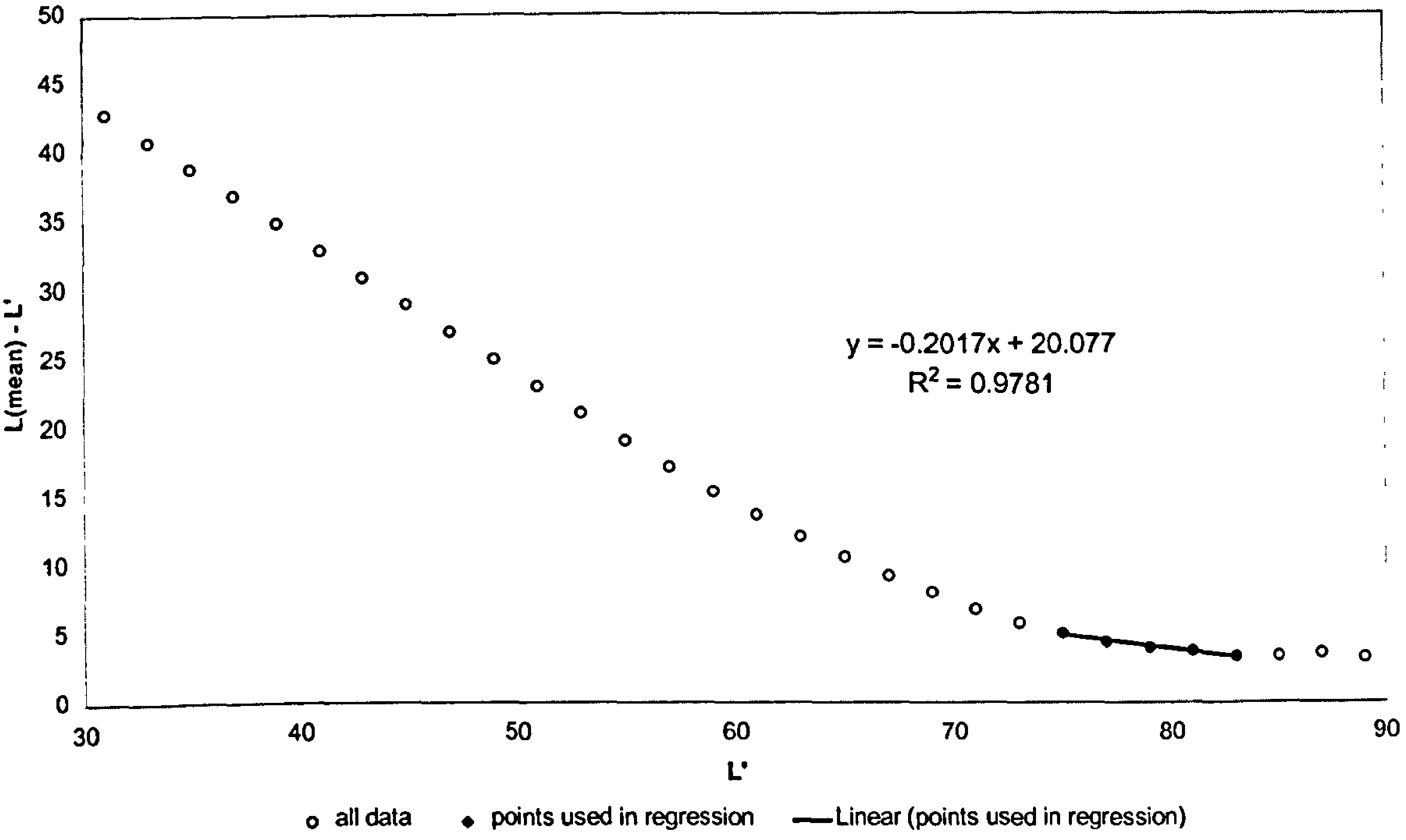


Figure 4.14 Powell-Wetherall plot for males, 1999

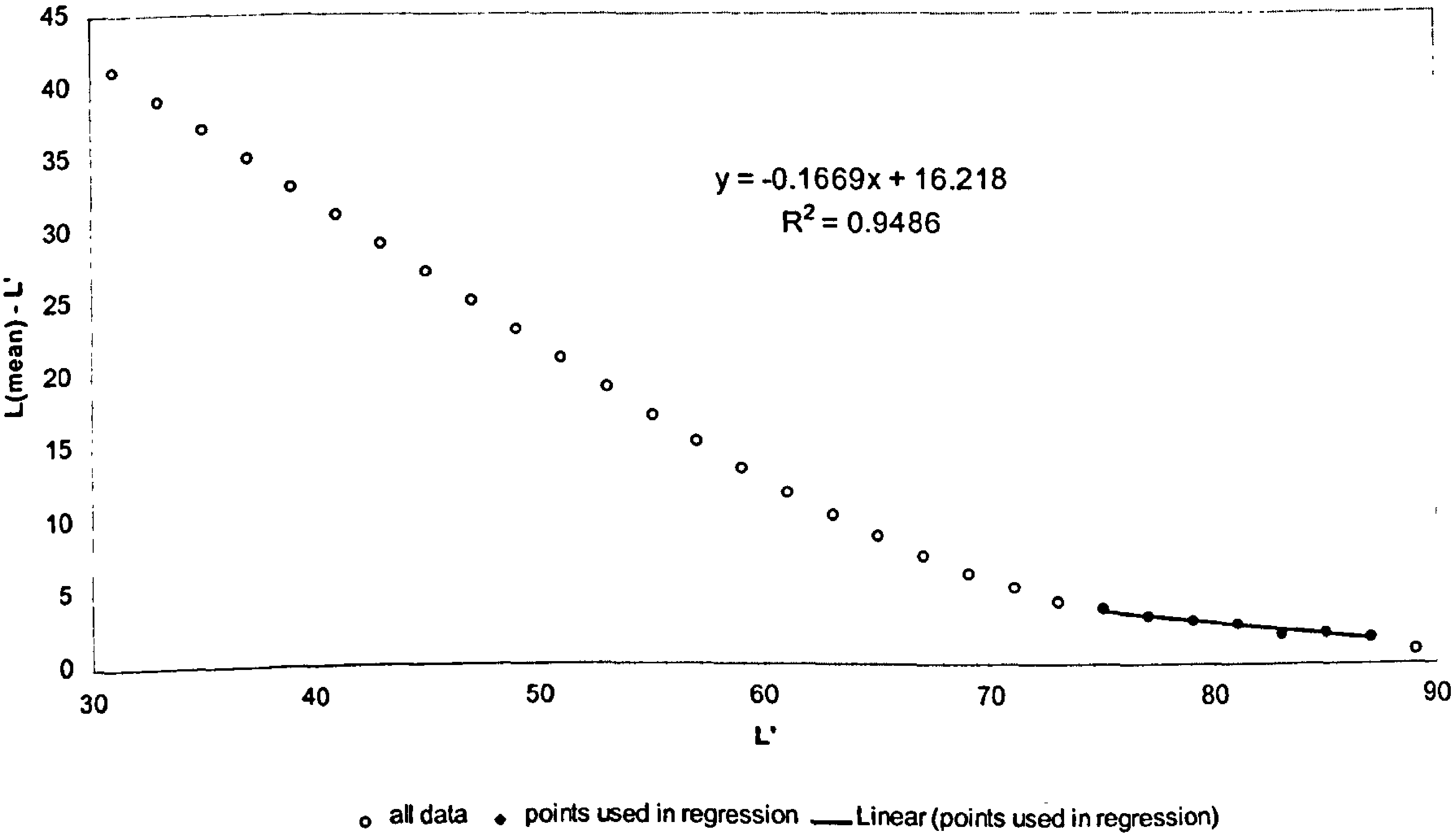


Figure 4.15 Powell-Wetherall plot for females, 1999

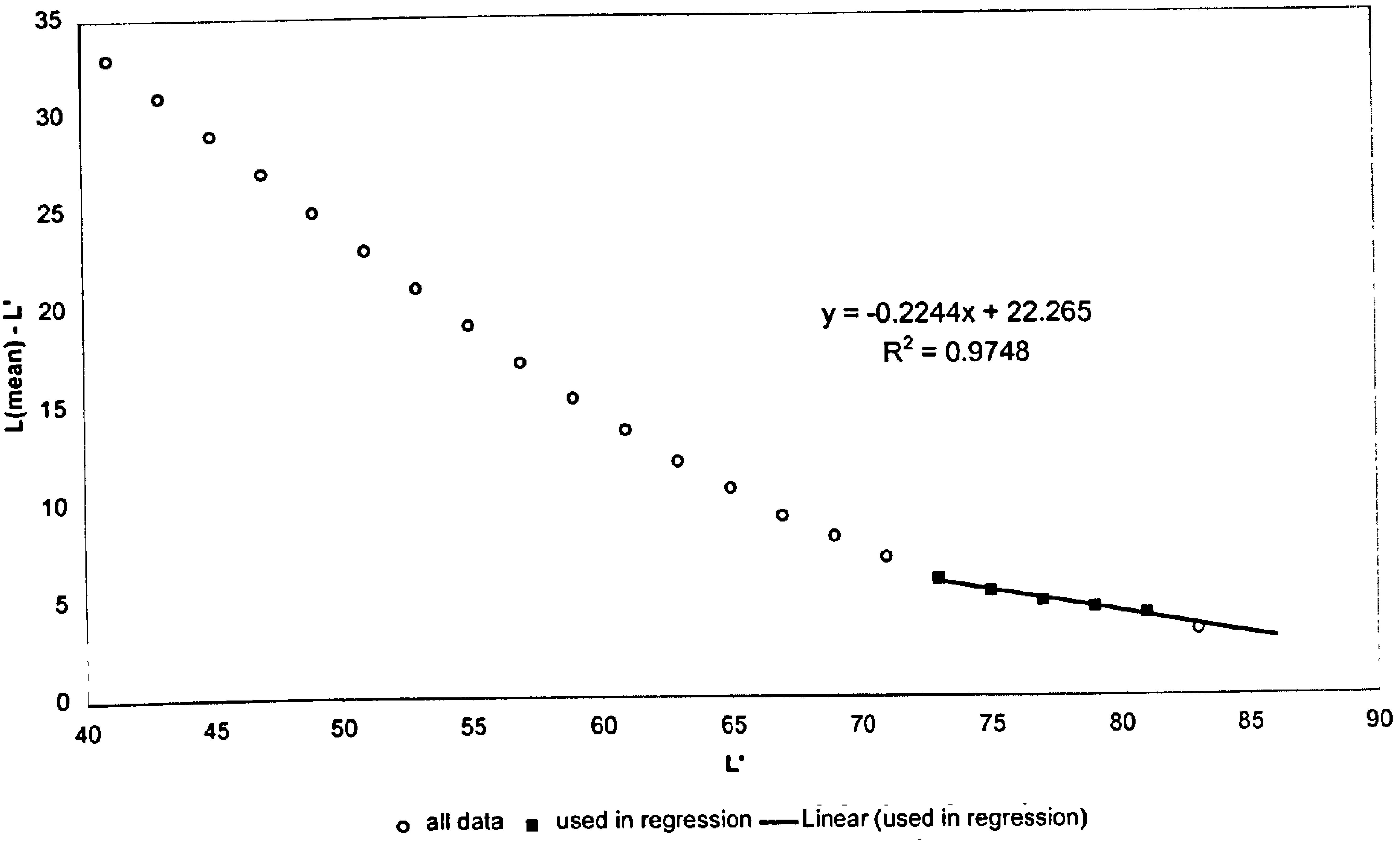


Figure 4.16 Powell-Wetherall plot for males, 2000

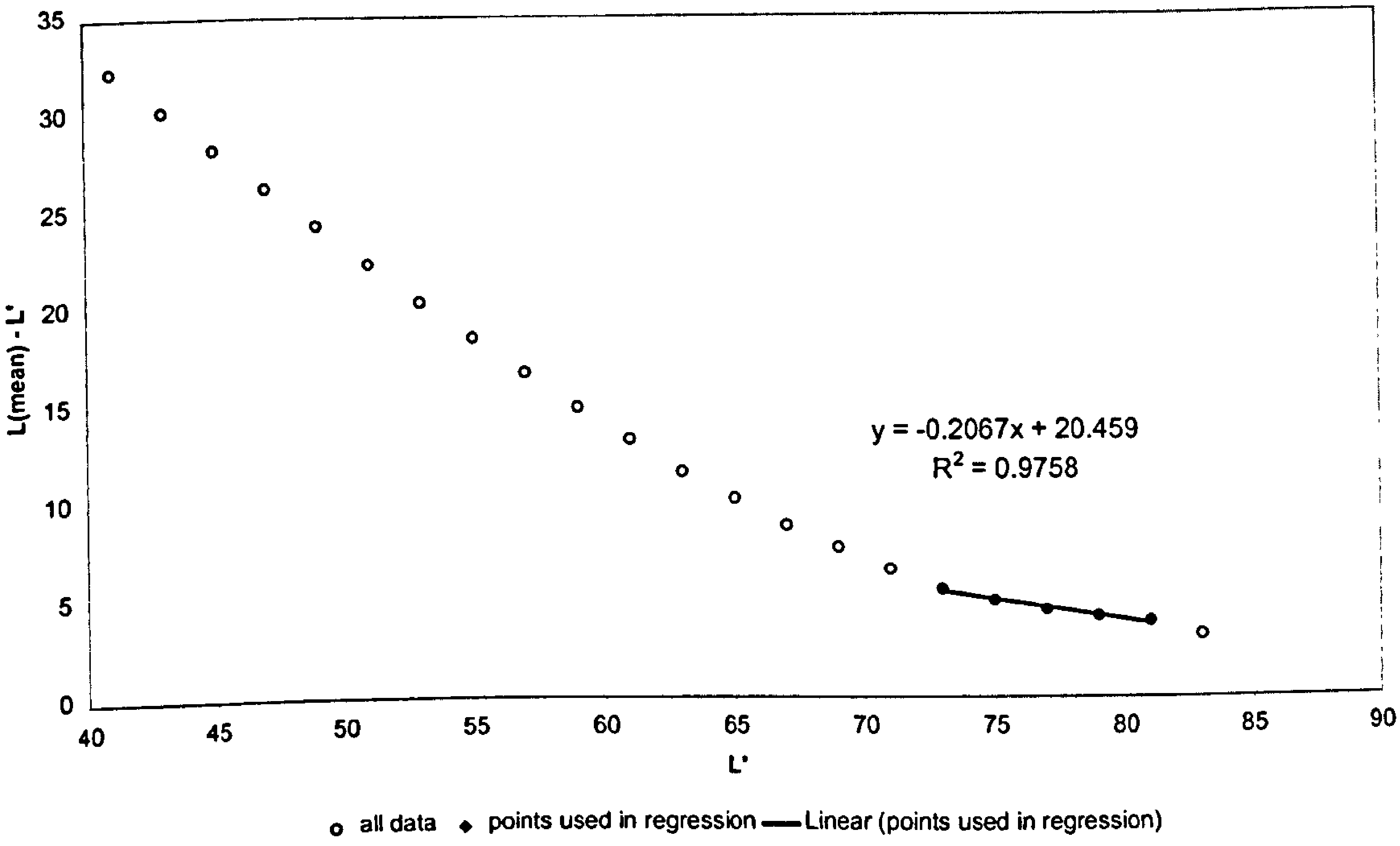


Figure 4.17 Powell-Wetherall plot for females, 2000

The results from the regressions give the following L∞ and Z/K values:

Sex	**Male 99**	**Male 00**	**Female 99**	**Female 00**
L∞	94.3 mm	99.2mm	97.17mm	98.98mm
Z/K	3.14	3.45	4.99	3.84

The data for both years for each size was combined and run through the Powell-Wetherall analysis, giving the following results:

Parameter	**Males**	**Females**
L∞	98.67	95.23
Z/K	3.52	3.26

Another method for obtaining an initial estimate of L∞ is to use the Pauly approximation:

$$L\infty = L(max)/0.95$$

Using this formula, L∞ for males was estimated to be 103 mm for both 1999 and 2000, whereas L∞ for females was estimated to be 95mm in 1999 and 96mm in 2000. This shows that there is a certain amount of variation in estimates of L∞, depending on the method used to estimate the parameter, and depending on the year of sampling. It is possible to modify the Pauly equation to make L(max) the mean of the ten largest animals in the sample, making it less dependent on one individual. In any case, it can be said with some measure of confidence that L∞ lies between 94-103mm for males and 95-98.9mm for females.

4.3.6 Monthly Size-Frequency Graphs

Figures 4.18-21 show the monthly size frequency distribution of males and females caught over the two-year sampling period. In February 1999, the weather conditions were such that it was not possible to obtain any samples.

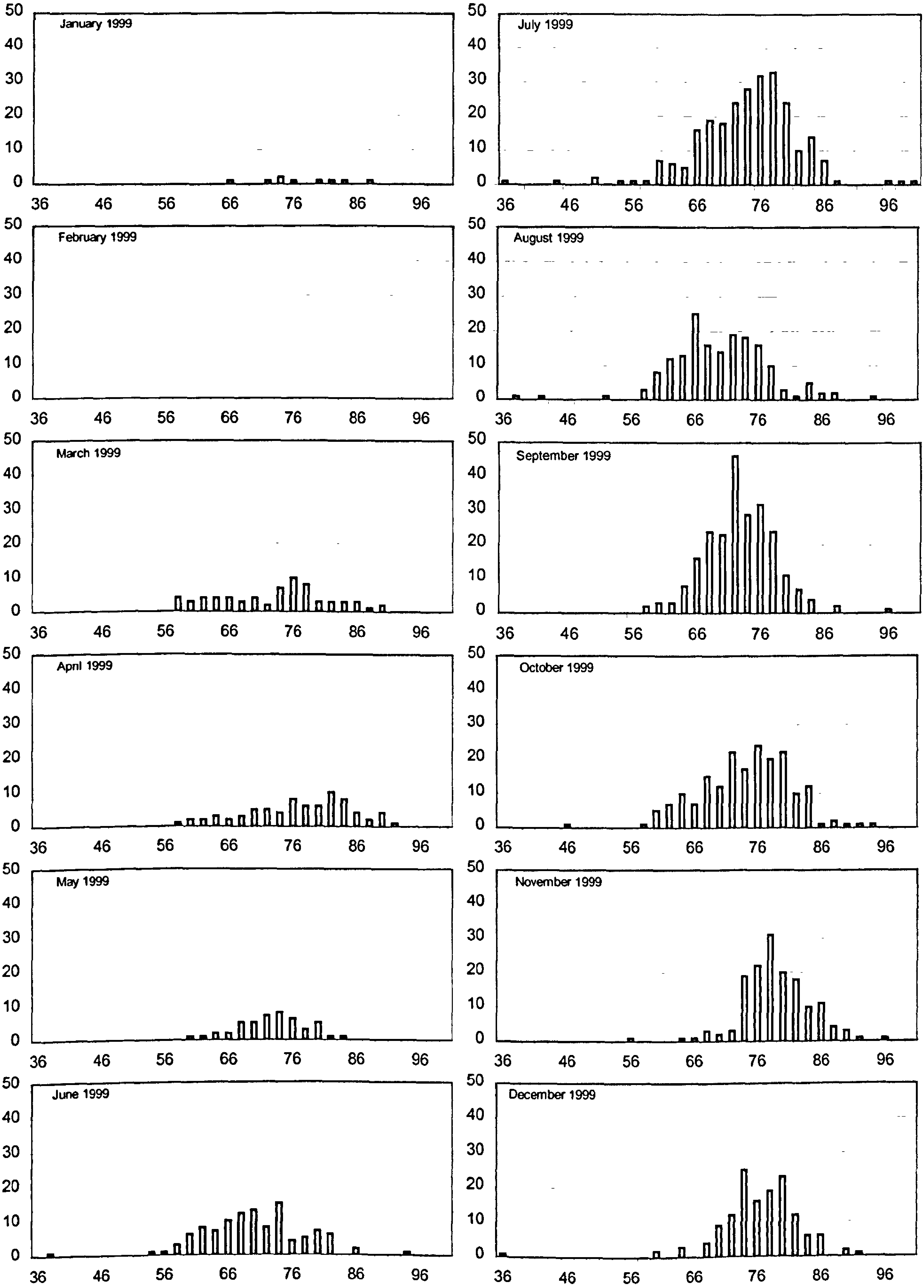


Figure 4.18 Length frequency graphs for male samples 1999 (horizontal axis = carapace width (mm); vertical axis = frequency)

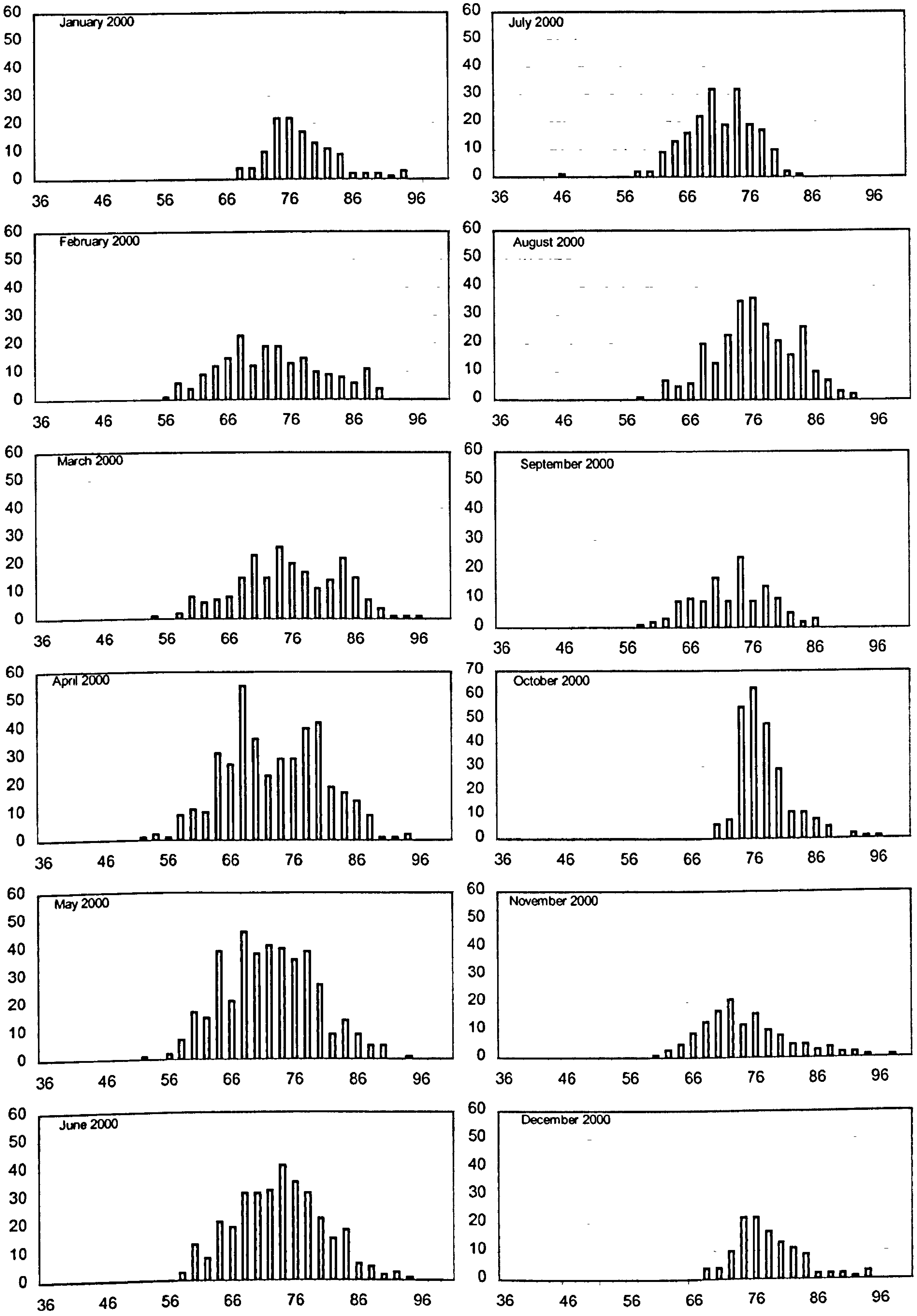


Figure 4.19 Length frequency graphs for male samples 2000 (horizontal axis = carapace width (mm); vertical axis = frequency)

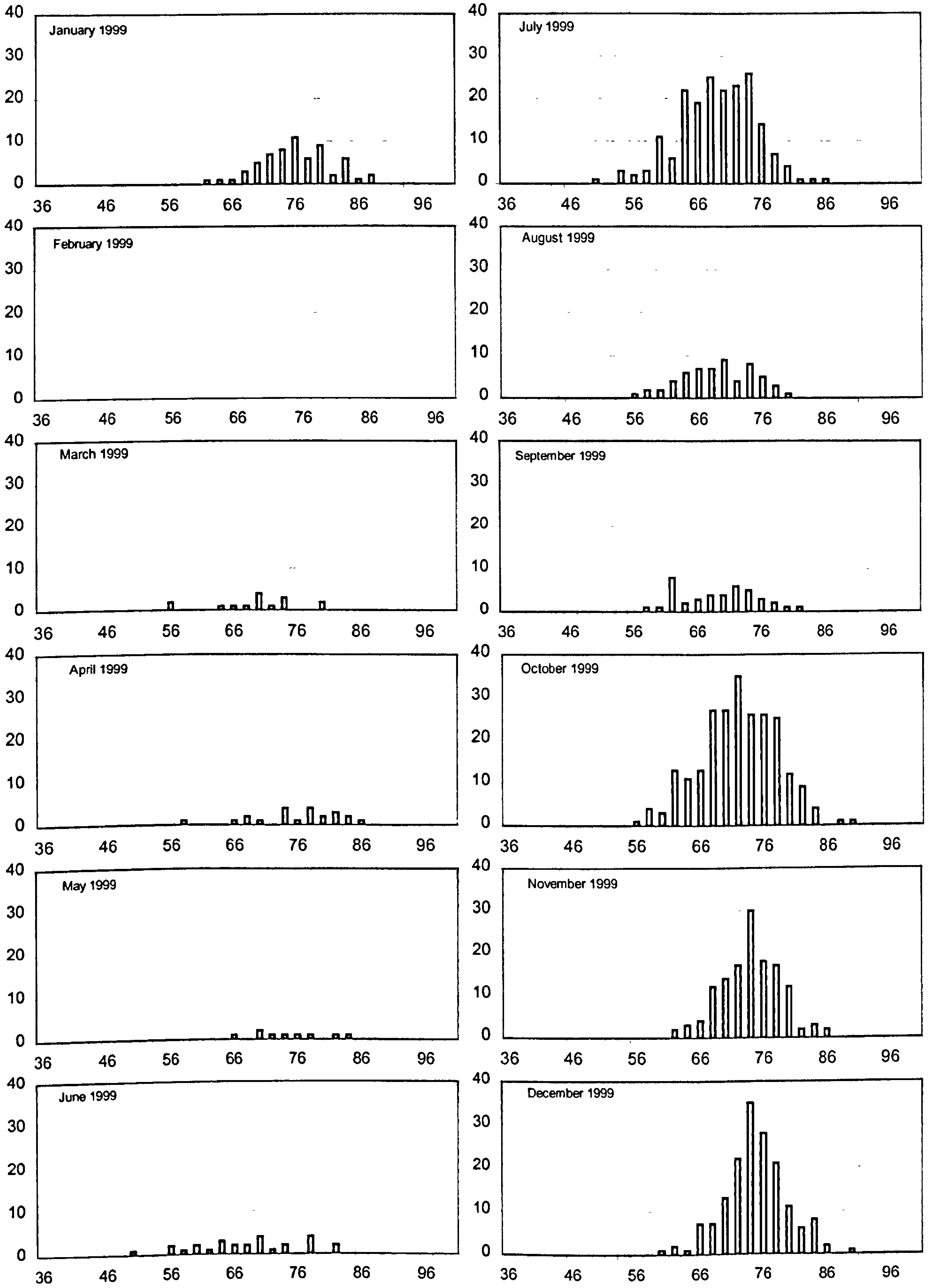


Figure 4.20 Length frequency graphs for female samples 1999 (horizontal axis = carapace width (mm); vertical axis = frequency)

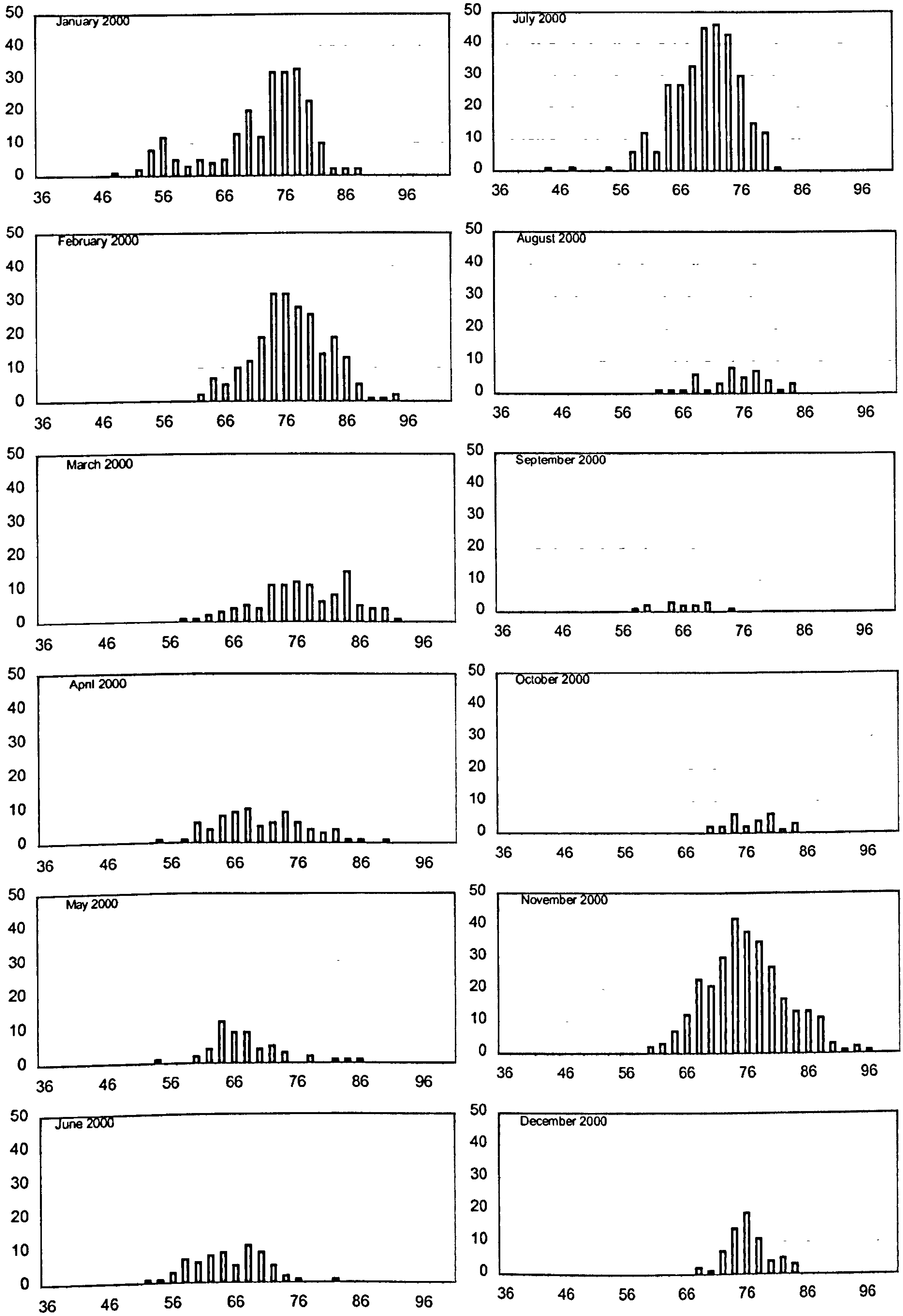


Figure 4.21 Length frequency graphs for female samples 2000 (horizontal axis = carapace width (mm); vertical axis = frequency)

Each monthly sample shown in the previous figures was analysed using the Bhattacharya technique. The results of this are shown in the tables below:

Month	Modal sizes (from Bhattacharya analysis)			
January		75		
February				
March	64	71.3	77.21	85
April	62	73	76	83.9
May	66	74		80
June	63.4	70.9	74	81.4
July	63	69.7	77.8	80.3
August	64.2		74	80
September	62	69.9	77	81.9
October	64.7	70	77.3	80
November		69.5	78.4	83.4
December		71.1	78.2	80

Table 4.2 Results of Bhattacharya analysis for males 1999

Month	Modal sizes (from Bhattacharya analysis)					
January			77.4	84.4	90	
February	59.6	68.8	74.4	82.7		
March		61.7	70.8	74.8	85.8	
April	55	65.8	67.7	79.7	86.6	
May		61.9	64	68.5	78.9	86.5
June		61.5	70	78.2	85.5	
July		66.5	71.3	74	78.4	
August		62	69.6	76.3	84.9	87.8
September		67.2	74.2	78.2		
October				78.2	86.8	
November						
December				77.3	83.9	

Table 4.3 Results of Bhattacharya analysis for males 2000

Month	Modal sizes (from Bhattacharya analysis)				
January				74.4	80.8
February					
March				71	
April				69	
May					
June		60	65.5		
July	54	61.5		69.4	78.7
August		60	67.6	71.4	78
September		63.2	69.9	74.8	
October		59.7	62	72.6	78.5
November					
December					

Table 4.4 Results of Bhattacharya analysis for females 1999

Month	Modal sizes (from Bhattacharya analysis)						
January			64	71.8		77.6	
February	56.5	65.6	71.8		78.6		84.9
March			68.7		77.3		84.9
April	61.6		67.2	75.3			84.9
May		65.6	72.6			82	
June	59.9	65.1	68.4				
July	61		72.7		78		
August			69	73.4	78.3		
September		64	72				
October				75	80.4		
November			70.6		78.7		87.6
December		67.9		76.5		82	

Table 4.5 Results of Bhattacharya analysis for females 2000

The process of determining modal sizes using this technique was found to be subjective and therefore not very satisfactory. Different results were obtained using the Bhattacharya package in the FiSAT computer programme than for longhand analysis on a spreadsheet. The tables above show the results for the latter method, as the FiSAT programme was found to be unreliable overall (see Section 4.3.7).

The low numbers of females obtained during some months made analysis of some samples extremely difficult. The modal sizes of each month in a year were collated to give mean modal sizes each year for each sex. These sizes were used in Gulland-Holt plots to give estimates of L∞ and K. These plots are shown below.

