

Bangor University

DOCTOR OF PHILOSOPHY

Population ecology of dab (*Limanda limanda* L.) in the eastern Irish Sea, North Wales.

Seisay, Mohamed B.D.

Award date:
2001

[Link to publication](#)

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Download date: 22. Nov. 2024

Population Ecology of Dab (*Limanda limanda* L.) in the Eastern Irish Sea, North Wales

Thesis submitted for the degree of
Doctor of Philosophy

By

Mohamed B.D. Seisay

B.Sc. Hon (Sierra Leone)
M.Sc. (Bangor, Wales)

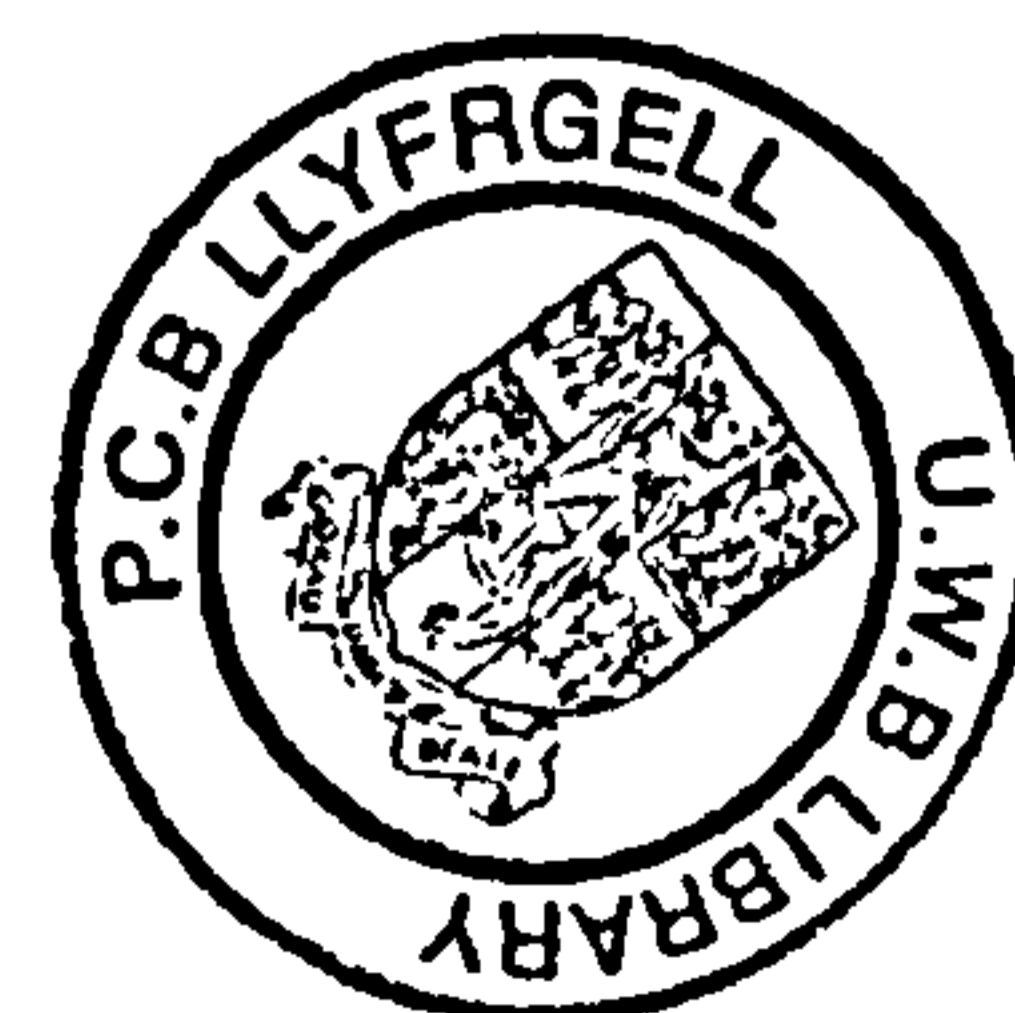
School of Ocean Sciences
University of Wales, Bangor
Menai Bridge, Anglesey

LL59 5EY

United Kingdom

I'W DDEFNYDDIO YN Y
LLYFRCELL YN UNIG
—
TO BE CONSULTED IN THE
LIBRARY ONLY

June 2001



DEDICATED

To

My brother M.B.D Seisay

ACKNOWLEDGEMENTS

I wish to express my deepest gratitude to my supervisor, Dr. David J. Grove, for his invaluable contribution, guidance and support throughout the period of this study. His participatory method of 'online' supervision contributed largely to the production of this thesis. In this regard, I owe a debt of gratitude (and also offer my unreserved apology) to his family for any inconvenience caused by his continued commitment to my thesis even after his retirement.

I also wish to extend my sincere thanks to Dr. Graham Walker for the technical assistance rendered to the section on '*histology*' in this thesis. I would like also to take this opportunity to thank all the staff on the 1986/87 'M.Sc. Fisheries Biology and Management' course in Bangor for their immense contribution to my professional development in the field of fisheries science.

I am very grateful to all the *R.V Prince Madog* crew, including Captain Steve Duckworth, Chief Mate Alan Price, the Boatswain Phil and crew Tom and Dave as well as the Pier Master John Owen for their kind 'helping hands' during the numerous sea trips, sometimes in very 'hostile' weather conditions. I also appreciate the effort of the following technicians: Gwyn Parry Jones, Gwyn Hughes and Berwyn Roberts for laboratory support and sample collection from the commercial fishery, including also the photographer Dave Roberts, who kindly did the pictures in this thesis.

I wish to thank the Commonwealth Scholarship Commission and the British Government for providing the funds that enabled me undertake this study. In addition let me seize this opportunity to register my appreciation to the British Government for their continuous assistance and engagement in my country at this very difficult period in the history of Sierra Leone. I am very grateful to the Sierra Leone Government, and in particular the Fisheries Department, for nominating me and also granting me study leave for the duration of this study. I am confident that the knowledge and skills acquired during the course of this study will contribute in no small measure to the scientific and rational management of the abundant and diverse fish resources in Sierra Leone.

On a personal note, I take this opportunity to thank my wife for her continuous support and understanding during the course of this study. I am indebted to my children, Kona, Mohamed and Sarata, for their patience and courage during my frequent absence from home due to either laboratory or sea duties. Also, my heartfelt thanks and sympathy to all my relatives in Sierra Leone (my mum Kona Seisay, brothers and sisters), who had been through the agony and trauma of war during the last three years.

Finally, I wish to thank all my numerous friends and colleagues throughout the duration of this study, particularly Mazlan, Lokmal, Hamdan, Adnan, Lyn and Peter Bridson for exchange of views on subject matters and also the numerous friendly discussions outside the realm of academia.

ABSTRACT

Population density, growth and mortality rates, reproduction, feeding ecology and energy mobilization of dab (*Limanda limanda* L.) on the North Wales Coast have been investigated between 1998-2001. The total population number is estimated as 2.34×10^6 . Average catch rates were lower in winter-spring than in autumn-summer: 42 hr^{-1} in February 2000; 141 hr^{-1} in July 2000. Catch rates were generally higher at night than daylight: 1549 hr^{-1} at 02:00 hr; 17 hr^{-1} at 10:00 hr in November. The 2-year old fish form the dominant year class. There was seasonal variation in sex ratio (Females: Males). In the long-term data, in autumn, the females were more abundant (1.83: 1) in trawl catches but the contribution of the males increases in spring (1.15: 1). There were seasonal variations in length and weight relationships: the average relationship was nearly isometric (power $b \approx 3.0$); in male $W = 0.01 \times TL^{2.91}$ and in female, $W = 0.01 \times TL^{3.04}$. April 1st was established as the birthday of the fish and the greatest deposition of the opaque zone in the otolith occurred in summer. The male grows at a faster rate than female in autumn 2000: ($L_{\infty}=25.7 \text{ cm}$; $K= 0.30 \text{ y}^{-1}$) and ($L_{\infty}=33.4 \text{ cm}$; $K= 0.25 \text{ y}^{-1}$) respectively. The long-term average total mortality rate was significantly higher in males ($Z= 1.95 \text{ y}^{-1}$) than females ($Z= 1.16 \text{ y}^{-1}$). This difference was calculated to be largely due to the relatively higher fishing mortality rate on the males.

There were cyclical cycles in the gonad, liver weight and condition factors. The peak spawning activity in males was in December-January whilst it occurred in February-March in females. In the 16-20 cm male, the maximum gonadocarcass ratio, GCR, (1.8 %) and hepatocarcass ratio, HCR, (2.9 %) were in January and August respectively. In female, the maximum GCR (17.1 %) and HCR (3.8 %) occurred in February. The GCR was at a minimum in spring-summer. The minimum HCR occurred in spring. The maximum condition factor (K) was in summer for male ($K=0.97$) and female ($K=1.02$) but, after spring spawning, declined to 0.67 and 0.72 respectively. The maximum average oocyte diameter (0.56-0.67 mm) was observed in fully ripe fish in the spawning season but, after spring spawning, reduced to between 0.10-0.22 mm. The total estimated egg production was 2.47×10^{11} eggs but the average per mature female was 3.51×10^5 eggs. Relative fecundity declined from 3045 eggs g^{-1} in fish aged 1 to 1917 eggs g^{-1} in fish aged 8. The fecundity-total length ($F= 41.6 TL^{2.86}$) and fecundity-somatic weight ($F= 4804SW^{0.88}$) relationships are estimated to be good predictors of dab fecundity. In autumn 2000, the length ($L_{50\%}$) and age ($A_{50\%}$) at 50 % maturity were lower in males ($L_{50\%} = 13.3 \text{ cm}$; $A_{50\%} = 1.3 \text{ yr.}$) than females ($L_{50\%} = 18.0 \text{ cm}$; $A_{50\%} = 2.4 \text{ yr.}$). The long-term averages showed relative stability in the females but a decrease in males, $A_{50\%}$ from about 2 years to about 1.5 years.

Five major taxonomic groups dominated the diet of dab: the ophiuroids, bivalves, crustaceans, polychaetes and hydroids. The ophiuroid, *Amphiura brachiata*, predominated. However, the study suggests size-selective preference for some prey groups. The composition of polychaetes in the diet declined with increasing size of the fish; 22.9 % by weight in the 11-15 cm length group to 5.7 % in the 26-30 cm group. On the contrary, the bivalves increase in the diet with increasing size of the fish, from 11.2 % (by weight) in the 11-15 cm group to 31.4 % in the $\geq 31 \text{ cm}$ group. There is however a significant diet overlap ($C \geq 0.60$) between the size groups. In general, daily food intake was higher in late spring-summer than in autumn-winter. In May, for example, daily food intake for the 21-25 cm and 26-30 cm female dab was estimated as 1.49 g and 4.61 g respectively. In February it was 0.52 g and 1.76 g respectively.

There were distinct seasonal changes in lipid and energy composition in the liver. Lipid content was significantly higher in the summer-autumn period than spring season. In September, it was about 62 and 69 % in male and female livers respectively. After spring spawning, the composition declined to 28 and 24 % respectively. The energy content per dry weight of liver peaked in October (8.50 kcal g^{-1} and 8.61 kcal g^{-1}) in male and female dab respectively. Also, after spring spawning, the energy levels declined to 6.18 and 5.86 kcal g^{-1} respectively.

The energy requirement for routine metabolism and gonad development in a 20 cm female is estimated as 111.3 kcal but energy gained from food intake and carcass and liver reserves is estimated as 117.9 kcal. In male, the total energy requirement was 83.4 kcal but energy gained from food intake and carcass and liver reserves is estimated as 113.3 kcal. Feeding (in late autumn and winter) and carcass tissues are the main suppliers of energy for activity and the spawning process.