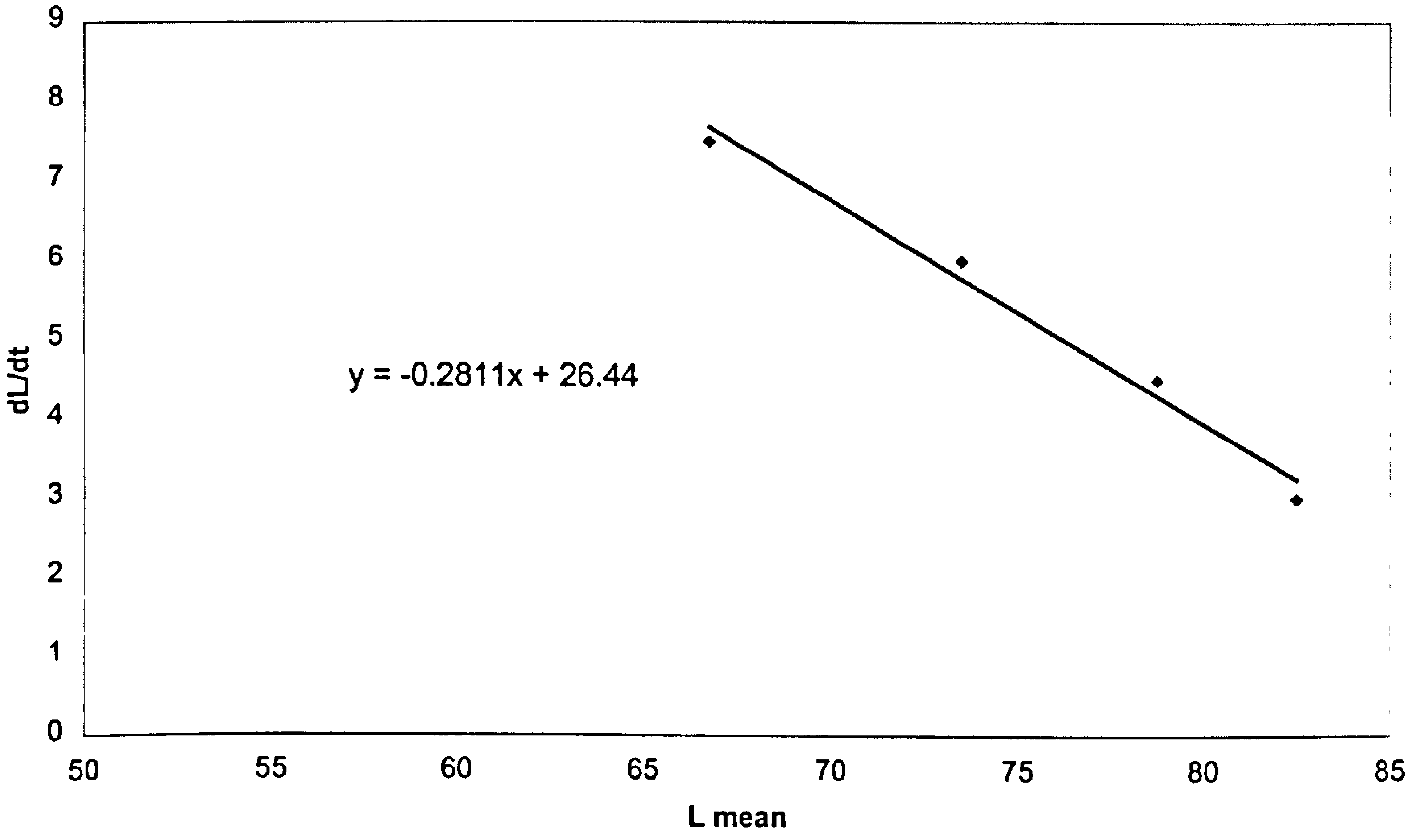


Figure 4.22 Gulland Holt plot for males 1999

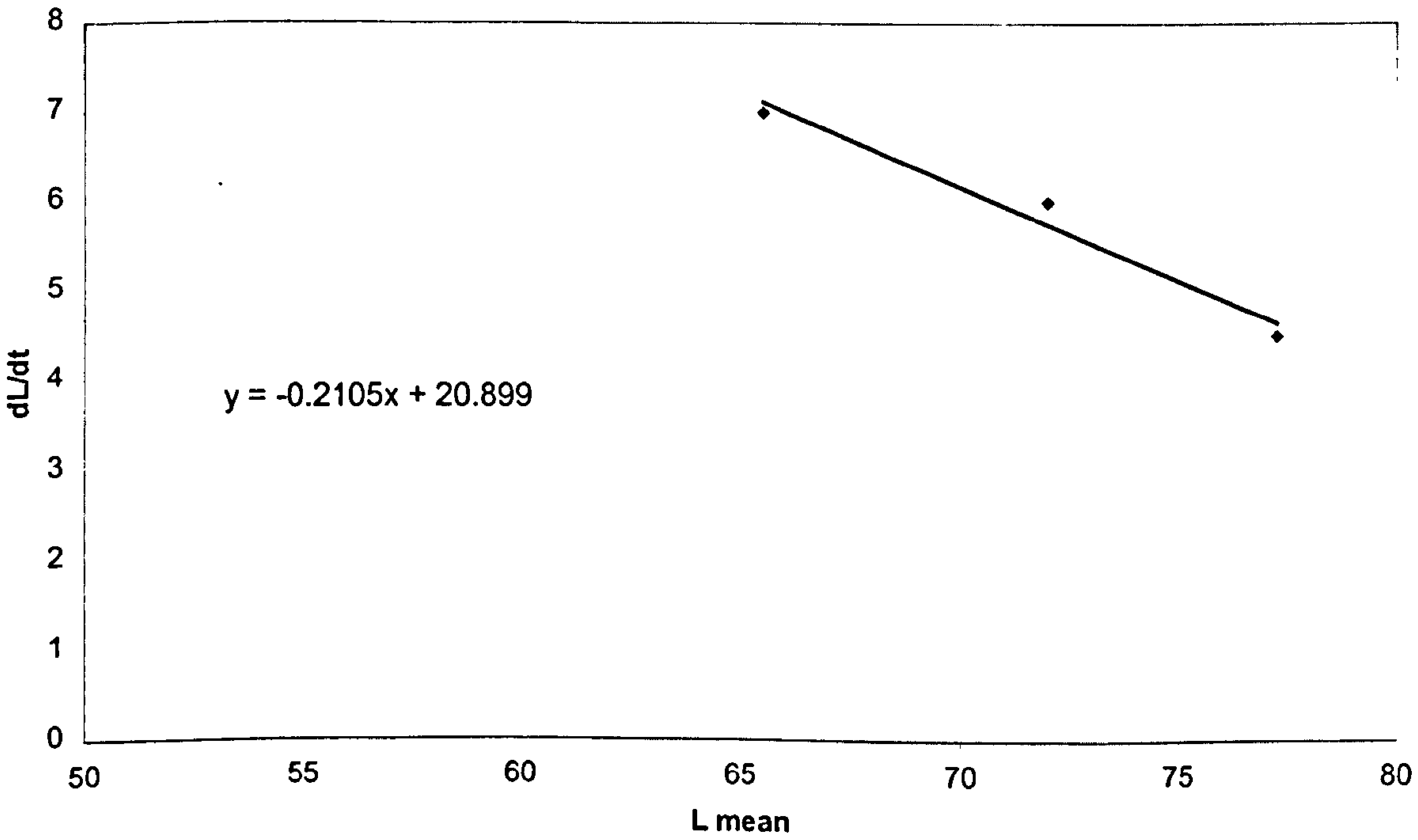


Figure 4.23 Gulland Holt plot for males 2000

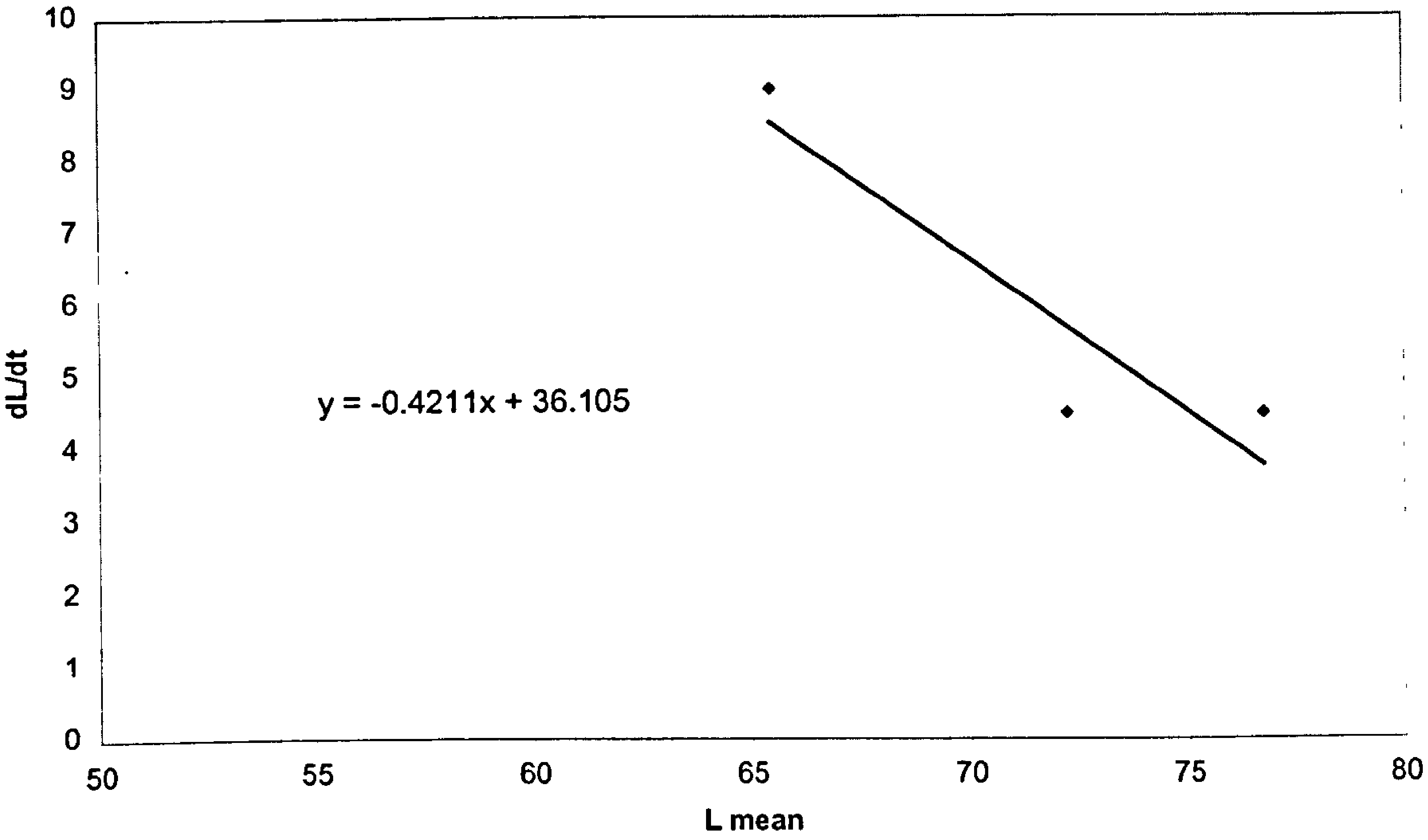


Figure 4.24 Gulland Holt plot for females 1999

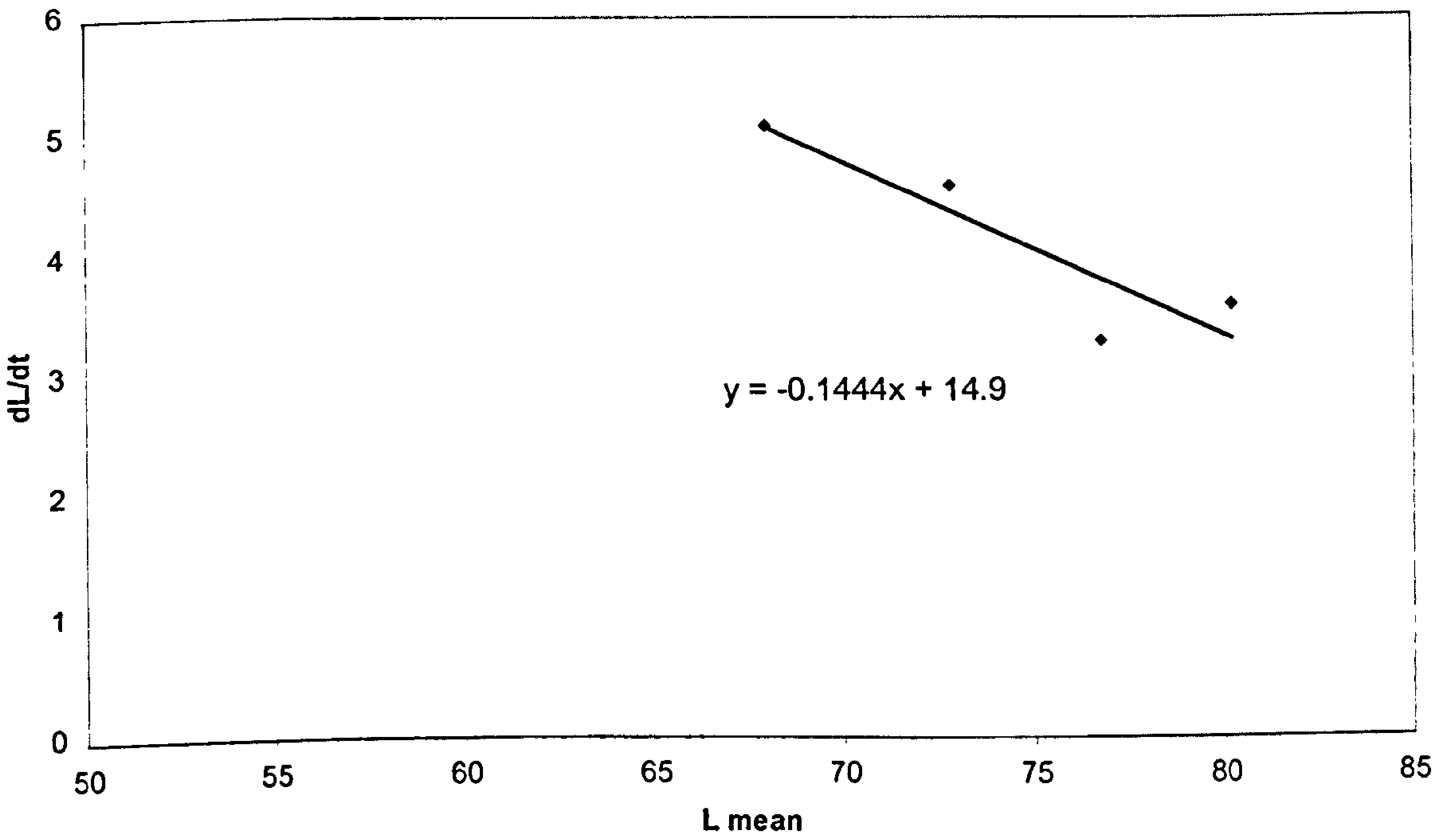


Figure 4.25 Gulland Holt plot for females 2000

From the regressions carried out on each plot, estimates of $L\infty$ and K were obtained using the following formulae:

$$L\infty = -a/b$$

$$K = -b$$

Thus:

Parameter	Males 99	Males 00	Females 99	Females 00
$L\infty$	94	99.3	85.75	103.16
K	0.28	0.21	0.42	0.144

These results are not only different from previous estimates of $L\infty$, but they are also, in the case of females, vastly different from one another. This is possibly due to the small numbers of females obtained during many months of the year, but is also probably a result of the difficulties of using methods to break down a length-frequency distribution into its component sizes using data obtained from fishing gear, which excludes smaller sized individuals.

At this point, before further analysis may be carried out, values of $L\infty$ and K must be decided upon. It was felt that the key issue surrounding the variability of the results was the difficulty in splitting the length-frequency distributions into their components at large sizes. Bhattacharya analysis depends on the first slope of the composite distribution being the uncontaminated slope of the first cohort. Clearly, when dealing with a sample that is made up mainly of adults, this is not the case, and the selectivity of the fishing gear also influences this. It was therefore decided that the growth parameters obtained from the juvenile sampling in Section 3B should be used in further work. Although this implied that there was no difference in these parameters between the sexes, the work carried out in Section 4.3.6 indicates that any differences between the sexes are, in any case minor, compared to those in other study areas. The growth curves constructed in Section 3B are those which best represent the stock in question, and from which further work is carried out.

4.3.7 Use of ELEFAN

The table below shows the results of the scan of K-values run by the ELEFAN programme given the following values for the remaining parameters: L∞=98.4, C=1, WP=0.0837.

sample	Males 99	Females 99	Males 2000	Females 2000
K value	1.6	8	3.4	0.82

Table 4.6 Estimates of K-values from ELEFAN.

These results are wildly disparate and do not fit into the pattern of events observed using other methods. Table 4.7 shows the results of the automatic search routine carried out on each set of 12-monthly samples, using seeded values for L∞, K, C and WP, all of which were varied in steps of the order described below:

L∞ = 98 +/- 0.5

K = 0.268 +/- 0.05

C = 1 +/- 0.1

WP = 0.084 +/- 0.08

Parameter	Males 99	Females 99	Males 2000	Females 2000
L∞	100	98	95	99.5
K	0.618	0.268	0.568	0.518
C	0.6	1	1	1
WP	0.484	0.324	0.004	0.244
Rn value	0.142	0.174	0.142	0.156

Table 4.7 Growth parameters for *Necora puber* estimated from automatic search routine in ELEFAN.

Whereas the L∞ values given above lie in the range expected from this study, The K values vary so much that little meaning may be derived from them. The Rn values are goodness of fit values (0<Rn<1), and in these cases, are all low. The ELEFAN results were therefore disregarded in further calculations.

4.3.8 Estimation of mortality

Length converted catch curves were constructed for males and females for 1999 and 2000. The figures for the parameters L∞ and K (98.4 and 0.268 respectively) were those obtained in the analysis of growth of the juveniles (Section 3B) and did not differ for the sexes. As a guide to the expected results, Table 4.8 below shows Z values calculated from the Powell-Wetherall plots in Section 4.3.5, using 0.268 as the value for K:

Parameter	Males 1999	Males 2000	Females 1999	Females 2000
Z/K	3.14	3.45	4.99	3.84
Z	0.84	0.925	1.34	1.03

Table 4.8 Initial estimate of Z from Powell-Wetherall plots (4.3.6)

The catch curves are shown on the Figures below (4.26-29):

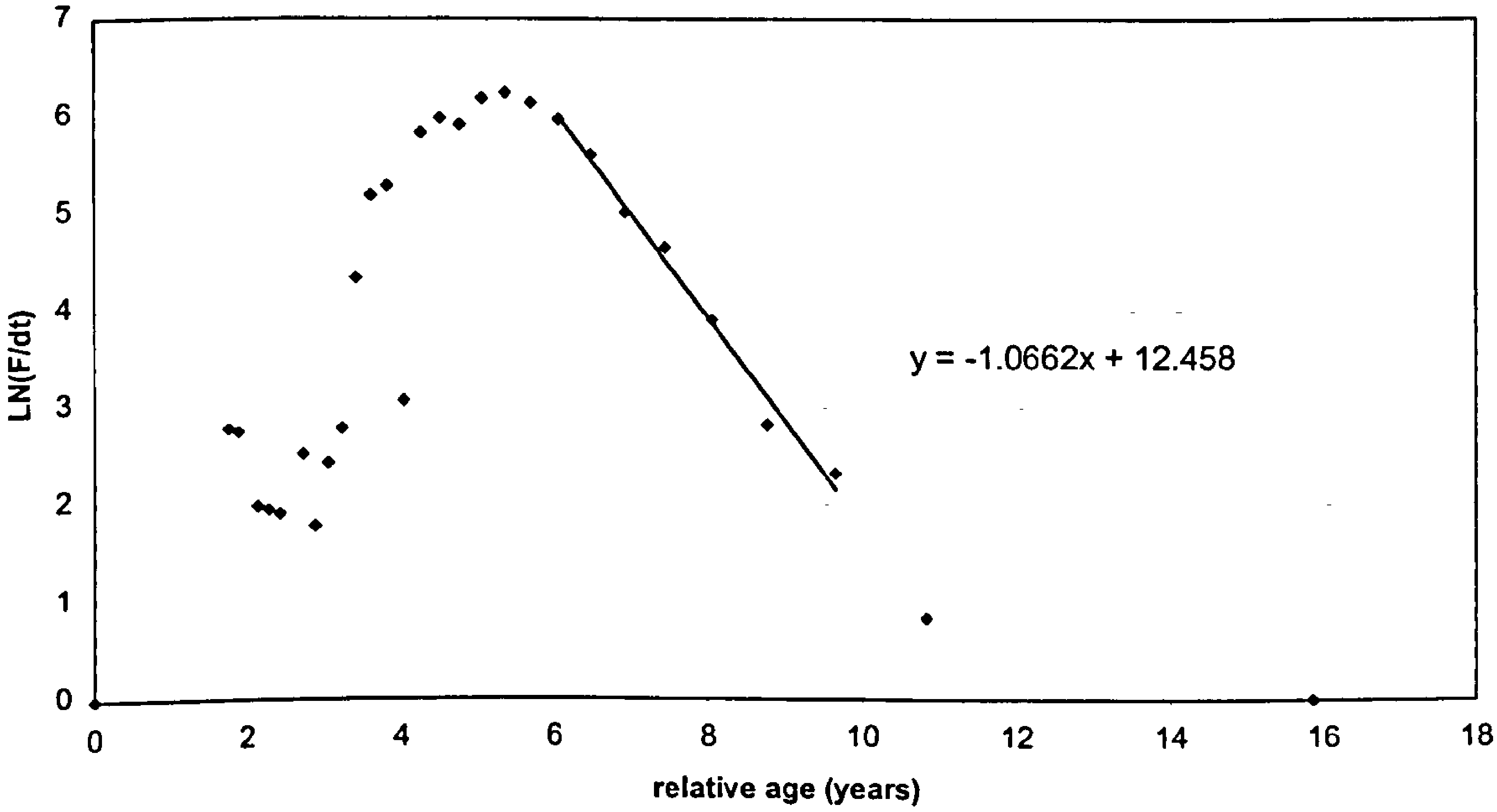


Figure 4.26 Length converted catch curve for males 1999

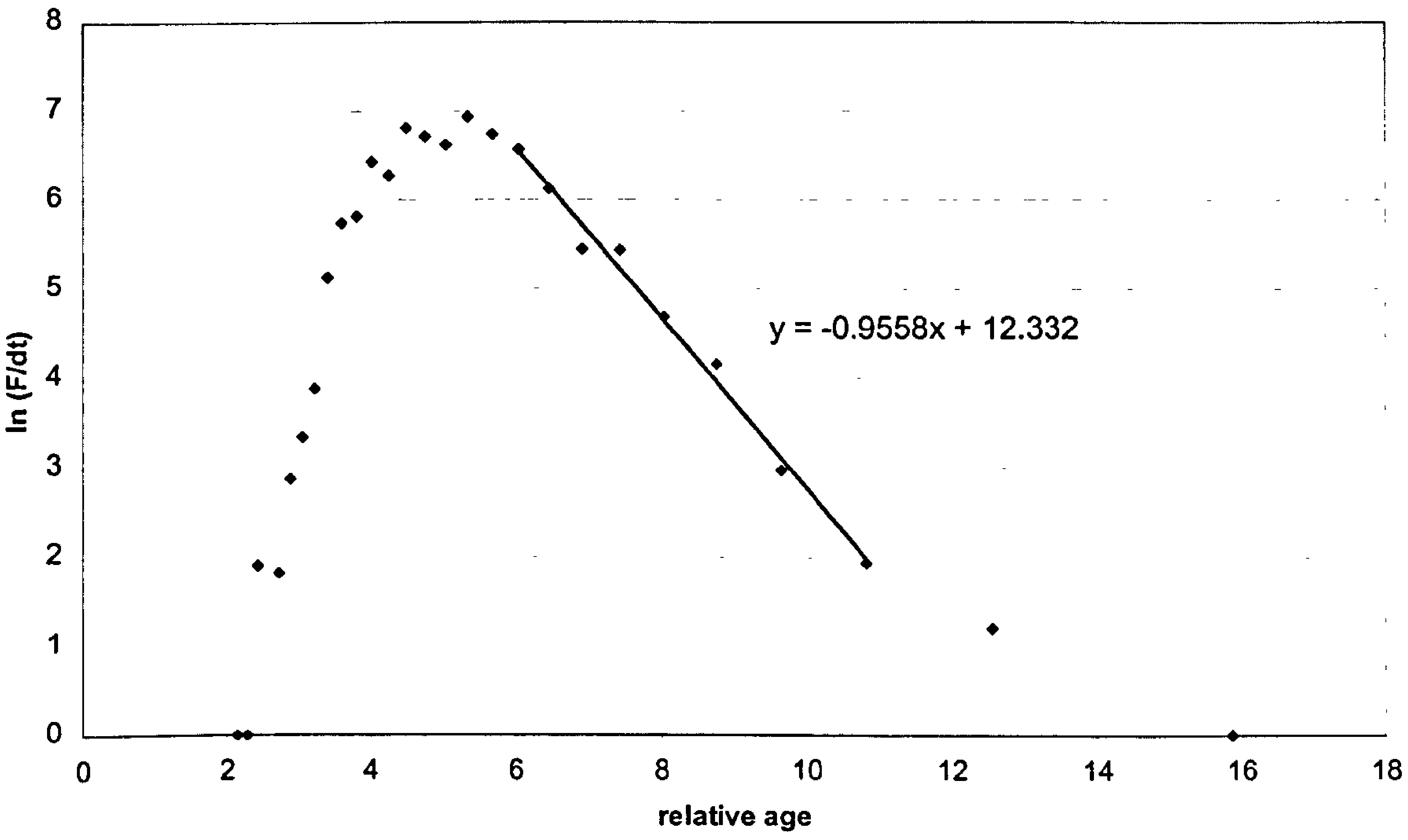


Figure 4.27 Length converted catch curve for males 2000

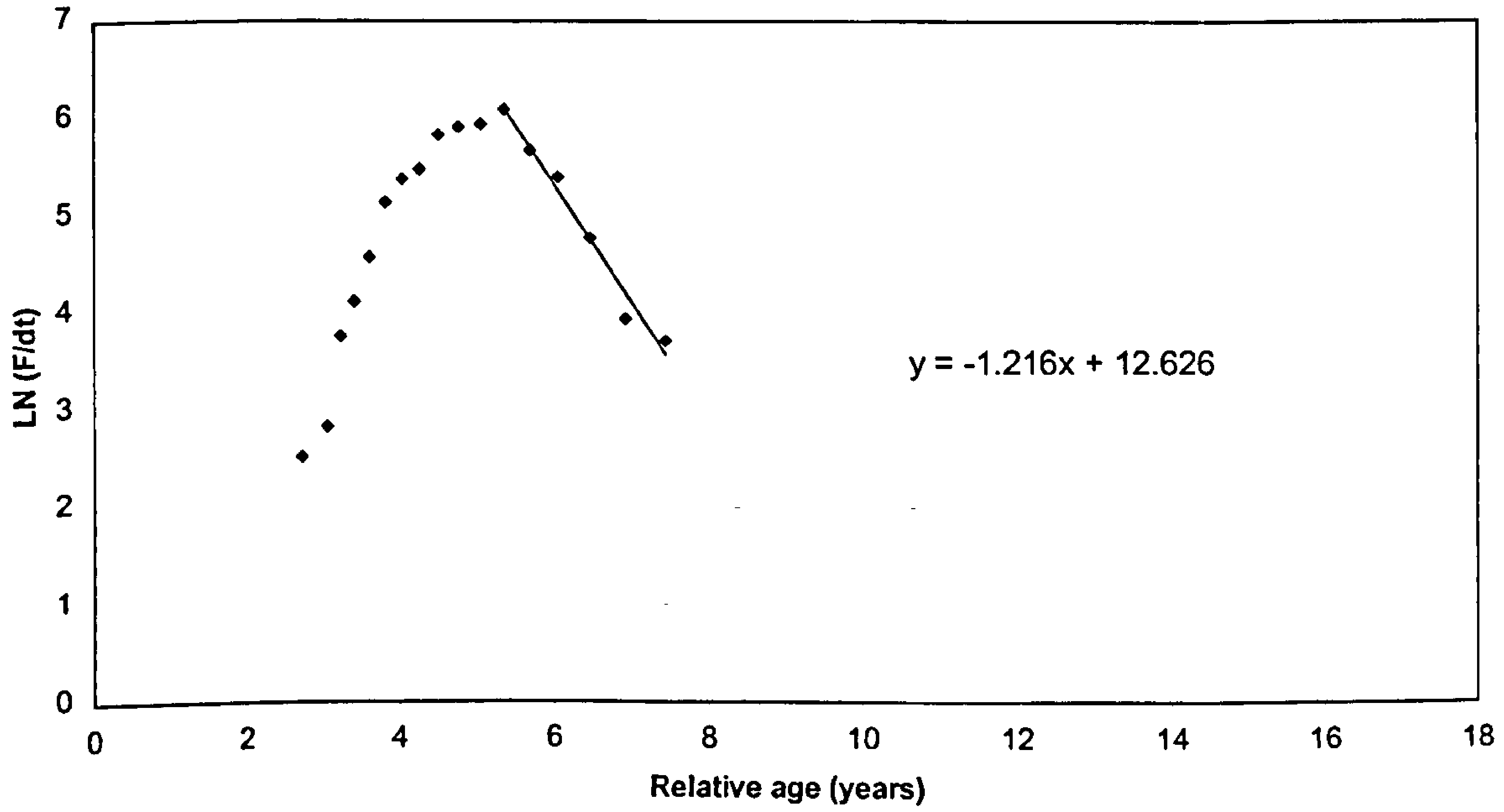


Figure 4.28 Length converted catch curve for females 1999

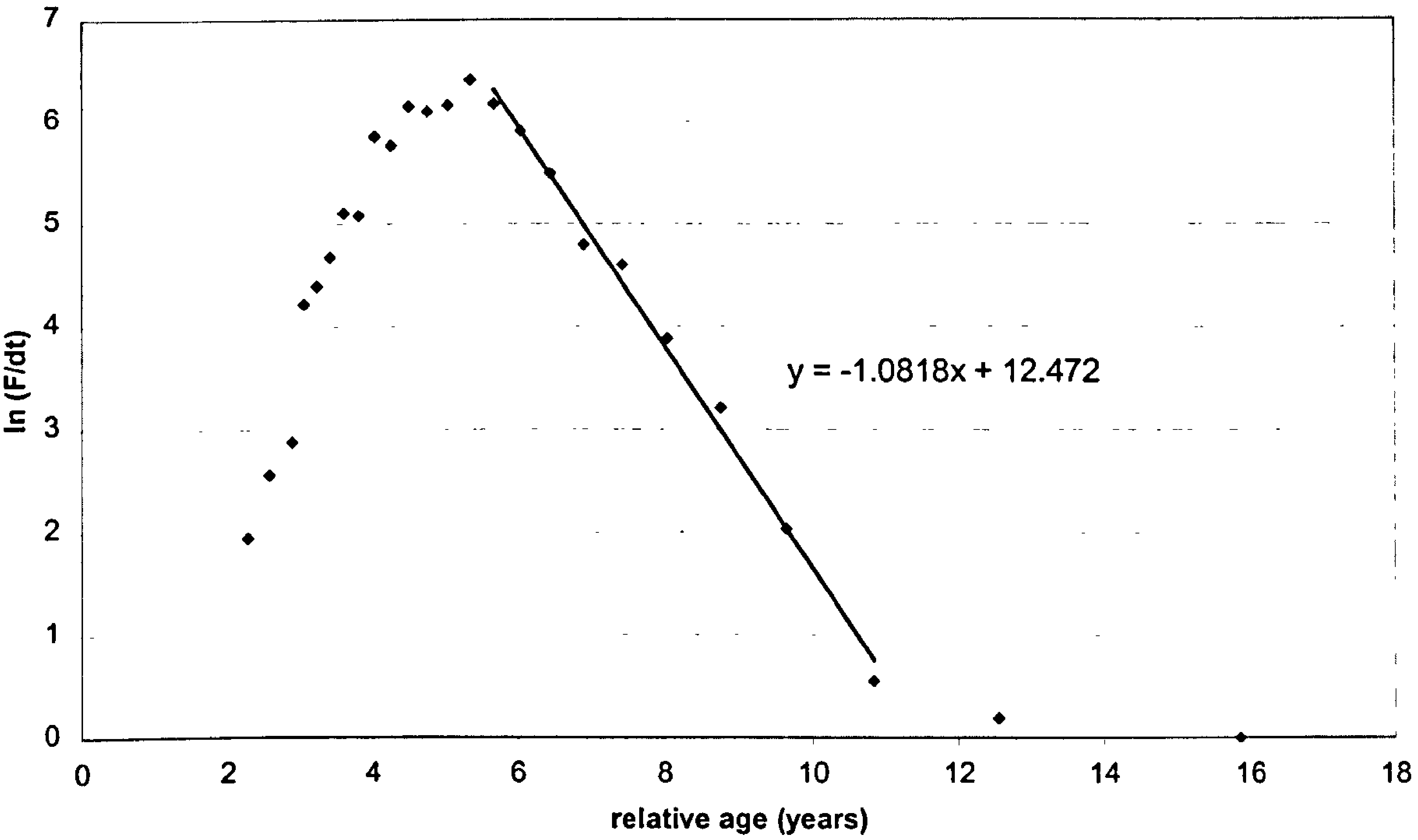


Figure 4.29 Length converted catch curve for females 2000

From the curves, total mortality (Z) was calculated to be:

Males 1999	Males 2000	Females 1999	Females 2000
1.066	0.956	1.216	1.082

Table 4.9 Estimates of total mortality (Z)

Natural mortality was the hardest figure to estimate because all the methods used are simple approximations. M, as estimated using the Alagaraja (1984) method, and taking longevity to be 10 years. Thus:

$$M1\% = -\ln(0.01) / 10 = 0.46$$

This can be compared with the result given by use of the Rikhter and Efanov (Rikhter *et al.* 1977) model, using 3 years as the age of massive maturation. Thus:

$$M = 1.521 / (3^{0.720}) - 0.155 = 0.535$$

The Pauly approximation gave M values of:

$$\mathbf{M = -0.0152 - 0.279*ln98.4 + 0.6543*ln0.268 + 0.463*ln9.74 = 0.33}$$

These figures are very different from one another, but it would appear that, if the range of M for the Spanish stock, which exhibits fast growth and short life-span, is between 0.3 and 0.6, then the figure should be lower for the Orkney stock. In this sense, it may be sensible to use a range of M values lower than 0.5 for further work.

If M is subtracted from Z, an approximation of fishing mortality (F) is obtained. The ranges for Z, M and F are summarised in Table 4.10 below.

Parameter	Male	Female
Z	0.956-1.066	1.082-1.216
M	0.2-0.5 (?)	0.2-0.5 (?)
F	0.456-0.8066	0.582-1.016

Table 4.10 Summary of mortality figures for *Necora puber*

The results show similar figures for males and females, but with slightly higher mortality values for females in all types of mortality.

4.3.9 Simulations

Figure 4.30 shows the simulated size-structure of a population of velvet crabs assuming the growth parameters obtained from section 3B ($L\infty$ = 98.4, K = 0.268). This simulation assumes all individuals moult at the same time, but with a variation of 10% around K. The variation around K was assigned randomly for each individual during each year, so the actual value of K for an individual bore no relation to its value in the previous year.

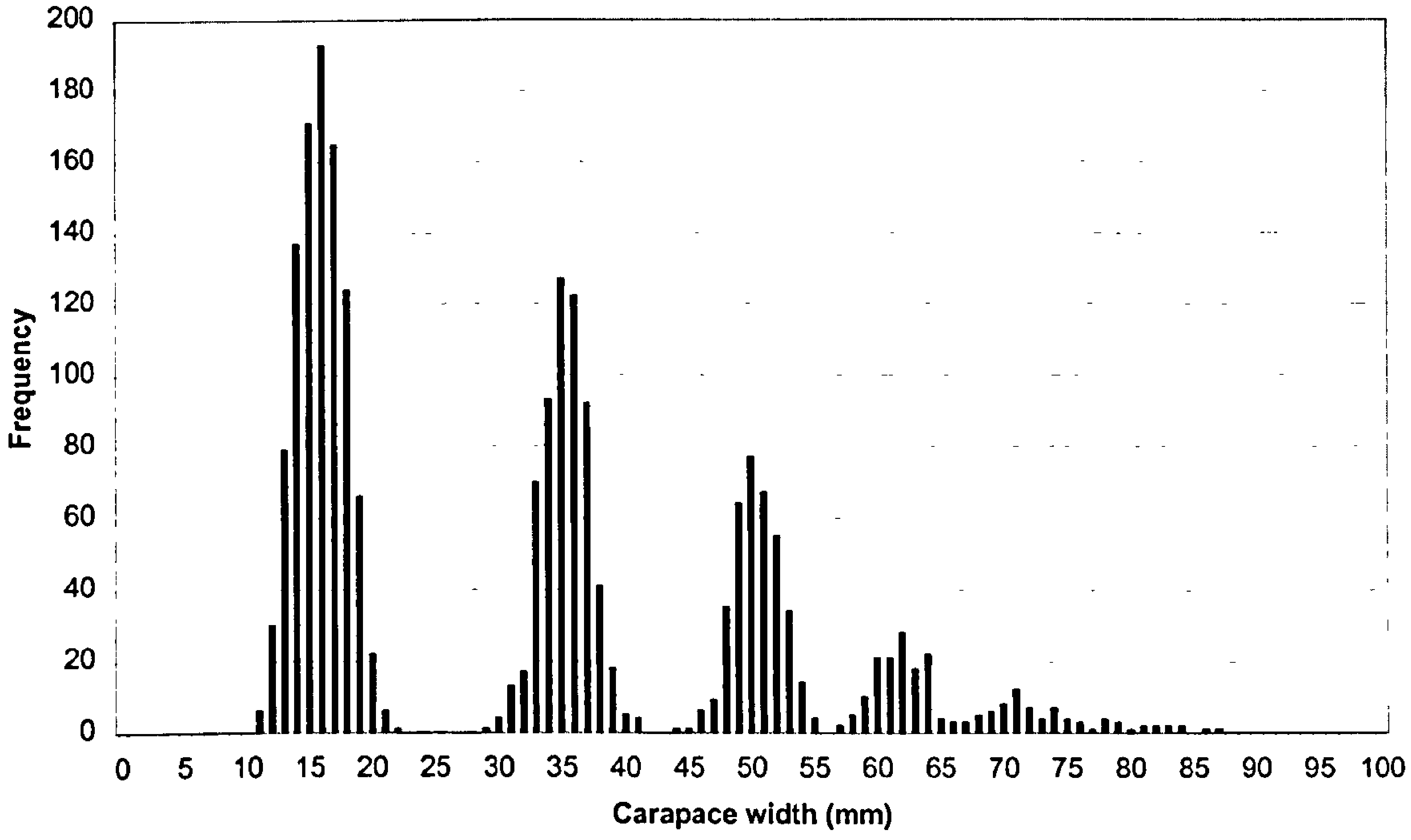


Figure 4.30 Simulated velvet crab population (M=0.5, F=0.5)

The population structure constructed using this model does not follow the pattern shown by the monthly samples found in the wild, nor to the juvenile size-distribution patterns displayed during beach sampling. It would therefore seem that variations in K alone are not enough to explain the variations seen in the wild.

Figure 4.31 shows the resulting population structure of the velvet crab according to the simulation based on moult increments, and including a natural mortality of 0.5, with no fishing involved.

This assumes that each moult stage is present at all times in equal proportions (allowing for mortality). However, this is not the case in the wild. The model can be used to illustrate expected findings on surveys at different times of the year, with different weight given to different moult sizes, depending on the month. Thus, for May, the 10mm moult size might be fully represented, with a small proportion of the following moult size, and none of the following few moults. The 34mm moult size might be fully represented and those moult sizes immediately before and after may be partially represented. All adult sizes would be expected to be present at all times.

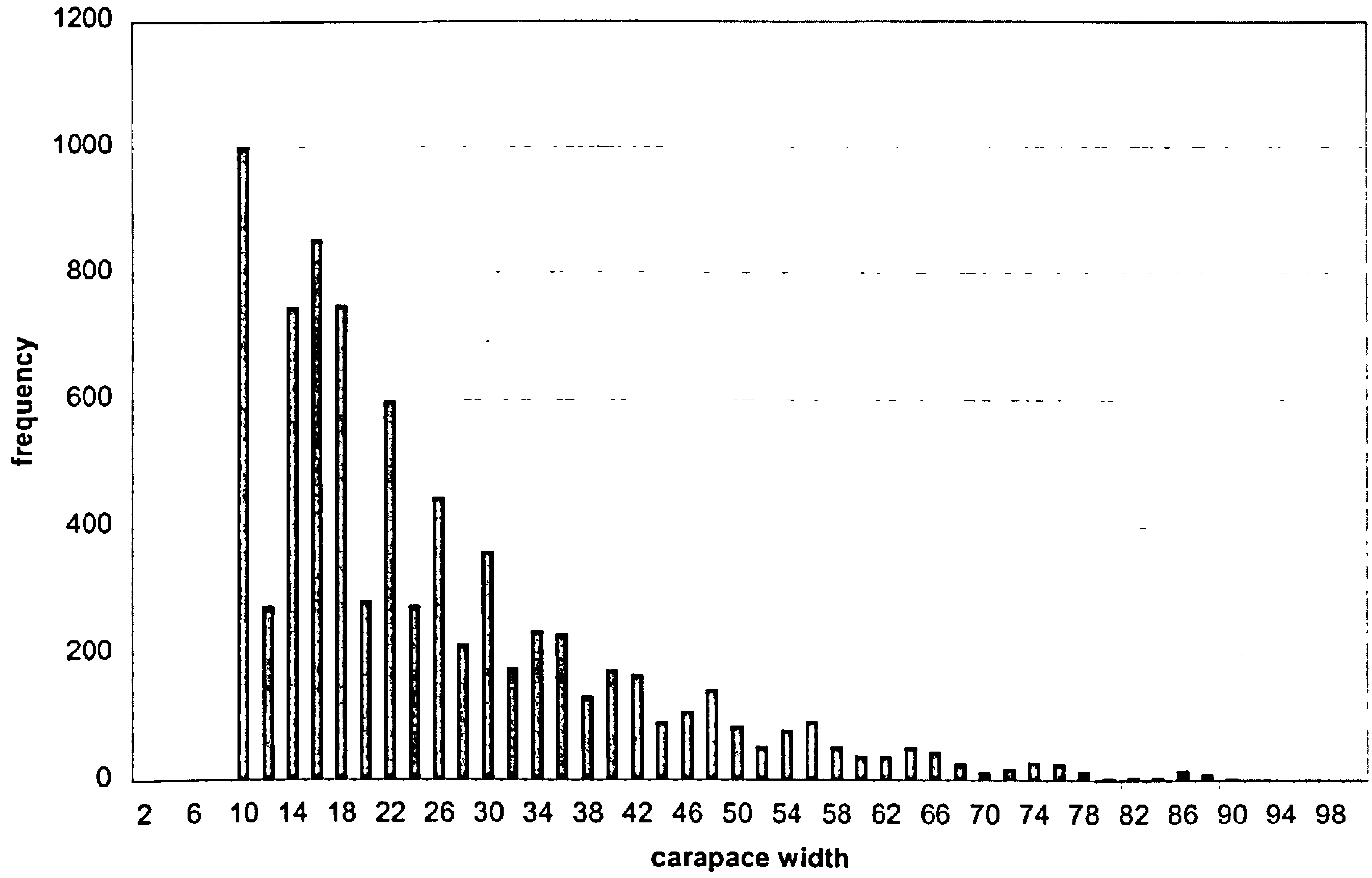


Figure 4.31 Moult increment simulation of a population of velvet crabs (M=0.5, F=0)

Figure 4.32 shows the predicted population structure for May, after differing proportionality coefficients have been applied to each moult size.

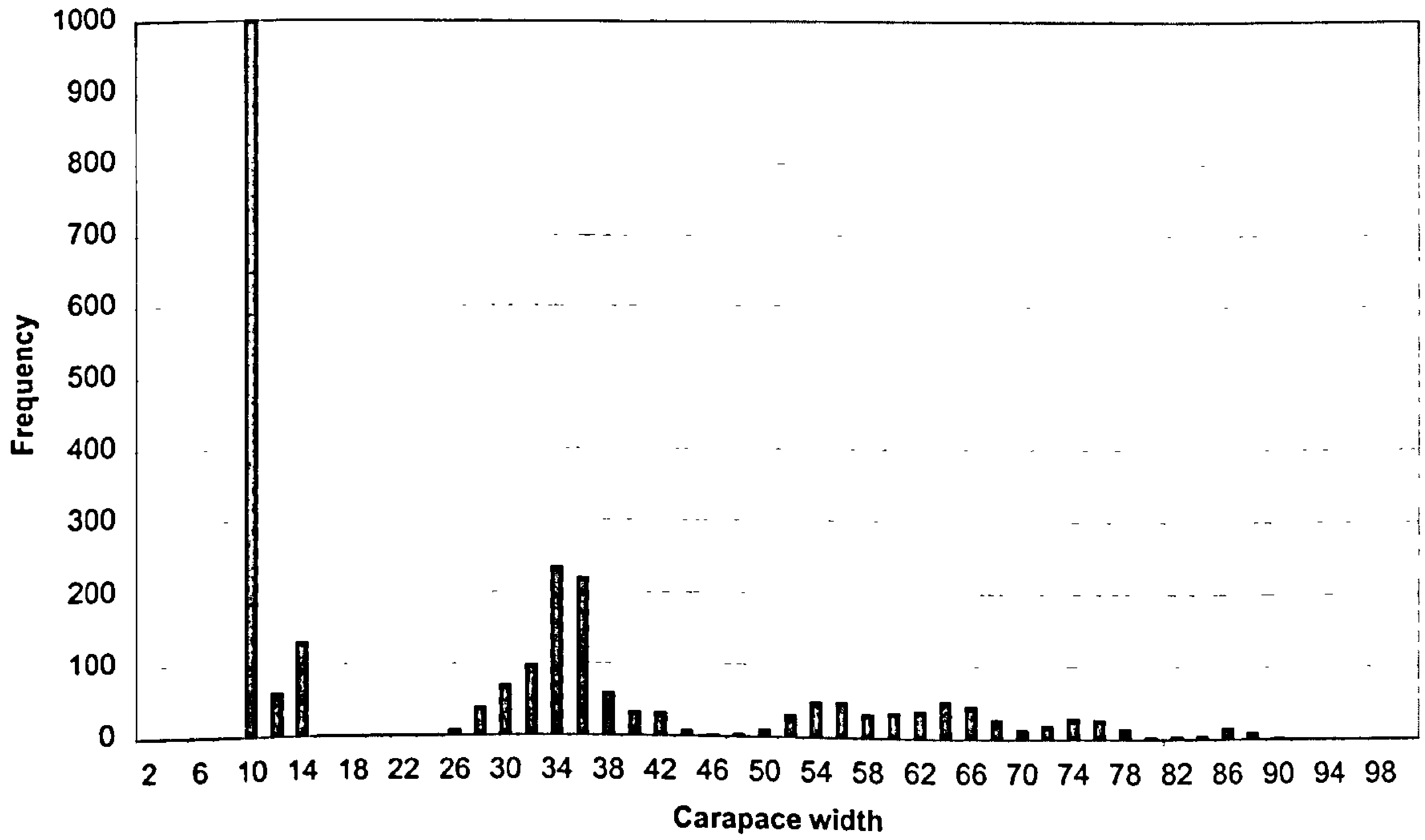


Figure 4.32 Simulated population structure (M=0.5, F=0) for May, using moult increments.

If this graph is compared with those graphs for May at Gritness, Gurness and Westness beaches (Section 3B, Figures 3.13-15), it can be seen that there is a closer resemblance than from the graph in Figure 4.30. There are two clear modal points, after which the pattern breaks down somewhat, making identification of modal sizes more difficult. Expected patterns can be produced for each month, once information about the proportion of individuals at each moult size is available.

4.4 Discussion

The general length-width and weight-width relationships of the velvet crabs in the Orkney stock are comparable with those in other studies in the UK (Bakir, 1990; Kinnear and Mason, 1987; Tallack, 1998). However, they are slightly different from the study carried out in Galicia (González-Gurriarán, 1981, 1985b), where there was more of a difference between males and females in terms of carapace shape. Females in that study appeared to be slightly longer in proportion to width. Bakir (1990) found there to be no significant difference in the CW:CL ratio between the sexes, and suggested that the weight differences were mainly due to the positive allometry displayed by the chelae after puberty.

The differences displayed between the sexes once puberty has been attained can be attributed to reproductive functions. The increase in positive allometry displayed by males in terms of the growth of their appendages, and especially, the chelae, implies a greater increase in weight compared to females, whose energy is diverted to egg production rather than chelar growth.

The sex ratio of mature individuals was overall male biased (1.86:1). This was also the case in Plymouth (Norman and Jones, 1992), where the overall sex ratio was 1.46:1 biased towards males. They found evidence to suggest that this was partly due to an offshore movement of females over the winter months. Bakir (1990) also found a sex ratio heavily biased towards males (3.1:1), also suggesting that offshore migration was partly responsible for this. As eggs display a low tolerance to reduced temperature and salinity (Choy, 1991; Mene *et al*, 1991; Valdés *et al*, 1991) females leave the littoral zone in search of more constant conditions in deeper water.

However, there is little evidence for long distance migratory behaviour (Kinnear and Mason, 1987; Bakir, 1990), and this movement may be of only a few metres (Norman and Jones, 1992). Choy (1988) found a strong male bias throughout most of the year (1.8:1), although from December to April in the sublittoral he found a higher proportion of females.

Differences in sex ratio may be due to a number of reasons, including migration of part of the population, increased predator pressure (or mortality in general) on one of the sexes, or sampling bias (Norman and Jones, 1992). In the case of this study, Figure 4.6 provides evidence that sampling bias may be the main reason for this difference. The low numbers of females found between February and June correspond to the period when females are ovigerous, and known to feed less (Choy, 1986b; Norman, 1989). If they are also moving offshore at this time, then both factors will combine to give a predominantly male sample. The proportion of females rises in early summer and becomes larger than that of males at the time of the male moult. This is also due to sampling bias, as males undergoing moult are unlikely to enter creels. The moult process is when individuals are at their most vulnerable, so crabs tend to hide until their carapace is hard enough not to be threatened. The ratio changes again in favour of males after this, coinciding with the female moult, during which mating also occurs. In the last months prior to spawning, the proportion of females rises once again. It is possible that females feed more than males during this time, as a preparation for the ovigerous period, when they consume much less. No significant difference was found between the numbers of males and females in the juvenile sampling programmes, which suggests that, unless there is a large difference in mortality, the nominal sex ratio of the stock is 1:1 and that differences arise due to sampling techniques.

As creels are passive fishing tools, they are very susceptible to behavioural changes in the population regarding diet and feeding, and for this reason above others, sampling bias must be considered the main factor in the changes in sex ratio. Whether this bias towards males will have an effect on the population structure in the long term, remains to be seen. However, if fishing activity is selective towards males both in terms of the gear and the practice of returning ovigerous females to the sea, it is possible that this may have a long-term effect on the reproductive capability of the population.

The moult cycle displayed by the Orkney stock is a clear yearly moult pattern, with males moulting in the months of July-August, and females moulting in the months of September-October. Recently moulted animals are less likely to enter traps because they display cryptic behaviour due to their vulnerability. Soft females are even less likely to enter traps than soft males, because at the time of the moult, they are accompanied and protected by males, and this is when copulation occurs. The male tends to stay with the female for a few days after the moult has been completed (González-Gurriarán, 1985b), and it is usually not until after this that she begins to feed.

Moulting occurred once a year in Irish stocks (Bakir, 1990), with males moulting from April to July, and females from May to August. Choy (1986b) found a male moulting period between April and July, and a female moult period between September and November. Norman (1989) found that males moulted in summer and females in autumn. All these studies carried out in the United Kingdom follow a similar trend in that moulting occurs on a yearly basis, and that males moult before females. The reason for the delay in the female moult may be related to reproduction. If the male must compete in order to gain the right to mate, and must then protect the female, it is an advantage to have moulted prior to this; the size of the male will be larger, and the condition of the chelae will be optimal. There is a difference however, in the length of this delay between the male and female moulting periods. In Plymouth and Swansea, the two periods are separated, whereas in Dalkey, they displayed some overlapping (although the scarcity of recently moulted individuals in this study may have distorted the results). In Orkney, the farthest north of the study sites, the time lag between male and female moults was the shortest of all the study areas. This may be attributed to the short summer period compressing all summer activity. In this sense, the peaks of moulting are more pronounced than in other areas.

The moult cycle in Galicia, as described by González-Gurriarán (1985b), displays considerable variations with respect to the cycles shown by British stocks. Individuals moult 11 times in their first year, 3 times in their second year and yearly after that, having a lifespan of four years. This may also be due to more favourable environmental conditions, in terms of temperature and food availability (the Galician stock of *Necora puber* inhabits the substrate beneath mussel rafts) allowing more rapid growth. The moult periods observed by González-Gurriarán were late spring/summer and winter for males and late summer and late winter for females.

Generally, British authors agree that that *Necora puber* undergoes several moults during its first year, a small number of moults in the second year, followed by yearly moults thereafter (Choy, 1986b; Norman, 1989; Bakir, 1990). The Orkney stock fits this pattern generally, although it appears to be the only stock where maturity does not occur until the third year. As discussed in section 3B, the Orkney stock undergoes around 7 moults in its first year, 5 in its second, 2-3 in its third, followed by yearly moults once sexual maturity has been attained. Photoperiod may be an important factor controlling the moult cycle (Passano, 1960). If this is the case, it is not surprising that in Orkney, with its short summer, the stock takes longer to go through the necessary moults to achieve sexual maturity.

The growth increment at moulting was observed during this study and found to be extremely variable under laboratory conditions. Traditionally, growth in crustaceans was thought to be in the form of a fixed percentage length or width increment at each moult (Przibram, 1929). This was usually in the order of 25% (doubling in size). However, this has proved not to be the case in this study and in other studies under laboratory conditions. González-Gurriarán (1981) found the laboratory growth factor to vary between 13.95-31.03%. He noted that only individuals moulting within a few days of capture were taken into account, as time spent in the laboratory reduced growth. Norman (1989) explained the growth differences between wild and laboratory females as linked to problems in spawning for laboratory females in unfavourable conditions. It was concluded that laboratory observations were unreliable as estimates of growth patterns in the wild.

The growth parameters of *Necora puber* have been studied previously for different stocks (González-Gurriarán, 1981, 1985b; Choy, 1986b; Norman, 1989; Bakir, 1990). Most of these studies have relied on the discrimination of modal groups from size-frequency distributions. Norman (1989) states that this can readily be carried out with juvenile instars, but that definition of adult year classes is limited to species with determinate growth and those with terminal anecdysis at sexual maturity. Hartnoll (1982, 1985) suggests that there is no clear growth pattern for portunids. This study suggests that this holds true for *Necora puber*, with the most reliable results being those based on juvenile sizes rather than adults. Possible reasons for this are discussed later in this section.

These studies showed that *Necora puber* is subject to plasticity in terms of its growth and development. Table 4.11 summarises the main growth parameters for *Necora puber* in different areas, bearing in mind that different methods were used.

Study	**Parameter**	**Male**	**Female**
Wilhelm (1995)	$L\infty$	111	100
Brittany	K	0.55	0.7
Bakir (1990)	$L\infty$	103	94
Ireland	K	0.53	0.8
	t_0	-0.046	-0.033
Norman (1989)	$L\infty$	107.25	97.8
Plymouth	K	0.337	0.363
	t_0	-0.214	-0.268
Choy (1986)	$L\infty$	107	83
Swansea	K	0.608	0.65
	t_0	-0.03	-0.05
González-Gurriarán (1985b)	$L\infty$	109	96
Galicia	K	0.65	0.67
	t_0	-0.041	-0.048
Current study	$L\infty$	98.4	98.4
Orkney	K	0.268	0.268
	t_0	0.345	0.345

Table 4.11 Growth parameters estimated for different stocks.

The table shows that the Orkney stock achieves a slightly smaller asymptotic length than in other stocks. The Orkney figures displayed are those obtained from the juvenile sampling programme. Hence, they are the same for both sexes, as growth differences between the sexes do not occur until puberty (González-Gurriarán, 1985b; Choy, 1986b; Norman, 1989). Female growth may be slightly slower, with a lower L∞ than males, if females in Orkney follow the same pattern as in other areas.

The main observable difference between the Orkney and other stocks is the K-value. It is the lowest value of all the stocks. This is not surprising, as growth rate is linked to ambient temperature (and therefore to latitude). The metabolic rate of crabs is slower in cooler waters, and they feed less. However, some results are surprising, such as the 0.8 K-value for females at Dalkey (Bakir, 1990). Not only is this far higher than the value for males, but it is also higher than values for the Spanish stock (González-Gurriarán, 1985b), which is in warmer waters. However, the growth parameters for Dalkey were based entirely on an adult population, so should be viewed with caution.

Various studies have been conducted to determine the life span and maximum size attained by *N. puber*. The results vary according to the geographical location of the site sampled. According to Gonzalez-Gurriarán (1981, 1985b) the velvet crab in Galician waters reaches a maximum size of 101-112mm CW for males and 89.3mm for females and has a life span of 4 years. Choy (1986b) identifies a maximum size of 78-85mm for males and 68-73mm for females with terminal ecdysis occurring after 5.5 years. Bakir (1990) disagrees and finds no evidence of terminal ecdysis in Irish waters- crabs growing to a CW of 91-96mm for males and 90-92mm for females, showing a much smaller difference in size due to sex than those crabs studied in the other areas. According to Bakir (1990), the growth rate in females slows down after the first year and a half of life, corresponding to the time of the first brood. This would appear logical as energy reserves are diverted from growth to reproductive effort. However, it is data from the other areas, and not his that would point to this conclusion.

The current study shows a smaller asymptotic size, slower growth rates but a longer life span of around 10 years. In comparison with Gonzalez-Gurriarán (1981, 1985b), the actual number of moults over the life of a velvet crab is comparable. It appears that the moult frequency may therefore determine the life span of the animal.

The difficulty in determining cohorts from adult size-frequency distributions can be linked with the variation in moult sizes apparent at the juvenile stages (section 3B), as shown by the simulations in 4.3.9. According to Mauchline (1977), growth in crustaceans is a function of increments at moult and moulting frequency. The first population simulation assumed a random variation around K for each individual and each year causing a variation around a mean size. In actual fact, it is more likely that those individuals growing slowly initially, will continue to do so, with the same occurring with those growing faster than the mean. The variation around each moult size will then increase with increasing size. As puberty is not attained until the fifteenth moult, at this point, the overlap with make distinctions extremely blurred. Added to this, and more importantly, are the differences in the intermoult periodicity. With individuals taking different lengths of time to go through moult stages, added to the inherent variations around K, there comes a size at which age distinction is very difficult.

The reasons for the variation in intermoult time may be related to resources and competition. At the same time, the reproductive season is spread over a series of weeks, so those individuals settling earlier have a greater chance of undergoing more moult before the winter quiescent period.

The total mortality (Z) for the Orkney stock of *Necora puber* was 0.96-1.1 for males and 1.1-1.2 for females. The difference between the sexes is consistent with figures obtained in other areas. In Galicia (González-Gurriarán, 1985b), Z was estimated to be 1.53 for males and 1.79 for females, whilst in Swansea (Choy, 1986b), Z was estimated at 1.71 for males, and 2.01 for females. The fact that total mortality for a virtually unfished stock (Wales) is lower than total mortality for an overfished stock (Spain) is somewhat surprising. Choy (1986b) suggests that the reason for the high mortality figures with respect to the Spanish stock lies in the use of "peelers" (pre-moult crabs) by anglers for bait in summer. However, it is unlikely that a seasonal informal practice can account for such differences with a commercially exploited stock. Bakir (1990) studied an unexploited stock, therefore assuming that Z=M. He used the Pauly M equation (Pauly, 1980), which gave mortality figures of 0.58 for males and 0.79 for females. He suggested that this mortality differential between the sexes was responsible for the lower numbers of females obtained during the study. However, the use of the Pauly equation to determine Z is suspect, as this is an empirical equation derived from fish species. Choy (1986b) justifies his use of the Pauly equation to determine M, by referring to Pauly *et al.* (1984), where it is suggested that decapods are similar to small, high K-valued fish. Choy (1986b) estimated natural mortality to be 1.2-1.4; values which are double those estimated in this study. This may partly be explained by the different methodology in obtaining these results and partly by the much faster growth and therefore shorter life span of the species in Wales. González-Gurriarán (1985b) takes a range of values for M in carrying out stock assessment, and concludes that M must lie between 0.3-0.6. The methods used in this study, which relate M with longevity, age of sexual maturation and temperature respectively, gave comparable results (around 0.3-0.5). However, with the different life pattern displayed in Orkney, it is probable that M is overestimated for this stock.

The tagging programme was relatively unsuccessful in that very few returns were obtained. One of the main reasons for this is probably the small number of individuals which were tagged (only 1000). In a population as large as the velvet crab population in Orkney (see chapter 5, section B) at least ten times the number should have been tagged, if not more. At the same time, tag retention was a problem, possibly accounting for up to 30% of losses. Early laboratory studies showed a mortality of around 10% to be implicit in the tagging programme. Kinnear and Mason (1987) and Bakir (1990) also found problems of mortality from tagging. Bakir (1990) suggested that the presence of tags might inhibit moulting. The individuals recaptured in the current study were done so before the moult period, so increase in size was not expected. No individuals tagged and released before the moulting season were recaptured during or after the season. All recaptures occurred within a short time of release, so the only results that could be obtained from this were indications of movement. None of the four individuals which were recaptured had moved from their release area, a fact that suggests velvet crabs may be territorial in nature. Further work however, is necessary in order to verify this. A tagging programme for *Necora* *puber* is currently underway in Millport (pers. comm, Combes, Marine Lab Aberdeen) which is meeting with successful results.

In terms of the methods used to determine growth and mortality parameters, many of these were found to be either subjective or unreliable. ELEFAN gave results which deviated wildly from the true patterns displayed by the stock. The reason for this may be the same reason why size-frequency analysis of monthly creel samples was also suspect. It was not possible to split the size distributions obtained during the sampling programme into separate curves with any confidence. This was partly due to the limitations of the gear. Creels undersample small individuals. Very few individuals under 50mm CW were obtained from creels. This meant that only the sexually mature part of the population was being sampled, and the difficulty of this has already been mentioned (Hartnoll, 1982, 1985). The best indirect method for obtaining growth parameters was found to depend on the pre-pubertal stages, when modal sizes were more easily identifiable. If settlement time and frequency can be identified, and initial estimates of L_∞ from adult sampling obtained, use of juvenile size-frequency distributions gives more reliable estimates of K, at least for males.

Currently, fisheries management is based on the process of determining parameters (L_∞, K, Z etc.), which are not frequently revised for a given stock. In many cases, different methods to obtain these parameters achieve different results. However, it is likely that these parameters (especially those involving mortality) change from year to year and between cohorts. If a standardised method can be devised to obtain and quantify the pre-pubertal cohorts, then each year class can be taken in turn and managed depending on its own particular parameters. As there are around 4 years from settlement to entry into the fishery, this gives time to monitor a cohort and decide upon management strategies depending on the strength of that particular year.

The final values for the population parameters were decided upon, not as fixed absolutes obtained using a particular method, but as those values which were thought to best represent the stock using a range of methods. Thus, for the prediction models used in Section 5B, there is a consistency in these values. L_∞ was derived from initial estimates using the Pauly approximation and the Powell-Wetherall plot. Ranges of possible L_∞ values were applied to the von Bertalanffy growth equation in conjunction with ranges of possible K values. These were inferred from past literature, preliminary estimates using the first year group of juveniles, and size-frequency analysis of juvenile shore searches to find a best combination of $L\infty$ and K, which was found to be around 98.4 mm ($L\infty$) and 0.268 (K). The values were then compared with moult increment and frequency values (both from the laboratory and the wild). Whereas there were some indications of a difference in $L\infty$ (and therefore, probably K) between the sexes, this difference was so slight (less than 3mm) that, in the interests of simplicity for prediction models, it was ignored. Overall mortality values were simplified to $Z = 1$. However, as the confidence in the value of M is low, due to the methods used to obtain it, ranges of M values are used in further analysis.

PART 5: FACTORS AFFECTING THE FISHERY

Section A: Fishing Practice

5.1 Aims

Section 1.7 outlined some of the studies carried out regarding fishing practices on different shellfish species. Section 1.9.6 highlighted the fact that very little work had been aimed specifically at velvet crabs. The aim of this section is to address the effects of bait type and soak time on the velvet fishery in Orkney. The question of bait type in Orkney lies not so much in the species used, but in its condition. The first part of this study aims to determine whether there is a difference in catch using fresh, frozen or salted bait. The second part of the study is aimed at determining whether leaving creels for an extra day as opposed to the usual 24 hours has a positive effect on the catch. The numbers of lobsters caught throughout both parts of the study were recorded and used to analyse possible links between lobster and velvet crab catches.

Part of the reason for these studies was to determine whether changes in fishing practice over time would have an effect in terms of the accurate estimation of fishing effort if not considered appropriately. If determined to be important in the estimation of fishing effort, these results were to be included in section B of this chapter.

The most commonly used bait for catching velvet crabs is frozen skad or horse mackerel (*Trachurus trachurus*), which is bought in 9kg slabs from shellfish merchants at £9 a slab. One third or half a fish is placed in each bait bag. Fresh bait is considered by the fishermen as far superior, but is often difficult to obtain in large enough quantities. It is sometimes available in slabs for around £15. Salted bait is mainly used to catch lobsters. The theory behind salted bait is that it keeps other species out of the creels. An experiment was devised to determine whether the use of fresh, frozen or salted bait affects the amount of velvet crabs caught in a creel. Trials also took place to determine whether leaving creels for 2 days rather than 1 day would double the catch.

The questions asked in this section are summarised below.

1. Is there a difference between fresh, frozen and salted bait?
2. Does soak time affect catch?
3. What are the reasons for creels not fishing?
4. Do lobsters and crabs interfere with one another in terms of catch?

5.2 Methods and Materials

The study site was in Wass Wick (59°04.95N: 003°01.54W), an east facing bay on West Mainland in Orkney. The substrate in the area was rocky hugging the coastline, with abundant wracks and laminarians. The centre of the bay was characterised by rocky areas and sandy patches, where green crabs *(Carcinus maenas*) were abundant. The waters were tidal, with a depth varying from 1.5-6m. Sampling was carried out from 16-29 April, 2000, and the water temperature was 9.5°C.

All the creels used in this experiment were of the following design: a rectangular steel base 66cm by 45cm and 38cm high, with two soft eyes. The mesh size used was 4cm at full stretch. The bait bags were suspended in the centre of the creels.

For the bait experiments, three backropes of 10 creels were used. Each creel was separated by 5m from its neighbour. On each rope, alternating creels were marked and baited with fresh or frozen bait. These were checked daily for five days and the catch recorded, in terms of size, species and sex in each creel. The procedure was repeated, using frozen (as the most commonly used) and salted bait.

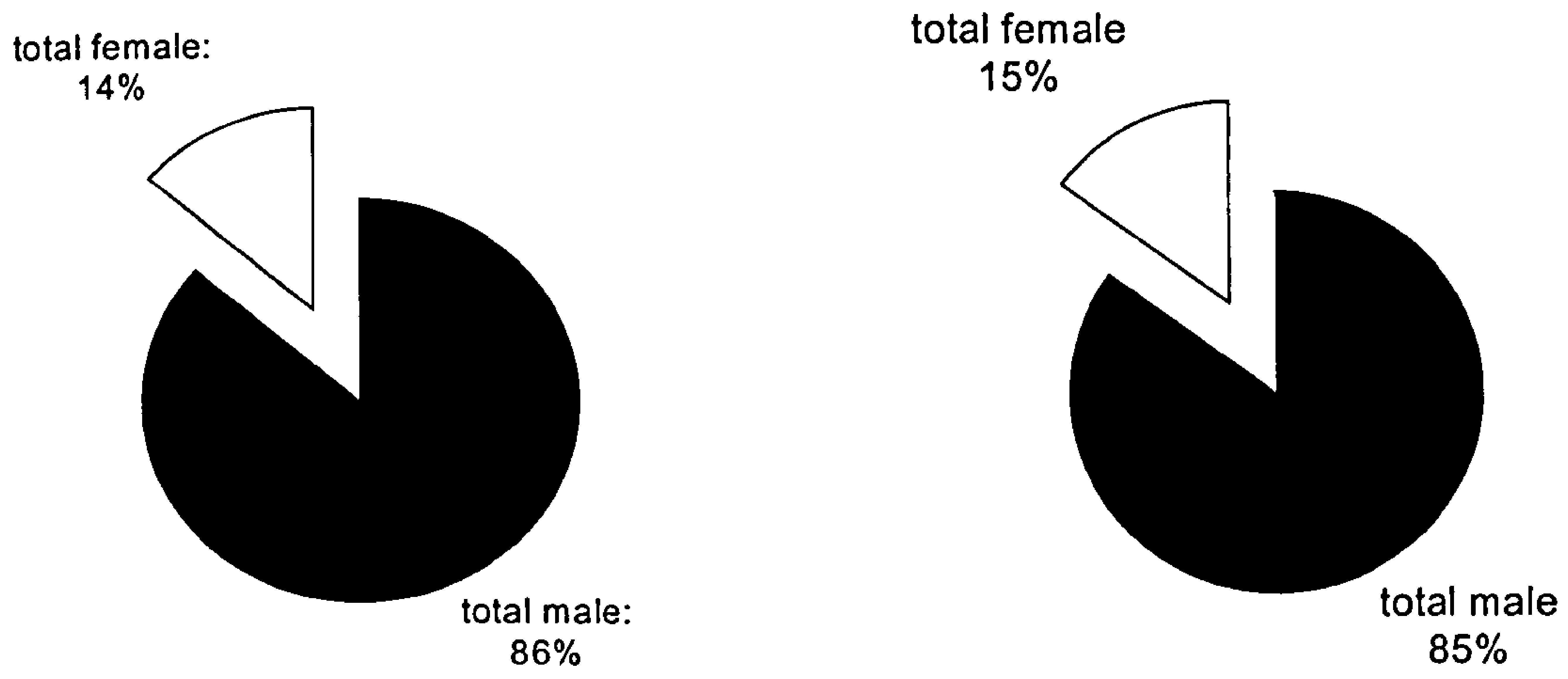
In order to examine the effects of different soak times, twenty single creels were numbered and shot randomly into the study area. Creels 1-10 were hauled and re-baited daily, whilst 11-20 every two days. For each creel, number, size, sex and species were recorded over a period of ten days (Dataset 6, Appendix A).

In all trials, effort was made to set the creels as close to the shore as possible, this being regarded traditionally as the best fishing ground (various fishermen, pers. comm.). Further into the bay, sandy areas of low velvet crab density, sometimes unavoidable, would detract from the aims of this study.

5.3 Results

5.3.1 Bait

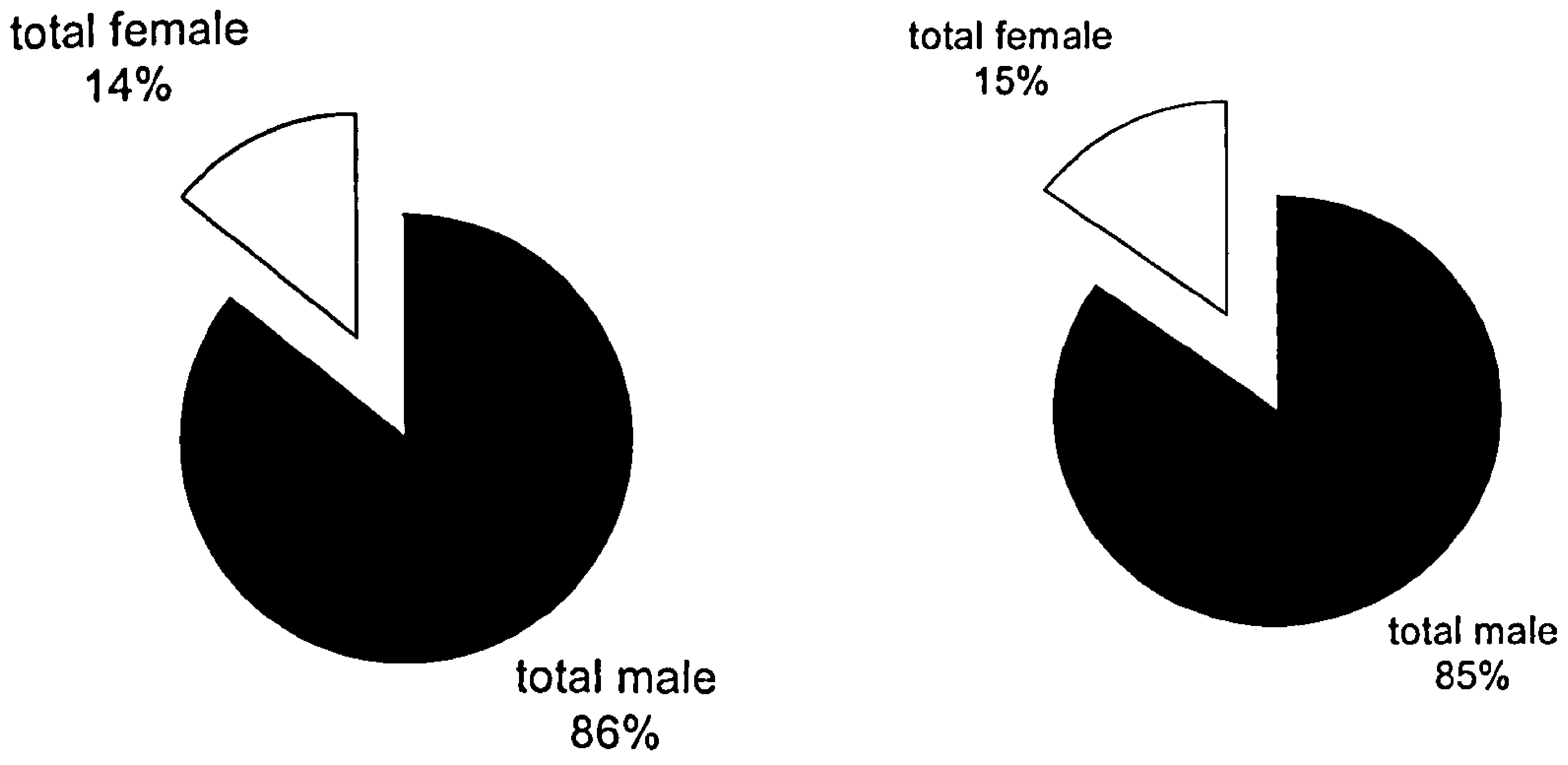
Figures 5.1 and 5.2 show the sex ratio of velvet crabs caught using fresh-frozen and salted-frozen bait regimes.



Fresh bait

Frozen bait

Figure 5.1 Sex ratio of catch (fresh and frozen bait)



Salted bait

Frozen bait

Figure 5.2 Sex ratio of catch (salted and frozen bait)

The first point to notice is the imbalance between males and females caught during these trials. In a stable population, a 1:1 ratio of males to females should be expected. However, this ratio does not occur in this situation. There is a large imbalance towards male dominance in all trials to an almost identical extent (86% : 14% for both fresh and salted bait, and 85% : 15% in both trials for frozen bait). There is no significant difference in the sex ratios caught with fresh, salted and frozen bait.