LIST OF CONTENTS

	<u>Page</u>
Abstract	i
List of Contents	ii

CHAPTER ONE

Population studies of the common dab (*Limanda limanda* L.)

Literature Review

1.1	GENERAL INTRODUCTION	1
1.2	RATIONALE	3
1.3	SPECIFIC OBJECTIVES	5
1.4	POPULATION BIOLOGY OF DAB	6
1.4.1	Distribution and abundance	6
1.4.2	Exploitation	8
1.4.3	Meristic and morphometric characters	9
1.4.4	Age determination	11
1.4.4.1	Hard parts	11
1.4.4.2	Age length frequency key	12
1.4.5	Variability in population parameters	12
1.4.5.1	Growth and mortality rates	12
1.4.5.2	Length and weight relationship	16
1.4.5.3	Cyclical changes in condition factor	18
1.4.6	Life-history strategy in flatfish	20
1.4.7	Reproduction	21
1.4.7.1	Temporal and spatial variability in sex ratio	21
1.4.7.2	Fecundity	24
1.4.7.3	Variability in fish fecundity	25
1.4.7.4	Gonad maturation	30
1.4.7.5	Age and length at maturity	34
1.4.8	Feeding ecology	36
1.4.8.1	Diet composition	36
1.4.8.2	Food resource overlap	40

1.4.8.3 Gastric emptying rate and food consumption	41
1.5 Aims of present study	44

CHAPTER TWO

The Local Population of *Limanda limanda* L. Population size and stock identity

2.1 INTRODUCTION	46
2.2 MATERIALS AND METHODS	47
2.2.1 Sampling area and method	47
2.2.2 Population size	48
2.2.3 Meristic and morphometric characters	50
2.2.4 X-ray technique	50
2.3 RESULTS	51
2.4 DISCUSSION	73

CHAPTER THREE

Growth and mortality rates of *Limanda limanda* L.

3.1 INTRODUCTION	79
3.2 MATERIALS AND METHODS	83
3.2.1 Age determination	83
3.2.2 Otolith accretion and seasonal growth	83
3.2.3 Estimation of growth rates	83
3.2.3.1 Seasonal growth in length and weight	84
3.2.3.2 Annual growth rates	84
3.2.4 Estimation of mortality rates	85
3.3 CURVE FITTING	87
3.4 RESULTS	87
3.5 DISCUSSION	109

CHAPTER FOUR

Reproductive biology of *Limanda limanda* L.

4.1	INTRODUCTION	115
4.2	MATERIALS AND METHODS	115
4.2.1	Gonad maturity staging	115
4.2.1.1	Visual assessment	116
4.2.1.2	Histological classification	119
4.2.2	Length and age at maturity	121
4.2.3	Determination of fecundity	122
4.2.3.1	Volumetric method	122
4.2.3.2	Gravimetric method	122
4.2.4	Egg production	125
4.2.5	Seasonal changes in egg size	125
4.2.6	Cyclical changes in gonad, liver and condition factor	126
4.3	RESULTS	126
4.4	DISCUSSION	154

CHAPTER FIVE

Feeding ecology of *Limanda limanda* L.

5.1	INTRODUCTION	163
5.2	STOMACH CONTENT DATA ANALYSIS	163
5.2.1	Occurrence method	164
5.2.2	Numerical method	164
5.2.3	Gravimetric method	165
5.3	MATERIALS AND METHODS	165
5.3.1	Stomach-Gut Index	166
5.3.2	Diet composition	167
5.3.3	Diet overlap index	168
5.3.4	Seasonal variation in diet composition	168
5.3.5	Diet diversity, breadth and evenness	169
5.3.6	Gastric evacuation rate	170
5.3.7	Daily ration and total food consumption	171

5.4	RESULTS	172
5.5	DISCUSSION	198

CHAPTER SIX

Lipid composition and energy allocation in *Limanda limanda* L.

6.1	INTRODUCTION	205
6.2	MATERIALS AND METHODS	206
	6.2.1 Energy determination	206
	6.2.1.1 Bomb calorimetry	206
	6.2.1.2 Wet oxidation	208
	6.2.2 Lipid determination	209
	6.2.3 Ash determination	210
	6.2.4 Energy allocation	210
6.3	RESULTS	211
6.4	DISCUSSION	231

CHAPTER SEVEN

SUMMARY AND CONCLUSIONS

7.1	INTRODUCTION	235
7.2	Population Size and Stock Identity	235
7.3	Growth and Mortality Rates	237
7.4	Reproductive Biology	238
7.5	Feeding Ecology	240
7.6	Lipid Composition and Energy Allocation	241
7.7	Constraints and Future Research	242
8.0	REFERENCES	244
9.0	APPENDICES	272

CHAPTER ONE

Population Studies of the Common Dab (*Limanda limanda* L.)

LITERATURE REVIEW

1.1 GENERAL INTRODUCTION

Fisheries research should be a standard component of any fisheries management system (Charles, 2001). More than two decades ago, however, most fisheries scientists relied on accumulated time series data for fish stock assessment purposes. This was particularly true in the case of Surplus Yield Models (Pitcher and Hart, 1982). The Surplus Yield Models require accumulated data of at least ten years of fish catch and fishing effort for their valid applications. But recent failures of important fish stocks have given mathematical models a poor reputation as tools for fishery management (Schnute and Richards, 2001); quantitative stock assessment methods provide no guarantee that a fish stock will remain sustainable. Modern approaches in fish stock assessment methods now consider parameters which can be monitored on short term or seasonal bases, which can be responded to at short notice (*Optimal Control*), (Pitcher and Hart, 1982). These parameters include growth, mortality and recruitment, the age (and size) at maturity and sex ratio but also sexual, seasonal and geographical variations in these population parameters are important areas of study. Environmental factors such as temperature, salinity and weather as well as food supply, predation and prey relationships have been correlated with the survival, recruitment, abundance and yield from fish stocks (Bailey, 1994; Rijnsdorp and van Leeuwen, 1996; Rogers and Millner, 1996). For instance, population parameters, meristic and morphometric features have been observed to differ between dab (*Limanda limanda* L.) populations in the North Sea, Baltic Sea, Icelandic Waters, Isle of Man, Coast of Brittany and Anglesey waters (Jonsson, 1966, Lee, 1972, Ortega-Salas, 1980, 1988a, Bakhsh, 1982, Deniel, 1990, Lozan, 1989, 1992 and Rijnsdorp *et al.*, 1992). Similarly, Basimi and Grove (1985a) found evidence of sexual and seasonal variability in population parameters (e.g. growth, length/ weight coefficients, length and age at maturity) for plaice (*Pleuronectes platessa* L.) in waters around Anglesey. Interannual and sexual variability in the biology and population parameters of the North Sea plaice have been discussed extensively by Rijnsdorp and van Leeuwen (1985, 1992, 1996), Rijnsdorp (1991) and Rijnsdorp and Millner (1996). Seasonalised growth models have therefore been developed to account for changes in growth patterns due to

periods of slow growth, for example in winter, and enhanced growth in summer (Pitcher and Macdonald, 1973a, Lockwood, 1974, Pauly and Gaschutz, 1979 and Basimi and Grove, 1985a).

Attention has also been focussed on studies involving the intraspecific and interspecific competition for food in the locality of fish stocks and the effects of fish stocks on the ecosystem (Daan, 1973; Ortega-Salas, 1988c; Carter, 1987; Carter *et al.*, 1991; Knust, 1996, Mookerji *et al.*, 1998; Seyhan and Grove, 1998; Jennings and Kaiser, 1999). As a result, ecosystem-based fisheries management and the setting up of marine reserves (habitat protection) are now under intense discussion as tools for potentially sustainable and rational fisheries management (Guenette *et al.*, 2000; Pitcher, 2000; Charles, 2001). The positive correlation found between nutrient concentration, primary productivity and fish production in lentic waters (Downing *et al.*, 1990) has led fishery scientists to conclude that production of fish in most waters is primarily limited by food supply (Ney, 1990). Diet analysis and estimation of feeding rates are thus central to fish stock assessment methods.

Fisheries science now tends to examine discrete questions in fish biology. These aspects have mainly involved diet composition of the fish, growth performance and exploitation, reproductive cycles involving gonad maturation, fecundity and recruitment and also food resource partitioning as a survival strategy. For example, Jobling (1995) noted that food supply might be expected to be the over-riding factor limiting growth rates and determining the onset of maturity. He suggested that the recent increase in the rate of growth of North Sea plaice probably reflects an increase in food supply due to reduced adult survival. He further attributed the reduction in average length and age at maturity to this reduced adult survival. Laboratory studies have shown that the key factors determining the daily growth in average length of individual flatfish are size of the fish, food availability and temperature (Jobling, 1993). Annual growth rate can be affected by both density-dependent and density-independent processes and are thought to act mainly by variability in water temperature and by differences in food quality and quantity. Density-dependent processes will be induced by competition for food among individual flatfish (Van der Veer *et al.*, 1994). Survival tactics by fish have been noted by Beddington and Cooke (1983), Stearns (1995) and Jennings and Kaiser (1999). It has been frequently noted that fish exhibit a range of life history tactics, presumably shaped by natural selection. It is expected that fishing will affect fish with different life history traits in different ways. Thus it is important that fisheries management incorporates important parameters which are relevant to growth, reproduction, diet and survival (Adams, 1990).

1.2 RATIONALE

This study, 1998-2001, investigates the population ecology of the common dab, *Limanda limanda* L., in the Eastern Irish Sea on the North Wales Coast (Figure 1.1), U.K.

Taxonomic classification:

The fish: The Common Sand Dab

Scientific name: *Limanda limanda* L. (1758)

Family: Pleuronectidae

In European waters, the Order Pleuronectiformes comprises of a large number of equatorial species, which are grouped into three families, viz. Bothidae (Scophthalmidae), Pleuronectidae, and Soleidae (Wheeler, 1969). The plaice (*Pleuronectes platessa* L.) and the common dab (*Limanda limanda* L.) belong to the family Pleuronectidae. Other important members of the family include flounder (*Platichthys flesus* L.), lemon sole (*Microstomus kitt* W.), halibut (*Hippoglossus hippoglossus* L.), witch (*Glyptocephalus cynoglossus* L.) and long rough dab (*Hippoglossoides platessoides* F.).

In the case of the dab (Figure 1.2.), the mouth is terminal, directed to the right of the eyes. The lateral line is strongly arched over the pectoral fin. The scales are finely serrated along the margins giving a rough feel to the eye-side. It is yellowish-brown on the eye-side, often with indistinct blotches and small dark spots. The blind side is smooth and white.

Whilst there have been recent studies on the population of dab in other European waters, there are very few published studies on the dab in Anglesey waters in the last decade. The population ecology of dab has been intensively investigated in recent years principally in the North Sea (Lozan, 1989, 1992; Rijnsdorp *et al.*, 1992, Knust, 1996, Saborowski and Buchholz, 1996, 1997), the Isle of Man (Ortega-Salas, 1988a-c; Nash *et al.*, 1994b) and the Coast of Brittany (Deniel, 1990). The dab populations in Anglesey waters were investigated in detail more than a decade ago (Gwyther, 1978, Bakhsh, 1982, Carter *et al.*, 1991). Since the dab populations in Anglesey waters have been continually fished over this period, it is hypothesized here there might be long-term fisheries-induced changes in abundance, growth rate, meristic and morphometric features, maturation and/or fecundity in these stocks.