The individuals caught in these trials were sized and grouped into four categories: discard (those individuals which were either undersized (<65mm CW)), berried (and therefore not saleable), small (CW 65-75mm) and large (CW >75mm). The results are summarised in Figures 5.3 and 5.4:

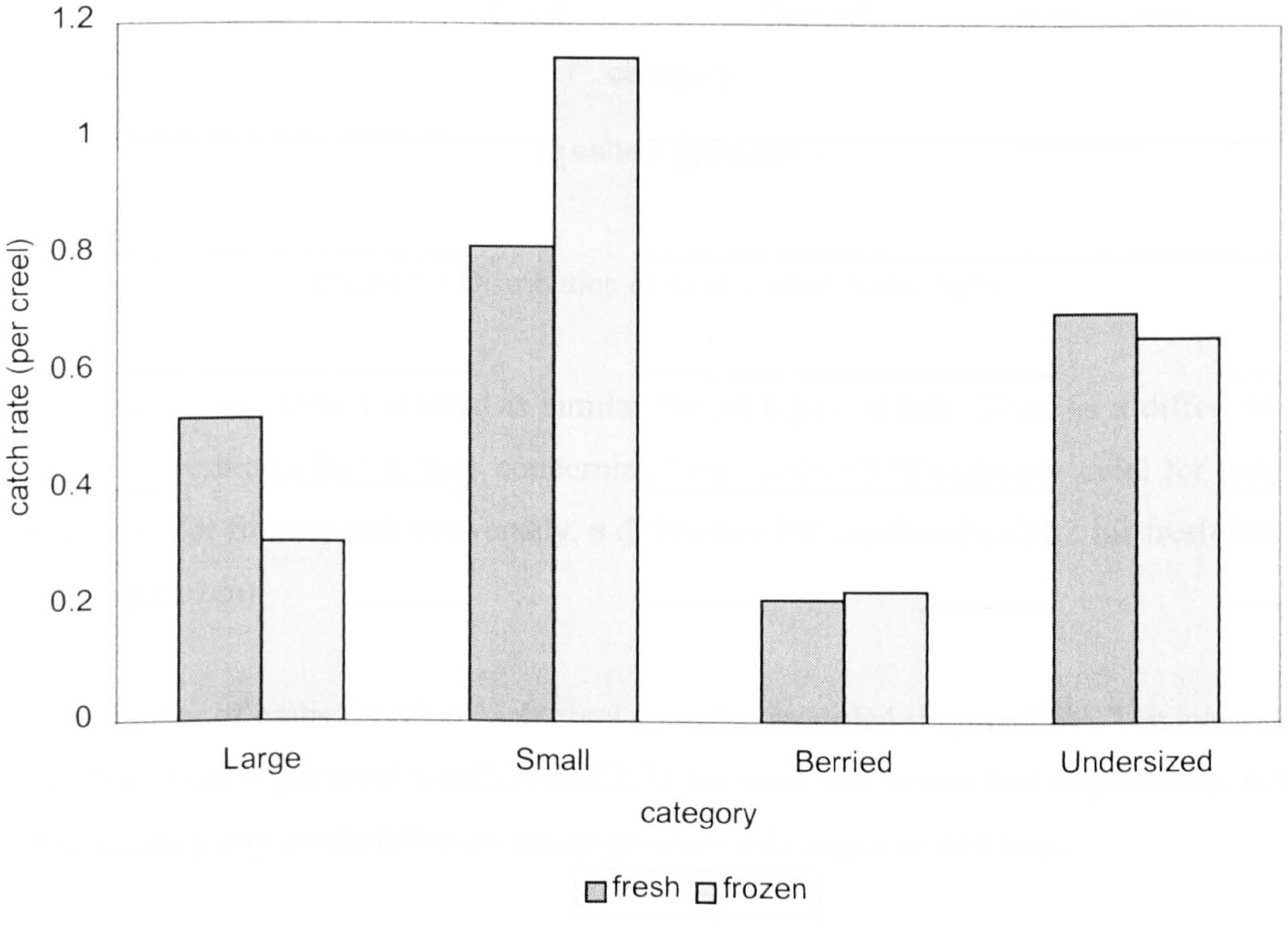


Figure 5.3 Distribution of catch (fresh-frozen bait)

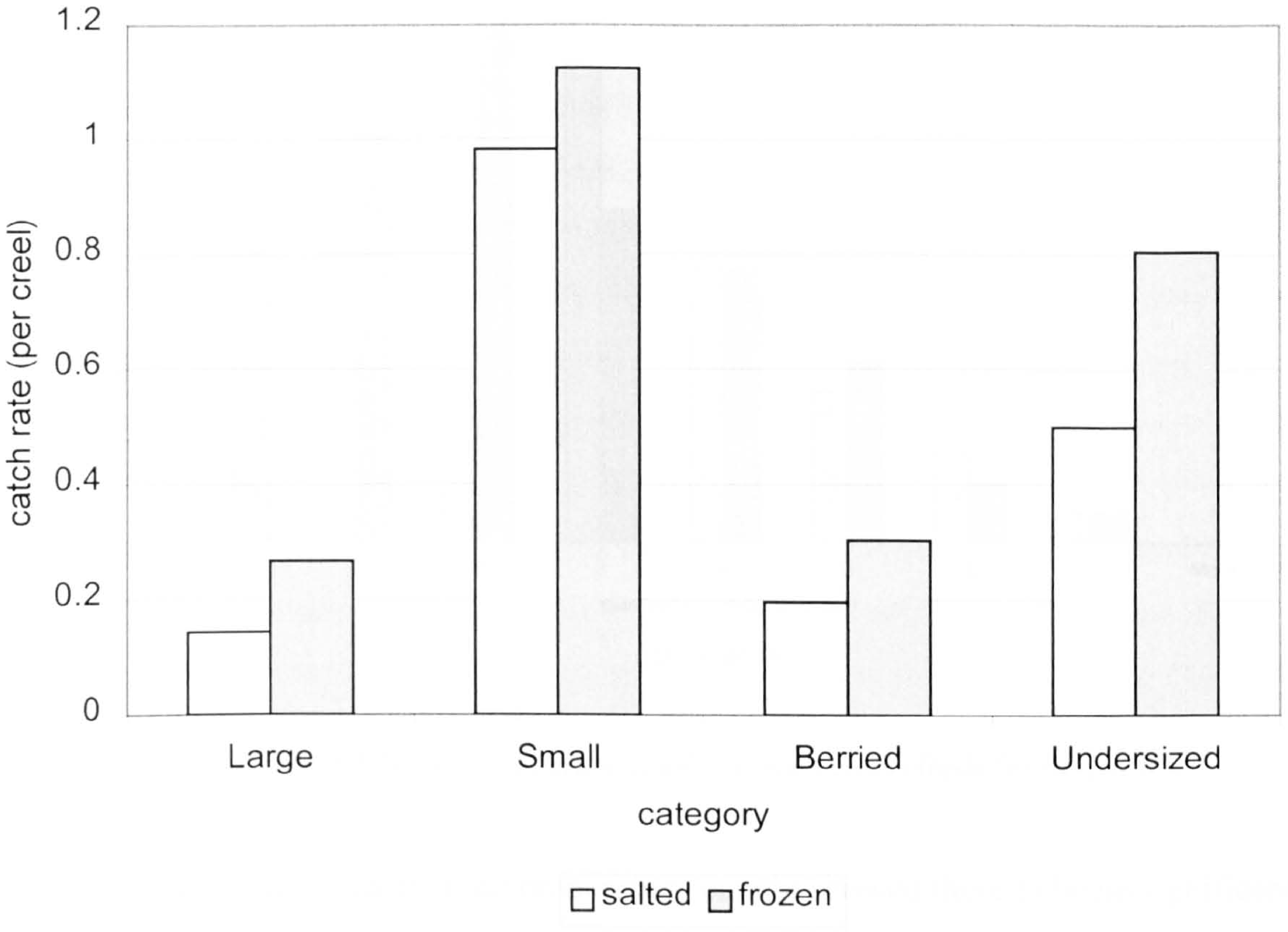


Figure 5.4 Distribution of catch (salted-frozen bait)

The amount of catch discarded is similar for all types of bait. There is a difference between fresh and frozen baits concerning large crabs (0.52 crabs per creel for fresh bait, 0.31 for frozen) and, conversely, a difference for small crabs (0.82 for fresh bait, 1.14 for frozen).

The number of crabs found in each creel was also recorded (Figure 5.5). The average number of crabs per creel was 2.24 and 2.33 for fresh and frozen bait respectively, not disregarding any creels fallen on sandy ground or damaged in any way.

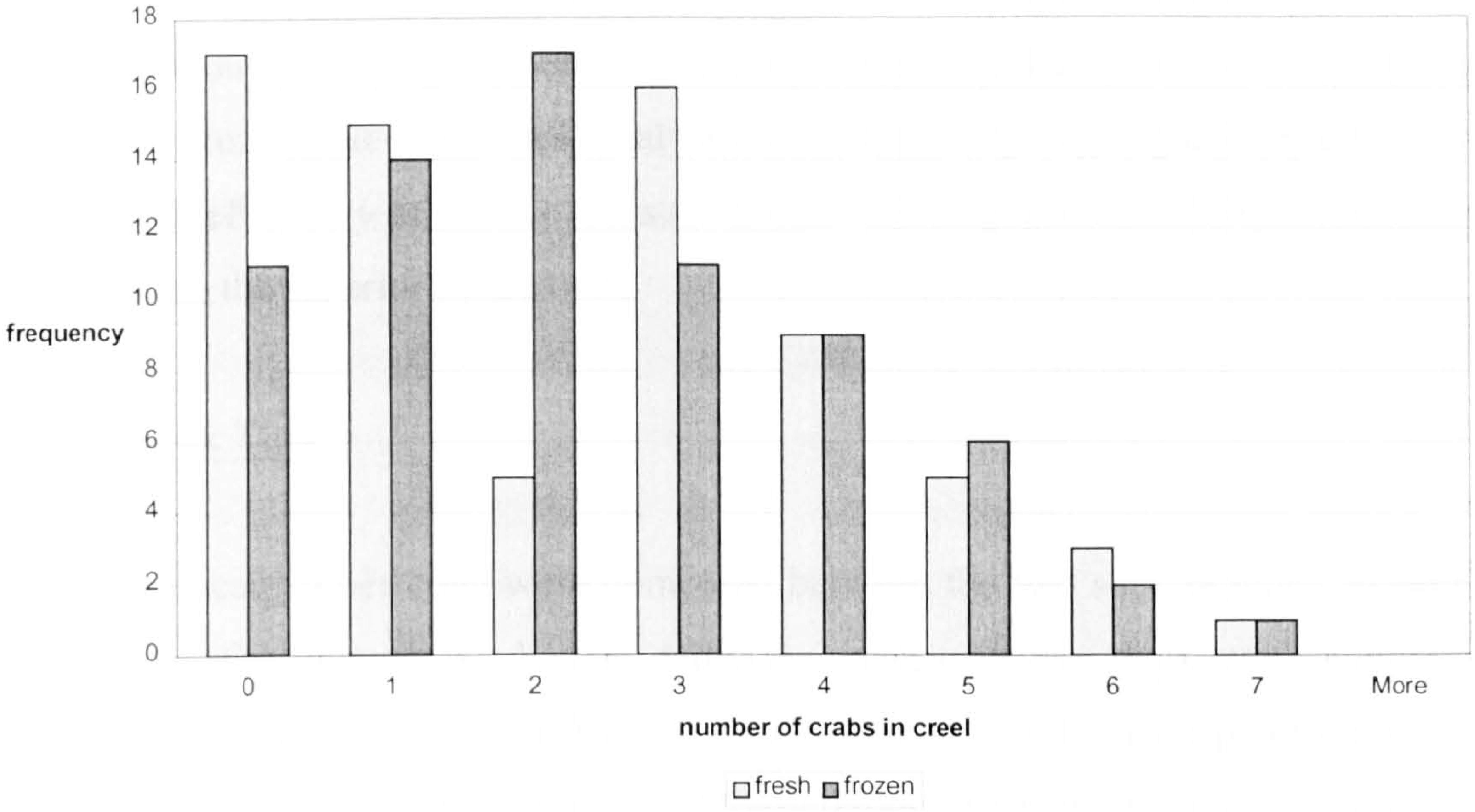


Figure 5.5 Numbers of crabs caught in each creel (fresh-frozen bait)

T-test data analysis carried out on numbers caught showed there to be no significant difference between the two baits (n=71, t=0.349).

Figure 5.6 shows the numbers caught per creel for salted versus frozen bait:

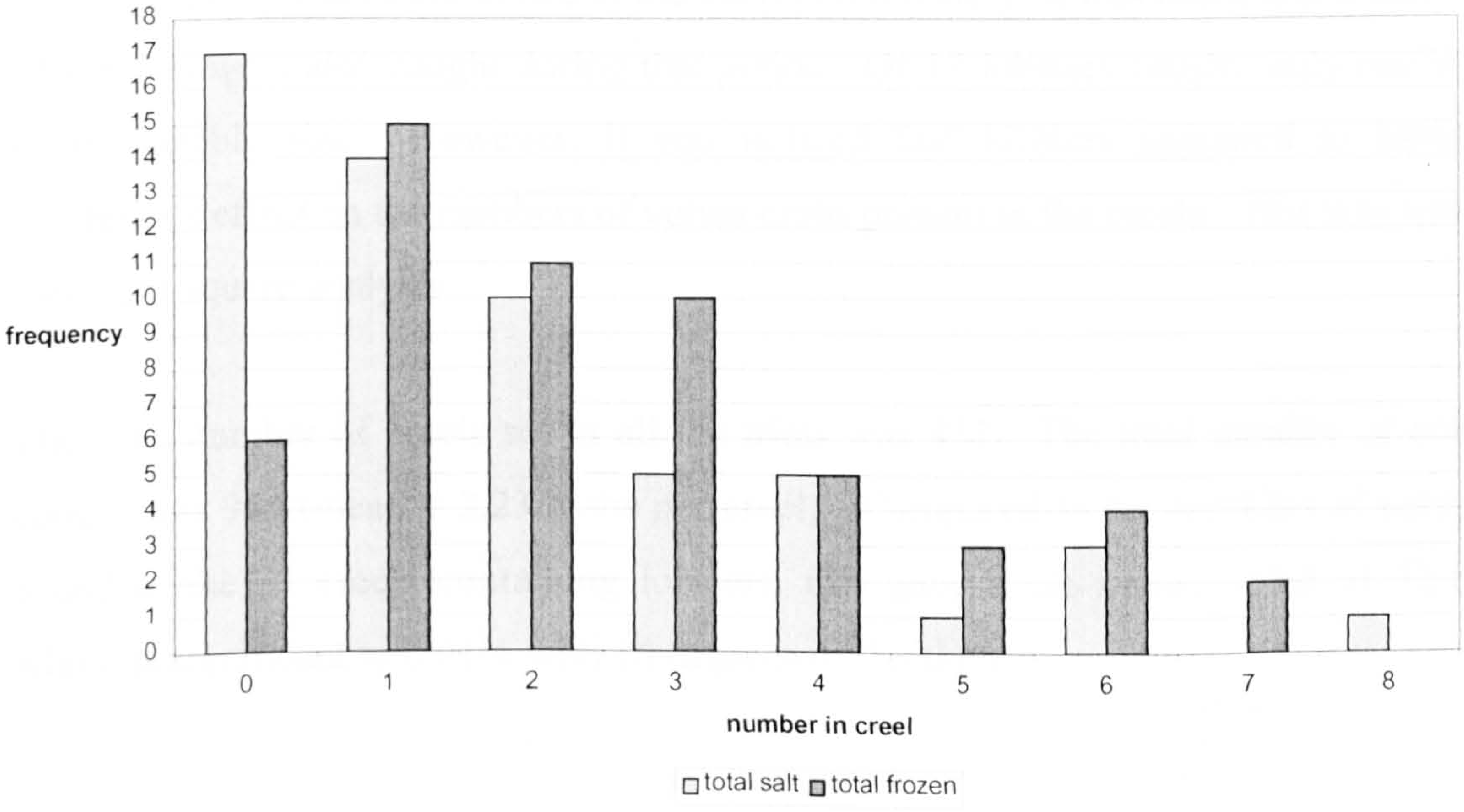


Figure 5.6 Numbers of crabs caught in each creel (salted-frozen bait)

The average number caught in each creel was 1.79 for salted bait and 2.5 for frozen bait. Although the range of numbers caught using salted bait (0-8) was slightly higher than for frozen bait (0-7), t-test analysis showed there to be a significant difference in the catch efficiency of the two baits (n=56, t=2.158, significant to 0.05%), with frozen bait being the superior of the two.

5.3.2 Soak Time

Numbers caught per creel were compared between the two soak regimes, using t-test analysis. For those creels hauled daily, the catch over two days was combined and compared with the single haul made every 48 hours to its corresponding creel. In order to reduce the effects of spatial differentiation, daily creels were set as closely as possible to their corresponding 2-day counterparts.

A total of 166 individuals were caught using a daily regime. 88 individuals were caught using the 2-day regime. This was found to be significant to 0.001% (t=3.52, n=50)

5.3.3 Effect of lobsters

Although these trials were aimed at the velvet crab fishery, it was noted that a number of lobsters were also caught during this period. Of 17 lobsters caught, only one was of marketable size. However, it was noticed that lobsters appeared to have a deleterious effect on the numbers of velvet crabs present in the creels. This was tested using chi-square analysis.

The total number of creels set in all the trials was 432. The total number of crabs caught was 964 (mean = 2.23 crabs per creel). Compared to the numbers of velvets found in the 17 creels containing lobsters, this gave a chi-square value of 32.13, which is significant to 0.01% with 16 degrees of freedom.

5.3.4 Empty Creels

Creels which did not contain any velvet crabs were examined for explanations. These are summarised in Table 5.1:

reason	number
Lobster	8
Sandy ground	73
Sea star around bait	8
Damaged creel	12
Other	7
Total	**108**

Table 5.1. Reasons for empty creels

As can be seen from the table, the main reason for no velvet catch is the creel falling on the wrong substrate. This was easily verified from the surface when the water was clear, and also by the abundant presence of green crabs in these creels. The damaged creels were fixed on hauling, but were not disregarded, so that the trials could resemble the real fishery as closely as possible.

5.4 Discussion

The sex ratio observed in these trials was constant throughout and coincided with other studies currently being undertaken in the same area. Whether this majority of males in the catch is a real reflection on the population as a whole in that area or is simply a result of behavioural differences between males and females, is not entirely clear. However, the operational sex ratio of crabs is often heavily male biased (Emlen and Oring, 1977), and the velvet swimming crab is no exception (Wilber, 1986; Choy, 1988; Smith, 1990). It is possible that egg-bearing females feed less than males and are therefore less vulnerable to traps. This has been proposed for *Homarus gammarus* (Branford, 1979) and *Homarus americanus* (Templeman and Tibbo, 1945) and corresponds with laboratory observations carried out in current studies in Orkney.

From the results, it can be seen that there is no significant difference between the use of fresh or frozen bait. Fresh bait has the disadvantage of not being as readily available as frozen bait, and is also approximately twice as expensive when purchased. Given this, and considering the amount of time potentially consumed in fishing for fresh bait, the current general practice of using frozen bait would appear to be sound. However, there is a possibility that the distance separating the creels is not sufficient, and that the crabs become confused as to the choice of bait. This would appear unlikely, as if this were the case, we should expect no differences between salted and frozen bait either.

Differences did arise when using salted bait, which is commonly used by fishermen in order to target lobsters. The thought behind this practice is that it keeps other animals out. Whereas this is not precisely the case, there is nevertheless a clear decrease in the numbers of velvets caught.

The trials examining soak times showed that only the shortest period is required in order to maximise the catch efficiency of each creel. Creels hauled daily obtained the same catch as those hauled every two days. It can be concluded from this, that an overnight soak, coinciding with the most active period of the species, is enough to keep the catch at its highest levels. Where this is not possible, due to weather or time constraints, it appears that the creels quickly reach a saturation point where either the rate of entry into the creel is equal to rate of escape, or the bait is stripped, and the numbers will remain constant, at least over 2 days. Although a soak time of one day may be the most efficient in terms purely of catch, other factors come into play in actual practice. Many fishermen use more creels than they are able to haul in one day, and so will alternate their fishing and leave them to soak for 48 hours or longer. The reason for this is partly in order to be able to cover more territory and exclude other boats from good ground. However, the weather often has a large role in determining the soak time. There are some areas that will only be accessible infrequently and at certain times of the year, so gear may have to be left for a number of days before it is possible to return and haul. Miller (1990) states that a fisherman may choose to use longer soak times in order to increase landings when catches are low. This is the case in Orkney, where many fishermen targeting lobsters will leave creels for a number of days before hauling them.

The negative effect of lobsters on the catch of velvets has been noticed locally. Lobsters have been known to prey on velvets, and this may be a reason for the avoidance on their part of creels containing lobsters. Another reason may be the defence of the bait by the lobster against any other creature seeking to enter the creel. However, the question must be asked as to whether the reverse is true. If velvet crabs tend to avoid creels containing lobsters, do lobsters also avoid creels containing a large number of velvet crabs? Another question arising from these results is whether the creels were empty before the lobsters entered them. It is possible that this is not the case, but that the presence of a lobster is an incentive for those velvet crabs in the creel to leave. If this is true, then the interaction of lobsters and velvet crabs in and around creels merits further study in order to determine at which density of velvet crabs the behaviour of the lobster changes from entering the creel to avoiding it. This may have consequences in terms of the fishery and the species targeted at specific times of the year.

Although the trials have shown that frozen bait in creels hauled every 24 hours is perhaps the best fishing regime to be practised, what it has also shown is that there is a large number of creels that do not catch the target species. There are a number of reasons for this. About 68% of the creels that did not contain a single velvet had fallen on sandy substrate, as could be verified from the surface and by the presence of green crabs in the catch. When setting a line consisting of a number of creels, it is difficult to ensure that all creels fall on the right ground. However, it is interesting to note that a distance of 5 metres may make the difference between an empty creel and one full of velvets. This indicates that velvet crabs are very substrate specific in their foraging behaviour and are unlikely to venture away from their preferred rocky substrate to feed. Of the remaining creels that did not contain velvets, 8 contained lobsters, another 8 had sea stars (*Asteris rubens*) tightly enveloping the bait and were otherwise empty, and the remaining few were either damaged or offered no explanation.

One of the initial reasons for this study was to determine whether changes in fishing practice (in terms of bait type) over the last few years should be taken into account when attempting to quantify fishing effort. The results of this study point to the fact that this is not necessary, thus simplifying these estimates to the consideration of creel, vessel or fisherman numbers. With regard to soak time however, for accurate estimates of effort, it should be taken into account, if only as a guide to the general practice at any particular time and place.

Section B: Estimation of Fishing Effort and Stock Assessment

5.5 Introduction

There are some indicators that a stock is being overfished, which are rudimentary and yet give preliminary insight into the state of the fishery. One such indicator is the mean size of individuals. However, as this may fluctuate throughout the year, several years of data are required in order to achieve meaningful results.

Models involving the assessment of fish stocks are useful in fisheries in that they suggest approaches in order to successfully meet management objectives.

Most models are applied to a single stock of a species, even where there is a mixed fishery clearly operating. The basic assumption of a single stock is that a geographical border can be drawn around its population, and that this can be treated as a self-sustaining stock. This implies that there is no migration of individuals either into or out of the predetermined area, neither of adults nor of juvenile or larval stages.

For the Orkney shellfish fishery, it is likely that some mixing of stocks occurs, especially at the larval stage. The length of the larval life may determine the extent of this mixing, but in the case of the velvet swimming crab, once the larvae have settled, there appears to be relatively little movement, and there is no evidence for large-scale migration.

In general, there are two types of model used in fishery management. The first type, surplus yield models, are based on the assumption that there is an equilibrium in the fishery, such that the rate of production is equal to the rate of removal of individuals, either by fishing or by natural mortality. The Schaefer model, used in this section, makes estimates of sustainable yield based on catch figures and changing amounts of effort applied to the fishery. The basic thought behind this model is that sustainable yield increases with increasing effort, up to a maximum point, known as the maximum sustainable yield (MSY), after which the yield decreases and, in extreme cases may drop to zero, indicating a total collapse of the fishery. Whilst rudimentary, the advantage of this model is that relatively little input is required in order to get some insight into the state of the stock. The parameters used and the reasoning behind this decision are discussed in 5.6.

Another kind of model used in this study is Jones's (1981) length cohort analysis model. This makes the assumption that there is constant recruitment throughout time, a case that does not necessarily always hold true in reality. However, with this assumption in mind, this model estimates the average numbers (and weights) of individuals of each size class in the sea from catch data and also estimates fishing mortality at each length.

The next stage of the Jones model is to predict the effects of changing effort on the long-term condition of the stock. This stage is equivalent to the Thompson and Bell (1934) model. Whereas length-cohort analysis is used to determine the numbers of individuals that must be present in the sea in order to account for a known catch, the Thompson and Bell model predicts the effects of changes in fishing effort on future yields.

Yield per recruit analysis (Beverton and Holt, 1957) requires slightly less data and provides insight into the relative benefits of exploiting smaller or larger individuals. Some measure of the selectivity of the fishing gear is required for this, as it depends on the size at first capture of individuals.

None of the models used in this section make any allowance for the relationship between stock size and recruitment, and generally focus on relationships between stock and fishing effort and gear.

Creels are passive tools for fishing. In essence, they fish by attracting the target species to them by means of some bait. The animal finds it easy to enter through the eye, but as it tapers inwards, exit proves more difficult, and the animal is trapped inside the creel on account of it being too large to pass through the mesh.

The selectivity of creels depends on a number of intrinsic and extrinsic factors. These include the mesh size and eye size of the creels, as well as biological factors such as differences in the behaviour of the crabs due to size, sex and reproductive state.

Environmental factors (temperature, weather, time of day) may also have an effect on what is caught, as well as the substrate on which the creels are placed

The gear used in the velvet crab fishery is biased towards larger crabs. The main reason for such a bias to exist is due to the legislation regarding minimum landing size imposed on the industry. The most efficient way to implement a MLS is to use gear that will simply not catch individuals below the approved size. Thus, general practice is that the mesh size on creels is about 4.5cm in diameter.

The aims of this section are:

1. Does the mean size of individuals caught change over time?
2. What is the selectivity of the fishing gear used?
3. Can we observe changes in catch and effort over the years?
4. Is it possible to carry out length-cohort analysis on the stock?
5. Can yield per recruit analysis be used as a tool for predicting results of changing the MLS?

5.6 Methods and Materials

Data collection was carried out in the form of sampling the state of the catch once it had reached the packing stage at the marketplace (Orkney Fisherman's Association, Pierhead, Stromness). At this point, the catch has been landed by the fisherman, and has probably spent a few days tied to a mooring point at sea, then another few days in the ponds at the sorting place. Thus, the catch may be up to a week old, and it has undergone preliminary sorting by the fisherman (it is illegal to land individuals under 65mm CW).

From September 1999 to December 2000, monthly sampling took place. One crate of velvet crabs was chosen at random, and the individuals therein were measured for the following characteristics: sex, carapace width, weight, moult state and presence of eggs (see dataset 5, appendix A). In addition to this, measurements were also carried out from May-July, 2001, in order to begin constructing a long-term database beyond the time constraints of this particular study.

The mean monthly size of males and females were compared with mean monthly sizes obtained during the sampling period at sea (January 1999 - December 2000, Dataset 1, Appendix A). The size distributions (in 2mm size groups) of the market samples were obtained.

Schaefer's (1954) surplus yield model was applied to catch and effort data for the velvet fishery in Orkney as a whole (i.e. considering all the velvet crabs in Orkney to consist of one stock).

The Schaefer surplus yield model of catch and effort is only as good as the data put into it. Catch data is quite easy to obtain. The following assumptions however, must be made:

1. All catch is landed into the area.
2. None of the catch landed in the area was fished elsewhere.
3. The stock is totally enclosed in the area and has no influences outside it.
4. By-catch and black fishing are both negligible.

Bearing these assumptions in mind, the landings statistics are available from official sources (OIC, SOAEFD). However, estimation of effort is not straightforward. Various changes have occurred in the recording of fishing statistics since the velvet crab fishery began in the early 1980s.

There has been the obvious change from imperial to metric measurements which took place in the early 1990s, as well as legislation changes in registration requirements which have led to anomalies in the data. The increase in fishermen between 1992 and 1993 is unrealistic; especially if we consider that the actual number of registered boats only increased slightly. In order to overcome this problem, the data from 1993 to the present day were considered to be correct. The numbers for 1992 were taken to be 90% of those of 1993, then the previous years were modified proportionally to the new figures for 1992.

In terms of species targeted, it must be taken into account that in the early 80s, when the velvet fishery began, lobster and partan (brown crab) were the main targets of the creel fishery. The change to integrating velvets was gradual and is not necessarily reflected by changes in the number of creels. In order to accurately account for this, the proportion of time and resources spent targeting each species would have to be ascertained, with the further complication that in many cases, there would be overlapping.

The number of creels involved in the fishery is the key parameter for estimating effort. The measure of effort used in this model was the number of creels and the proportion of time spent targeting velvet crabs.

Gear selectivity was estimated using experimentally obtained data. Two ropes of five creels were laid over one another in the study area (Wass Wick). One rope comprised the normal creels used for collecting data in this survey. The other rope was made up of prawn creels, which have a smaller mesh size. The characteristics of the creels are summarised in Table 5.2 below. The ropes were hauled every day for 10 days, and the size of each velvet crab caught was recorded (Dataset 6, Appendix A).

The relative standardised proportions of individuals of each size (in 2mm size groups) were calculated and used to determine the selectivity of the gear.

Parameter	**Normal creel**	**Prawn creel**
Mesh size	4cm	2.5cm
Eye diameter	15cm (soft)	8cm (hard)
Base area	45 x 65 cm	44 x 58 cm
Height	33cm	30cm
Bait	Frozen skad	Frozen skad

Table 5.2 Creel Parameters

Length-cohort analysis (Jones, 1981) was carried out using 2mm size groups, relating the proportions of individuals sampled to the structure of the entire catch for that year. Conversion of catch weight to catch numbers was carried out using the size-weight equations obtained in Section 4.3.1. The parameters used ($L\infty$, M/K, and F/Z) were those obtained from previous work in Sections 3B and 4. From the resultant figures, effects of changes in fishing effort were calculated.

Yield per recruit analysis (Beverton and Holt, 1957) was carried out separately for each sex, using various estimates of natural mortality (0.2-0.5); this being the least easily estimated parameter of those used. Curves were constructed to depict the fishery using the current gear (for a MLS of 65mm), and then simulated for an increased MLS to 68mm. $W\infty$ was obtained using the size-weight equations in Section 4.3.1, and applying them to $L\infty$. The parameter t_0 was estimated for a range of juvenile stages (Section 3B) and a mean value of 0.345 was obtained.

5.7 Results

5.7.1 Size distribution of market data

Figure 5.7 shows the relative proportions of males and females in each 2mm size class between 1999 and 2001 (Dataset 5, Appendix A).

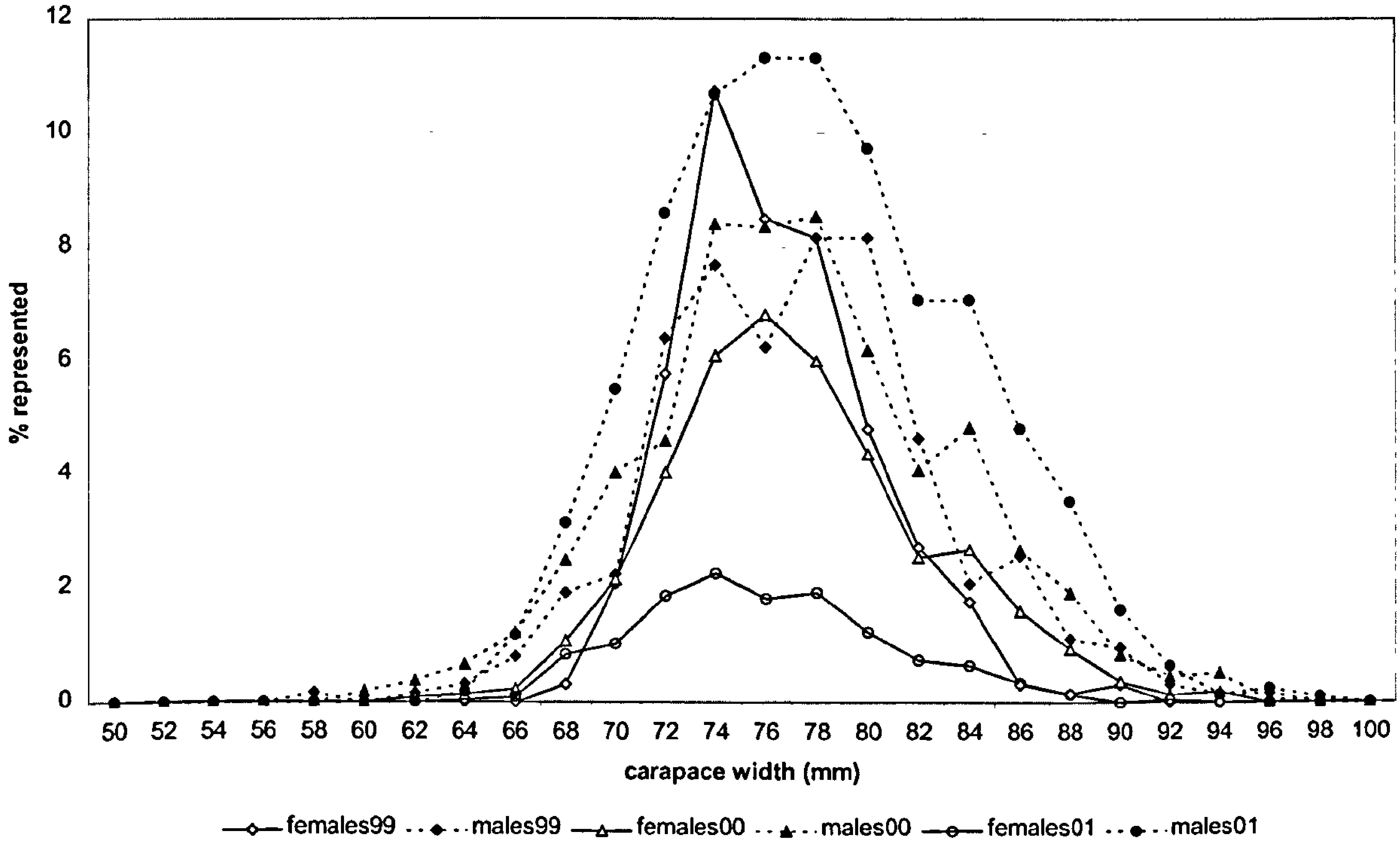


Figure 5.7 Proportional size-frequency distributions for market samples.

The graph indicates that the range of sizes being captured has not changed over the three years. Although there is a marked difference in the proportion of females represented in the 2001 sample, this is due to the timing of the sampling rather than to changes in the sex ratio of the population itself.

This can be contrasted with a study carried out by Tallack (1998), who compared the size-frequency distributions for velvet crabs at the same packing centre (Stromness Pier). She compared the distributions for 1990, 1993 and 1996, finding no changes between 1990 and 1993, but a slide in mean size in 1996, from around 70mm to 65mm (using 5mm size-cohorts). For comparison, these graphs are shown in Appendix D.

Figure 5.8 shows the mean monthly size of males and females during the market sampling (Dataset 5, Appendix A), compared with those from the catch sampling (Dataset 1, Appendix A).

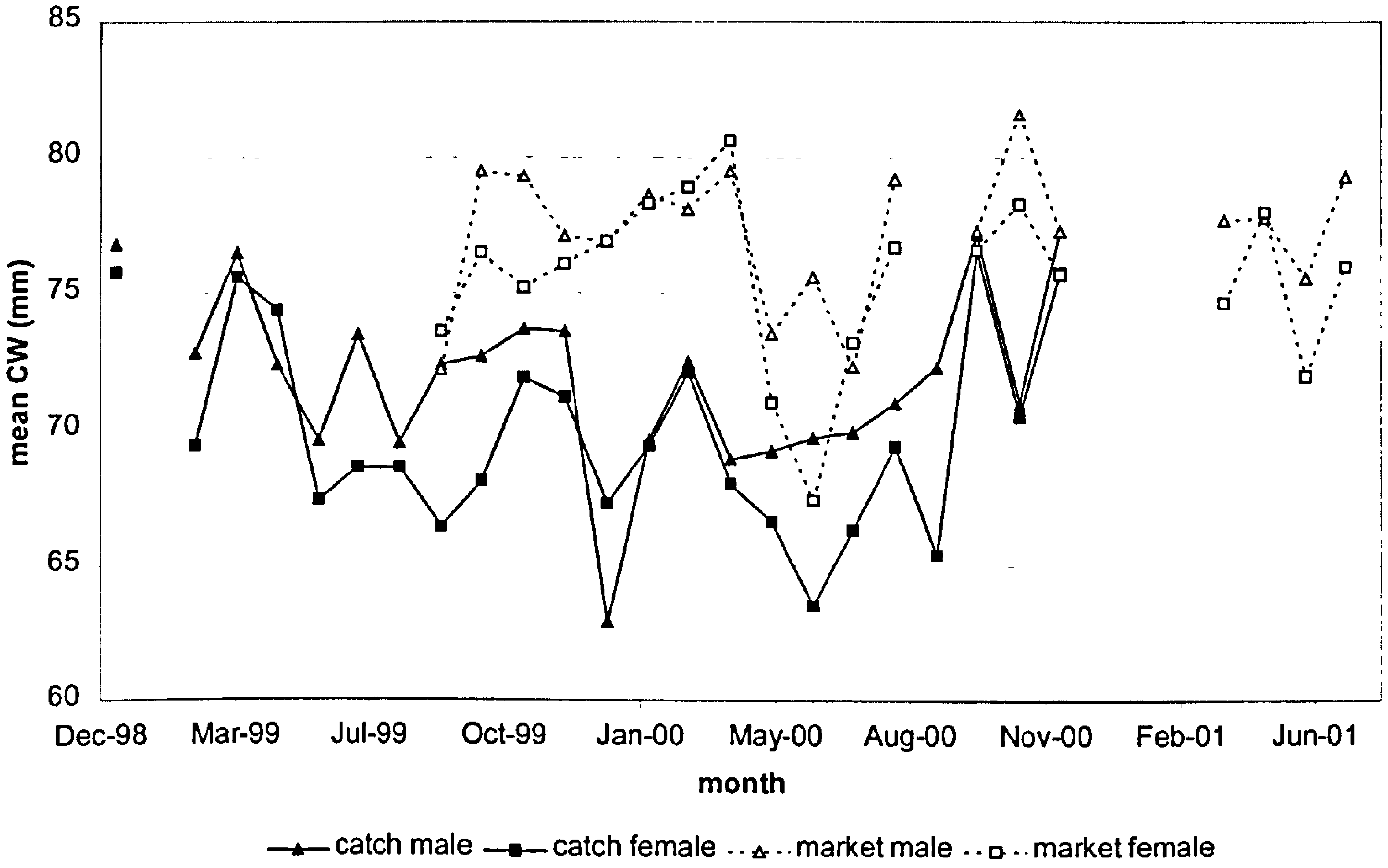


Figure 5.8 Mean monthly sizes of catch and market males and females.

The graph above shows considerable fluctuation over the months, with no clear trend, either of increasing or decreasing mean size. The mean size of the catch sample is mostly lower than that of the market sample. This is related to the discarding of undersized animals at the catch stage (see Section 5C for further details).

The size distributions and sex ratios in Figure 5.8 can be used to determine the numbers of individuals caught commercially over the study period. This is summarised in Table 5.3.

Year	1998 (Tallack)	1999	2000
Total weight (mt)	687.9	650	674
Numbers (millions)	5.72	5.49	5.65

Table 5.3 Total weight and numbers of velvet crabs caught commercially in Orkney

From this table, it can be seen that around 5.5 million velvet crabs are removed from Orkney waters annually, with some fluctuation but no clear trend.

5.7.2 Gear Selectivity

Table 5.4 summarises the catch obtained using the normal fishing gear compared with that using the smaller-meshed prawn creels.

Length L1	Length L2	No. in creel	No. in prawn crl	Total number
48	54	0	0	0
54	60	1	4	5
60	66	10	18	28
66	72	40	33	73
72	78	38	29	67
78	84	18	26	44
84	90	12	6	18
90	96	2	3	5
96	102	0	0	0

Table 5.4 Catch from normal creels and prawn creels (for selectivity analysis)

This information was used to produce a selection ogive for the gear used, forcing the curve through a 0.99 chance of capture at 84mm, as is shown in Figure 5.9.

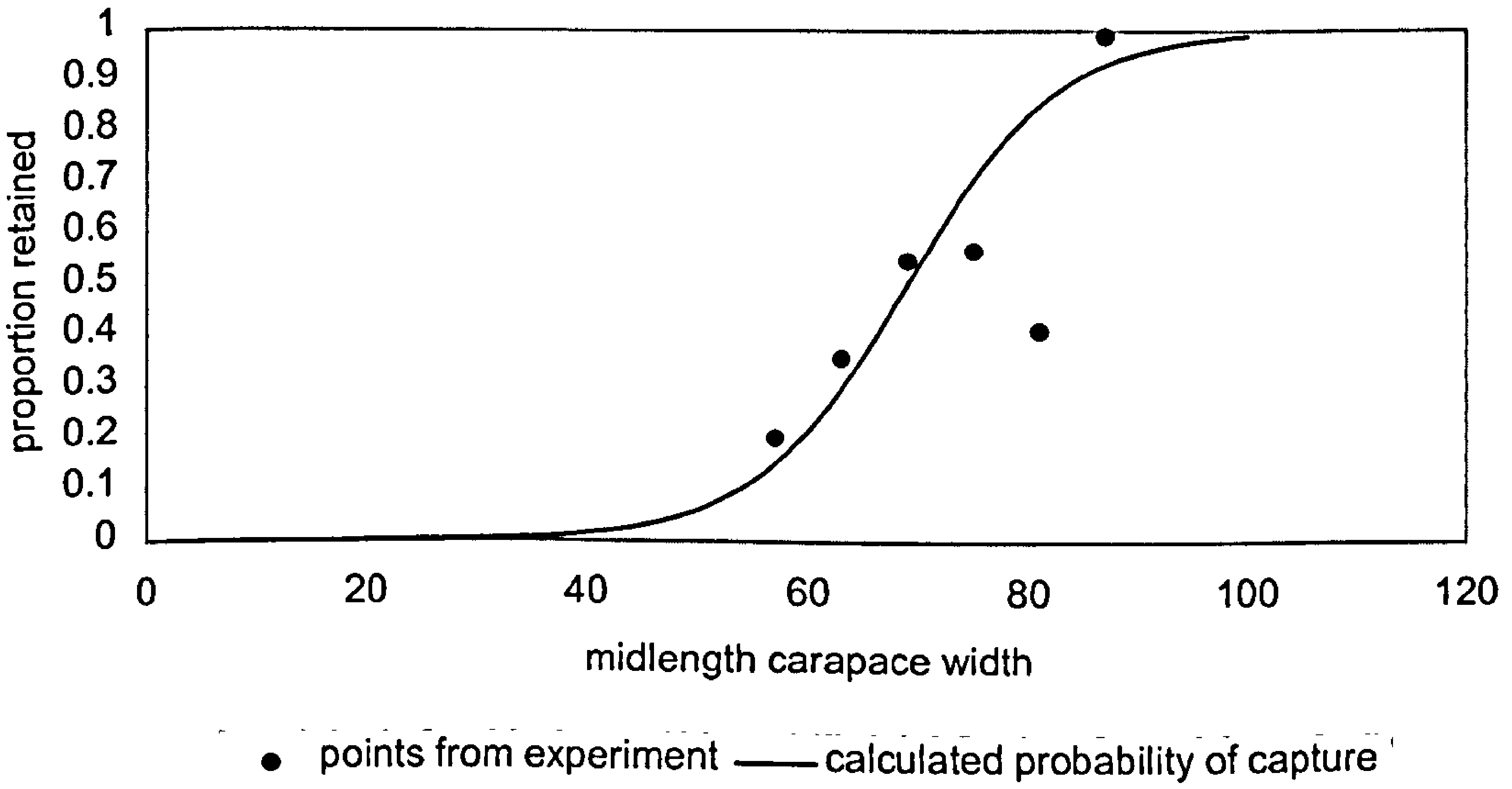


Figure 5.9 Trendline showing changing gear selectivity over size for commercial creels.

The size at which there is 50% chance of retention is around 65mm. There is virtually no retention below 50mm, and virtually 100% retention above 80mm.

5.7.3 The surplus yield model

The numbers of full time and part time fishermen were gathered using the Orkney Economic Reviews, along with data on the structure of the fleet. This information is summarised in Figure 5.10.

Due to a change in legislation between 1992-4, the raw data for numbers of fishermen shows a large discontinuity from 1992 to 1993 (see Figure 1.8). This discontinuity is unreal, and in order to compensate for this, on the advice of the Fisheries Office and Orkney Fishermen's Society (OFS), the trend after 1993 is applied to the 1992 data and all years previous to that are modified accordingly. This gives the pattern shown in Figure 5.10, which is more consistent with the reality of the inshore fishery.

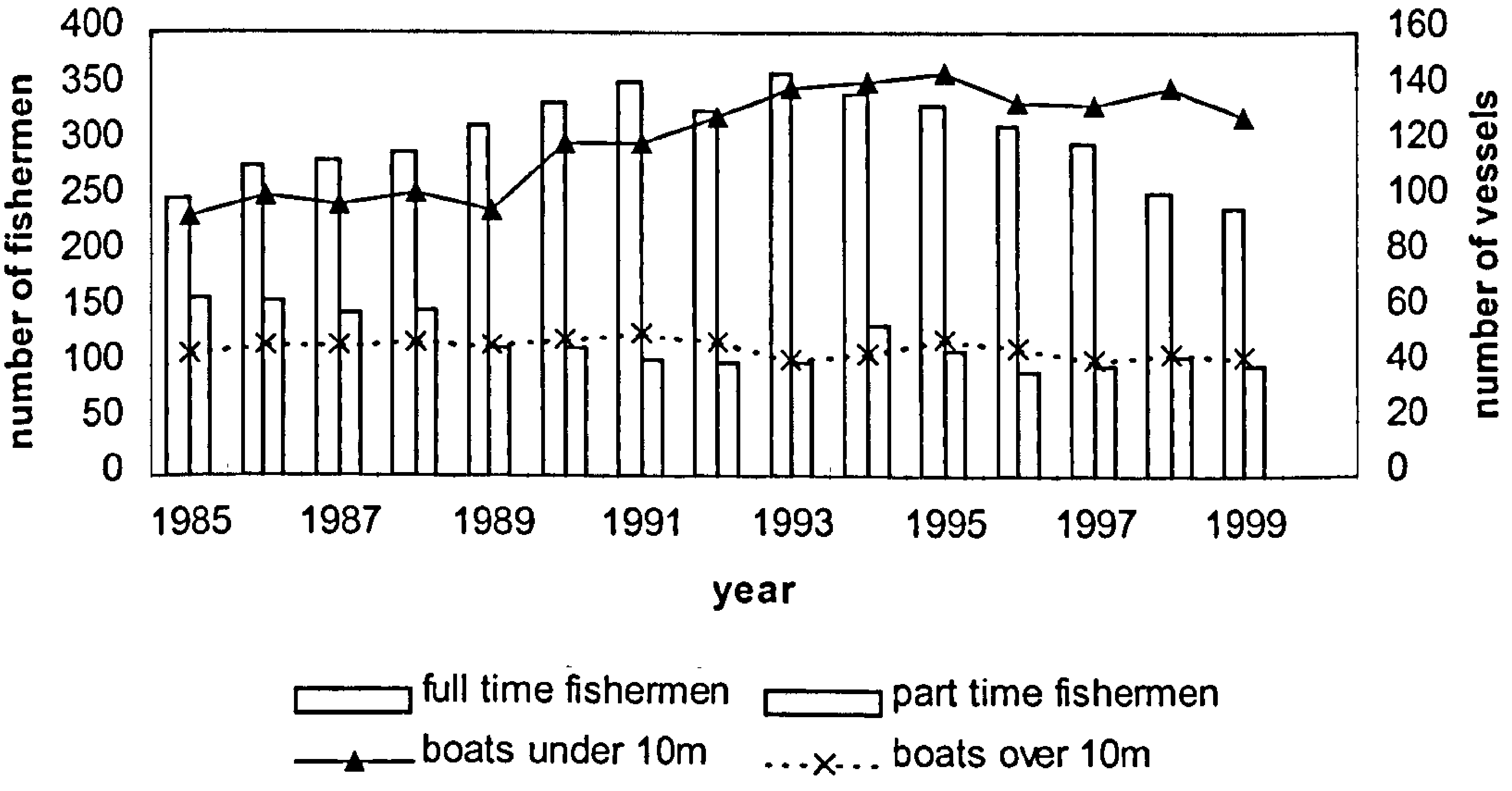


Figure 5.10 Numbers of vessels and fishermen in shellfish industry, Orkney (data from Orkney Economic Reviews)

The numbers of part time fishermen have remained relatively constant, compared with a steady decrease in full time workers since 1993. In the same manner, the number of large vessels has also remained fairly steady with respect to the smaller vessels, which have also decreased slightly in recent years.

Catch data for velvet crabs, edible crabs (partans) and lobsters was also collated for the same period in Orkney, using the same sources (Orkney Economic Reviews). This is shown in Figure 5.11.

It can be seen how, in the last two or three years, catches of edible and velvet crabs have decreased with respect to their peaks, both in 1997. The lobster catch is declining slowly and steadily since the mid-1990s (although it is little different from the late 1980s).

For the purposes of the surplus yield model, the catch data was used in its original form. In order to determine effort, the number of fishermen involved in the practice was taken to be the main cause of effort. Total effort was calculated as the number of full-time fishermen and half the number of part-time fishermen, multiplied by the number of creels per person and modified by a proportionality constant relating to the time spent targeting the species. After conversations with local fishermen, it was assumed that the fishery began with 100 creels per person, and increased by 10 creels per person per year. The proportion of time spent targeting the velvet crab was assumed to be 0.1 in 1985, and was increased by 0.05 each year, reaching 0.8 in 1999.

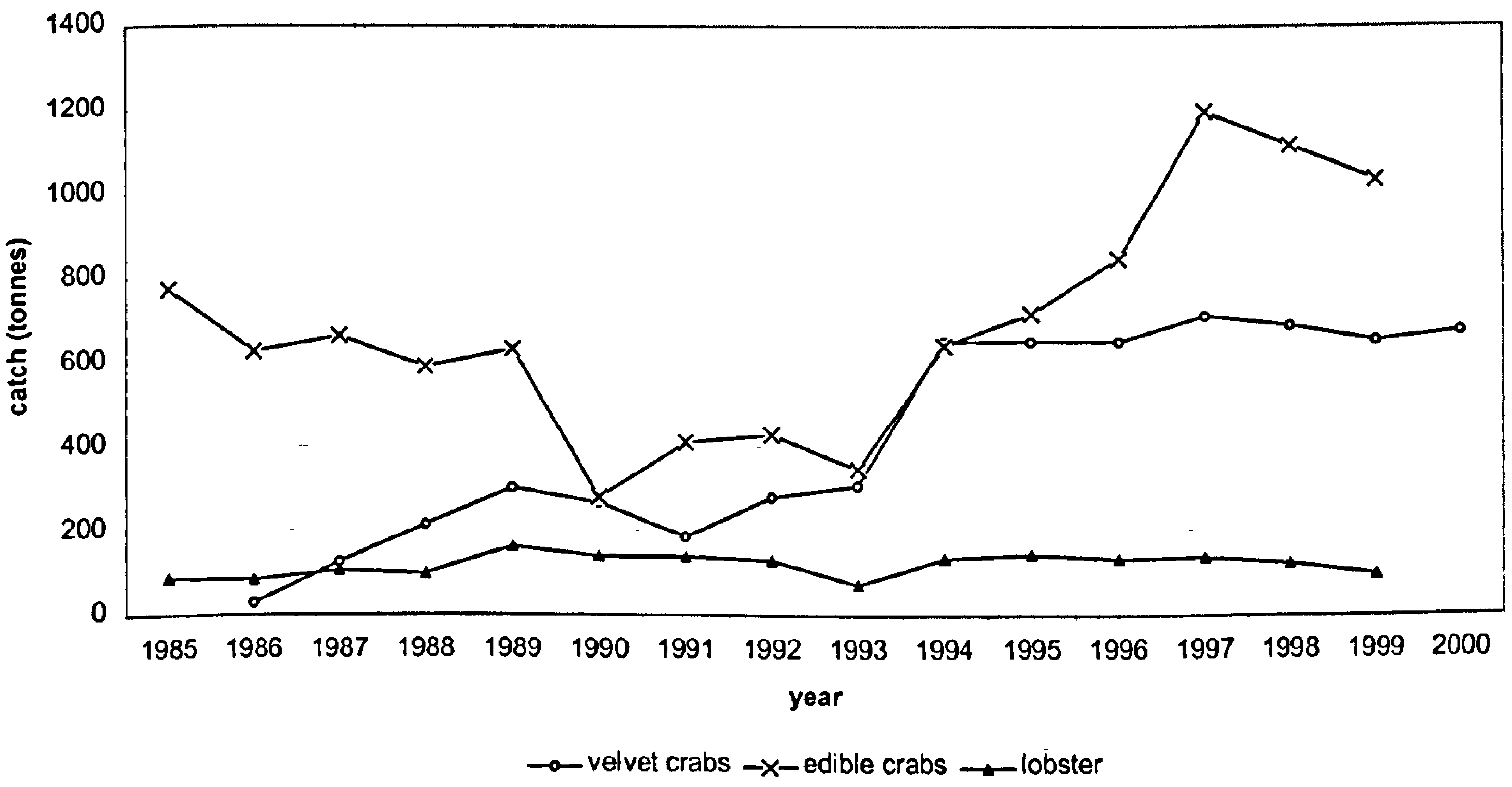


Figure 5.11 Shellfish catch in Orkney since 1985 (from Orkney Economic Reviews)

The yearly catch of velvet crabs (in tonnes) was plotted against the resultant creel effort, in Figure 5.12 below.

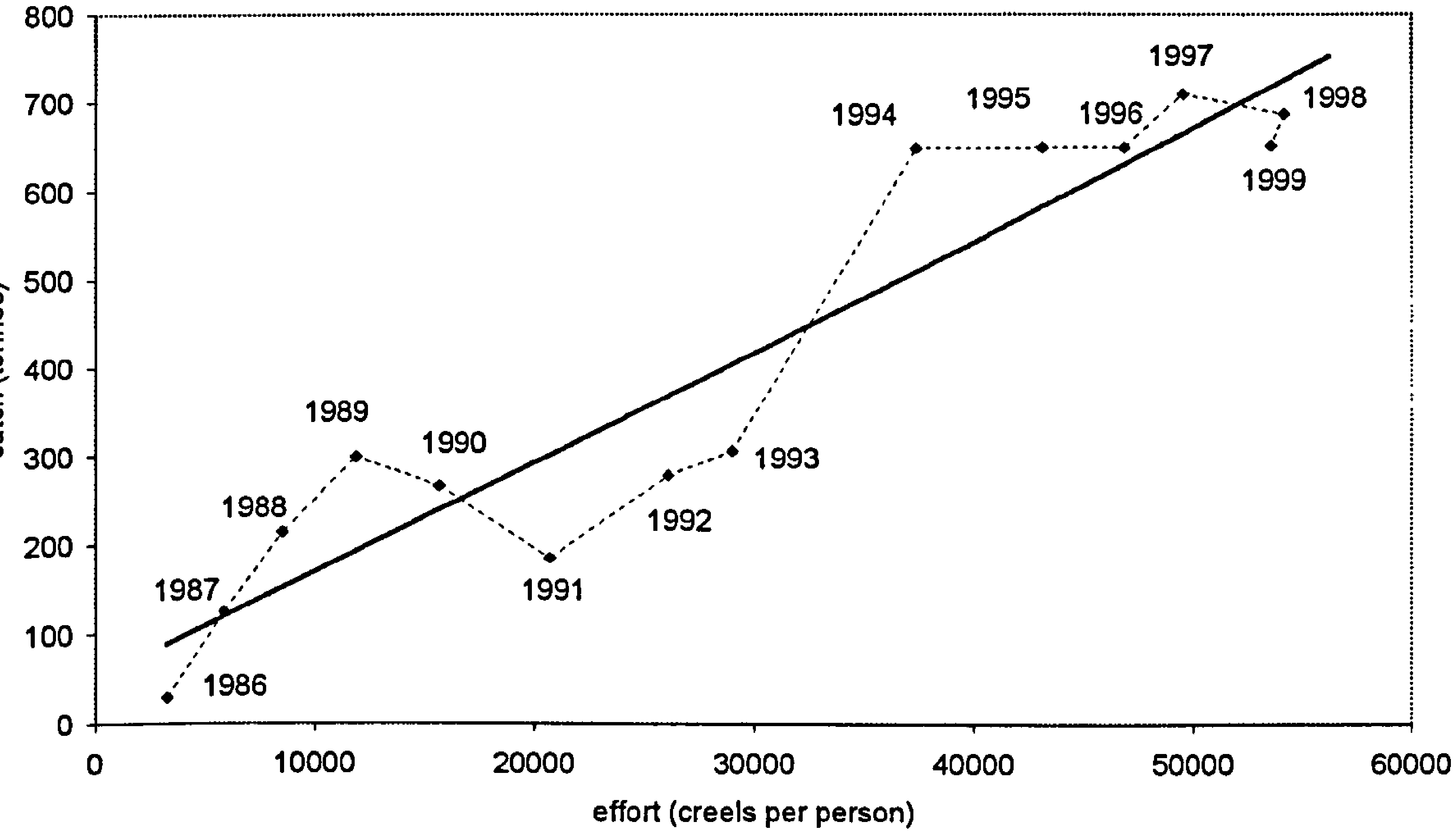


Figure 5.12 Catch-effort data for velvet crabs in Orkney.

The dotted line on the graph shows data for consecutive years. The figure shows a trend of a straight line relating increase in catch with increasing effort. The graph clearly shows that the fishery is not in equilibrium (one of the basic assumptions of this model). Therefore, no firm conclusions can be made from this. However, in recent years (corresponding to those catches around 650 tonnes), there is no clear increase in catch with the increasing amounts of effort put into the fishery. This may suggest that the fishery is currently approaching its maximum sustainable yield. However, this model should be viewed with caution, as the estimation of effort is rudimentary and based on generalised assumptions. Further work required in order to produce a more reliable model of catch and effort is discussed at the end of this section (5.8).

5.7.4 Length Cohort Analysis

This is a procedure which allows scientists to understand what is happening to fish stocks by looking at the numbers of fish caught during successive intervals in their lives. The intervals in this case are not age intervals, but intervals of size (2mm size groups). The following figures were used in the analysis:

$L\infty = 98.4$
M/K = 1.12
F/Z for the largest size group = 0.8

Values for M (and therefore M/K) were varied from 0.2 to 0.5 in 0.05 increments to examine the effects of M on the estimation of the total population size. These are summarised in Table 5.5.

M	**Adult population size (millions)**
0.2	27.5
0.25	31.2
0.3	35.9
0.35	42.2
0.4	51.9
0.45	65.3
0.5	89.3

Table 5.5 Estimations of adult population size using different M values in length cohort analysis.

It can be seen that the total population size estimates vary greatly depending on the natural mortality value used. In further analysis of effects of changes in effort, M was assigned a value of 0.3, after comparison with the higher values of 0.5 assigned to the shorter-lived Spanish stock (González-Gurriarán, 1985b).

The length-frequency distribution of the fishery was determined by using the distributions obtained from the market data (Dataset 5, Appendix A) and the total annual weights of velvet crabs caught in Orkney waters, using weight conversion factors obtained in Section 4.3.1.

Length-cohort analysis is usually carried out on a time series equivalent to the life-span of the species in question, but in this case, only one complete year of fishery data was available, so the procedure was carried out on 2000 data (Dataset 5, Appendix A). The remaining data collected (2001) is to be continued on a long-term basis in order to carry out more meaningful analysis once the time series is long enough. It was assumed that all individuals reaching the packing stage die, including those undersized. This is not an unreasonable assumption, as although undersized individuals are returned to the sea, the time lag between catch and release, and the state in which they are kept before release are not conducive to high survival rates. According to the analysis there are around 35.9 million individuals of 50mm CW and greater in Orkney waters, out of which around 5.5 million are removed annually. This represents a catch of 15% of the total adult population. Table 5.6 shows the results of the length-cohort analysis.

Length Cohorts to be used (cm)			Numbers Caught Millions	Numbers In Length Class Millions	Survival Rate: Sdt (=exp^-Zdt)	Zdt (-ln(Sdt))	F/Z (CL/total losses)	Fdt (Zdt*F/Z)	Total Mortality Rate (M/(1-F/Z))	dt	**Average Numbers in the sea Millions**
Length Cohorts L1	L2	XL	CL	NL	SdeltaT	ZdeltaT	F/Z	FdeltaT	Z	dt	**Stock numbers**
98	100	#NUM!	0.001224	0.00153				0.221458			
96	98	2.726041	0.001302	0.014919	0.102552	2.277381	0.097243	0.221458	0.332315	6.853075	0.040291
94	96	1.403901	0.021262	0.059255	0.251781	1.379194	0.479572	0.661423	0.576448	2.392572	0.076911
92	94	1.233328	0.019587	0.114289	0.518461	0.65689	0.355903	0.233789	0.465768	1.410336	0.118159
90	92	1.164395	0.042085	0.203959	0.560355	0.579185	0.469335	0.271832	0.565328	1.024512	0.158615
88	90	1.126976	0.105736	0.378205	0.539281	0.617518	0.60682	0.374722	0.76301	0.809318	0.228367
86	88	1.103455	0.169523	0.647568	0.584039	0.537788	0.629347	0.338455	0.809382	0.664443	0.332801
84	86	1.087295	0.319223	1.112652	0.582004	0.541277	0.686378	0.371521	0.956565	0.565855	0.486202
82	84	1.075506	0.302857	1.612742	0.689913	0.37119	0.605604	0.224794	0.760657	0.487986	0.657446
80	82	1.066524	0.521344	2.390476	0.674653	0.393557	0.670337	0.263816	0.910021	0.43247	0.854633
78	80	1.059453	0.774424	3.503631	0.682285	0.382307	0.695702	0.265972	0.985875	0.387785	1.129104
76	78	1.053741	0.874117	4.81142	0.728191	0.317192	0.668393	0.212009	0.904685	0.350611	1.445573
74	76	1.049031	0.903251	6.242343	0.770772	0.260363	0.631237	0.164351	0.81353	0.320041	1.758906
72	74	1.04508	0.585587	7.429828	0.840173	0.174147	0.493132	0.085878	0.59187	0.294232	2.006328
70	72	1.041719	0.452667	8.534242	0.87059	0.138584	0.409871	0.056801	0.508363	0.272608	2.17249
68	70	1.038824	0.283104	9.503874	0.897975	0.107613	0.291971	0.03142	0.423711	0.253977	2.288426
66	68	1.036305	0.124852	10.33587	0.919504	0.083921	0.150063	0.012593	0.352968	0.237758	2.357142
64	66	1.034093	0.075123	11.13034	0.928621	0.074054	0.094558	0.007002	0.33133	0.223506	2.397815
62	64	1.032136	0.048657	11.90741	0.93474	0.067486	0.062616	0.004226	0.32004	0.210869	2.428053
60	62	1.03039	0.021139	12.66393	0.940262	0.061597	0.027942	0.001721	0.308624	0.199586	2.451267
58	60	1.028825	0	13.40453	0.94475	0.056835	0	0	0.3	0.189449	2.468656
56	58	1.027413	0	14.14951	0.947349	0.054088	0	0	0.3	0.180293	2.483298
54	56	1.026133	0	14.89871	0.949714	0.051595	0	0	0.3	0.171982	2.497328
52	54	1.024967	0	15.65195	0.951876	0.049321	0	0	0.3	0.164403	2.510801
50	52	1.023901	0	16.40908	0.953859	0.047239	0	0	0.3	0.157464	2.52376
Total			5.647064								35.87237

Table 5.6 Length cohort analysis based on market data for 2000.

A fishing factor (F-factor) was applied to the analysis in order to predict the effects of changes in fishing effort on the catch and stock numbers. The F-factor is simply a proportion of the current fishing mortality (i.e. where F-factor = 2, fishing mortality is doubled). The effects of changing effort on catch levels are shown in Figure 5.13.

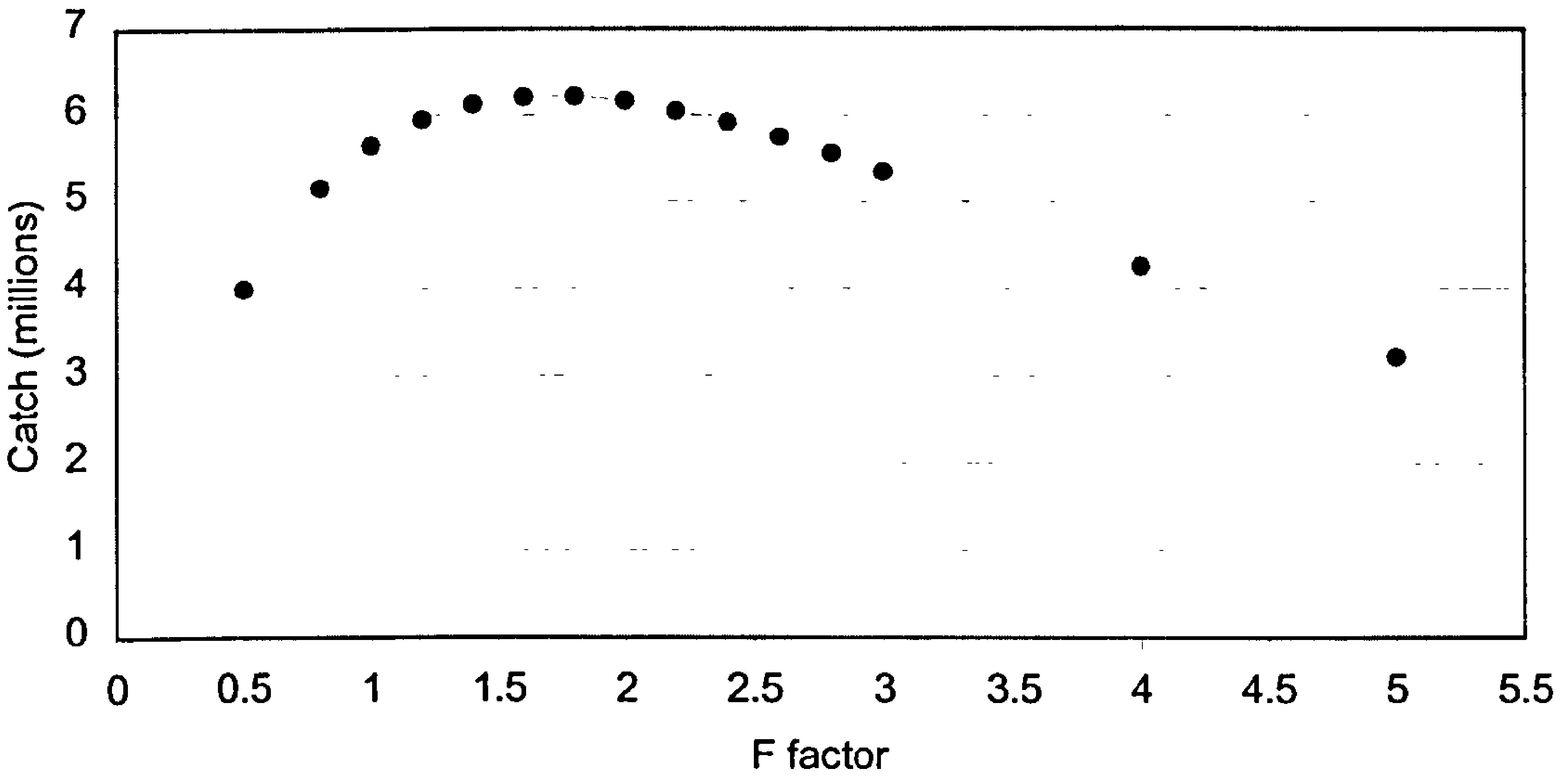


Figure 5.13 Predicted catch (in millions of individuals) with changing effort

As is shown in the graph, a reduction of fishing effort from the current level (1) causes a reduction in the numbers of individuals caught. At present effort levels, around 5.5 million individuals are caught. The maximum catch predicted by this model is around 6.25 million individuals at fishing levels around 1.8 times the present levels. After this point, there is a steady decline in catch as effort increases. When yield was plotted for different F-factors, the same pattern was displayed (Figure 5.14).

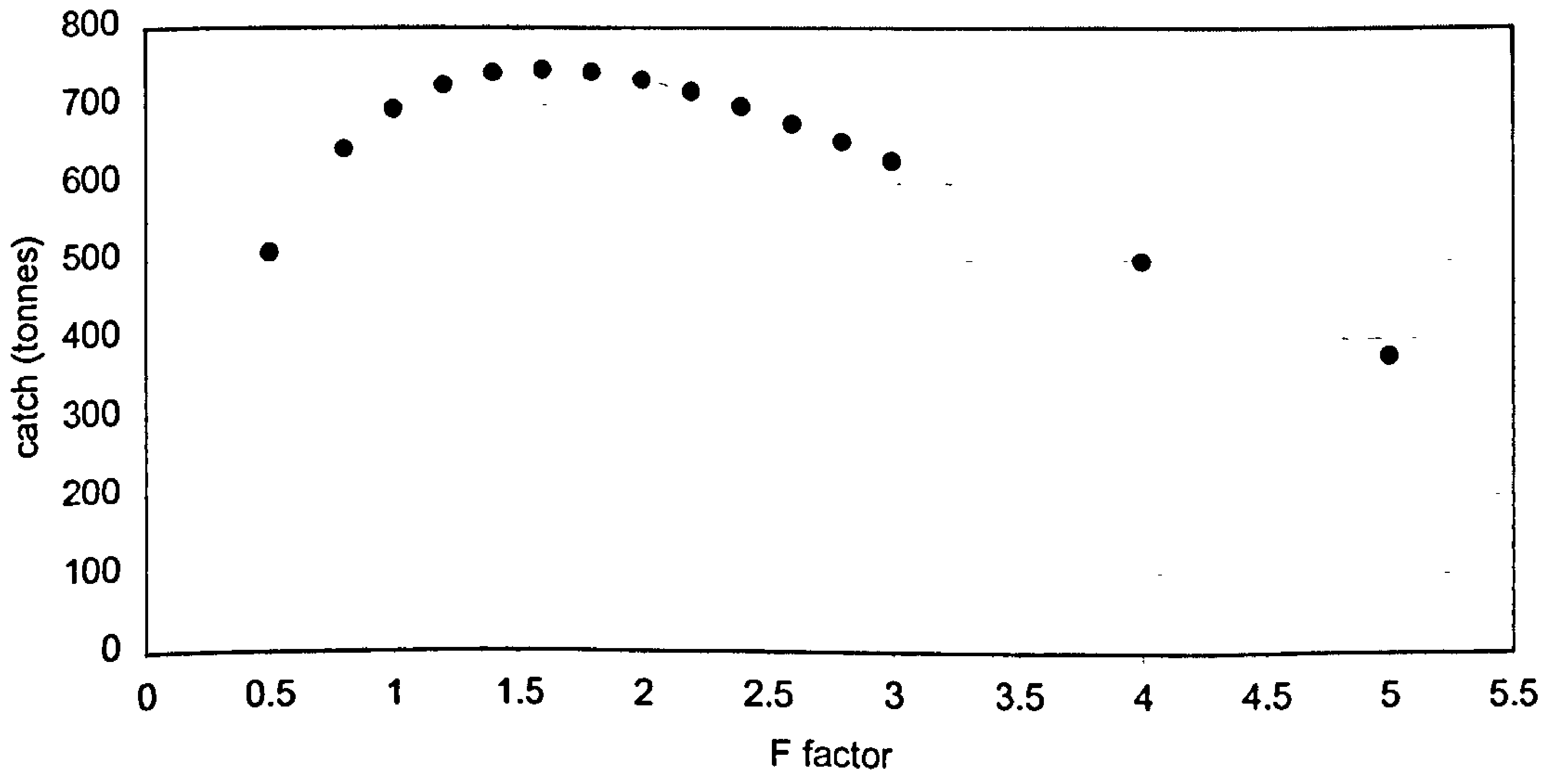


Figure 5.14 Predicted yield of velvet crabs at different levels of fishing effort (F).

The effects of changes in fishing effort are also noticed in the numbers of individuals in the sea. As fishing effort increases, the population structure of the stock becomes increasingly skewed towards smaller sizes. At very high levels of fishing effort, very few large individuals are left at all. Figures 5.15 and 5.16 show the relative numbers of individuals in the sea and total biomass respectively at different F-factors.

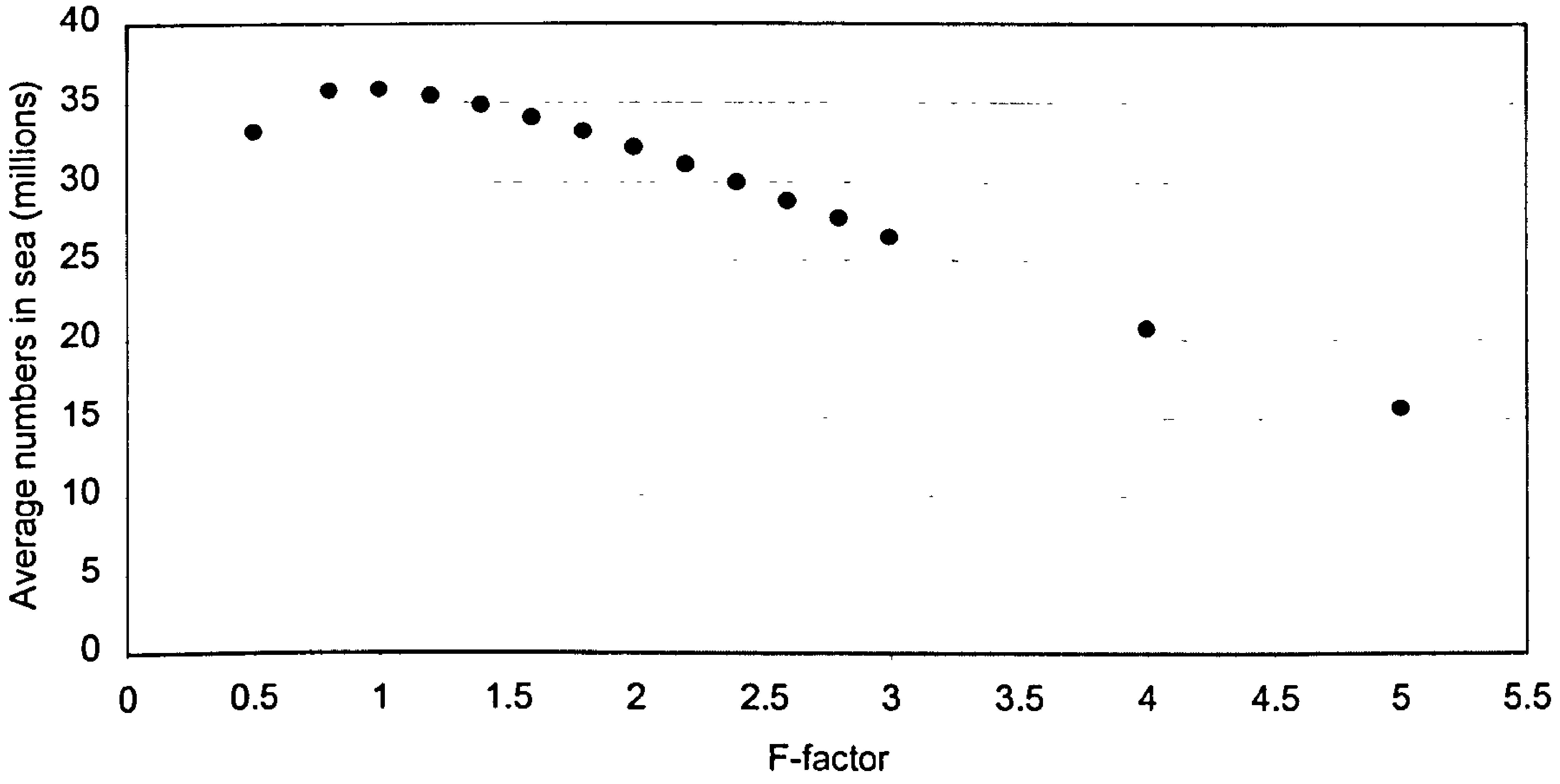


Figure 5.15 Average numbers (millions) in the sea at different levels of effort.