Sexual differences in rates of growth, mortality and length and age at maturity have been well documented in flatfish species. This pattern of differential growth, mortality and maturity has also been found by Bakhsh (1982), Basimi and Grove (1985a), Ortega-Salas (1988a),

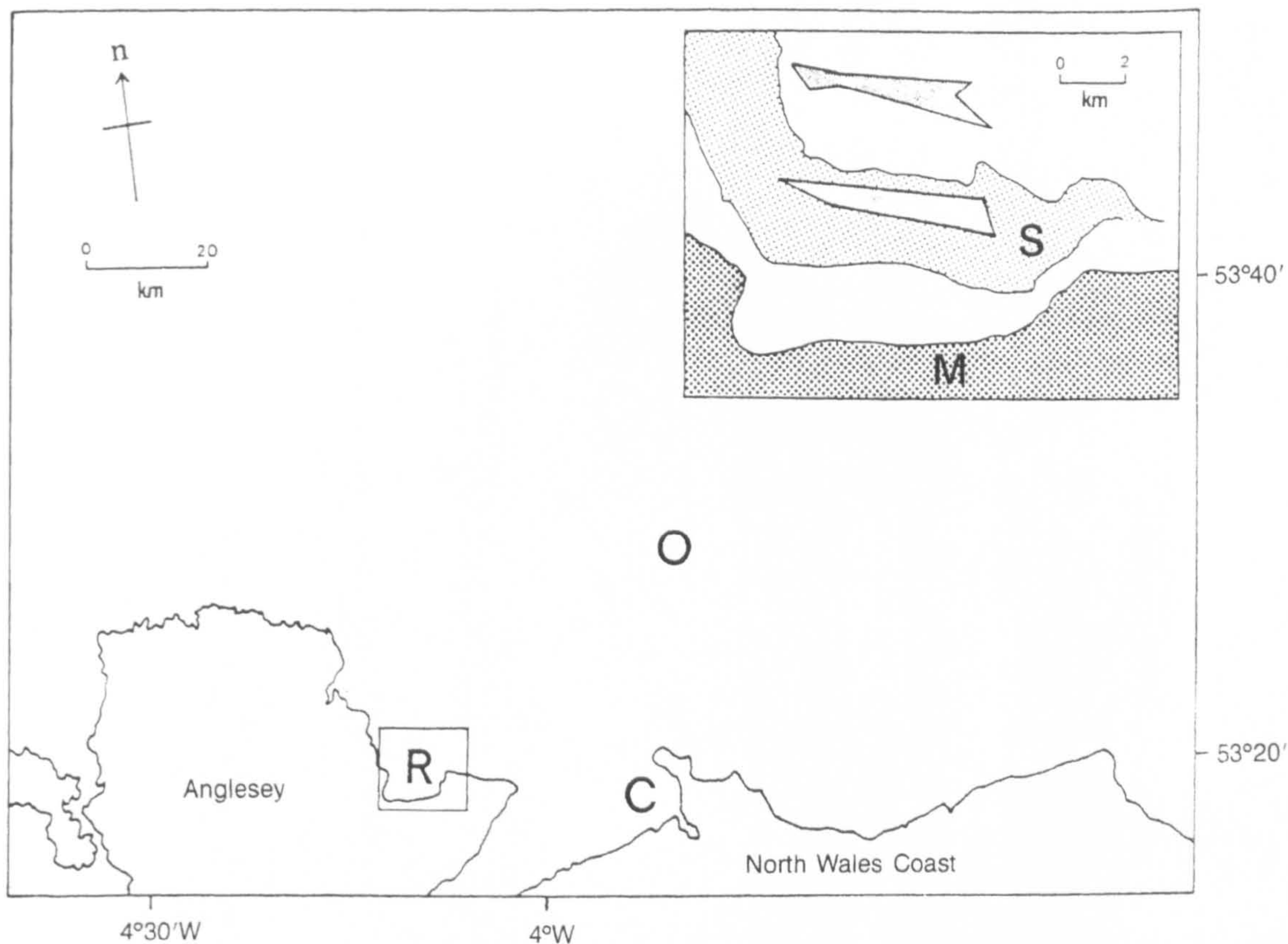


Figure 1.1 Map of the study area on the North Wales Coast showing Red Wharf Bay (R), Conwy Bay (C) and Offshore (O) sites. The inset shows the positions of mud (M) and sand (S) substrates in the areas trawled in Red Wharf Bay.

Figure 1.2. The common dab (*Limanda limanda* L.): mature female, caught 6th July 2000 by trawling survey in Red Wharf Bay. During this period, the gonads are 'resting' (that is, maturity stage III). Classification of the various maturity stages in dab is undertaken in Chapter 4.



Deniel (1990) and Rijnsdorp *et al.* (1992). They were also able to establish seasonality in the condition of the fish. Detailed studies on the population biology of dab (maturation cycle, fecundity, sex ratio, growth, feeding, distribution and abundance) were carried out by Bohl, (1957), Jonsson (1966), Lee (1972), Htun-Hun (1978a,b and c), Ortega-Salas, 1980, Bakhsh (1982), Bagge and Nielsen (1989), Deniel, (1990), Lozan (1992), Rijnsdorp *et al.* (1992), Bolle *et al.* (1994), Campos *et al.* (1994), Nash *et al.* (1994b), Bels and Davenport (1996) and Knust (1996). An examination of earlier studies concluded that, two decades ago, the female and male dab in Anglesey waters reached sexual maturity earlier than their counterparts in the North Sea and the Isle of Man. Studies on the racial characters showed differences between the dab populations in the North Sea, Baltic Sea, Icelandic waters, Danish waters and the waters of Eastern Anglesey (Poulson, 1933, Jensen, 1937, Jonsson, 1966 and Bakhsh, 1982).

The feeding ecology of dab in Anglesey waters has been investigated by Macer (1967), Jobling (1974), Gwyther (1978) and Carter *et al.* (1991). Population density estimates of dab have been reported for Anglesey waters (Bakhsh, 1982), the Isle of Man (Ortega-Salas, 1988b) and the North Sea (Stefan *et al.*, 1996). The effect of the dab population on the benthic populations needs serious attention in view of the voracious and opportunistic feeding habit of this species (Arntz, 1971; Kaiser and Ramsey, 1997).

This study thus presents an opportunity to update the population biology of dab in Anglesey waters and make comparisons with dab populations in other European waters and earlier studies on dab in the present study area.

1.3 SPECIFIC OBJECTIVES

- a. To estimate the population abundance of dab in the study area, which will include diurnal and seasonal variation in catch rates.
- b. To estimate population parameters and compare with estimates derived from earlier studies in the same area and also from different regions like the North Sea, Isle of Man, Baltic Sea, Coast of Brittany and Icelandic waters. The parameters will include growth rate, mortality rate and length /weight studies.
- c. To study the gonad maturation cycle of dab by both visual assessment and simple histological methods. This study will enable estimates of length and age at maturity in both sexes to be derived, as well as spawning seasons.
- d. To estimate the fecundity and establish the relationship between fecundity and length, weight, ovary weight and age. Seasonal variations in egg diameter will be undertaken. The gonadocarcass and hepatocarcass indices will be estimated on a monthly basis.

- e. To study the composition, diversity and breadth of diet for dab between seasons and between size groups. The intraspecific diet overlap index between size groups, and also between dab populations in different localities will be determined on a monthly basis.
- f. To study feeding patterns on a seasonal basis and for diel periodicity to compare with earlier studies.
- g. To conduct energy mobilisation studies which will entail determining changes in the gross energy content as well as total lipid and ash content, of the gonad, carcass and the liver for individuals of each sex.
- h. To estimate the gastric evacuation rate and food consumption in the wild

1.4 POPULATION BIOLOGY OF DAB

1.4.1 Distribution and abundance

The dab has a wide range of distribution throughout the waters of north-eastern Europe. Its distribution extends from the Bay of Biscay to the coast of Murmansk and across Iceland (Bohl, 1957; Jonnson, 1966).

Surveys along the coast of England and Wales, which covered a depth range (0-30 m), indicate that the distribution of 0-group dab is not restricted only to waters less than 10 m in depth (Riley *et al.*, 1981). Although juvenile dab seem to be concentrated in coastal waters, small specimens (< 9 cm) have been caught in offshore stations in the Dogger Bank area and in the Eastern Central North Sea (Rijnsdorp *et al.*, 1992) between 10-20 m deep and in Red Wharf Bay (present study), 10-15 m deep. It is unclear whether these are juveniles from coastal or from open sea nursery grounds.

Both plaice and dab spawn in offshore waters (Bolle *et al.*, 1994). In the southern North Sea, the spawning period for plaice is from December until March, whereas the spawning period of dab runs from September to January with a broad peak from February to April (Harding and Nichols, 1987; Van der Land, 1991). Rijnsdorp *et al.* (1992) further observed that in March and April 1989, spawning of dab occurred all over the south eastern North Sea with major concentrations of eggs in the German Bight and north of the Friesian Islands and along the southern bight of the North Sea. Developing plaice eggs are transported to the coastal nursery grounds by residual currents. The post-larval plaice reach the nursery grounds in March-April 2-3 months before dab do (Macer, 1967; Edward and Steel, 1968; Van der Veer *et al.*, 1990). Campos *et al.* (1994) also found that both dab and flounder

spawn during the winter and spring months in the south eastern North Sea, with flounder showing peak production in March and dab in late April. Juveniles of both species are known to be dependent on coastal nursery areas. Metamorphosing dab are known to settle in deeper waters and begin entering the coastal areas only as juveniles in summer and autumn. Kaiser and Ramsay (1997) reported that dabs are widely distributed throughout the whole North Sea and are found at depths of up to 100 m; however the vast majority of the population occurs in the south-eastern North Sea on shallow (< 30 m) sandy substrata.

Flatfishes of various species comprise a considerable proportion of demersal fish in the entire North Sea, representing more than 20 % of the total fish biomass in the area (Daan *et al.*, 1990; Campos *et al.*, 1994). It has been reported that dab larvae are the most abundant among the flatfish larvae in the North Sea, comprising, on average, 51.2 % of all flatfish larvae, with a mean density of 38.8 individuals per square metre (Campos *et al.*, 1994). There are however seasonal fluctuations in the post-larval abundance, becoming relatively low during winter. Bolle *et al.* (1994) found that 0-group dab was the most important juvenile species in the open North Sea (the Dutch coast zone and the estuarine Wadden Sea) and that the adults were distributed down to 150 m depth. The trawl catch rates of dab in Icelandic waters suggest that the dab is common at depths of 40-100 m (Jonsson, 1966) but decreases rapidly and becomes rare at depths of more than 120 m. According to Bohl (1957) the adult dab is more common at 20-40 m depth in the North Sea. The species is believed not to migrate long distances. During winter, however, it seeks deeper water but moves shoreward in late winter for spawning.

Rijnsdorp *et al.* (1992) showed that the dab is more abundant (Nh^{-1}) at depths ≥ 30 m in the North Sea. The abundance however declined at depths greater than 40 m. The lowest catch rate was observed at depth ≤ 29 m (Table 1.1).

Table 1.1. Abundance (catch by number per hour trawling) in the south-eastern North Sea (Rijnsdorp *et al.*, 1992).