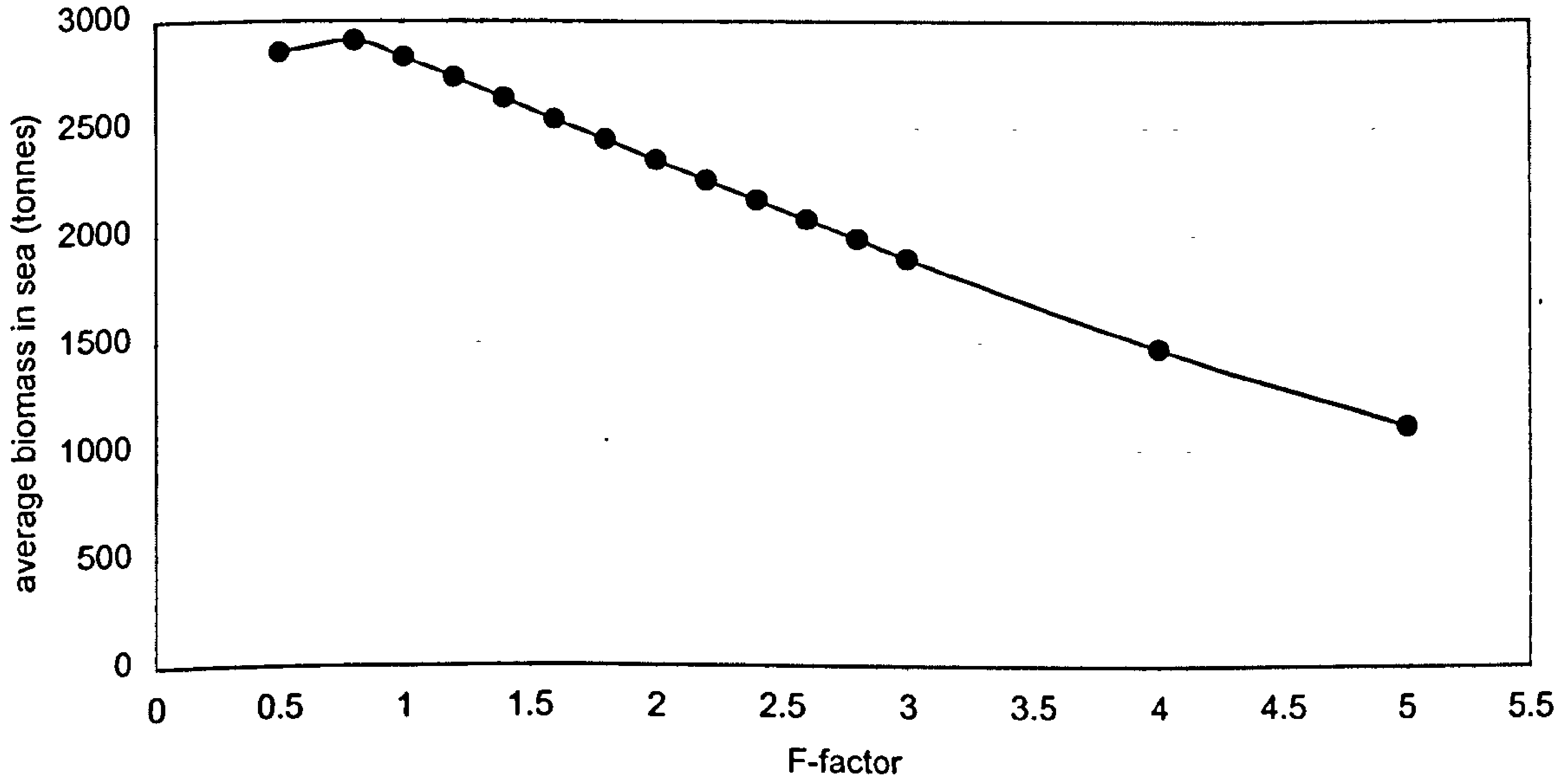


Figure 5.16 Average biomass in sea (tonnes) at different levels of effort.

5.7.5 Yield Per Recruit Analysis

Figures 5.17-18 show the yield per recruit curves for males and females, using M values of 0.2, 0.3, 0.4, and 0.5. Values for W∞ were calculated by using the growth equations in section 4.3.1 applied to and L∞ value of 98.4 for both males and females. The age of recruitment (t_r) was considered to be 3 years – this is the size of sexual maturity.

W∞ = 262g (males), 241g (females)

$K = 0.268$

$t_0 = 0.345$

$t_r = 3$

The age at first capture was assumed to be the age corresponding with the MLS; in this case: 65mm. This corresponds to the continuous lines on the graphs. Discontinuous lines represent yield per recruit at the same range of M values for an increased MLS to 68mm.

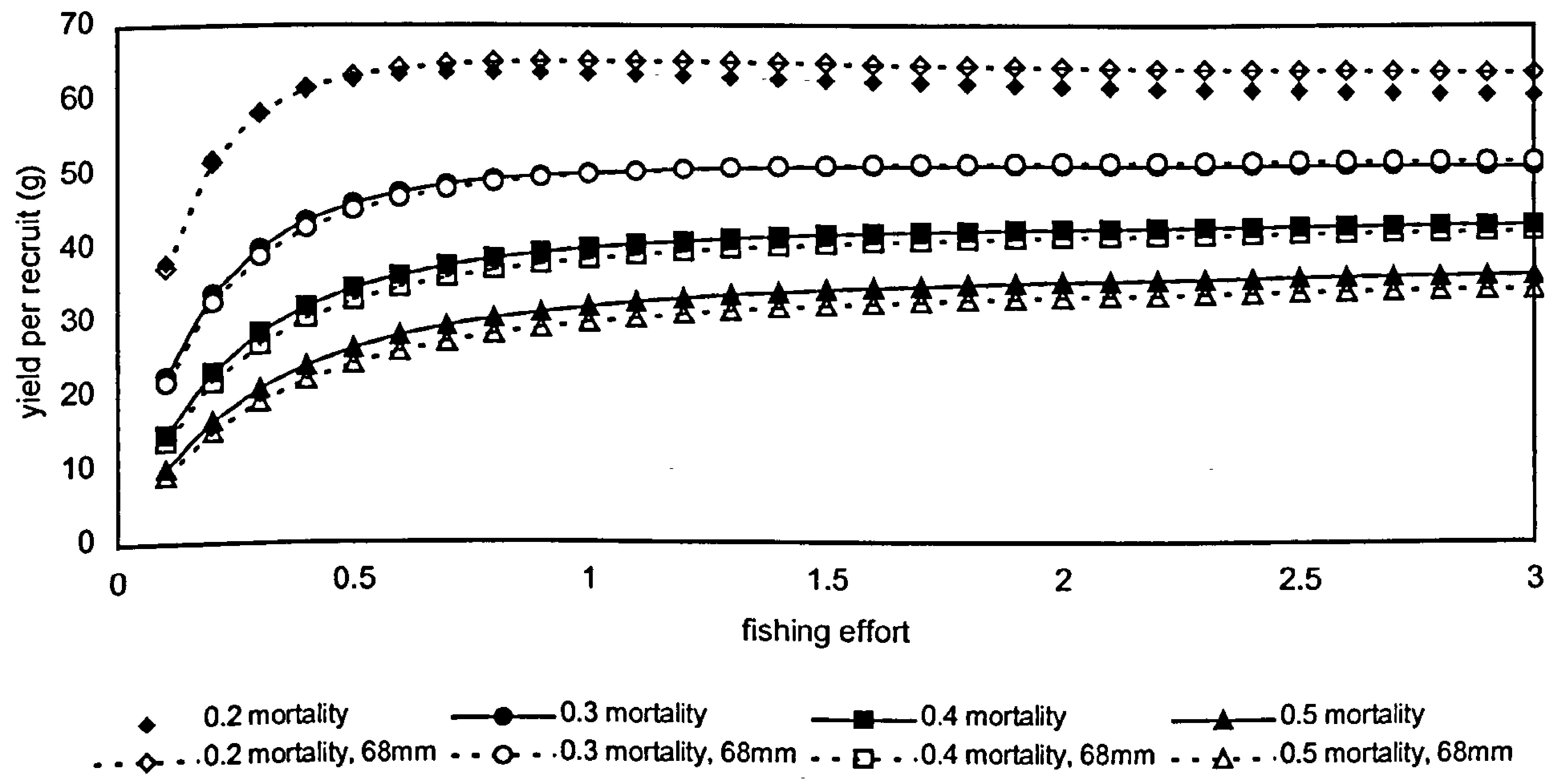


Figure 5.17 Yield per recruit analysis for males

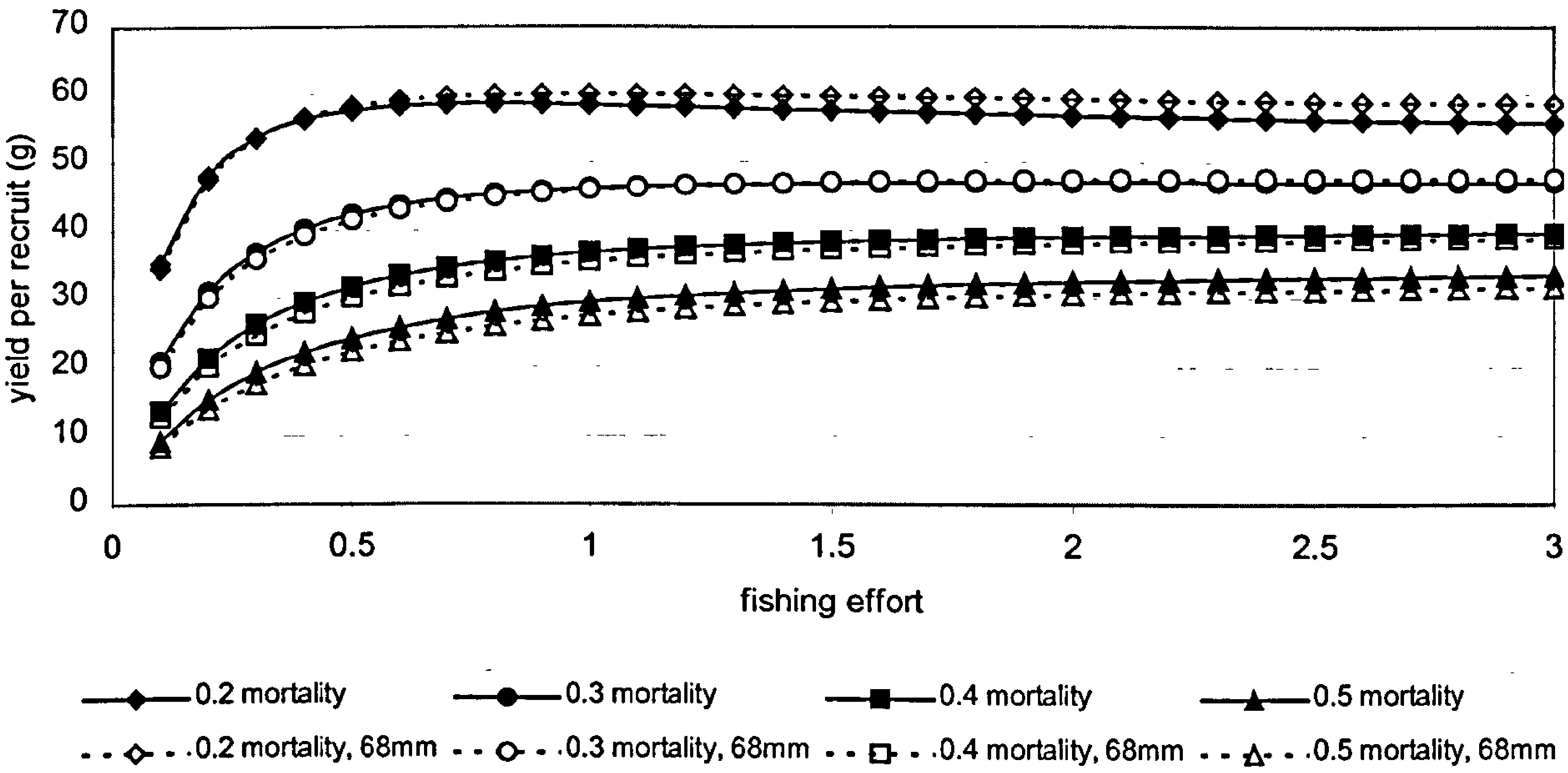


Figure 5.18 Yield per recruit analysis for females

At present, fishing levels are around 0.6-0.8. Regardless of the value for M, all series in both of the above graphs show a levelling of the yield per recruit, and in some cases, the beginning of a decline, at fishing effort above this. For mortalities of 0.2 and 0.3 (the most realistic, taking into account the life span of the animal), there may be a slight improvement in yield if the MLS is increased to 68mm, but this is virtually imperceptible. Although preliminary, what is important to note from these graphs is that fishing effort is around the maximum at present, and caution should be exercised if fishing effort is to increase.

In order to test the optimum age at capture further, curves were made up using a constant value of 0.3 for M, but with age at capture varying from 1-8 years. Figure 5.19 shows the results of this (for males only).

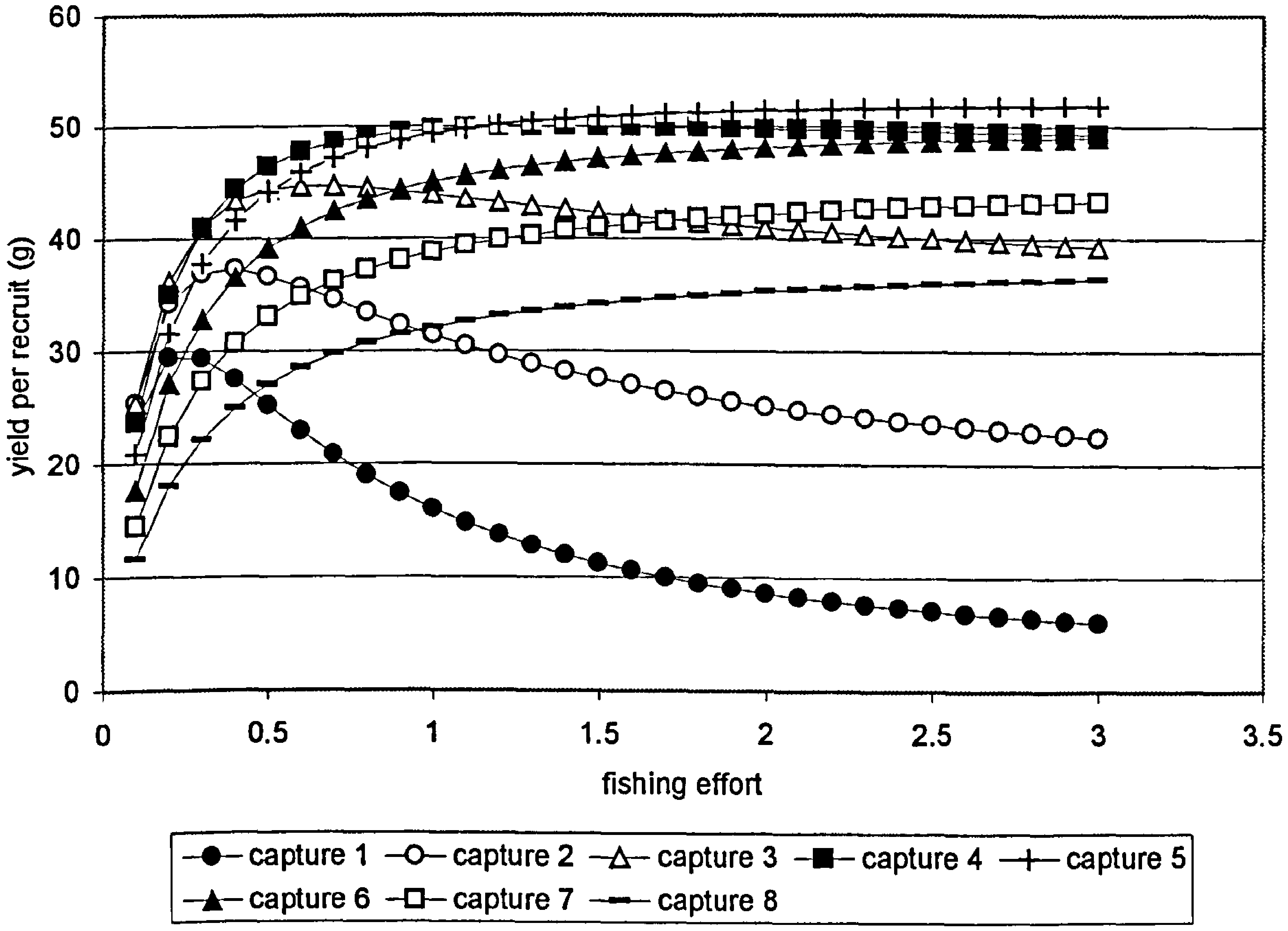


Figure 5.19 Yield per recruit analysis for males, showing different ages at capture

From the above graph it can be seen that yield per recruit increases over the first three years, but then decreases dramatically after the fourth year. The optimum yield at current fishing effort is obtained by using 4-year old individuals (around 65mm) for fishing effort between 0.5-1. There is a suggestion that the optimum yield at higher levels of fishing effort may correspond to an older (therefore larger) animal at first capture.

5.8 Discussion

Fisheries models are mainly based around the central assumption of a unit stock. However, anecdotal evidence points to the possibility that in Orkney, there is no unit stock of velvet crabs, but rather, a large number of substocks. The first indication of this is the fact that of the few tagged individuals recaptured (see Section 4.3.3), all of these were recaptured in the same general area of their release. In addition to this, fishermen speak of certain bays being "fished out". At the marketplace, it has been observed how fishermen bring in large animals for a period of time as they discover a new area to exploit, and how the animals decrease in size until a new area is exploited. This fluctuation in sizes is apparent in figure 5.8. Thus, instead of having a unit stock, which is homogeneously distributed throughout the Orkney Islands inshore fishing area, there may a large number of stocks, each exploited to varying extents, making up areas as small as bays or sounds, between which there is relatively little mixing. However, it is likely that at the larval stage, more mixing does occur, and that this separation takes place once settlement and/or recruitment occur. In this case, for the purposes of population dynamics, parameters such as $L\infty$ and K are likely to be comparable for the entire Orkney archipelago, whereas in terms of fishery models, the existence of substocks may produce anomalous results.

The surplus yield model displays a straight-line relationship between catch and effort. This does not really tell us much about the state of the fishery. However, the figures used in this calculation were broad simplifications of reality, assuming a steady increase in targeting and creel numbers over the history of the fishery, since its commencement in the mid-80s. The accurate estimation of long-term effort changes must be addressed. One conclusion which can be made from this exercise is that the fishery is not in equilibrium.

Undoubtedly, the most significant hindrance in the analysis of available data for Orkney's shellfisheries is the lack of any accurate and definitive data on fishing effort. The Orkney creel fishery is a mixed creel fishery and it is difficult to apply any analysis of the available historical data on vessels and fishermen to separate shellfish stocks. The introduction of some programme involving local fishermen recording data on their activities in the form of a logbook would be highly beneficial for the management of the fishery. This would allow the gradual accumulation of accurate data on many aspects of the mixed fishery, most importantly effort expended in relation to catch.

The Marine Laboratory in Aberdeen has operated a voluntary logbook system with some fishermen. This included a chart of Scotland upon which fishermen were asked to shade the area in which they fished. The logbook sheet is shown in appendix C. As can be seen, "creel type" was specified by the fisherman, in the event that several different types were utilised at any one time. "Total number" highlighted the number of creels actually in the water, for example, they may have had 1,000 creels in the water, yet only managed to haul the same 500 every second day. A tick in one of the boxes identified the weight unit to be used. If the creels were specifically targeting lobsters, then the number hauled on a certain day would be entered in the left-hand column, and any other species caught as by catch were entered under the appropriate title. Yet if, for example, 200 creels were on lobster ground and 800 on brown crab ground then the figure of 200 would be entered to the left of the lobster column, and 800 under the brown crab title. The remarks area at the bottom of the sheet is present to allow such aspects as market prices, boat upgrades, unusual sightings etc to be recorded (this information was supplied by the Marine Laboratory, Aberdeen).

Another consideration which must be taken into account is the relationship between the creels and effort. This is not necessarily a straight line, as doubling creel numbers may not double effort if they are laid in the same area in such a way that they compete with one another, or if the numbers of creels exceed the capability for daily hauling.

The length-cohort and yield-per-recruit analyses are more reliable in that they depend on more robust data, although they also involve assumptions and omissions, which may detract from their validity. Ideally, length-cohort analysis should be carried out on data representing several years of sampling, or at least as long as the average life-span of the species in question. In this case, only one year has been used, but a long-term database has been set up in order to monitor the development of the fishery.

The inference from the length-cohort model is that the fishery is nearing its maximum sustainable yield. The current levels of fishing appear to be optimum. This is in sharp contrast with a similar study carried out by González-Gurriarán (1985b), on the Galician stock. He estimated an 11.69-16.53% increase in yield per recruit for males and a 8.08-12.59% for females by increasing the MLS from 50mm CW to 66mm for females and 67mm for males. He concluded that the values of F at the time were 33% above the optimum values. However, it has been shown that the Galician stock of *Necora puber* differs greatly from the Orkney stock in two important factors that affect yield per recruit: growth rate and life span. The Galician stock is fast growing and short lived, and is first caught at a relatively young age. In Orkney, the age at first capture is much later, and growth is slowing down, so that an increase in the MLS is not balanced (mortality exceeds growth), and is therefore not necessarily recommendable.

It must be taken into account that the Orkney inshore fishery is a mixed fishery incorporating the edible crab (*Cancer pagurus*) and European Lobster (*Homarus gammarus*) as well as *Necora puber*. Whereas there may be room for limited expansion in terms of the velvet crab, there is concern that the local stocks of edible crabs and lobsters may be overexploited (ICIT, 1999). Therefore, if any deliberate increase in fishing mortality for velvets was undertaken, it should take into account the more vulnerable condition of the remaining species and compensate for this in some way (such as an increase in the MLS for these species).

Overall, the methods used in this study seem to indicate that the state of the stock is not in immediate danger, but that optimum fishing levels are being approached. The average size of individuals fluctuates throughout the year but there is no discernible trend showing decreasing size. Overall catch weight is being maintained over several years. However, it must be taken into account that these studies are only preliminary, and long-term data collection (currently underway) is required in order to truly ascertain the state of the stock.

Section C Market Considerations

5.9 Aims

This section aims to look at some of the considerations that must be made regarding the logistics of the industry, when making decisions about the management strategy to follow. This includes a study of the monthly catch over a period of three years, the conditions of that catch and the price it fetches both at first sale and in the shops overseas. One of the main reasons for undertaking this part of the study is to present some facts that can be taken into account in the event that a closed season be considered again, a subject of debate among fishermen currently, since the voluntary ban was discontinued. It also presents some of the problems involved in the processes between capture and sale to foreign companies, an area that would benefit from technological and methodological innovations.

The specific questions asked in this section are:

1. What is the monthly catch of velvet crabs in Orkney, per port?
2. To what extent is mortality at the packing stage important?
3. Does the quality of the catch change throughout the year?
4. How much do discards affect the industry?
5. What is the price fluctuation throughout the year, at first sale and at the marketplace?

5.10 Methods and Materials

During a period of 2 years, sampling of velvet crabs at the marketplace (OFS, Pierhead, Stromness) was carried out. This involved the random selection of a box of velvet crabs. All individuals in the box were measured for the following characteristics: CW, CL (carapace length), sex, limb loss, moult stage, presence of eggs (in the case of females) and mortality.

The samples taken during the general survey at sea were reanalysed in order to determine the percentage discard during actual fishing and how this changes over the year, and the limb loss at catch was recorded for comparison with limb loss at packing.

In addition to this, the prices offered for velvets at a number of merchants were monitored throughout the year, as was the price at the market in Spain.

5.11 Results

5.11.1 Monthly Catch

The graph below shows data collected by the Scottish Office regarding the monthly catch of velvet crabs divided into the main ports in Orkney.

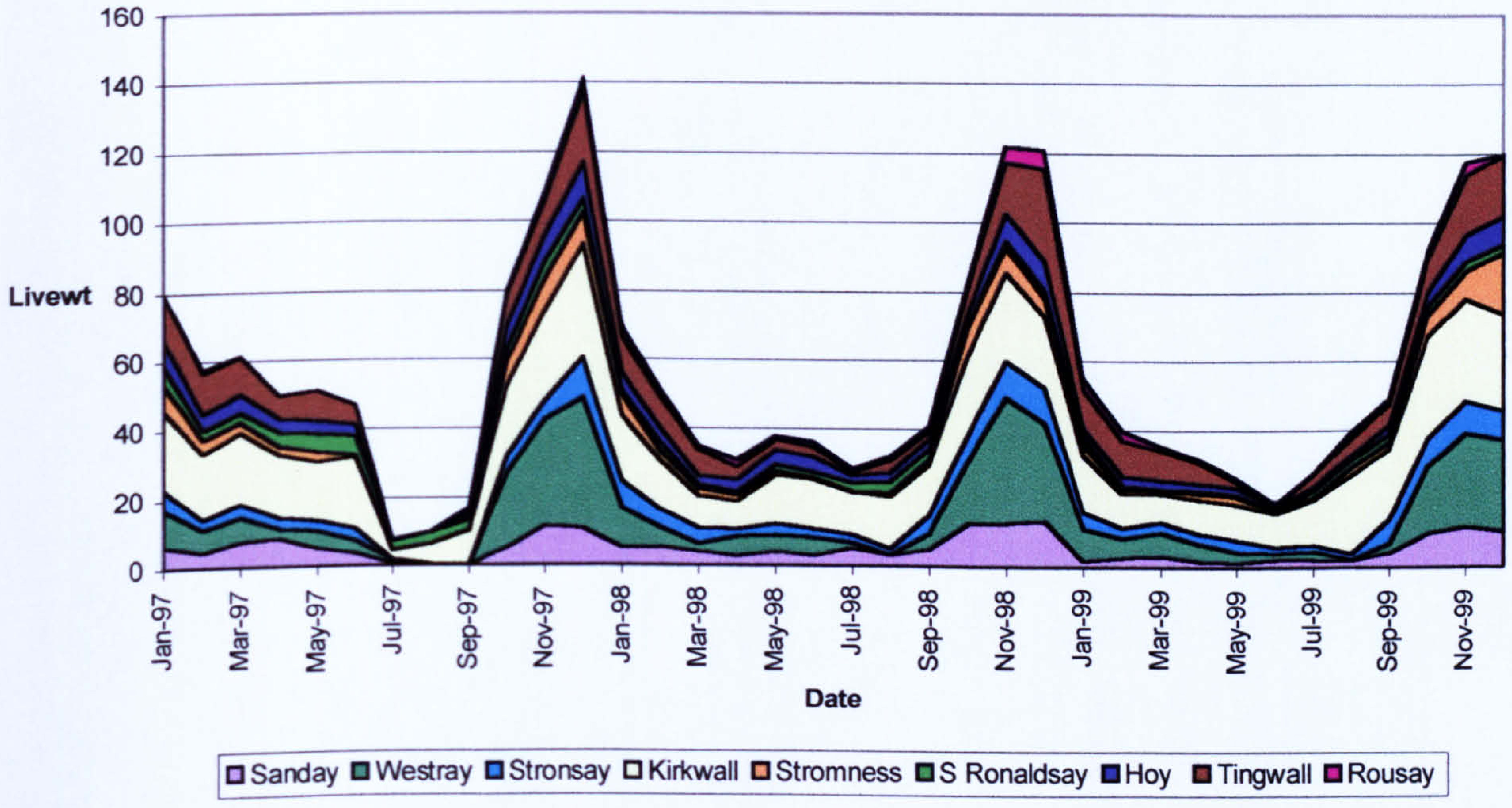


Figure 5.20 Monthly catch by port of velvet crabs in Orkney (data from Scottish Office)

As can be seen from the graph, the pattern of catches shows a distinct seasonality. Although in 1997, the almost-zero catch for July and August can be attributed to the voluntary ban, in the most recent years, this has been discontinued. The main port overall is Kirkwall, but Sanday and Westray produce a large catch in the winter months, reaching 36.7 tonnes in November 1998, although the catch throughout the remainder of the year is small. This trend is followed by most ports, with a relatively low catch during the spring and summer months, rising steeply in autumn and peaking around Christmas and New Year. It also appears that the winter peak in catch levels is decreasing slightly or becoming less pronounced. The sum of the catches from these ports in 1997, with the voluntary summer ban in place, is 709.77 tonnes, compared with 687.02 and 650.92 tonnes for 1998 and 1999 respectively, without a summer ban.

On Mainland, Tingwall followed by Stromness are the other important landing sites. Figure 5.21 shows the relative importance of each port with regards to its yearly catch over the last three years:

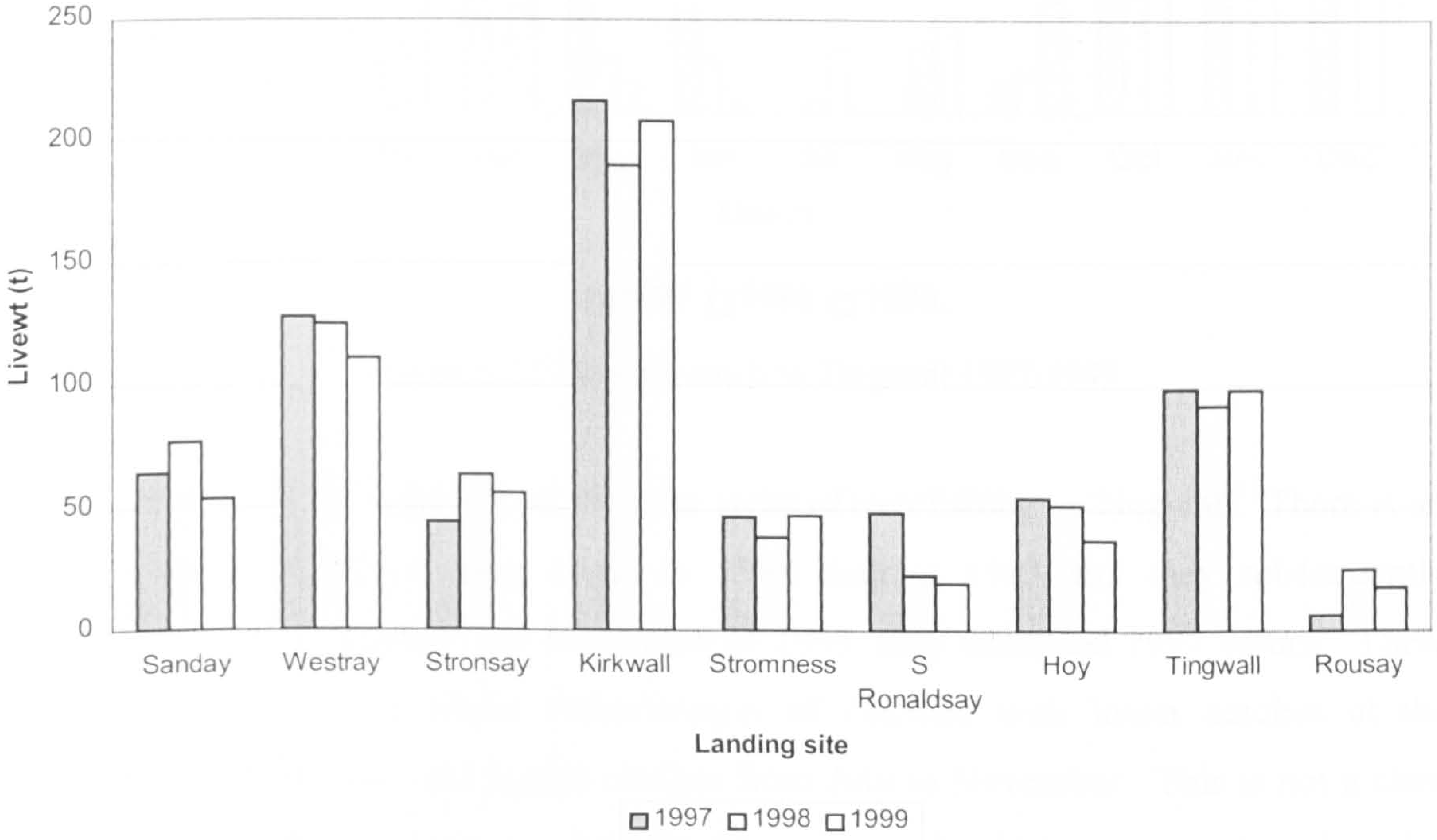


Figure 5.21 Yearly landings of velvet crabs by port (data from Scottish Office)

The importance of velvet crabs is clearly far greater in the northern part of Orkney, rather than in the southern ports of Mainland, South Ronaldsay and Hoy. Most of the fishing for velvet crabs is carried out from Eynhallow Sound northwards, making Tingwall and Kirkwall good access points to the best fishing grounds. Scapa Flow is generally not considered the best ground for velvet crabs, due to its sedimentary and enclosed nature. In most cases, it can be seen that the catch for 1999 is slightly lower than for previous years, although in Stromness the catch has remained mostly constant but low, and in Tingwall there does not appear to have been much change. This is somewhat surprising as in recent months (1999-2001), Tingwall fishermen have complained that the stock is being overfished and that catches are well below previous levels. In order to examine this in more depth, the monthly catches for Tingwall were isolated and plotted against each other for comparison. This is shown in Figure 5.22:

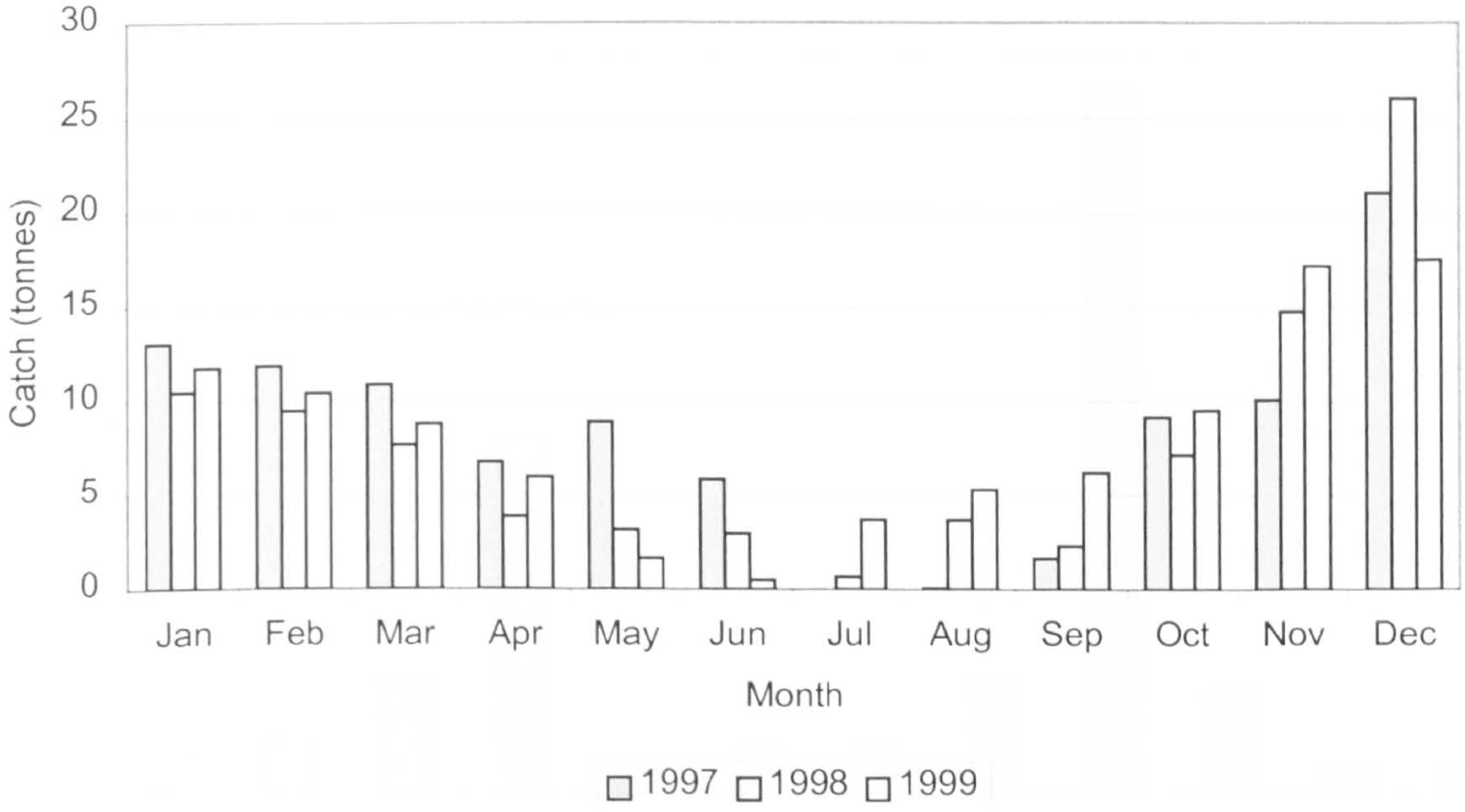


Figure 5.22 Monthly catch in Tingwall 1997-1999

The graph does not appear to show clear signs of overfishing in Tingwall. There is an indication that catches were lower in 1998 than in 1997, but they subsequently improved and in October and November of 1999, they exceeded 1997 values. There does appear to be a slight redistribution of catches, with lower catches at the beginning of the year, and higher catches from July to November. This is not a clear sign of overfishing. However, data for future years should be compared against this data in order to see whether some trend is emerging.

5.11.2 Losses

The catch figures correspond to the weights of animals in good conditions that are either exported or processed. However, the figures do not necessarily correspond to actual weights of animals removed from the water, as limb loss, mortality and discards due to size, moult stage or ovigerous state reduce the proportion of catch which reaches the merchant in a marketable state.

Figure 5.23 shows the mean monthly mortality of velvets at the packing stage, taken over a two-year sampling period:

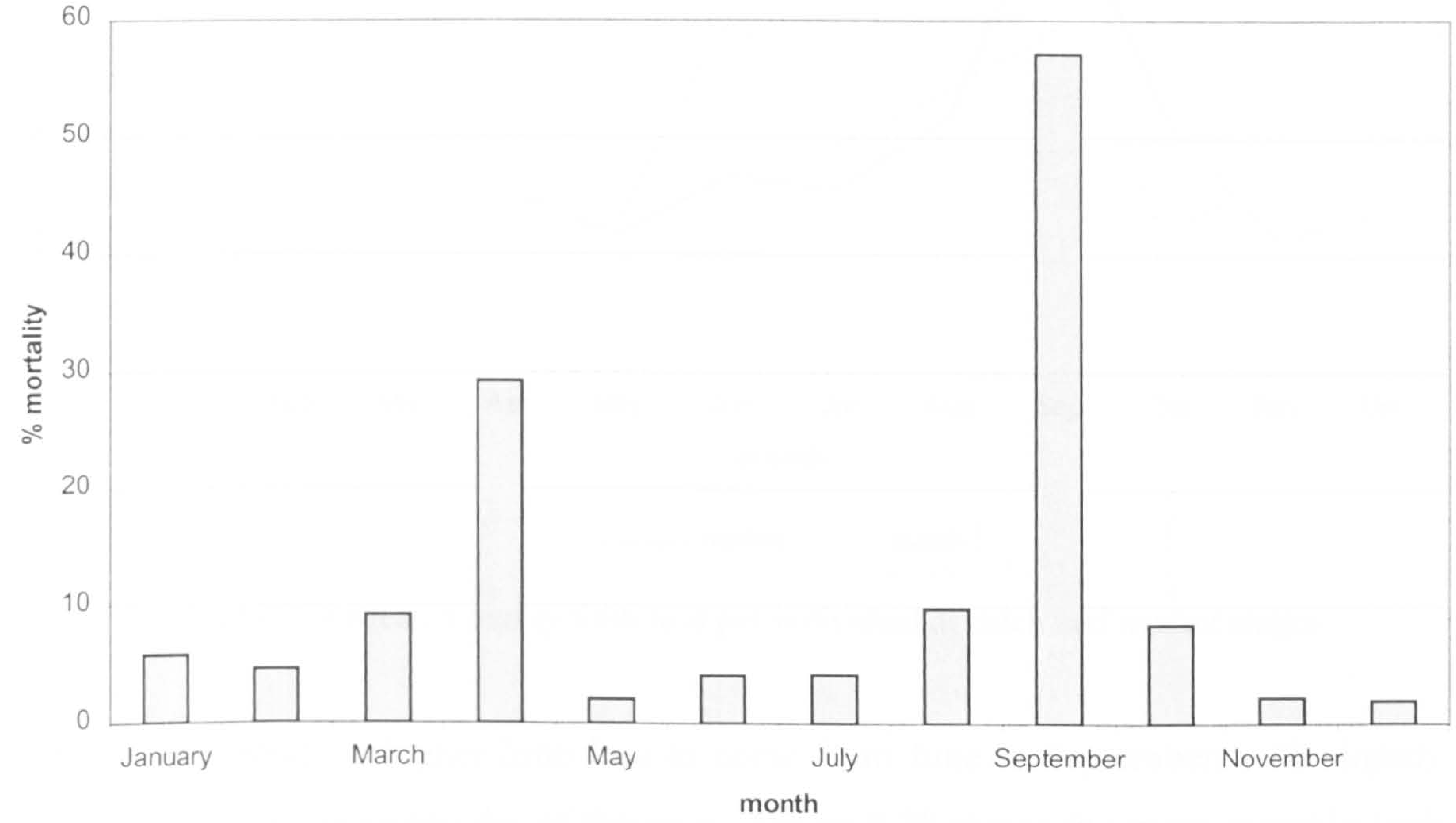


Figure 5.23 Monthly mortality of velvet crabs reaching packing stage

There are two results which stand out from the above graph. The largest mortality, corresponding to the month of September, may be misleading. In September 2000, OFS (Orkney Fisherman's Society) did not carry out any packing of velvet crabs, so these data correspond only to the measurements carried out in September 1999. These crabs were in a particularly bad state according to those working at the packing place, and should not be seen as representative. However, a mean mortality over the year of 11.5%, which is lower in November and December, and higher during the rest of the year, does represent the general mortality of the catch, and takes into account the fact that occasional catches are in a poor condition.

Figure 5.24 shows the average limb loss per individual over the year, both at the market and at the point of capture (as measured during the general sampling survey):

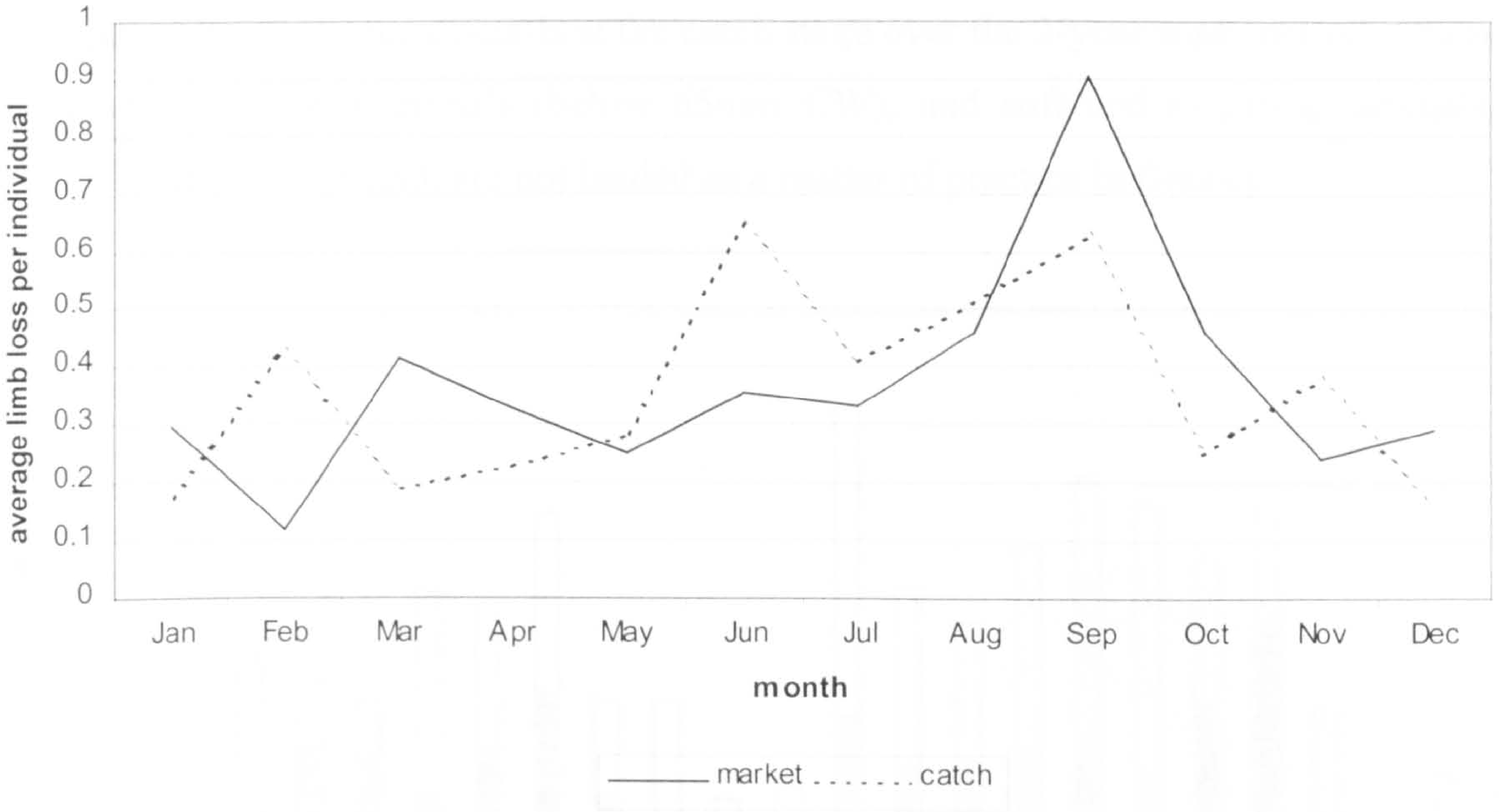


Figure 5.24 Mean monthly limb loss per individual at catch and market stages

There is a trend for higher limb loss to occur from June to September, with slightly lower levels in the remainder of the year. Figure 5.25 shows the mean monthly limb loss per individual broken down into the different sexes:

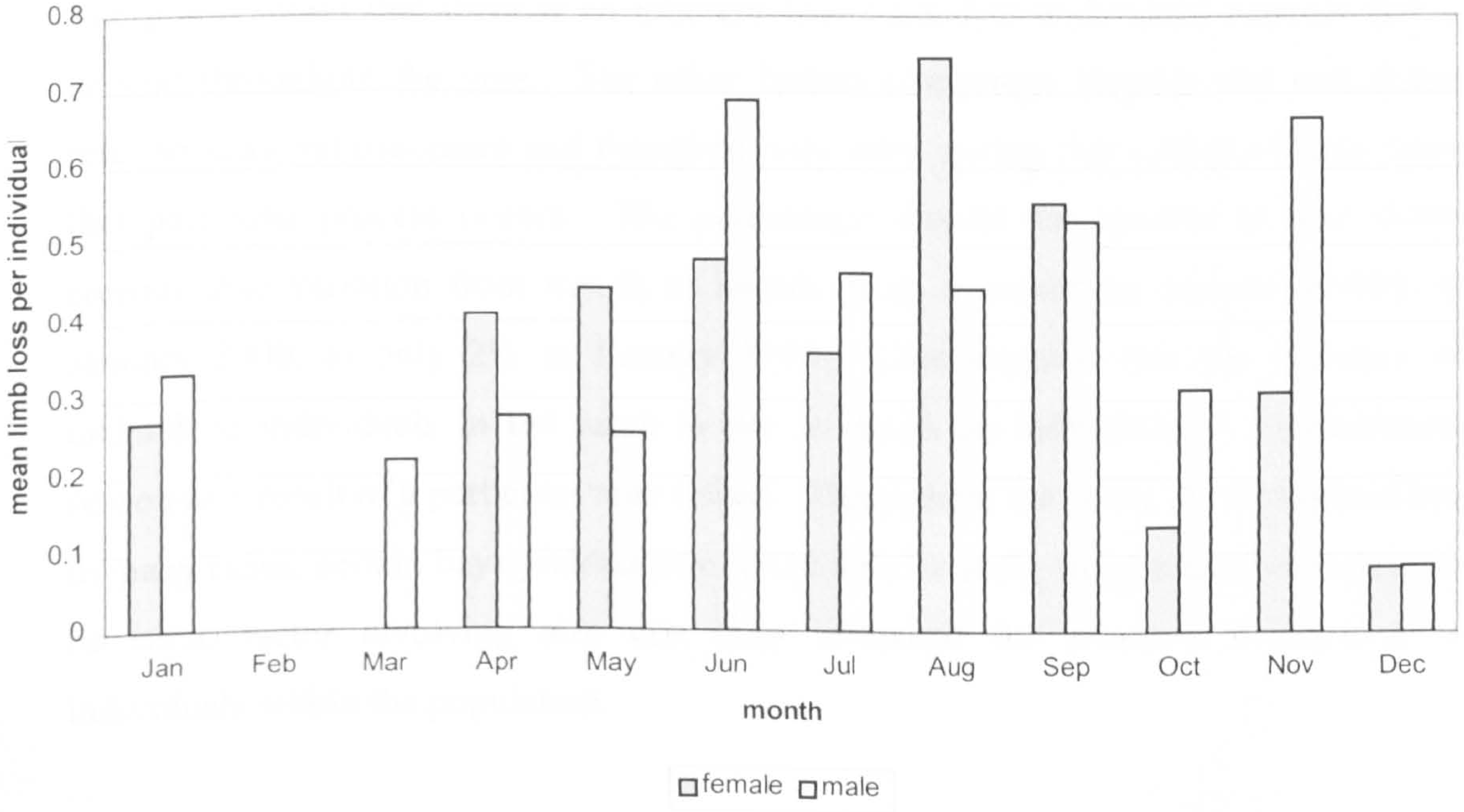


Figure 5.25 Mean monthly limb loss for males and females

The overall limb loss over the study period was 0.42 limbs for males and 0.32 limbs for females. A Student's t-test showed there to be no significance in this difference.

Figure 5.26 shows the discards at the catch stage over the 2-year study period. These include undersized animals (below 65mm CW), and soft and ovigerous animals, which, while not illegal, are not landed as a matter of practice in Orkney.

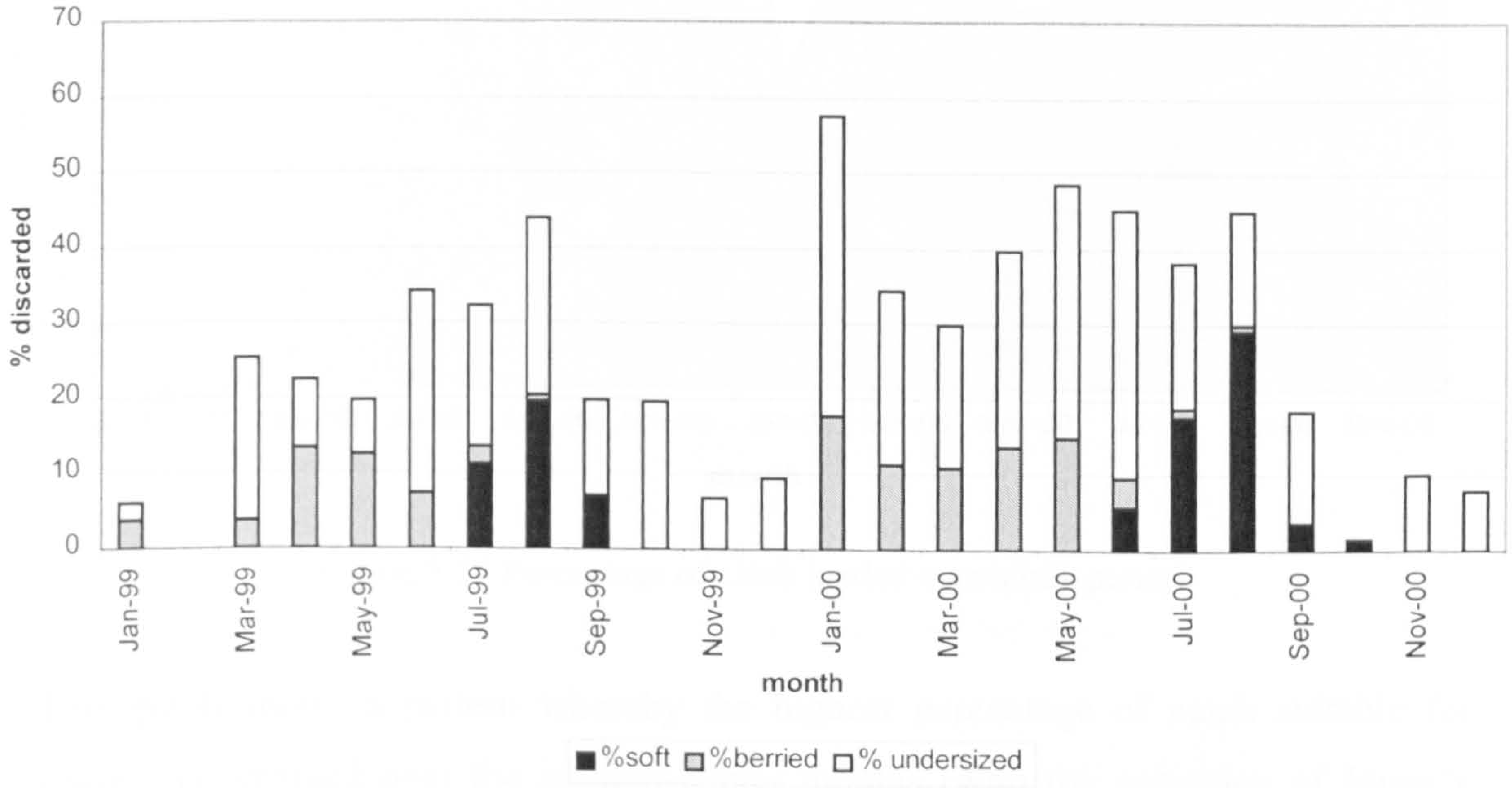


Figure 5.26 Percentage of catch lost for various reasons over time

The graph shows that there is an inherent loss related to undersized animals that is present throughout the year. The other factors (ovigerous females and soft crabs) refer to seasonal processes and therefore only arise during that period of time when that particular process occurs. The percentage discard for reasons of size shows considerable variation from month to month, from a maximum amount of 40% in January 2000, to only 2% in January 1999. This suggests that the presence of undersized individuals in the catch is not so much an indication of a recruitment season as a result of a particular area fished. Throughout the study, it was noticed that in many cases, certain bays yielded animals of similar sizes, suggesting that there may be some factor involving size that may influence the physical distribution of individuals within the population.

Translating the data on losses and discards into the percentage of the catch that is landed, the following graph is obtained (Figure 5.27):

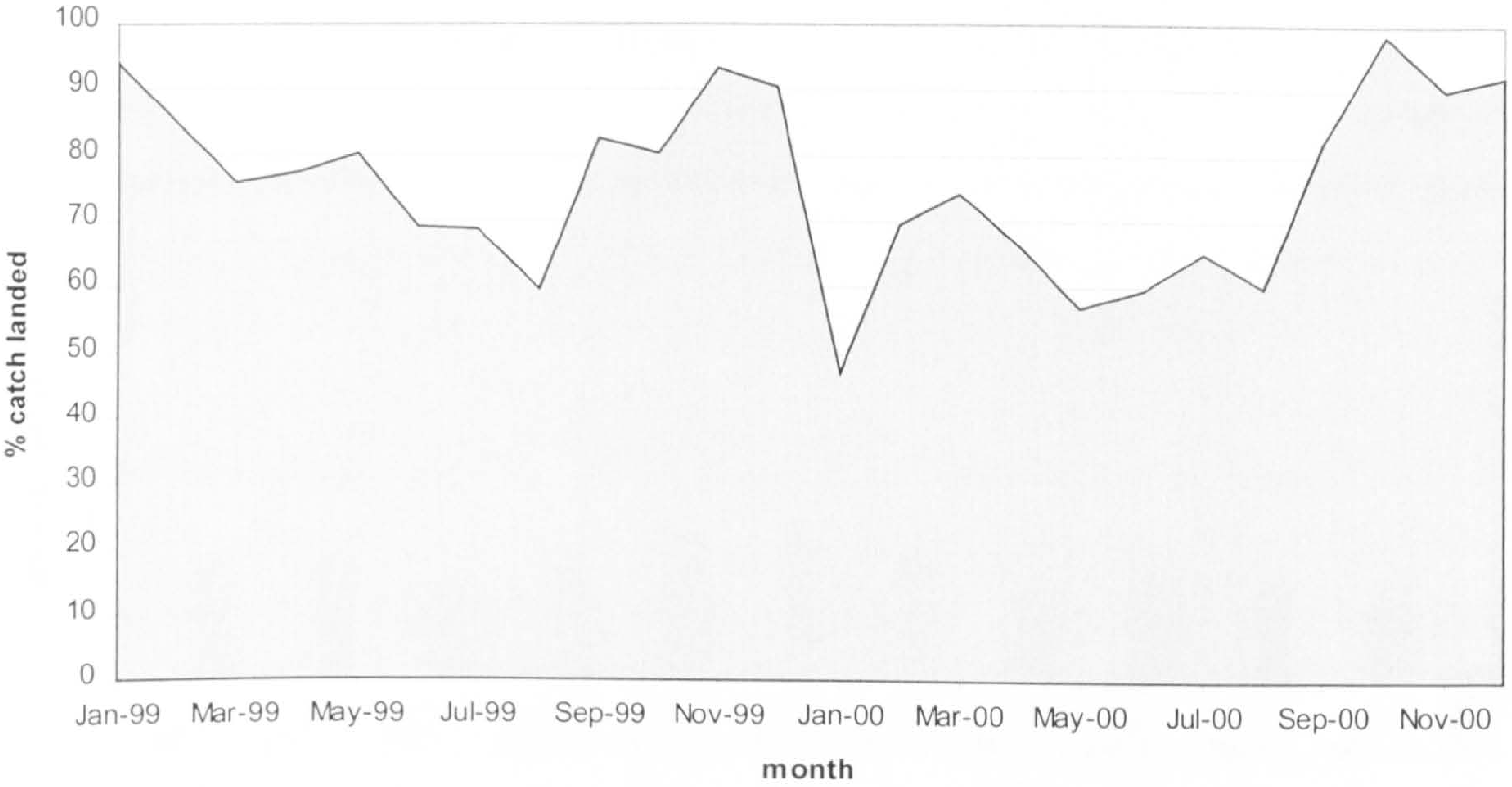


Figure 5.27 Percentage of catch landed over study period

This graph shows a pattern whereby the highest percentage of catch suitable for landing is obtained over the autumn-winter months (with the exception of January 2000 where only 47% of the sample was of marketable condition due to an unusually large proportion of undersized individuals caught). In these months, over 80-90% of the catch is landed, compared to the summer months where landings can be as low as 60% and below of the actual individuals caught. This coincides mostly with the ovigerous period of the females and the moulting season for both sexes.

5.11.3 Price Changes

Figure 5.28 reflects the changes in prices offered for velvet crabs both at the merchants and in the shops in Spain.

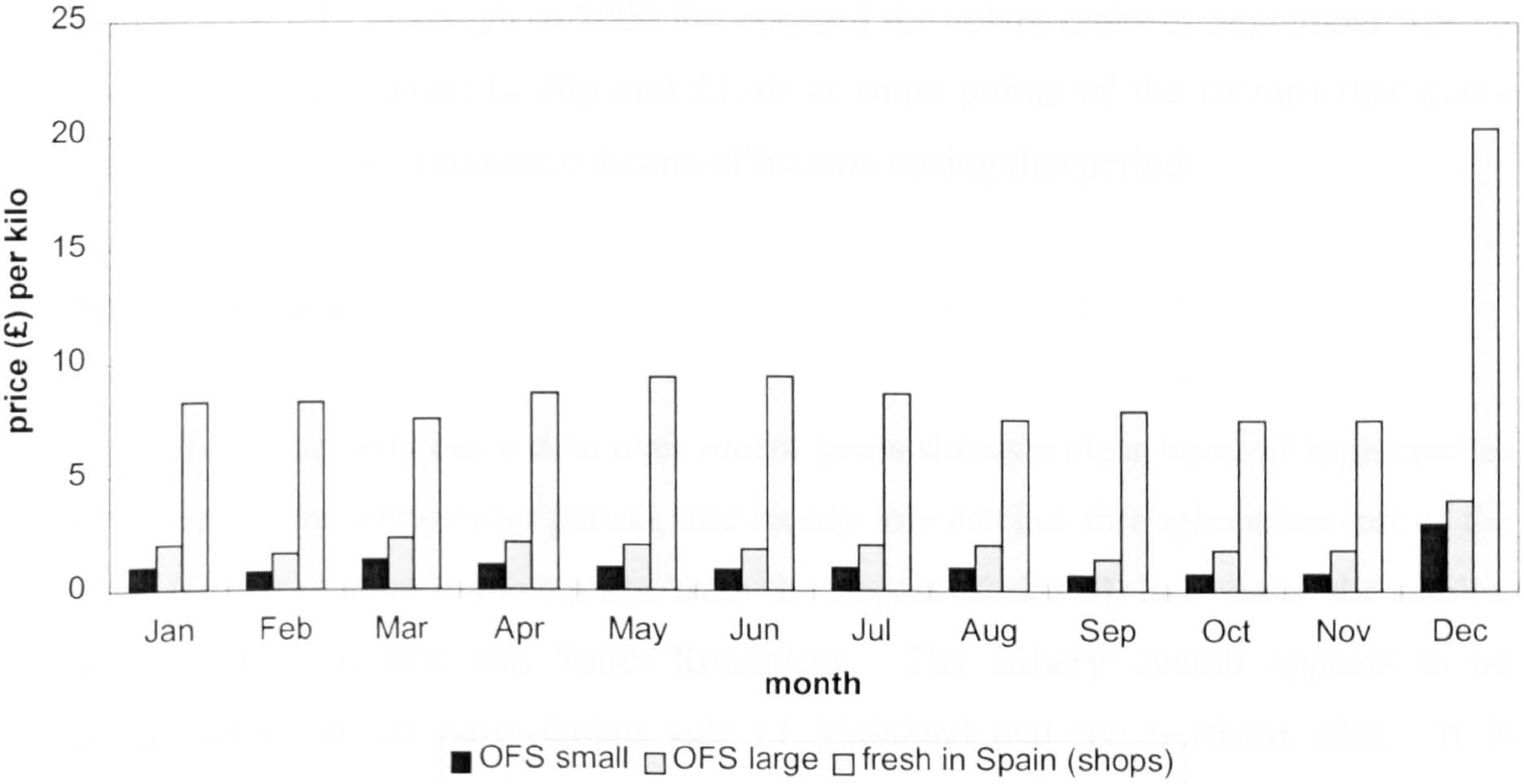


Figure 5.28 Velvet crab prices at merchant and Spanish market

Prices for large and small crabs are shown for the merchant (any crab with a CW of 75mm or greater is considered large), whereas price per kilo is shown for the shops in Spain (the approximate exchange rate at the time of study was 265 pesetas to the pound).

The price of velvet crabs in Spain remains relatively constant at around 2000 pesetas per kilo throughout the year with the exception of a small peak in April-May and a huge increase in price over the Christmas period. Both peaks can be attributed to times of year at which seafood is in great demand. The typical Spanish Christmas dish is the *mariscada*, a mixture of all sorts of shellfish, including the velvet crab. The period of April to May coincides either with Easter (when it is late) or with a number of long weekends celebrating certain saint's days. It is also the start of the good weather in most of the peninsula, when the typical family gatherings at weekends are resumed, at which seafood plays a prominent role in many homes.

The price obtained by the fishermen at the merchants in Orkney generally reflects the prices and demand in Spain. The highest prices are obtained over the Christmas period, of £3 per kilo for small individuals (<75mm) and £4 per kilo for large individuals (>75mm). Throughout the rest of the year, the prices fluctuate around the £1 and £2 marks, although in 2000 the demand for velvet crabs in September was so low (prices were down to 70p and £1.40 at some points of the month) that many fishermen turned to alternative means of income during this period.

5.12 Discussion

The official monthly catch data over recent years shows a clear trend of high catches over the late autumn-winter period, and steady low catches throughout the rest of the year. This is evident in most ports, from the largest (Kirkwall) to some of the smaller landing areas in Hoy and South Ronaldsay. The fishery overall appears to be concentrated on the north-facing side of Mainland and the northern isles. It is interesting to note that Tingwall is a more important landing site for velvet crabs than Stromness, the second largest town in the archipelago. However, this can be related to the distribution of the species. Those harbours looking onto Scapa Flow tend to be less important for the velvet crab fishery because this area is mostly soft sediment and is protected from most of the wave action, being virtually enclosed.

There has generally not been a significant change overall in the numbers landed, although some areas such as South Ronaldsay and Westray have experienced a decline in landings over the last three years. However, the general pattern is that of a constant total catch with some local fluctuations. If, as suggested in section 4, the velvet crab is territorial, then it may be susceptible to localised overfishing in areas that are heavily exploited. This may be the reason why some fishermen from Tingwall are expressing concerns about dwindling stocks. The catchment area of Tingwall is subjected to a very high fishing pressure, and it is possible that some regularly frequented areas have been exhausted. It is also possible that the removal of the summer ban has a negative effect on the winter catch.

There is a mortality of around 11.5% of the catch between the time it is caught and the time it is packed for transport to Spain. This is slightly higher in summer months and lowest in November and December. Occasional catches are in a very poor condition with over 50% mortality. There are a number of factors which contribute to the quality of the catch in this period. The first factor is the length of time that transpires from capture to transport. This period is shortest in the weeks leading up to Christmas, when there is a high turnover of catch, and packing is carried out almost on a daily basis. In the summer however, there are times when packing is carried out once a week or, in the case of September 2000, even less frequently. The longer the catch remains in crates, the more stress the animals are subjected to and the higher the mortality is likely to be. In the same way, the method of storage was also observed to affect the survival of the catch. Those animals packed tightly in crates were generally observed to be in a better state than those kept in mesh bags (this was also the case for observations of limb loss). Mortality is also influenced by temperature (MacMullen, 1983). In the summer months, there is likely to be a higher rate of mortality after capture, as velvet crabs are susceptible to stress by heat as well as overcrowding.

The pattern shown for limb loss is one of a generally higher loss during summer months, and a lower loss in winter. This can also be related to the length of time between capture and packing. The longer the crabs are kept in captivity, the more likely they are to lose limbs due to their agonistic behaviour towards one another. Limb loss also occurs in the wild, especially during courtship rituals between rival males (Smith *et al*, 1994), and in the creels, where a large number of individuals are artificially forced to share a relatively small area.

The discarding of individuals at the catch level, due to size, reproductive state or moult stage, shows a distinct pattern. The most efficient time of year in terms of the percentage of the catch which can be landed is October-December. At this time of year, the only discards are those due to size. From January to April, a large proportion of the catch must be returned to the sea because it consists of ovigerous females and, although the sex ratio at these times is heavily biased towards males, most of the females caught at this time are berried, and may account for up 10-15% of the catch. Although this figure diminishes by early summer, the moult season begins at this time, and at the height of the moulting season, in August, up to 30% of the catch must be returned due to its soft condition. Throughout the year, catches of undersized crabs fluctuate, generally being highest in the summer and lowest in the winter. This may be an indication of a recruitment period, but as certain areas were observed to consist of individuals of similar sizes (for example, the large number of undersized crabs obtained in January 2000 were all caught in one bay to the north of Rousay), it may be more likely that this is simply a reflection of the choice of fishing ground. Further work is necessary to determine this.

The overall picture as shown by Figure 5.20, shows a greater catch efficiency in terms of discards in the very months where prices are at their highest. During the period of time previously covered by the voluntary ban, prices are at their lowest, as is catch efficiency. Indeed, many fishermen do not bother fishing for velvet crabs at this time even though there is no ban. The amount of time and effort required to obtain the same income as in winter months is simply too high. There is some talk of resuming the summer ban on velvet crabs, and using this time to target other species. There is a worry among some fishermen that the summer fishery adversely affects the quality of the winter fishery, when prices are at their highest. It is not clear whether this is the case, but it does appear that there is sense in having a ban during this period, as it coincides with the moult season. Although recently moulted crabs are returned to the sea, the time spent in the creel may affect their quality later on, in terms of limb loss and shell state, as well as increasing mortality during this period.

However, there is a disadvantage to the implementation of a ban. Most merchants deal with Spanish businesses that want velvet crabs on a year-round basis, even if the summer quantities are lower. If the local merchants cannot satisfy this demand for part of the year, there is a chance that these businesses will go elsewhere, where a year-round fishery does exist. This would have a negative effect on the local economy as a whole. This should be taken into consideration when discussing the possibility of reintroducing the summer ban.

PART 6: FINAL DISCUSSION AND CONCLUSIONS

6.1 Restatement of Aims

The general aim of this study was to investigate the life history and fishery of the velvet swimming crab (*Necora puber*) in the Orkney archipelago, and to place into context its importance in local socio-economics.

The study was divided into parts which dealt with broad areas concerning the subject. Thus, reproduction, larval and juvenile stages, growth and the fishery were all dealt with separately. However, all these subjects are interwoven and must be seen as integral parts to understanding and improving the management of an important local resource.

The questions this study attempted to answer are summarised below:

Part 1: Background

1. What is the importance of *Necora puber* and other portunids in worldwide fisheries?
2. What is the importance of *Necora puber* to the Orkney Isles?
3. What knowledge of the Orkney stock can be obtained from studies of other stocks?
4. What are the gaps in our knowledge of the Orkney stock?
5. How may these gaps be addressed?

Part 2: Reproduction

1. At what size is sexual maturity attained?
2. When does mating occur, and is there a size relationship within a pair?
3. What is the brood size?
4. Is the brood size affected by the size of the female, limb loss?
5. Is there egg loss during development?
6. What are the stages (and duration) of egg development?

7. How often does reproduction occur, and what is the timing?
8. Can fecundity be used to estimate initial mortality (Z) figures?

Part 3A: Larvae

1. Is there a prezoeal stage for *Necora puber?*
2. Can the prezoeal stage be described?
3. What is the development time through each stage in the laboratory?
4. What is the mortality through each stage in the laboratory?
5. Is larval rearing on a large scale feasible?
6. Are larvae comparable in morphology with those from other stocks?
7. When are larvae present in the water column?

Part 3B: Juveniles

1. Where are juvenile *Necora puber* found in Orkney?
2. Can a measure of abundance be obtained?
3. Which is the best method of obtaining juveniles?
4. To what extent are juveniles morphologically similar to adults?
5. When does settlement occur?
6. Is the sex ratio 1:1?
7. How fast do they grow?
8. When do they reach sexual maturity?
9. When do they reach MLS?
10. How often do they moult?
11. What are the moult increments?
12. Can growth curves for the entire population be constructed from juvenile data?

Part 4: Population dynamics

1. What is the relationship between CW, CL and weight?
2. Does the sex ratio change over time, and if so, why?
3. How often and when do adults moult?

4. How long does the moult process take?
5. Is tagging an effective method to measure growth/movement?
6. What are the von Bertalanffy growth parameters ($L\infty$ and K) for the stock?
7. What are the advantages/limitations of the methods used?
8. Are there any differences between males and females?
9. What are the values for Z, M and F?
10. Can the population structure be modelled?
11. How do the population dynamics compare with other areas?

Part 5A: Baiting practice

1. Is there a difference between fresh, frozen and salted bait?
2. Does soak time affect catch?
3. What are the reasons for creels not fishing?
4. Do lobsters and crabs interfere with one another in terms of catch?

Part 5B: The state of the fishery

1. Does the mean size of individuals caught change over time?
2. What is the selectivity of the fishing gear used?
3. Can we observe changes in catch and effort over the years?
4. Is it possible to carry out length-cohort analysis on the stock?
5. Can yield per recruit analysis be used as a tool for predicting results of changing the MLS?

Part 5C: Market considerations

1. What is the monthly catch of velvet crabs in Orkney, per port?
2. To what extent is mortality at the packing stage important?
3. Does the quality of the catch change throughout the year?
4. How much do discards affect the industry?
5. What is the price fluctuation throughout the year, at first sale and at the marketplace?

Essentially, all the questions are parts of the objective of the study: to find out enough about the stock and fishery of *Necora puber* in Orkney waters in order to manage the resource in the long term, in a profitable and sustainable manner.

The following parts to this section summarise the findings from this study, bringing together results from all sections of the study in order to give an overall picture of the stock and its exploitation. Some management options are explored, and the potential for further work in this area is discussed.

6.2 The life cycle of the Orkney stock of *Necora puber*

The velvet swimming crab *(Necora puber*, Brachyura, Portunidae) is found in north-west European waters from Norway to the Spanish Sahara, and all round the British Isles. It is generally found on the lower shore down to around 70 metres on exposed, rocky substrate, unlike most other members of its family. In Orkney, those individuals found in deeper waters are lighter in colour and are locally known as "red" or "blonde" velvets. It has been suggested that these belong to a separate substock of velvet crabs.

Necora puber is an opportunistic omnivore. Its food varies according to season and availability, but it is known to feed on brown algae. It is thought that the algae aid in the moult process (Norman, 1989), although the exact mechanisms are, as yet, unknown. They are cryptic by day, and active by night. They display antisocial behaviour towards one another and towards other species. They are predated upon by a variety of larger fish (such as cod), and octopus.

Sexual maturity occurs at different sizes for males and females. Gonad examination showed 50% maturity sizes of 43mm CW for females and 51mm for males. The range of sizes over which puberty was attained was narrow for both sexes, suggesting that it occurred over one moult. External indications of sexual maturity include an increase in the positive allometry of the height of the major chela in males at around 51mm, and a discontinuity in abdominal segments 4 and 6 for females between 38-40mm.

Mating pairs were only found in the month of September during both years of study. In all mating pairs, the male was larger than the female by 6-11mm.

After mating has occurred, the female's ovaries begin to develop. The eggs are not fertilised until they are spawned. Spawning does not occur until January. In the laboratory, the female was observed to bury herself in the sand throughout the spawning process and for much of the time that she was in the ovigerous state. It is possible that migration onto soft sediment by females occurs in the wild at this time. There is only one spawning period each year. It is extended – from January to June, and the eggs develop slowly through the first stages, but faster in later stages (possibly partly due to increased water temperatures as summer approaches).

The eggs are carried under the abdomen, where they are frequently oxygenated by fanning movements. The mean egg diameter at spawning is 340µm. The eggs increase in diameter (and volume), so that at hatching, the mean diameter is 570µm. Females were observed preening their egg masses, and removing (presumably) inviable eggs. The maximum brood size was found to be 278,000 eggs, with a minimum brood size of 5,000 eggs. The mean brood size was 112,000 eggs. There was a general trend of increasing brood size with increasing size, but this was weak and subject to much variability. After around 80mm CW, the increase in brood size appeared to level off. Four developmental stages were identified. There was significant loss of eggs during development. Up to a third of the total egg mass may be lost during development. This may be due to intrinsic factors such as the viability of the eggs, or extrinsic factors such as inadequate ventilation, or excessive abrasion.