Depth (m)	N _{Male}	N _{Female}	N _{Total}	Duration (Min.)	N _{tot} h ⁻¹
29	62	417	479	300	96
30	1875	3192	5067	240	1267
35	10335	8224	18559	150	7424
40	7426	9685	17111	210	4889
42	2884	3815	6699	180	2233
43	2362	2003	4365	150	1746

Macer (1972) noted that the Great Orme is a spawning ground principally for plaice and dab but Red Wharf Bay is considered as an important nursery area for these species. Rogers *et*

al. (1999) reported that plaice and dab were the most abundant flatfish species in the Northeast Atlantic and were typical of shallow, uniform sandy and muddy seabeds, which occurred extensively throughout the southern North Sea, and to a limited extent in UK Western Waters. They also found that in the Irish Sea, commercial fish assemblage being dominated by plaice and dab.

1.4.2 Exploitation

Flatfish support major commercial fisheries in temperate and boreal systems of the Northern Hemisphere (Pauly, 1994). The European catch of dab in 1977 was 1.4×10^4 mt, with annual catches in France over 2000 mt and over 4000 mt in Holland and Denmark (Ortega-Salas, 1988b). Between 1988 and 1993, the annual catch of dab in Western European waters varied between 5.1×10^3 and 1.3×10^4 mt (FAO, 1995 and 1998), with Holland and Iceland contributing significantly higher amounts (average annual catches 2970 and 2968 mt respectively) than other European countries (Tables 1.2). The total European catch increased in the later 1990's to more than 1.3×10^4 mt *per annum*, which is closer to the 1970's catch. The landings by Iceland and Holland dominated the total catch of dab in the late 1990's. Iceland contributed 60.4 %, 59.3 % and 27.8 % to the total catch in 1996, 1997 and 1998 respectively. Landings by Holland contributed 43.8 % to the total catch in 1998.

Table 1.2. Production of dab by country in Western Europe (FAO, 1995 and 1998) in tonnes

Countries	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
England (& Wales)	693	471	429	650	565	684					
Scotland	1130	1191	744	1072	834	1721					
UK							1706	2225	2221	2590	2467
Holland	3419	2521	-	-	-	-	-	-	-	-	7983
Iceland	3776	2236	1897	2632	3045	4222	5159	5558	7954	7891	5061
Germany	503	406	501	671	627	1102	1944	2074	1880	1384	1129
France	3090	1963	1522	1460	1514	1567	1258	1062	1120	1446	1576
Total	12611	8788	5093	6485	6585	9296	10067	10919	13175	13311	18216
- = no data											

The biomass of dab in the North Sea is estimated as 2 million tonnes (Sparholt, 1987; Daan *et al.*, 1990). In terms of weight, Stefan *et al.* (1996) reported the biomass of fish in the North Sea as 14.1×10^6 mt and the biomass of dab and plaice as 1.6×10^6 mt. The total estimated fish landings in the North Sea were 2.7×10^6 mt. The estimated landings of dab and plaice were 7.0×10^3 mt and 1.5×10^5 mt respectively. Ortega-Salas (1988b) estimated the stock size of dab in the Irish Sea, using a VPA technique, as 2.0×10^4 mt. Bakhsh (1982)

estimated the numbers in the dab population on the North Wales Coast as 1.2×10^6 fish in 1979-1980. Dab are caught as by-catch in the commercial fishery for plaice and sole (*Solea solea* L.) in the North Sea. Their survival rate after capture has been estimated at 24 % (Kaiser and Spencer, 1995). Surprisingly, despite the high by-catch rate, this species remained the most abundant flatfish species in the North Sea. Kaiser and Ramsey (1997) have suggested that the combined effects of predator and competitor removal, plus increased food availability resulting from eutrophication and trawling disturbance, may have contributed to the observed resilience in the stability of the population of this species. On the other hand fishing pressure in the North Sea has led to the decline in the populations of larger target species such as cod and plaice (Greetstreet and Hall, 1996; Rijnsdorp *et al.*, 1996).

The magnitude of year-class abundance in many temperate flatfish appears to be determined by physical and environmental factors experienced early in life, and it is subsequently modified by potentially density-dependent processes within the nursery (Henderson and Seaby, 1994). Henderson and Seaby found that dab abundance was positively correlated with water temperature during their juvenile stages.

Due to its high biomass and wide distribution, dab plays an important role within the benthic system (Knust, 1996). Over the years it has become an important key species for monitoring biological and chemical pollution (Dethlefsen, 1984; Claussen, 1988).

1.4.3 Meristic and morphometric characters

Taxonomists have long been aware that counts of vertebrae, fin rays or scales vary among individuals. In many cases such counts are used to identify species. Fish of different stocks in a mixed fishery have been separated by the combination of meristic characters (de Veen and Boerema, 1959; Cushing, 1981; Templeman, 1981; Begg *et al.*, 2001).

Meristic characters have been used by Jensen (1937), Bohl (1957), Jonsson (1966), and Bakhsh (1982) to characterise dab stocks in the waters of Denmark, North Sea, Iceland and Anglesey respectively (Table 1.3). The species of juvenile flatfish (plaice, flounder and dab) have been differentiated by the number of vertebrae (Ellis and Gibson, 1995).

The shape of individuals can be described by ratios between sizes of body parts (Jennings *et al.*, 2001). Examples are head length, body depth and fish length. When such morphometric characters are compared in many individuals, distinct patterns can emerge that indicate

differences between stocks (Bakhsh, 1982). The length of skull and various parts of the vertebral column have also been useful for predicting original total length in flatfish juveniles from known sea areas (Ellis, 1994).

The role of environmental randomness on the formation of meristic characters has been extensively reviewed in Nikolsky (1963). Jensen (1939) found that the numbers of anal fin rays were positively correlated with water temperature experienced when the dab and plaice larvae are quite small. Jennings *et al.* (2001) also noted that morphometric and meristic differences may result from genetic or environmental factors. The relative roles of such factors have been discussed by Leslie and Grant (1990), Creech (1992), Kartavtsev *et al.* (1993) and Seventi *et al.* (1996).

Table 1.3. Variation in the mean count of meristic characters in dab in European waters

a). Mean number of vertebrae in dab at different localities

Area	Mean±95%CL	Author
Iceland S & SW	40.52±0.04	Jonsson (1966)
Iceland N	40.56±0.12	"
Iceland Larvae	40.70±0.08	"
North Sea	40.36±0.24	Lozan (1988)

b). Mean number of dorsal fin rays in dab at different localities

Area	Mean±95%CL	Author
Iceland S & SW	74.16±0.18	(Jonsson, 1966)
Iceland N	74.04±0.27	"
Iceland Larvae	73.81±0.41	"
North Sea S.E	73.72±0.47	"
Baltic Sea W	71.18±0.37	"
North Sea	71.65±2.84	Lozan (1988)

c). Mean number of anal fin rays in dab at different localities

Area	Mean±95%CL	Author
Iceland S & S.W	57.71±0.14	(Jonsson, 1966)
Iceland N	57.65±0.22	"
Iceland Larvae	57.56±0.33	"
North Sea S.E	56.57±0.37	"
Baltic Sea N	54.64±0.31	"
North Sea	55.72±1.55	Lozan (1988)

d). Summary results of mean counts of meristic characters in dab in Anglesey waters

Meristic characters	Mean±95%CL	
Vertebrae*	38.78±0.67	Bakhsh (1982)
Anal fin ray	57.22±1.45	"
Dorsal fin ray	73.91±1.92	"

* Vertebral count is without Urostyle

1.4.4 Age determination

1.4.4.1 Hard parts

A basic requirement in population biology is determination of the age composition within samples of the species being studied, from which estimates of the age structure, growth and mortality rates of the population as a whole can be obtained. It has become routine to use the observation that periodic changes occur in the growth or structure of hard, permanent parts of the fish, which appear to be related to seasonal cycles in the fish's metabolism. The correlation between the age of fish and morphological changes has been documented (Bagenal, 1974; Bagenal and Tesch, 1978; Campana and Neilson, 1985). The most common hard structures used are the otoliths (Lozan, 1989, Deniel, 1990; Rijnsdorp *et al.*, 1990), opercular bones (Mann, 1976; Banda, 1992) and scales (Hunt and Jones, 1975). In pleuronectids the age is frequently determined from the otoliths (Lozan, 1989; Rijnsdorp *et al.*, 1992).

The saggital otoliths are located in the sacculus of the inner ear. They are flattened, ovoid structures usually composed of a number of concentric rings with different radii. The appearance of the layers normally varies from extremely opaque to completely hyaline (transparent). The growth pattern of fish over its life span can be seen in the changing width of the opaque zone. Age is normally determined by counting the opaque zones. In the simplest case one complete annual cycle of otolith growth consists of laying down one opaque zone and of one hyaline zone. The first opaque zone is usually called the 'nucleus' of the otolith (FAO, 1981). The different densities of these concentric areas or zones form a series of light and dark rings when viewed under a microscope (King, 1995). This appearance depends on whether they are viewed under reflected light or transmitted light. In temperate areas, this deposition of alternate opaque (spring-summer) and hyaline zones (fall-winter) is a regular annual occurrence.

This methodology is suitable for ageing the younger, faster growing fish up to about 8 years old, but may seriously under-estimate the age of older, slow growing fish, for example like plaice (Rijnsdorp and van Leeuwen, 1992); otoliths from older fish require more detailed preparation.

1.4.4.2 Age length frequency key (ALFK)

A popular method to find the population structure that is widely used in Europe is the Age Length Frequency Key (ALFK) method. The age length key is a table showing, for each length class of fish, the percentage or fractional age frequency composition. It is used in cases where age determination is possible but time consuming (and impracticable) and therefore expensive to examine all the fish in large samples. In order to estimate the age composition of the catch from a particular stock, an age/length key is constructed based on a smaller sample of age readings. Afterwards, lengths are converted to ages by means of the key. A length stratified method, as opposed to random sampling (Basimi and Grove, 1985a, Seyhan and Grove, 1998) is used to obtain the subsample. Stratified length sampling ensures that very small fish and very large fish are included in the key. After the key has been prepared, a large number of fish which were only measured can be distributed on age groups according to the key. For species like flatfish, the ALFK is constructed with the sexes separated because their population parameters are different.

1.4.5 Variation in population parameters

1.4.5.1 Growth and mortality rates

The growth rate of fish is a characteristic that shows variation in response to locality, food availability, population density, temperature, salinity and fishing intensity (Ricker, 1981; Campana, 1984; Al-Hossaini and Pitcher, 1988; Tsai *et al.*, 1991; Rijnsdorp and van Leeuwen, 1992; Wang and Tzeng, 1999). Growth has also been found to vary seasonally with time (Burd and Cushing, 1962; Lockwood, 1974), with length of the growing season (Francis, 1994) and genetic factors (Paloheimo and Dickie, 1966)

Growth studies by Jonsson (1966) showed that the dab in cold water areas grow faster than the dab in the warm water area of the coast of Iceland. The possible reason could be that food conditions are better in the cold water area due to less crowded fish stocks and less interspecific competition between dab and other fish species living on the same or similar

diet (plaice, haddock). Because of great exploitation of the stock, together with exploitation of other flatfish species, the dab in the western Baltic grows faster than the dab in the North Sea where the population is dense and the competition for food is greater (Bohl, 1957; Jonsson, 1966). Comparison of the growth of dab around Iceland with that in the North Sea (Bohl, 1957) and western Baltic (Kandler and Thurow, 1959) showed that the growth of the Icelandic dab was intermediate between the fast growing dab in the western Baltic and the slow growing dab of the North Sea. The growth in length of the dab in Anglesey waters has been shown to be higher than in the North Sea (Lee, 1972; Bakhsh, 1982). The Anglesey dab were found to be a little larger than the southern North Sea and Icelandic dab in the first three years of their age but the situation reversed after age 3-4 years.

Many workers use the average size at age for a sex (or species) to fit the non-seasonal Von Bertalanffy growth function (formula in Chapter 3, Section 3.1) for length-at-age (See Table 1.5 below). A number of workers have derived estimates of the parameters of this function and established differences in growth rates between sexes of the same species by season and by locality (Bakhsh, 1982; Basimi and Grove, 1985a; Horn, 1993). Seyhan (1990) and Chuenpagdee (1990) demonstrated sexual and seasonal differences in growth rates in male and female plaice respectively between 1970 and 1990 in Anglesey waters. In flatfish the females usually grow to a larger size than the males. The investigations by Ortega-Salas (1988a), Deniel (1990) and Rijnsdorp *et al.* (1992) showed that dab fits into this category. The growth rate of both sexes of dab in Icelandic waters during the first 2-3 years is approximately the same but, from then onwards, the growth rate of the females exceeds the males. The reason is that the males reach sexual maturity at an earlier age and then growth slows down. It is generally held that somatic growth will be reduced with the onset of sexual maturity (Nikolskii, 1969; Roff, 1983).

Bakhsh (1982) considered 1st April as the official birthday of dab based on evidence from seasonal changes occurring at the edge of the otolith. Rijnsdorp *et al.* (1992) found that the dab population was dominated by 4 and 5 year old fish in the southeastern North Sea. Beyond 5 years, the number of dabs quickly declined. The length distribution of dab was dominated by size groups of 15-20 cm and few smaller than 10 cm were observed in the samples from a research net of 40 mm stretched codend mesh size. Differences in growth rates in dab were observed between the coastal areas, central areas and the offshore Dogger Bank in southeastern North Sea. These differences are in agreement with the observations of Bohl (1957), who found that the dab in the shallowest areas in the German Bight grew faster compared with dab at the offshore grounds. Deniel (1990) studied growth in ten flatfish species in the Bay of Douarnenez on the West Coast of Brittany in France and

found that in all the species, females attain greater ultimate size than males and also older specimens were mostly females. Males ($K= 0.64 \text{ yr}^{-1}$) grow relatively faster than females ($K= 0.54 \text{ yr}^{-1}$). Ortega-Salas (1980,1988a) also found that the rate of growth in length and weight in the dab was faster in summer than winter. The growth rate was found to vary with age and with area; growth rate was also affected by maturity in both male and female dab.

Basimi and Grove (1985a) demonstrated that 1st April should be the official birthday of plaice in Anglesey waters and the starting date for the onset of seasonal growth in length. They showed that initiation of opaque otolith growth zones and the subsequent change to the hyaline layers varies with age and sex. Lockwood (1974), however, considered 1st May as the starting point for seasonal growth in plaice in the North Sea. Rijnsdorp (1989) took 1st January as the official birthday of plaice in the North Sea.

It is therefore reasonable to infer from the above review that growth of fish is directly or indirectly affected by environmental conditions (supply of available food, temperature, intensities of competition for food). The extent of variability in mean length at age and Von Bertalanffy growth parameters in dab and plaice in European waters is illustrated below in Tables 1.4 and 1.5 respectively.

Table 1.4. Mean length at age of male and female dab from samples in March 1990 in southeastern North Sea (Rijnsdorp *et al.*, 1992)

The six station numbers run (beginning from station 3) from the shallow inner German Bight towards the deeper Dogger Bank

A. Male

Stations number	3	5	6	7	8	9
Age (yr.)	Mean length (cm)					
1	-	-	9.00	-	-	-
2	11.56	11.89	11.32	12.35	11.70	13.07
3	14.39	14.35	14.35	14.13	14.92	15.80
4	17.20	16.59	16.31	16.06	16.56	17.41
5	19.12	19.05	18.68	17.13	17.21	19.15
6	20.40	20.74	19.21	18.83	18.22	22.92
7	21.00	21.10	-	19.54	19.79	21.84
8	22.29	22.70	21.05	-	20.44	23.91
9	23.00	23.00	-	20.00	21.68	20.00
10	-	-	-	20.00	-	-
11	-	-	-	21.00	23.00	-

B. Female

Stations	3	5	6	7	8	9
Age	Mean length					
1	-	-	-	-	-	11.40
2	12.90	12.27	13.08	12.47	12.62	13.79
3	17.25	15.50	15.36	15.17	16.06	17.49
4	20.29	18.59	17.58	17.57	18.30	19.37
5	23.17	21.93	20.99	20.02	19.49	22.23
6	24.27	23.54	22.25	22.81	20.69	24.34
7	27.21	27.20	25.50	26.38	22.90	25.80
8	26.83	26.20	26.88	23.38	26.10	27.20
9	28.00	25.53	26.00	27.06	24.22	27.86
10	-	-	-	24.00	26.94	32.00
11	-	-	-	-	27.46	-

Table 1.5. Spatial, seasonal and sexual variability in Von Bertalanffy growth parameters (L_{∞} , K and t_0) in dab and plaice in various European waters. Detailed explanation of these parameters and their estimation is given in Chapter 3.

Spp.	Sex	L_{∞} (cm)	K (yr ⁻¹)	t_0 (yr ⁻¹)	Area	Author
Dab	M	20.67	0.44	0.12	North Sea (Central)	Lee(1972)
Dab	F	30.40	0.22	-0.17	North Sea (C)	"
Dab	M	24.08	0.48	0.29	North Sea (Southern)	"
Dab	F	42.40	0.18	-0.29	North Sea (S)	"
Dab	M	27.62	0.47	0.28	North Sea (S)-Dutch	"
Dab	F	35.59	0.37	0.27	"	"
Dab	M	21	0.419		Anglesey	Bakhsh(82)
Dab	F	28	0.302		"	"
Dab	M	25	0.26	-0.34	North Sea (SEast)	Rijnsdorp et al. (92)
Dab	M	22.9	0.28	-0.54		"
Dab	M	23.1	0.39	-0.29		"
Dab	F	30.5	0.28	-0.07		"
Dab	F	29.6	0.21	-0.67		"
Dab	F	33.4	0.19	-0.85		"
Dab	F	33.0	0.318	0.239	Isle of Man	Ortega-Salas (88a)
Dab	M	22.15	0.604	0.425	"	"
Dab	F	35.16	0.20	-0.29	German Bight	Lozan (89)
Dab	M	28.37	0.23	-0.63	"	"
Dab	F	41.8	0.540	0.24	Douamenez (France)	Deniel(90)
Dab	M	36.1	0.636	0.299	"	"
Plaice	F	61.7	0.372	0.209	"	"
Plaice	M	50.7	0.504	0.239	"	"
Plaice	all	68.50	0.095	-0.82	North Sea (C)	Bannister (77)
Plaice	M	44.60	0.122	-6.37	"	"
Plaice	F	57.20	0.175	-0.196	"	"
Plaice	M	40.84	0.337	-0.64	Dutch BT/Ger. BT	"
Plaice	F	52.20	0.175	-1.96	"	"
Plaice	M	43.10	0.195	-3.09	Cleaver Bight	"
Plaice	F	56.10	0.135	-3.01	"	"
Plaice	M	41.60	0.193	-3.92	South. Bight	"
Plaice	F	52.20	0.155	-2.99	"	"
Plaice	M	36.2	0.27	-1.97	Anglesey	Basimi(78)
Plaice	F	45	0.25	-1.20	"	"
Plaice	F	56.06	0.168	-1.56	" (1989 Summer)	Chuenpagdee (90)
Plaice	F	47.09	0.314	-0.77	" (1989 Autumn)	"
Plaice	M	47.51	0.188	-1.74	"(1989S)	Seyhan (90)
Plaice	M	43.02	0.219	-2.05	"(1989A)	"

The decrease in abundance of a cohort with time is treated as an exponential decrease with an (assumed) constant instantaneous coefficient of total mortality rate ($Z \text{ yr}^{-1}$) (Beverton and Holt, 1957). One of the important parameters in the studies of a fish population is the present instantaneous rate of total mortality, Z . This total mortality rate is the summation of instantaneous rates due to natural causes (M) and any fishing (F). Estimation of Z can be affected by net emigration or immigration. Z is initially assumed to be constant for all age groups, but it could vary of course for different age groups. For example, the effect of differential mortality should be observed since larger fish in a year class may die first. Also, younger fish may be more vulnerable to predation, diseases and the fishing gear in use. The older ones can swim faster and are liable to escape the fishing gear. The most commonly used method is the semi-log plot of population abundance against age, usually referred to as Catch Curve technique (Sparre and Venema, 1998). A detailed description of the technique and the underlying assumptions are given in Chapter 3. Basimi (1978), Seyhan (1990) and Chuenpagdee (1990) used catch curve analysis to determine Z for plaice and were able to demonstrate sexual and seasonal differences in rate. Bakhsh (1982) and Ortega-Salas (1988b) estimated the total mortality rate of dab and showed that sexual differences existed. Estimates of Z in dab and plaice in various localities are given in Table 1.6.

Table 1.6. Estimated total mortality rate ($Z \text{ yr}^{-1}$) of dab and plaice in different localities

Species	Female	Male	Area	Author
Dab	0.80	0.64	Anglesey	Bakhsh (1982)
Dab	1.04	1.39	Isle of Man	Ortega-Salas (1988)
Dab	1.18	1.12	North Sea	Lee (1972)
Plaice	0.78		Anglesey(1990S)	Chuenpagdee (1990)
Plaice	0.69		Anglesey(1989A)	"
Plaice	0.82	0.90	Irish Sea	Siddeek (1989)
Plaice	0.98	0.65	Anglesey	Basimi and Grove (1985a)

S = Summer

A = Autumn

1.4.5.2 Variation in length and weight relationship

Relationships between the length and weight of individual fish of varying sizes are recorded for several reasons. It is often difficult to record fish weights at sea due to accelerations or when sampling on a market due to space and time. Often large samples are analysed for length composition, and length and weight recorded for selected individuals within subsamples. This provides a means for back calculating weights of fish in the large sample. The length/weight relationship (usually) in the form

$$W = aL^b \text{ -----(1.1),}$$

can help decide if the individuals grow isometrically ($b \approx 3$); this was assumed for plaice in the Beverton and Holt basic yield equation (1957). Length/weight relationships may also give indications of taxonomic differences and events in the life history of fish such as metamorphosis and the onset of maturity and throw light on the seasonal variation in the condition ("nutritional well-being") of the fish. Individual variations from the general length weight relationship have been considered generally under the term 'condition', as indicated by the exponent of the length weight equation.

The power b generally lies between 2.5 and 3.5, usually close to 3 (Table 1.7). When $b = 3$, the growth in weight is isometric which implies that growth in weight proceeds in the same direction as the cube of the length. When $b \neq 3$, growth in weight proceeds in a different dimension (Pauly, 1984) and is considered allometric. In the vast majority of fish species, it has been found that the cube law is not obeyed. Most fish species have been observed to change shape as they grow (Basimi and Grove, 1985a). It is also observed that the exponential (b) in the length weight relationship may be influenced by many factors such as sex, time of year, stage of maturity, stomach contents and environmental variables.

Bagenal (1957b), Jones (1974), Ortega-Salas (1980) and Chuenpagdee (1990) used length and weight relationships to illustrate seasonality in growth of long rough dab, turbot, dab and plaice respectively. All the flatfish tend to be in good condition in November and December but the condition declined at or after spawning time, March and April, followed by a recovery.

Basimi and Grove (1985a) found no significant differences in the condition of the male and female plaice between early summer and late autumn (May to November). However as the spawning season progressed, in winter and early spring (Jan-March), it was discovered that spent female fish differed significantly in condition from other groups of fish due to the loss in weight as a result of spawning. Thus, seasonal differences in feeding rate and spawning activity affect the condition of the fish.