In the laboratory, at water temperatures constantly above 12°C, the total development time from spawning to hatching was 60 days. In the wild, data gathered on egg stages of ovigerous females suggests that development time is more than double this, with the main hatching period occurring in June. Larval release occurs at night and over several hours. Although the reproductive cycle of the Orkney stock is a yearly event, this appears to be limited by the females, as the males displayed no cycle in this aspect, tending to display mature gonads throughout the year.

The larvae hatch as prezoeae, enveloped in the prezoeal cuticle so that the dorsal spine of the zoeal stages is not obvious. The prezoeal stage lasts only a few minutes (up to 2 hours) and is followed by 5 zoeal stages and a megalops stage, which settles and undergoes metamorphosis to the first crab instar. The morphometry of the zoeal stages is comparable with that of larvae in other areas (Mene, 1987).

Total development time in the hatchery, from hatching to metamorphosis was 33 days. However, the survival rate was appalling, with only 2 larvae reaching the first crab instar, from an original 33,000. This was partly due to technical problems with equipment, and partly to the cannibalistic nature of the larvae, making batch rearing a difficult prospect. The expense of rearing larvae is, at present, prohibitive.

Necora puber larvae are found in the water column from June to September. Although megalops stages were not found during the study period, they have since been found at the end of July in a study by Hazlehurst (2001).

Settlement and metamorphosis therefore occur in August and September. The size of the first crab instar is about 2.4mm. Juvenile *Necora puber* were found at a number of beaches around Orkney. They inhabit a similar habitat to adults, being found at low water during spring tides under rocks and stones on exposed shores, in and among the *Laminaria* zone. It is not clear whether they only occupy a narrow band of shallow water, or whether they extend into adult grounds. If they are separate from the adults, some form of migration to adult grounds must take place at a certain time.

Length-frequency analysis of samples obtained at three sites around Eynhallow Sound showed there to be two peaks in juvenile sizes, followed by the adult distribution starting at around 50mm (sexual maturity). This implies that sexual maturity occurs after three years. In the first year, the juvenile crab undergoes around 7 moults, reaching a size of 15mm. In the second year after a further 5 moults, the crab reaches 35mm. There are three further moults in the third year. It is possible that the female attains puberty a moult stage or two before the male, as sexual maturity was estimated as occurring at a smaller size for females than for males.

There is no significant difference in the sex ratio of juveniles. Both sexes appeared to grow at the same rate whilst juveniles. Estimates of growth parameters from juvenile data gave $L\infty = 98.4$ and $K = 0.268$.

There was considerable variation in the moult sizes present on the shore. This led to some difficulties in identifying modal groups. It became apparent that the variability in sizes was due to individuals being at different moult sizes. As there is one, fairly extended reproductive season, some individuals settle earlier than others and therefore moult earlier. In addition to this, patchy food availability may cause some individuals to remain at a certain size for longer than others, so that within a year cohort, a variety of moult sizes are present at any given time.

Once sexual maturity has been attained, adults moult on a yearly basis. There is a time difference between the male and the female moult seasons. Male moulting peaks in late July, whereas female moulting peaks in early September. There is some overlap between the two moulting periods. The delay in female moults is probably related to reproduction. Males compete for females and attend them for several days prior to the moult, after which mating occurs while the female is still soft. Recently moulted females were rarely found in creels.

The sex ratio of adults appeared to fluctuate throughout the year. This was more due to relative reluctance to enter traps when ovigerous or moulting, rather than real differences in the population structure itself. There was no evidence of migration, although it is possible that females migrate to soft substratum in order to spawn. Tagging trials were unsuccessful but hinted at territoriality or little movement of individuals from an area.

The CW-weight relationship for the Orkney stock of *Necora puber* was $0.0003.CW^{2.9807}$ for males and $0.0003.CW^{2.9629}$ for females. There was no significant difference in weight between males and females until puberty. Males became heavier than females, mainly due to the increased growth of the chelae after puberty.

Methods of size-frequency analysis applied to adults were found to be unreliable, as cohorts are difficult to separate from a total size-frequency distribution after puberty.

Those parameters obtained using juveniles were adopted as being the most reliable. Although they did not differentiate between the sexes, there was evidence that any differences of $L\infty$ and K between males and females were small compared to differences in other areas.

Total mortality (Z) was estimated to be 1.01 for males and 1.15 for females. Natural mortality was estimated to be around 0.5, but was estimated using equations relating mortality to longevity and sexual maturation. Fishing mortality was estimated to be around 0.5.

Figure 6.1 summarises the processes in the life cycle of the Orkney stock of *Necora puber* and their timing.

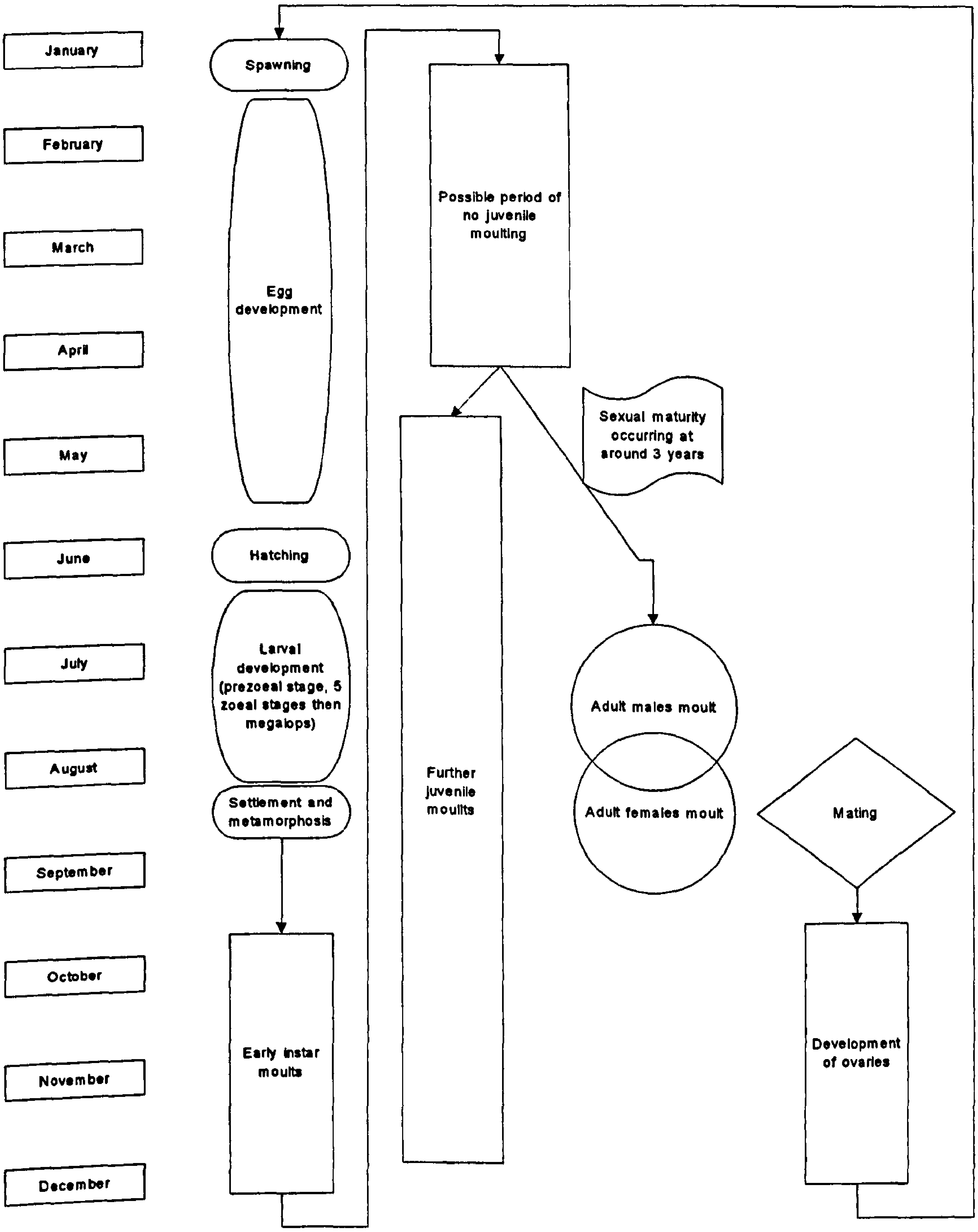


Figure 6.1 General pattern and timing of events during the lifecycle of the Orkney stock of *Necora puber*

6.3 The current state of the fishery for *Necora puber* in Orkney

The velvet crab fishery in Orkney has developed over the last two decades in response to demand for the resource in Spain, where stocks were severely depleted. It is currently the most important shellfish species in Orkney, not for its value (£1,043,509 at first sale in 2000), but because it has allowed the inshore fishery to become a year-round industry which also incorporates species such as the edible crab and the European lobster.

The velvet crab is fished using creels. These are usually baited with frozen skad. Fresh bait was not found to significantly enhance the catch, although both fresh and frozen bait was found to produce higher catches than salted bait. Creels are laid overnight where possible, although sometimes they are hauled every two days. This may be due to a boat operating more creels than can be hauled in a day's work. The optimum soak time was found to be one night, as there was no significant difference in catches between a soak time of one night and that of two nights. The advantage of a two-day soak is that a wider area can be covered and essentially monopolised by any given boat. It is thus due to competition, and not optimum fishing practice that this sometimes occurs.

The velvet crab is targeted all year round, although demand at the consumer level (in Spain) fluctuates. The highest prices are obtained in the weeks leading up to Christmas and New Year. Lowest prices coincide with the summer months, during which the state of the catch is at its poorest, with recently moulted individuals either being too soft to land, or susceptible to stress if they are landed.

Catches increased drastically from the start of the fishery in the mid-80s up until the mid-90s, after which the annual catch has levelled off around 650-700 tonnes. The mean size of individuals in the catch fluctuates throughout the year and may depend greatly on the area fished, but has not decreased over recent years. The surplus yield model (Schaefer, 1954) was applied to catch and effort data for Orkney and gave inconclusive results, mainly due to the difficulty of applying numerical values to effort both in the present and for past years.

Jones' length cohort implied that the current levels of fishing effort in Orkney were approaching the maximum, and that there may only be limited room for an increase in fishing effort. According to length-cohort analysis, at present, an annual yield of around 5.5 million individuals is removed from a total adult (>50mm CW) population of around 36 million. Yield per recruit analysis suggested that there was no point in increasing the minimum landing size and that maximum yield per recruit occurs when age at first capture is 4 years. Taking into account that onset of sexual maturity does not occur until the third year, leaving the MLS at 65mm (corresponding to around 4 years) allows for at least one chance at successful reproduction, whilst maintaining yield per recruit close to the maximum. This model also suggested that fishing effort was close to the optimum level.

However, these models have been carried out on short-term data. Collection of size-frequency data for these analyses is now being undertaken as a long-term project, in order to remove the uncertainties of using data from one year only. In addition to this, further work must be carried out into the definition of the stock and its dynamics, in terms of movements and mixing. This is discussed further in Section 6.5.

6.4 Options for the future management of the fishery

The velvet crab fishery in Orkney (and the rest of the UK) is legislated under the Sea Fish (Conservation) Act 1967. This act is mainly concerned with size restrictions on exploited fish and shellfish species. The Undersized Velvet Crabs Order 1989 (SI 1989 No. 919) makes it an offence to land or transport any velvet crab below a carapace width of 65mm.

The Sea Fisheries (Shellfish) Act 1967 allows the provision of orders for the establishment or improvement of a specified shellfishery, along with its regulation. A several order grants exclusive rights over an area of seabed for specified species. A regulating order, as applied to a defined area, for specific shellfish species and for a set time, is normally made to local sea fisheries committees or other public bodies with the aim of developing an efficient and sustainable shellfishery (ICIT, 1999).

There are various tools available for the management of a local fishery. Limitation of effort is favoured in many areas. Effort limitation can be focused on the gear in a number of ways, such as limiting the number of creels per person or per boat. An advantage of this in the case of the velvet crab fishery is that if creel numbers are used to determine effort in surplus yield models, then the effects of limitations on the numbers of these creels should be directly visible when using such models. However, there are problems in enforcing such limitations. Creels would have to be licensed and stamped, with marked buoys giving information on the number of creels on the backrope. The fishery would have to be policed and some penalty for infringement of the rules introduced.

Increasing the MLS is a way of changing the relative effort on different sizes of individuals. It is self-regulatory, in that merchants will not purchase undersized individuals. The cost to the industry would come in the form of larger mesh size or the inclusion of escape gaps in creels. A blanket MLS throughout the entire UK may not necessarily be the best option for a species such as the velvet crab, which shows considerable plasticity from one area to another. The local regulating body can act in accordance with scientific evidence from its stock and set a MLS which best suits the local fishery, taking into account age and size at sexual maturity, relative reproductive output at different sizes, and lifespan and maximum size.

The number and size of vessels operating within an area covered by a regulating order may be controlled by use of a permit scheme. Within this scheme, there may be limitations on number of days fishing permitted in a year, or there may be a ban on fishing on a particular day of the week. However, in a location such as Orkney, where fishermen already lose around 90 days a year due to bad weather, such limitations would be unpopular as well as inefficient.

Currently, there is a voluntary ban on the landing of ovigerous and recently moulted velvet crabs in Orkney. This is enforced at the marketplace by the merchants, due to the high mortality caused by transport of these animals, which are particularly susceptible to stress. The scientific rationale behind a ban on landing of ovigerous animals is that the stock is limited by egg number. This is not likely to be the case in the velvet crab in Orkney, so the effectiveness of this is debatable. However, if it forces greater awareness of the vulnerability of such resources as well as improving the quality of the product after transport, then such a scheme is positive.

Closed seasons and closed areas are other management options. A closed season was in use in Orkney up until 1998, but as it was voluntary and therefore only partially adhered to, it was dropped. Most fishermen agree that the re-introduction of a summer ban on velvet crabs would be a positive development in the fishery. The summer ban would coincide with the moulting and mating period of *N. puber*. This is the time when discards are highest, the susceptibility of the catch to stress is also high (due to the warmer temperatures and recently moulted condition of many of the animals) and prices are lowest. Many fishermen believe that relieving the pressure on the stock at this time would improve the winter catches, when prices are highest.

Closed areas are currently being investigated by researchers at ICIT, Heriot-Watt University. Research here is focused on the premise that if an area within a fishery is entirely closed to fishing, then depending on the size of that area and the mobility of the species involved, fishing effort outside that area could be increased without jeopardising the viability of the stock. Research is currently in the phase of mathematical modelling of the theoretical viability of such schemes (Papamatthaiaki, 2000). Before introducing this for an actual fishery, details must be known about migratory and reproductive behaviour.

Since October 1997 a consultation process has been initiated by the Orkney Fisheries Association within the Orkney Fishing Industry, addressing the potential for a Regulating Order for Orkney's shellfisheries (as provided for in the Sea Fisheries (Shellfish) Act 1967, amended by the Sea Fisheries (Shellfish) (Amendment) Act 1997).

It is proposed that the Regulating Order cover a six mile limit around the Orkney Islands with a median line in the Pentland Firth and some negotiation with Shetland on Fair Isle. The Regulating Order would be applied to lobster, brown crab, green crab, velvet crab, king scallop, queen scallop, common whelk, edible periwinkle, common mussel, native oyster, common cockle, razor clam and horse mussel.

The aims of the regulating order are the maintenance of a sustainable fishery of Orkney shellfish stocks and the improvement and enhancement of these stocks where feasible thereby boosting the overall viability of the fishery. The Regulating Order would involve the installation of an annual permit scheme, which would control the number of vessels operating in the area. Various measures of regulation are under consideration. Those affecting the velvet crab fishery include:

- Replacement of the ban on velvet crab landings with a controlled fishery over the summer months;
- Limitation of creel numbers;
- The requirement for some form of agreement between permit holders and buyers;
- Exchange of permits with areas adjoining Orkney;
- Limitation on earnings and residency requirements for a permit, bearing in mind the presence of outside fishermen with historical fishing records;
- Limitation on entry to various fisheries with respect to vessels over a certain size, VCU's or horsepower.

These considerations are currently under discussion between the various groups of fishermen in Orkney, with a view to reaching conclusions in early autumn of this year (2001).

However, as the evidence in this study suggests, there appears to be no need for alarmist measures. The introduction of a logbook scheme and permits would allow a detailed monitoring of the situation, and are advisable. The reintroduction of the closed season would respond more to market demands than to conservation demands, but for this reason, would also be recommendable. If the state of the catch during the summer months is poor, prices are low, and there are negative repercussions for when prices are higher, then it is reasonable to limit fishing during this period so as to maximise profit later in the year. The existence of a Regulating Order should be seen as an opportunity to maximise the sustainable use of the resource, which currently has room for expansion if managed with care.

6.5 Scope for further study

The completion of this study raised several new questions about the Orkney stock of *Necora puber*. In the interests of maintaining a sustainable industry, which can be managed with comprehensive understanding, the following points are recommended as aspects meriting further research:

The movements of individuals require documentation. The present study undertook a tagging survey, which gave insufficient results. It is important to know the details of movements within Orkney for a number of reasons. This study treats *Necora puber* in Orkney waters as a single stock. However, the extent of movements may help to determine the extent to which this is true. If there is little mixing between areas, the situation may be one of several substocks with a common larval pool. If this is the case, the basic assumption of most fisheries models is not fulfilled, and new ways of assessing the stock must be devised. Questions to be addressed in such a study include:

> Do juveniles migrate to adult grounds, and if so, when and at what size?
> Do females migrate in order to spawn, and if so, where to?
> How much general movement is there?

Such a study could be carried out on different levels. Surveys of general mixing of the populations of two adjacent bays could be carried out by mark-recapture methods. The results of these surveys could be used to investigate the potential effectiveness of introducing closed areas as a method of managing the fishery. Surveys of juveniles would require the use of tags that could be retained over a series of moults. Surveys of possible female migrations may require the use of tracking devices.

The plankton sampling programme that took place in this study had basic aims of determining when velvet crab larvae were found in the water column. A larger scale survey is recommended to look more closely at the numbers and timing of zoeal development, and at the movements involved. It is important to know to how the larvae are transported around Orkney waters, and to what extent their place of settlement depends on their place of release. As part of the work, those species in the larvae either utilised by or predating upon the zoeae should be identified.

Now that the habitat of juvenile *Necora puber* has been identified, further work must be carried out into the extent of its distribution. In addition to this, exact moult sizes and timings could be ascertained by means of a medium-scale rearing programme. Settlement and recruitment should be monitored yearly by use of a standardised collection method. This could then be used as a basis for accurate assessment of year classes, independent from the fishery.

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Appendix A

Raw Datasets (in diskette form EXCEL for Windows)

Dataset 3 Plankton Hauls

All hauls carried out around Tingwall Harbour, for 5 minutes at speed of 1 knot

59.06 N 3.02 W

	Larval stage						
Date	**1**	**2**	**3**	**4**	**5**	**megalop**	**total larvae**
15/05/99	0	0	0	0	0	0	0
15/06/99	0	0	0	0	0	0	0
15/07/99	4	1	0	0	0	0	5
26/07/99	0	1	2	0	0	0	3
18/08/99	0	0	3	0	0	0	3
15/09/99	0	0	0	0	0	0	0
15/10/99	0	0	0	0	0	0	0
15/11/99	0	0	0	0	0	0	0
15/12/99	0	0	0	0	0	0	0
15/01/00	0	0	0	0	0	0	0
15/02/00	0	0	0	0	0	0	0
15/03/00	0	0	0	0	0	0	0
15/04/00	0	0	0	0	0	0	0
27/04/00	0	0	0	0	0	0	0
15/05/00	0	0	0	0	0	0	0
21/05/00	0	0	0	0	0	0	0
10/06/00	0	0	0	0	0	0	0
28/06/00	6	0	0	0	0	0	6
06/07/00	7	1	0	0	0	0	8
16/07/00	2	1	1	0	0	0	4
28/07/00	0	0	2	0	0	0	2
07/08/00	0	0	0	0	0	0	0
18/08/00	0	0	0	0	0	0	0
12/09/00	0	0	0	0	0	0	0
07/10/00	0	0	0	0	0	0	0
22/11/00	0	0	0	0	0	0	0
07/12/00	0	0	0	0	0	0	0

2 of 7

Dataset 4 larval rearing

Larval numbers in batches

Date of hatching: 28/06/00

date	age	1	2	3	mean per100ml	total pop
28/06/00	0	62	60	60	60.66667	30333.33
30/06/00	2	21	21	20	20.66667	10333.33
03/07/00	5	8	5	5	6	3000
05/07/00	7	5	5	5	5	2500
07/07/00	9	5	5	5	5	2500
10/07/00	12	5	4	4	4.333333	2166.667
12/07/00	14	3	4	3	3.333333	1666.667
14/07/00	16	2	2	2	2	1000
17/07/00	19					100
19/07/00	21					35
21/07/00	23					13
24/07/00	26					4
26/07/00	28					3
28/07/00	30					2
31/07/00	33					2

date of hatching: 28-06-00

date	age	1	2	3	mean per100ml	total
28/06/00	0	12	12	12	12	6000
30/06/00	2	9	10	12	10.33333	5166.667
03/07/00	5	3	3	3	3	1500
05/07/00	7	2	4	3	3	1500
07/07/00	9					
10/07/00	12					
12/07/00	14					

Percentage of larvae at each stage of development

age	pre	1	2	3	4	5 mega	crab	
0	100	0	0	0	0	0	0	0
0.3	2	98	0	0	0	0	0	0
2	0	100	0	0	0	0	0	0
3	0	100	0	0	0	0	0	0
4	0	100	0	0	0	0	0	0
6	0	0	100	0	0	0	0	0
8	0	0	100	0	0	0	0	0
10	0	0	0	100	0	0	0	0
13	0	0	0	50	50	0	0	0
15	0	0	0	30	70	0	0	0
17	0	0	0	17	66	17	0	0
19	0	0	0	0	0	100	0	0
21	0	0	0	0	0	100	0	0
23	0	0	0	0	0	38	62	0
26	0	0	0	0	0	0	100	0
28	0	0	0	0	0	0	100	0
30	0	0	0	0	0	0	100	0
33	0	0	0	0	0	0	0	100

Morphometric measurements

stage1

date	a	b	c	d
11/07/00	2.025	0.92	0.72	1.02
icit batch	2.225	0.89	0.73	1
1 day old	2.3	0.91	0.7	0.95
	2.2	0.85	0.7	1.05
	2.35	0.93	0.7	1.05
	2.3	0.95	0.75	0.95
	2.2	0.89	0.74	1
	2.27	0.94	0.72	1.02
	2.25	0.91	0.72	0.98
	2.1	0.87	0.68	0.94
26/06/00	1.925	0.82	0.65	0.85
batch 1	1.925	0.92	0.75	0.85
2 days	1.9	0.9	0.73	0.75
	2	0.96	0.75	0.9
28/06/00	1.95	0.85	0.7	0.85
batch 1	1.9625	0.82	0.75	0.8
4 days	1.925	0.85	0.7	0.82
28/06/00	2.05	0.84	0.68	0.8
batch2	1.9	0.7	0.73	0.85
1 day old	2.02	0.76	0.7	0.88

	2.02	0.88	0.72	0.88
	1.95	0.81	0.72	0.88
	2	0.78	0.7	0.87
	1.9	0.75	0.73	0.88
	2.08	0.76	0.71	0.81
	1.9	0.73	0.72	0.8
	1.95	0.83	0.72	0.88
average	2.058426	0.852593	0.715556	0.90037

stage 2

date	a	b	c	d
03/07/00	2.6	0.87	0.82	1.09
batch 2	2.5	0.8	0.87	1.05
	2.45	0.88	0.8	1.03
	2.65	0.92	0.8	1.1
	2.55	0.85	0.82	1.04
	2.55	0.86	0.84	1.05
	2.5	0.85	0.8	1
	2.5	0.825	0.83	1.01
batch3	2.6	0.875	0.875	1.075
03/07/00	2.45	0.85	0.825	1.075
average:	2.535	0.858	0.828	1.052

stage 3

date	a	b	c	d
07/07/00	2.8	1	0.95	1.1
	3.2	1.125	1	1.4
	3	1.2	1	1.3
	2.8		0.95	1.13
	3.25		1	1.53
	3.25		1	1.5
	3.25	1.05	0.95	1.3
	3.2	1.2	1.02	1.5
	3.6		1.1	1.6
	3.05		0.975	1.375
average	3.14	1.115	0.9945	1.3735

stage 4

date	a	b	c	d
10/07/00	3.6	1.2	1.125	
batch2	3.9			1.75
12/07/00	3.75		1.2	1.8
batch2	3.9		1.2	1.87
	4		1.25	1.75
	3.375		1.22	1.6

	4.03		1.275	1.9
	3.8		1.2	1.75
14/07/00	3.8	1.2	1.175	1.7
batch2	3.55	1.2	1.2	1.65
	3.75	1.2		1.72
	3.625	1.2	1.15	1.7
average	3.756667	1.2	1.1995	1.744545

stage 5

date	a	b	c	d
17/07/00	4.75		1.4	2.125
	4.5		1.55	2.1
	4.5		1.5	2.125
			1.525	1.925
	4.5		1.5	2.175
	4.4		1.5	2
average	4.53	#DIV/0!	1.495833	2.075

megalopa measurements

date	a	b
	1.9	1.475
	2.025	1.45
average	1.9625	1.4625

a	total length
b	cw
c	cl
d	dorsal spine

Dataset 9 Egg Development

tank temperature: 7C at start 12C at end

Date	x	y	z	diameter	long diam.	stage	vol (mm3)
09/03/00	195	210	200	403.3333	420	1	0.034306
	220	215	215	433.3333	440	1	0.042598
	215	225	240	453.3333	480	1	0.048632
16/03/00	200	205	210	410	420	1	0.036065
	200	210	215	416.6667	430	1	0.037825
	195	205	207.5	405	415	1	0.034745
23/03/00	200	210	205	410	420	1	0.036065
	200	210	200	406.6667	420	1	0.035186
	200	200	205	403.3333	410	1	0.034348
30/03/00	220	215	205	426.6667	440	2	0.040617
	215	210	220	430	440	2	0.041607
	220	210	210	426.6667	440	2	0.04064
06/04/00	220	205	220	430	440	2	0.041561
	210	220	215	430	440	2	0.041607
	215	205	210	420	430	2	0.03877
13/04/00	230	220	215	443.3333	460	3	0.04557
	215	225	220	440	450	3	0.044579
	220	225	220	443.3333	450	3	0.045616
20/04/00	225	225	225	450	450	3	0.047713
	230	220	230	453.3333	460	3	0.048749
	230	215	225	446.6667	460	3	0.046606
27/04/00	235	235	235	470	470	4	0.054362
	235	240	245	480	490	4	0.057881
	240	235	235	473.3333	480	4	0.055518
04/05/00	240	240	250	486.6667	500	4	0.060319
	245	250	240	490	500	4	0.061575
	250	240	235	483.3333	500	4	0.059062
09/05/00						**5 (hatched)**	

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Appendix B

Regression results for allometric growth measurements

1 of 2

Appendix B: Regression results for allometric growth measurements (chapter 2)

The table below shows the linear and log-transformed regression analysis carried out on the relationship between carapace width (as the independent variable) and other characteristics. For all cases, the correlation was significant ($p < 0.01$). Linear regression: $Y = a + bx$ Log transformed regression: $Ln(Y) = a + b\ (Ln(x))$.

		linear regression		**log regression**		**Allometry**
Variables	**sex/stage**	**a**	**b**	**a**	**b**	
fourth abdominal segment width	male	0.094	0.3068	-1.2346	1.014	0
	Fem. juv.	-1.1041	0.3995	-1.6659	1.1949	+
	Fem. adult	-3.5889	0.5533	-1.3066	1.1449	+
sixth abdominal segment width	Male	0.2194	0.1859	-1.4435	0.9439	0
	Fem. juv.	-0.9973	0.3043	-1.9799	1.194	+
	Fem. adult	-6.692	0.5403	-1.9977	1.2782	+
Major chela height	male juv.	-0.0545	0.238	-1.4688	1.0066	0
	male adult	-11.488	0.4659	-3.5594	1.5533	+
	female	-0.4596	0.2489	-1.5405	1.0263	0

Allometry was determined by testing the slope (b) of the log transformed regressions against the isometric slope of 1 with Student's t-test.

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Appendix C

Sample of logbook scheme used in Aberdeen

1 of 2

Sheet No ____________

S	E	
E	C	
N	C	
O	R	
S	H	

H	E	
U	L	
M	A	
S	M	
C	L	

O	N	
N	O	
O	W	
N	M	
S	M	
I	L	
C	L	

I	S	—
F	L	—
M	F	—
O	C	—
A	R	
F	F	
F	D	

Boat ____________ Landing Place ____________ Week Ended Sat ____________ 19

Creel type | *Parlour Traditional Steel*

Total Number

☐☐☐☐

		Lobsters			Brown Crab			Velvet Crab			Other Species
	Creels Lifted	legal number	kilo ☐ lbs ☐ legal weight	number undersized	Creels Lifted	kilo ☐ st ☐ legal weight	number undersized	Creels Lifted	kilo ☐ st ☐ legal weight	number undersized	kilo ☐ st ☐ weight
Mon											
Tue											
Wed											
Thur											
Fri											
Sat											
Sun											

Fishing Ground Grid Ref

☐☐E☐☐

Any other comments Sea state Wind strength

Signed ____________

Total Number of Creels

☐☐☐☐

		Prawns	Other Species
	Creels Lifted	kilo ☐ st ☐ weight	kilo ☐ st ☐ weight
Mon			
Tue			
Wed			
Thur			
Fri			
Sat			
Sun			

Fishing Ground Grid Ref

☐☐E☐☐

Any other Comments Sea state Wind Strength

Signed ____________

Marine Laboratory Aberdeen: Voluntary Logbook Sheet

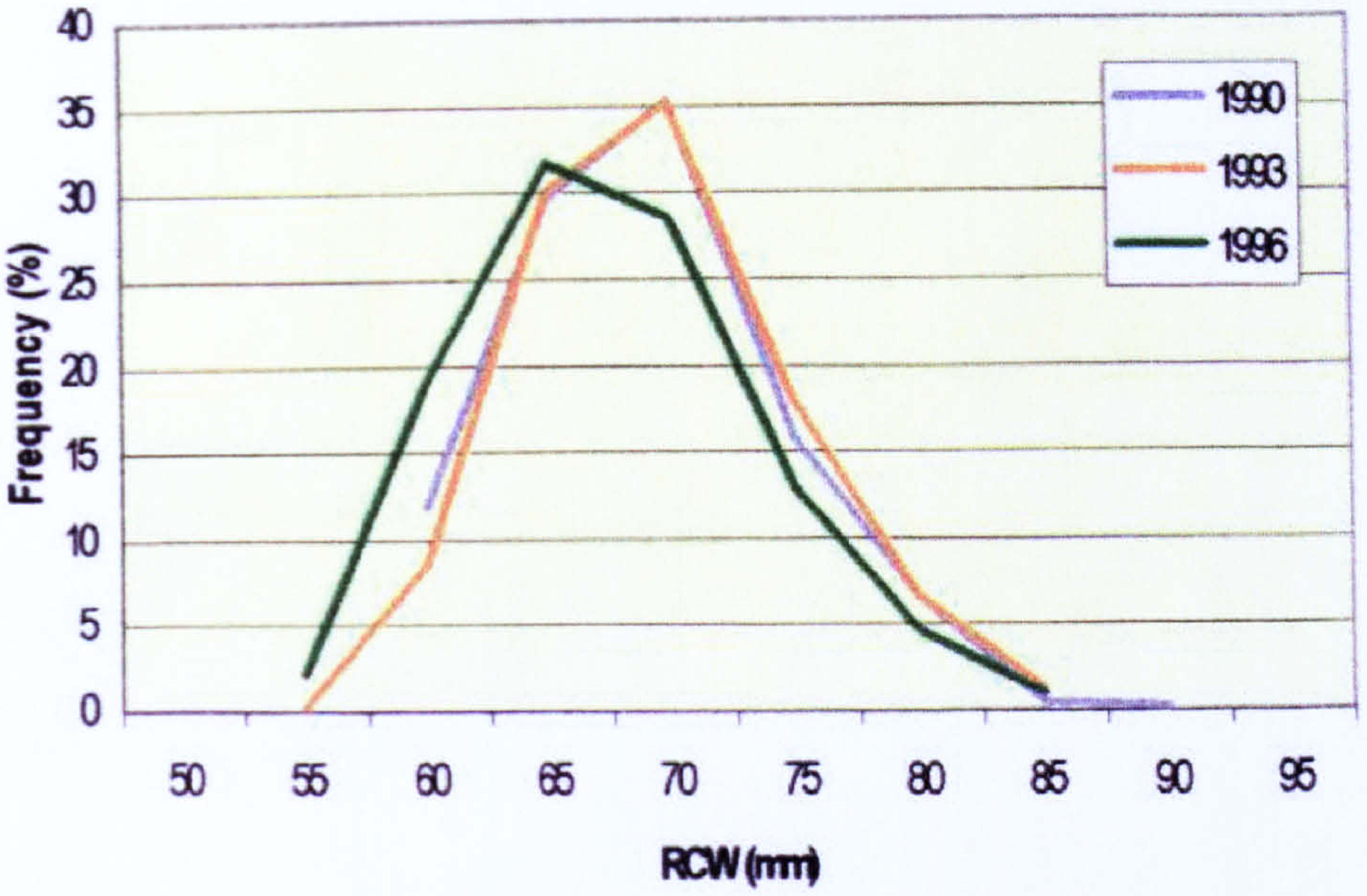
2 of 2

Appendix D

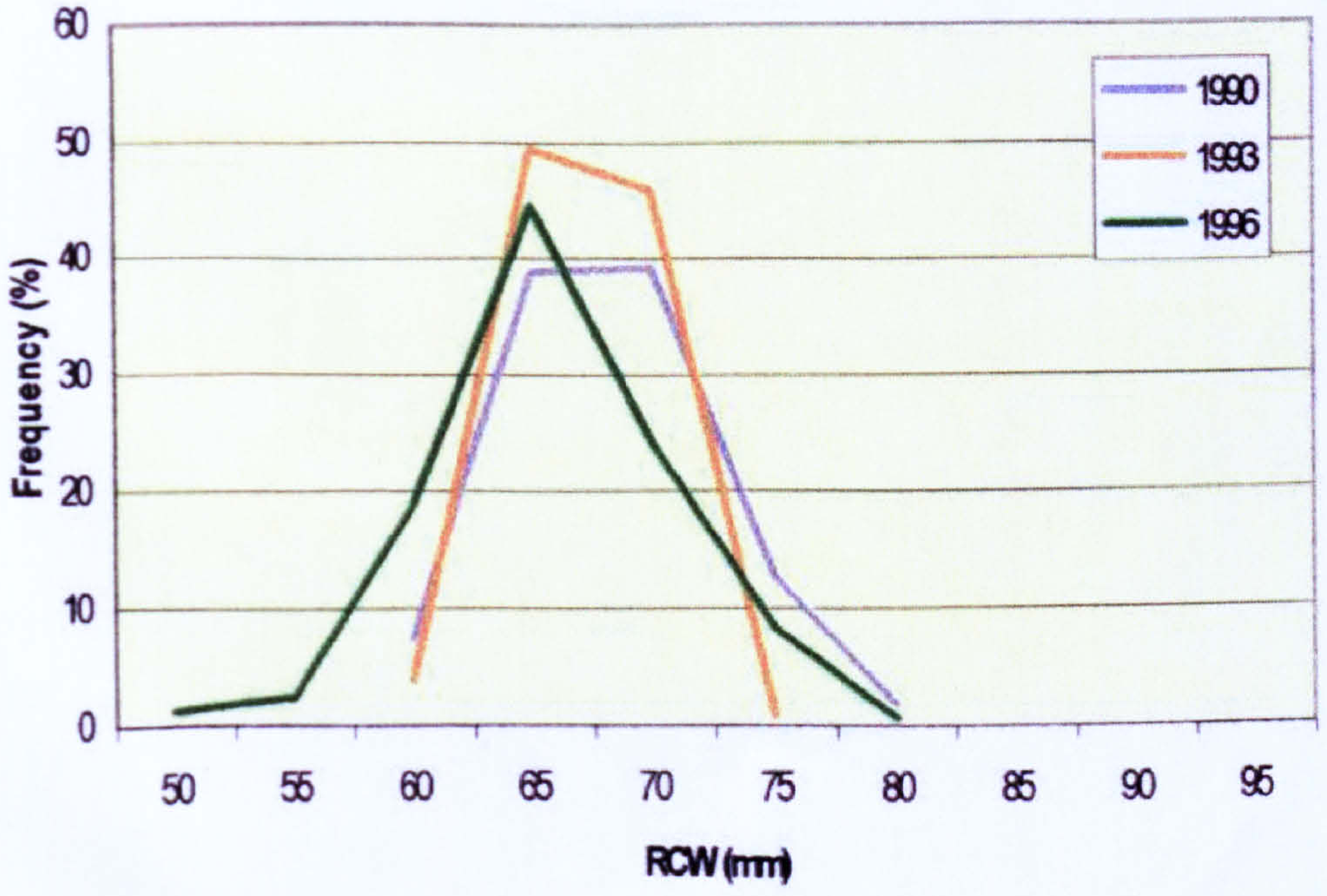
Size distribution of velvet crabs landed in Orkney in 1990, 1993 and 1996 (from Tallack, 1998)

1 of 2

a) Males.



b) Females.



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