Table 1.7. Fitted constants (a and b) of length and weight relationships for some flatfish species ($W = aL^b$ with W in g and L in cm).

a) Female plaice, Chuenpagdee (1990)

Year	Season	a	b
1978	Autumn	0.006	3.163
1979	Autumn	0.004	3.256
1987	Autumn	0.001	3.588
1988	Autumn	0.011	3.009
1989	Summer	0.008	3.013
1990	Summer	0.015	2.858

c) Dab

Ortega-Salas (1980)	a	b	r
Male	0.006	3.057	0.92
Female	0.005	3.114	0.98

c) Turbot

Jones (1974)	a	b
Male	0.054	2.745
Female	0.045	2.793
Combined	0.049	2.769

1.4.5.3 Cyclical changes in condition factor

Various workers have used empirical formulae to describe seasonal changes in condition of dab, as opposed to using the coefficients of length and weight relationships. 'Condition' is an indicator of the changes in the food reserves stored in the muscles. It is generally defined as the ratio of the weight of fish to the cube of the length (when the growth in length and weight is isometric). A simple way of measuring the variability of the condition of the fish is by means of the condition factor. Rather ambiguously, authors have used the symbol "K" for condition factor, which must not be confused with the instantaneous growth rate ($K \text{ yr}^{-1}$) used in the Von Bertalanffy Growth formula. There are variations in the definition of condition factor, as shown below:

Purchase and Brown, 2001 defined condition factor as:

$$K = \frac{\text{Body weight}}{\text{Length}^3} \times 100 \text{-----} (1.2)$$

Htun-Han (1978a) defined condition factor as:

$$K = \frac{\text{Body weight} - \text{Gonad weight}}{\text{Length}^3} \times 100 \text{-----} (1.3)$$

Knust (1996) defined condition factor as:

$$K = \frac{\text{Carcass weight}}{\text{Length}^3} \times 100 \text{-----} (1.4)$$

Where carcass weight is the eviscerated body weight (that is body weight without the gonad, liver and gut). The last equation (1.4) seems more realistic since it eliminates error that may be introduced by variation in stomach fullness, gonad and liver weight.

The usefulness of the study of condition factor is that it is possible to define the seasonal changes in the condition of fish in relation to age and sex of the fish. Differences in condition in different localities might serve as an index of the productivity of the water mass. Seasonal variations in condition factor have been reported for dab (Lee, 1972; Bakhsh, 1982; Knust, 1987; Saborowski and Buccholz, 1996, 1997).

Ortega-Salas (1980) showed that the maximum value of the condition of dabs in the Irish Sea is obtained around August-September and the minimum after spawning in May. The decline in condition in May coincided with the minimum weight of the liver. This observation has earlier been made by Htun-Han (1978a) who also confirmed depletion in body reserves during seasonal maturation in dab. He found that the annual cyclical changes in the condition factor of dab were almost parallel with the hepatosomatic index (total body weight divided by liver weight). The condition reached a peak in the pre-spawning periods. He observed striking similarity in the value of the condition for both males and females, with a range between 0.8 to 1.1. Bakhsh (1982) also observed a high hepatocarcass ratio (carcass weight divided by liver weight) for both male and female dab for most of the year but which declined

considerably in May after the spawning period. The lipid content of the female dab was high in summer (probably due to active feeding) and also during vitellogenesis (November-December) but falls at the end of the spawning season. In the German Bight, the values for condition factor range from 0.88 in April to 1.08 in August (Knust, 1987).

1.4.6 Life history strategy in flatfish

Study of the life history strategy of fish is important in elucidating the survival tactics and resilience exhibited by exploited fish populations. It is frequently observed that fish species that are subject to the highest rate of natural mortality (M) have the fastest rate of relative growth (high K), a relatively small body size (low L_{∞}), maturity at an early age and smaller size, and investment of a high proportion of their available resources into gonad (towards reproduction) rather than somatic growth (high GSI, Gonadosomatic Index), (Jobling, 1995). Such a species is referred to as r-selected whilst the k-strategist, on the other hand, would be characterised by a high age at first maturity, a low K and a large L_{∞} , low M and a high maximum age (Pitcher and Hart, 1982 and Jobling, 1995). It should therefore be obvious that fishing will affect fish with different life history traits in different ways. Fisheries based on fast growing fish which mature earlier at a smaller size may be sustained at younger ages at higher levels of mortality, whereas slow growing fish which mature later at a larger size will be in danger of extinction with high fishing effort (Jennings and Kaiser, 1999).

For example, Deniel (1990) found that ten flatfish species on the coast of Brittany segregated according to their longevity; those reaching their asymptotic lengths rapidly have shortest life spans and also highest values of K . The growth rate and total mortality rate of the males are higher and they reach maturity earlier than their female's counterparts. In plaice, the males are present at the spawning grounds at the beginning of the spawning period and stay there until the end. Female plaice, however, visit the spawning grounds several times to shed a batch of eggs and aggregate in the areas adjacent to the actual spawning grounds in between the spawnings (Simpson, 1959a; Rijnsdorp, 1989). Rijnsdorp estimated the average duration of the spawning period of plaice is 11 weeks and 5 weeks in male and female plaice respectively, which ensures that an average male is able to fertilise eggs over nearly the complete spawning period. He also noted that male plaice remain stationary during the spawning period whereas the females may move within a restricted area around the actual spawning grounds. Tagging experiments have suggested that dab migrate seasonally between spawning and feeding areas in the North Sea (Bohl, 1957) and the effect of this on the sex ratio is discussed below.

Flatfish, in common with other marine teleosts, also produce a large number of small eggs spawned in several batches (Rijnsdorp, 1994). This reproductive strategy is held to be an adaptation to the patchiness of the food resource in both space and time (Rothschild, 1986; Cushing, 1990).

1.4.7 Reproduction

Reproduction is the link in the life cycle of a fish, which, in connection with other processes like recruitment and growth, should ensure the continuity of a species. Various aspects of the reproductive biology of fish are documented in Nikolsky (1963), Donaldson (1977), Rijnsdorp (1989), Rijnsdorp *et al.* (1991) and Jobling (1995). The focus of the present review is to discuss variability in sex ratio, maturation and fecundity in dab.

1.4.7.1 Temporal and spatial variability in sex ratio

Sex ratio is normally calculated as the number of males divided by the number of females. It can vary considerably from species to species, from population to population, from one locality to another, from season to season, from year to year, from one length or (age) range to another of the same species (Table 1.8). This variability in sex ratio could be crucial to the formulation of management plan for fish stocks.

Saborowski and Buchholz (1997) have made observations on the seasonal distribution of dab by sex in the southern North Sea. The sex distribution was characterised by a reduced proportion of males during autumn and winter. As a result of the immigration of large females in autumn and winter for spawning purposes, the male proportion decreased rapidly, reaching less than 15% of the total number of dab in samples in January. From March to July the ratio was about 50 %: 50%. In summer, the females were less frequent than males, comprising only 40 % of the total number of dab. Thus the sex ratio changed continuously throughout the seasons reflecting a cyclic annual succession.

Along the German and Danish coasts, Bohl (1957) investigated the spatial occurrence of dab during summer and found that females were predominantly present in the shallow coastal waters. Males were rare in this shallow area, but become more abundant in deeper waters (>15 m) further away from the coast. After spawning, female dab were observed to return to the coastal areas earlier than males and the older fish also return earlier than the younger

ones. The males were observed to spend a longer time in spawning condition than females. The sex ratio in Icelandic dab was variable with time, depth and area. Out of 7035 dabs examined in Icelandic waters, Jonsson (1966) found that 51.7 % were males as against 48.3 % females. The males were more common in the younger age groups from age I to V (53.9 %). The male proportion was largest in age group IV (59.5 %). Then the males decreased in proportion in larger age groups; but the female proportion increased accordingly. This proportional decrease of males with increased age has been attributed to the higher mortality rate for this sex. The possibility of large scale fertilising of the eggs by the males is ensured by the fact that a) the males reach maturity earlier b) males of younger age groups are more common than females and c) the reproductive organs of the males are active for a longer period each year than the female. Comparison of the sex ratio among length groups in Icelandic waters show that the proportion of females and males are equal in the younger length groups (7-14 cm). Males however dominate between 16-27 cm and females dominate in the bigger length groups.

Bakhsh (1982) observed that the sex ratio for dab in Anglesey waters was 1:1 in the 13-18 cm total length group, but also noted that the females dominate outside this length group. The females were also found to dominate the inshore areas throughout the year. In the samples taken offshore in April, the proportion of males (48.8 %) nearly equalled that of the female. The proportion of males was higher in May (55.06 %) and July (53.04) and decreased to 25.12 % in January and 38.09 % in February. Generally, the females formed a greater proportion (52.86 %) than males (46.16 %).

Ortega-Salas (1980) also observed changes in sex ratio in the Isle of Man dab throughout the year. There were more female dabs in shallow waters (15-50 m) during summer but male dabs were dominant during the spawning period in winter. There were fewer males (40 %) than females (60 %) at all ages and in all trawl catches of dab in the Isle of Man and he attributed this to differential mortality between the male and female dab. The estimated mortality rate of the male dab was 34 % higher than the female dab in the Isle of Man.

On the coast of Brittany, the usual pattern of female dominance among the older age groups was also evident in the dab sex ratio distribution (Deniel, 1990). This observation was again attributed to differential mortality among the adult population and/or migration. Simpson (1959a and b) attributed the dominance of females among the older fish in the North Sea and Irish Sea plaice to the higher mortality among the males during fishing on the spawning ground. Simpson (1959a) observed higher male proportions in the Southern Bight of the North Sea and attributed this to the continued decrease in the numbers of the older

spawners, combined with a strong recruitment of the young spawners. Rijnsdorp (1994) noted that differences in sex ratio may affect spawning success of a population by its influence on the chances that males and females may find each other to spawn successfully.

Table 1.8. Variability in sex ratio in dab in different locations in Europe

a) With season in Anglesey (Bakhsh, 1982)

Year	Month	Female (%)	Male (%)
1979	May	44.94	55.06
	July	46.96	53.04
	September	55.61	44.39
1980	January	74.83	25.12
	February	61.91	38.09
	April	51.12	48.88

b) With depth in Anglesey (Bakhsh, 1982)

Locality	Male (%)	Female (%)
Offshore	46.14	52.86
Inshore	26.06	73.94

c) Variation in sex ratio of dab with season and depth in the Isle of Man (Ortega-Salas, 1980)

Month	Year	Males (%)	Females (%)	Depth (m)
February	1977	80	20	80
January	1978	30	70	15-30
February	1978	75	25	80
August	1978	38	62	80

d) Variation in sex ratio (in %) with age and depth in Icelandic dab (Jonsson, 1966)

Sex	Age (yr.)	Depth (m)		
		< 40	40-80	> 80
Male	I	45.6		
Female	I	54.4		
Male	II		55.3	
Female	II		44.7	
Male	III			78.6
Female	III			21.4

e) Sex ratio of dab according to age in Icelandic waters (Jonsson, 1966)

Age (yr.)	Male (%)	Female (%)
I	52.3	47.7
II	47.8	52.2
III	55.8	44.2
IV	59.5	40.5
V	54.0	46.0
VI	49.4	50.6
VII	48.8	51.2
VIII	43.4	56.6
IX	41.3	58.7
X	39.4	60.6
XI	31.5	68.5
XII	33.3	66.7
Total	51.7	48.3

f) Sex ratio of dab according to length class in Icelandic waters (Jonsson, 1966)

Length range (cm)	Male (%)	Female (%)
7-10	48.9	51.1
11-14	50.2	49.8
15-18	65.0	35.0
19-22	65.0	35.0
23-26	60.3	39.7
27-30	47.2	52.8
31-34	35.1	64.9
35-38	26.1	73.9
39-42	0	100

g) Sex ratio (in numbers) by length and age groups of dab on the West Coast of Brittany (Deniel, 1990)

TL cm	Age 0		Age 1		Age 2		Age 3		Age 4		Age 5+	
	F	M	F	M	F	M	F	M	F	M	F	M
5-10	13	3	4	2								
10-15			42	23								
15-20			32	23	3	8						
20-25			30	23	13	24		1				
25-30			10	2	19	28	7	24		1	2	3
30-35					16	13	42	37	10	24	29	3
35-40							16		48	1	14	
40-45									1			
Total	13	3	118	73	51	73	65	62	59	26	45	6

h) Sex ratio of dab in the south-eastern North Sea (Rijnsdorp *et al.*, 1992)

Depth (m)	Male %	Female %	Total
29	12.94	87.06	479
30	37.00	63.00	5067
35	55.69	44.31	18559
40	43.40	56.60	17111
42	43.05	56.95	6699
43	54.11	45.89	4365
TOTAL	47.71	52.29	52280

1.4.7.2 Fecundity

The fundamental biological process which takes place in the spawning season is the production of fertilised eggs, from which develop subsequent recruits to the fishable stock. It is generally agreed that there must be a critical level of egg production below which recruitment to the stock would decline. The maintenance of egg production above this limit is a first essential step to the attainment of maximum productivity. The studies of egg production and the development of the gonad in fish are essential components of fish stock assessment and dynamics of fish populations. The estimates of fecundity and gonad development can be used in fish population parameter derivation like mortality rates and

hence in fishery management models (Beverton and Holt, 1956; Rikhter and Efanov, 1976; Gunderson and Dygert, 1988; Van Eenennaam and Doroshov, 1998).

Fecundity has been defined as the number of eggs spawned by an individual female in a spawning season and can be estimated by counting the number of oocytes in the ovary (Jones, 1974 and Rijnsdorp, 1994). Bagenal (1957a) defined fecundity as the number of unshed eggs in the ovary before spawning. Nikolsky (1963) referred to this definition as individual, absolute or total fecundity whilst Kraus *et al.* (2000) called it potential fecundity. The use of the term potential fecundity is based on the consideration that the realised fecundity, that is the number of eggs spawned per season, cannot be determined prior to spawning as a bias through subsequent atresia might occur and, furthermore, some vitellogenic eggs could remain in the ovary after spawning. Pitcher and Hart (1982) also defined fecundity as the potential number of offspring present before fertilization. Relative fecundity is defined as the number of eggs per unit weight or length (Bagenal, 1963, Nikolsky, 1963, Rijnsdorp, 1994 and Kraus *et al.*, 2000). Relative fecundity is generally used for comparison of fecundity of fish in different years or localities or fish of different sizes or age (Pitcher and Hart, 1982). Population fecundity is the number of eggs produced by all the females in the spawning population (Pitcher and Macdonald, 1973b; Marteinsdottir *et al.*, 2000).

1.4.7.3 Variability in fish fecundity

Simpson (1951) showed variation in fecundity between plaice of the same size, irrespective of age, and also observed differences in fecundity of plaice between different localities. Baltic plaice were shown to have higher fecundity than the North Sea or Barents Sea plaice. Nikolsky (1963) suggested that the variation in egg number among fish of the same size could be accounted for from the effects of food supply and temperature acting as critical factors in the development of the fish. Tyler and Dunn (1976) showed that food limitation can lower fecundity by restricting the recruitment of the oocytes rather than by increasing atresia of maturing oocytes in the winter flounder (*Pseudopleuronectes americanus*). Not all the ripe eggs are spawned in the spawning season. Some may be resorbed in the spent fish and this phenomenon is termed atresia. The 'atretic follicles' may be identified under a microscope (further note on this is given in Chapter 4). The percentage of females with ovaries that developed yolk was observed to increase with meal frequency, and fish on higher rations were also observed to develop heavier ovaries. Ration size was positively correlated with yolk-bearing oocytes per ovary but not with the percentage of atretic oocytes. Other workers have also attempted to establish relations between fecundity, food ration or population

density. Increased food supply has been shown to enhance fecundity in a number of experimental studies involving Brown trout, *Salmo trutta* (Bagenal, 1969; Townsend and Wootton, 1973; Horwood *et al.*, 1989). Fecundity and relative fecundity have also been said to be a density-dependent, population-regulating mechanism (Kipling and Frost, 1969). They suggested that high population density, with increasing behavioural interactions, may cause reduction in fecundity in the pike, *Esox lucius*.

Recent studies have also illustrated the variability in egg production among individuals and populations of different fish species. This results from differences in age and size of the female (Thorpe *et al.*, 1984), life history strategy (Morita and Takashima, 1998), competition (Fleming and Gross, 1989) and food supply and temperature (Fleming and Gross, 1990). Jonsson and Jonsson (1999) showed that individual egg mass and fecundity increased with somatic mass in first time and repeat spawning wild anadromous and freshwater resident brown trout, *Salmo trutta* in streams of Norway. Jonsson and Jonsson (1997) had noted that fecundity increases with body size because the amount of energy available for egg production and the body cavity accommodating the eggs both increase with size.

Individual fecundity in flatfish has been shown to be highly variable (Simpson, 1951; Bagenal, 1963; Rijnsdorp, 1991). Jones (1974) noted that the turbot was the most fecund local flatfish in the North Sea due to its large size, but relative fecundity was highest in dab and flounder. Relative fecundity varies enormously between flatfish species from approximately 4000 eggs g⁻¹ in the dab to 150 eggs g⁻¹ in plaice (Table 1.9). This variability in relative fecundity was directly related to egg size. The egg diameter of a ripe ovary in dab in the North Sea was estimated to be 0.75 mm and in plaice 1.93 mm. The egg size of brill (*Scophthalmus rhombus* L.) was estimated as 1.30 mm. Bakhsh (1982) also showed that the fecundity of dab is relatively high, varying between one and five thousand eggs per gram body weight. Rijnsdorp (1991) suggested that favourable conditions for growth will result in an above average growth in length and consequently an increase in absolute fecundity. He pointed out that the condition of the plaice at the critical time of maturation is expected to be closely associated with the food supply and the temperature of the environment. Bagenal (1957b, 1963) found significant differences in the fecundity of long rough dab and plaice in different years and concluded that these differences were due to the variation in food supply and population density between years. Bagenal (1966) showed that the plaice fecundity was lowest in the North Sea, in comparison to the Barents and Icelandic plaice. He found that the fecundity of plaice is low in areas where the population is high. Conversely in those areas where the plaice are scarcer, the fecundity was high. He correlated fecundity with larval drift and spawning areas of plaice and found that where water currents were favourable for good

survival of eggs and larvae, the parents were less fecund and where the currents are likely to carry the planktonic stages far, and to decimate the broods, the fecundity was high. Simpson (1951) stated that the high variation in fecundity of fish of the same size indicates that the number of eggs produced by plaice is heavily influenced by internal or external factors. He defined two critical periods in the maturation of the plaice in which the number of eggs laid might be influenced. One is the period when the germinal epithelium is laid down during the first year of life and secondly, the time when the new primary oocytes are being formed each year. Simpson recognised that the former period might fix the general level of fecundity for life whilst the latter period would be expected to affect the number of eggs laid year by year. He acknowledged that the growth rates and fecundity of individuals are both affected by food supply and therefore faster growing fish would be expected to have a higher fecundity than a slower one, and that temperature might affect egg production since all metabolic processes, within certain limits, are expected to increase with temperature.

In his review, Wootton (1979) acknowledged that the rate of food consumption was temperature dependent and thus low temperature could lead to reduced fecundity indirectly through a reduction in feeding rate. At high stock densities, food is expected to be limiting, growth rate should decline and absolute fecundity fall (Rothschild *et al.*, 1989). At low stock densities, growth rate increases, the size of the individual at the end of the year is large and fecundity is therefore greater. Jobling (1995) similarly noted that where there is a high population density and the spawning stock is large, density dependent factors related to the amount of food available to the individuals might be expected to lead to reduced individual fecundity. He further noted that despite reduced individual fecundity, the population fecundity may be higher for a small spawning stock. The spawning population should give an indication of the potential numbers of recruits immediately after spawning, although the spawning stock/recruitment relationship is unlikely to be linear (Pitcher and Hart, 1982).

i) Fecundity and length relationship

Fecundity is a function of body size (Bagenal, 1978; Wootton, 1979; Ali and Wootton, 1999). Abundant food leads to larger body size and so to higher fecundity (e.g. Wootton, 1973; Townsend and Wootton, 1984; Karlsen *et al.*, 1995). Wootton (1990) has speculated that small females might need to maximise egg number because their fecundity is low, whereas large females of the same species may be able to sacrifice some fecundity in order to increase the quality of their eggs in terms of mass.

Jones (1974) showed that fecundity varies nearly to the cube of the length of turbot. Van Eenennaan and Doroshov (1998) found that fecundity exhibited a significant linear relationship with fork length in the Atlantic surgeon (*Acipenser oxyrinchus*). They observed that the individual and relative fecundity for this species showed rapid increase in the early ages of reproduction followed by a dampened rate in the older fish. The relationship between fecundity and age was non-linear, with a decrease in fecundity in older fishes. In dab, the number of eggs were found not to vary directly in proportion to the cube of the length (Bakhsh, 1982). The relative fecundity increased between a 13 cm dab and 24 cm dab but declined when approaching the size of 35 cm.

ii) Fecundity and body weight relationship

Fecundity has been frequently shown to have a linear relationship with weight. Bagenal (1957a) argued that fecundity may be linearly related to body weight since the relationship of weight to length is similar to that of fecundity to length, and also weight is more closely connected with the condition and food reserve of the fish. Simpson (1951) and Lee (1972) illustrated a linear relationship between fecundity and weight in plaice and dab respectively. Other workers have found non-linear relationships between fecundity and body weight (Schopka and Hempel, 1973; Bakhsh, 1982). The coefficients 'a' and 'b' in the fecundity/weight relationship have been demonstrated to vary in plaice between 0.24 and 1.14, and between 0.98 and 1.36 respectively in the North Sea (Bagenal, 1973). Similarly for the Long rough dab, he showed that 'a' varied between 0.04 and 0.49, and 'b' between 0.79 and 1.52 in the Clyde Sea area. The different use of total body weight, somatic weight or carcass weight by different authors may be responsible for the differences in the coefficients.

iii) Fecundity and ovary weight relationship

There should be a trade-off between egg mass and fecundity as individuals have limited resources available for egg production (Roff, 1992). Factors influencing this trade-off have been discussed in recent literature (Beacham and Murray, 1993) but genetic and phenotypic plasticity appears to be involved (Fleming and Gross, 1990).

Bagenal (1957b) showed a non-linear relationship between fecundity and ovary weight in the long rough dab. He observed that the number of eggs does not increase in proportion to the weight of the gonad and therefore postulated that the heavier gonads produce fewer eggs per gram than do the lighter ones. The eggs in the bigger gonads would thus be larger and heavier. Rijnsdorp (1991) compared changes in fecundity and ovary weights for the North

Sea plaice in different locations and concluded that the relationships vary according to locations. In one area, it was found that fecundity increased by 70-100 % whereas the ovary weight increased by only 13 %. In another area, fecundity increased by 26 % whereas the ovary weight did not increase. The observed discrepancies might be due to the difference in egg size between the two areas. Again, the validity of this conclusion would very much depend on the assumption that the proportion of the connecting tissue in the ovary is constant. Bakhsh (1982) established a power relationship between fecundity and ovary weight in dab whilst Morse (1981) showed a linear relationship in the summer flounder.

Table 1.9. Data on fecundity of teleost flatfish, including oocyte diameter and relative fecundity; also fecundity versus length, body weight and ovary weight relationships

a) Variation in fecundity in some flatfish species in the North Sea (Jones, 1974)

Species		Ripe oocyte Diameter (mm)	Average Fecundity N	Body weight (g)	Relative Fecundity (N/g)
<i>Scophthalmus rhombus</i> L.		1.30	601550	1293	465
<i>Limanda limanda</i> L.		0.75	549340	131	4193
<i>Hippoglossoides platessoides</i>		1.10	81840	64	1279
<i>Pleuronectes platessa</i>	Flamborough	1.93	125480	741	169
	Southern Bight	1.93	84030	590	142
<i>Lepidorhombus whiffagonis</i>		1.43	440600	794	555
<i>Solea solea</i> L.		1.30	571340	785	728
<i>Microstomus kitt</i> (Walbaum)		1.30	411210	730	563
<i>Scophthalmus maximus</i> L.		1.02	3658740	3394	1078
<i>Glyptocephalus cynoglossus</i>		1.15	220670	244	904

b) Coefficients of fecundity/length relationships in flatfish in different localities:

Species	Author	Area	$F = a.L^b$
Dab	Bohl (1957)	North Sea	$F = 7.2783 L^{3.4525}$
Dab	Kandler and Pirwitz (1957)	North Sea (SE)	$F = 25750 (L-20.6)$
Dab	Bakhsh (1982)	Kattegat	$F = 44900 (L-20.3)$
Summer flounder	Morse (1981)	Anglesey	$F = 17.461 L^{3.263}$
		Atlantic Bight	$F = 0.045 L^{3.402}$

c) Variations in fecundity with body weight in flatfish in different localities:

Species	Author	Area	F / W relationships
Plaice	Simpson (1951)	Flamborough	$F = 169.33GW^*$ 1948/9
		Southern Bight	$F = 142.80GW^*$ 1947/8
		Southern Bight	$F = 143.33GW^*$ 1948/9
		Southern Bight	$F = 142.93GW^*$ 1947-9
		Flamborough	$F = 165.1W + 3124$
		Southern Bight	$F = 143.4W - 254$
Dab	Kandler and Pirwitz (1957)	North Sea (SE)	$F = 1364TW - 86000$
Dab	Lee (1972)	Kattegat	$F = 1751TW - 89000$
Dab	Bakhsh (1982)	North Sea	$F = 3996.17TW - 9214.83$
Dab	Bakhsh (1982)	Anglesey	$F = 3650SW^{1.006}$
Summer Flounder	Morse (1981)	Middle Atlantic Bight	$F = 3668.83TW$
			$F = 908.864W - 101867.5$

* = Lines pass through the origin
 GW = Guttled weight
 SW = Somatic weight
 TW = Total body weight
 W = Not clarified

d) Some examples of coefficients of fecundity and body weight relationship from $\ln F = \ln a + b \cdot \ln W$ in flatfish

Species	Author	Area	b	a
Turbot	Jones (1974)	1967 North Sea	0.9991	0.1406
		1969 North Sea	0.9672	-0.1016
Long rough dab	Bagenal (1957b)	North Sea	0.9234	1.1388
Solea solea L.	Millner <i>et al.</i> (1991)	North Sea	0.787	-48.85
		Eastern channel	0.787	11.48

e) Fecundity (F) and ovary weight (OV) relationship of flatfish:

Morse (1981)	Summer flounder	$F = 10998.048OV + 552515.161$
Bakhsh (1982)	Common dab	$F = 41093.28OV^{0.8312}$

1.4.7.4 Gonad maturation

Maturation can be defined as the process of gonad development leading to first spawning. The rates of gonad development and reproductive performance are important parameters for stock assessment, which may be used in the development of models for the management and restoration of depleted stocks. An understanding of the reproductive development of fish is therefore important for population management (van Eenennaam and Doroshov, 1998). Maturation is usually defined as the length ($L_{50\%}$) or age ($A_{50\%}$) at which 50 % of the fish reach maturity for the first time. Once matured, individual fish contribute to the spawning stock.

In fisheries studies, focus is mainly concentrated on the time of spawning (King, 1995). There are generally two common methods of studying the reproductive cycle and time of spawning in fish.

- b) Assessment of the gonads on pre-determined stages of maturation over time. This includes visual assessment of the appearance of the gonads, and histological methods (Nikolsky, 1963; Htun-Han, 1978b and c; Erickson *et al.*, 1985; Rijnsdorp, 1989; Johnson *et al.*, 1998; Yoneda *et al.*, 1998)
- c) Measurement of relative size of gonad over time and the gonadosomatic index (Ortega-Salas, 1980; Slotte *et al.*, 2000).

Temporal changes in the weight of gonads in mature fish can be a useful indicator of the reproductive state of the fish. The maturation stage is assessed by calculating the gonadosomatic index (GSI). The GSI expresses gonad weight as percentage of the whole body weight, (Lee, 1972 Htun-Han, 1978; Ortega-Salas, 1980; Rijnsdorp, 1989). There are in any case variations to this definition. In some cases much of the population is of uniform size, so the absolute gonad weight is used (Scott, 1979). Several workers have followed the reproductive cycle of fish using the mean monthly gonad weights (Hellawell, 1974, Huber and Bengtson, 1999). However when great variability in weight occurs within a year class, as for example in the Pleuronectidae, more analytical methods must be used. Hence the use of the carcass weight, Bakhsh (1982).

Ortega-Salas (1980) observed that in winter gonad weight was greatest for both male and female dab. Lozan (1992) estimated the GSI for five year-old female and male dab, related to whole weight prior to spawning, as 8.8 % and 2.1 % respectively. It is important to follow the seasonal development of the gonads and establish the timing of reproduction in the male and female. Ovaries and testes may be examined microscopically and classified into various developmental stage of gametogenesis. Htun-Han (1978b and c) classified maturation stages for the North Sea dab ovary and testes based on both external and histological appearances (Table 1.10). He showed that the annual reproductive cycle in dab in the North Sea can be histologically divided into four periods, namely:

Period	Female	Male
Pre-spawning	Oct-Jan	Sep-Nov
Spawning	Feb-Apr	Dec-Mar
Post-spawning	May-Jun	Apr-May
Resting	Jul-Sep	Jun-Aug

He noted a gradual increase (recrudescence) in the GSI in the prespawning period, reaching a peak in the spawning period. There was a gradual decline in the GSI value in the postspawning period and a relatively stable value in the resting period. The marked increase in weight of the ovary during the spawning period has been attributed to the intake of fluids by the fully ripe ovaries (Stages V and VI), which result in their swelling and becoming hyaline.

Histological assessment of gonads is now commonly used for maturation studies due to the detailed information it reveals on spermatogenesis, oogenesis and also changes in the supporting tissue. The developmental stages of the dab ovaries and testes were classified histologically by Htun-Han (1978b and c) into 6 and 5 stages respectively. The investigation shows that gonad development in the dab reached a peak in February-March, with a short and precise spawning season. The duration of the spawning season was observed to be around 6 weeks, which also agreed with that found by Lee (1972) for dab in the North Sea. Bakhsh (1982) assessed the maturation cycle for dab in Anglesey waters using the scale of Lee (1972) and also by histological methods. Bakhsh (1982) found that females undergoing pre-spawning maturation began to appear in the population from November and became more common until December and January. Females in ripe condition were present up to May. The pre-spawning period in males begins early in September and were in ripe condition between February and March.

Table 1.10. Macroscopic and microscopic characteristics of each stage of development in the dab gonad, from Htun-Han (1978b and c)

(a) Ovary

Spawning periods	Maturity stage	External appearance	Histological appearance
	Immature	Small, slender and conical; each ovary is pinkish and translucent, enveloped in a coat of silvery epithelium and has a maximum length of 15 mm	Maturity stage I and II oocytes, few larger than 70 μm ; oocytes have densely staining cytoplasm without vacuoles; the ovarian wall is about 30 μm thick.
Resting	Developing immature/resting matures	Larger, reddish and translucent	Stage II oocytes predominate, but stage III, which are larger and have cytoplasmic vacuoles, are beginning to appear; oocytes up to 150 μm ; the ovarian wall is about 50 μm thick.
Pre-spawning	Developing	Pink, full, completely opaque and sometimes appears granular from effect of developing eggs showing through ovarian wall; vascularization slight	Mainly stage III present, but stage IV oocytes (with small yolk droplets and vesicles) and a few stage V (with densely-staining yolk granules) are beginning to appear; oocytes up to 250 μm ; the ovarian wall is about 150-200 μm thick
Spawning	Ripe and/or running	Ripe or running with eggs; most of the eggs are translucent and some may be completely transparent (Hyaline), producing a speckled appearance; ovary is full and vascularization is heavy; eggs run from vent on slight pressure	Stage V and VI (Hyaline) oocytes predominate; latter are irregular in shape (due to Histological process) and are up to 700 μm in diameter; in a running fish, hyaline oocytes are present in lumen; the ovarian wall is thinner (100-150 μm) probably due to distension of ovary
Post-spawning	Partly spent	Partly spent and may appear flabby; eggs, which may be opaque or translucent, give ovary a granular appearance; vascularization heavy	Few hyaline oocytes remain; conspicuous spaces (empty follicles) present in septa; the ovarian wall is about 200-250 μm thick
Post-spawning	Spent	Fully spent and resembling an empty bag; a few eggs may be still seen through translucent wall	Oocytes of all stages are present, but stage I and II, predominate; atretic follicles in various stages of absorption are evident; the ovarian wall is up to 400 μm

(b) Testis

Spawning periods	Maturity stage	External appearance	Histological appearance
	Immature	Barely visible as a thin filament, adhering closely to the rear wall of the abdominal cavity	Only spermatogonia (Stage I, each up to 12 μm in diameter with a nucleus of about 7 μm) are present either singly or in small groups; the testicular wall is about 5 μm in thickness
Resting	Developing immature/resting mature	Pink, translucent and has developed from immature stage; if traces of spermatozoa are found in the vas deferens, the fish probably has spawned in the immediately preceding season and the testes is at the start of another cycle	Larger stage I cells present in nests around the periphery of the testes; the bulk of testes made up of smaller stage I and primary spermatocytes (Stage II, each up to 8 μm in diameter with a nucleus of about 5 μm); the testicular wall is about 10 μm in thickness
Pre-spawning	Developing	Not distinctly lobed, white, opaque and large compared to above stage; vas deferens filled with spermatozoa to varying degrees but none exuded on applying slight pressure to flanks	Secondary spermatocytes (Stage III, small, dense and irregular in shape, about 4 μm) and spermatids (Stage IV, cup-shaped like spermatozoa but without tails) predominate; a few ripe spermatozoa (Stage V) present but are attached to lobular wall; the testicular wall is about 15 μm in thickness.
Spawning	Ripe and/or running	Distinctively lobed, white, flat and soft to the touch; if running ripe, spermatozoa runs out of genital pore on slight pressure to flanks	Some stage IV present, but mainly consists of ripe spermatozoa, active and unattached, in the lumen and vas deferens; the testicular wall is about 10 μm in thickness
Post-spawning	Partly spent	Appears thin, flabby and reddish; vas deferens generally empty and but there may be a little residual milt	Lumen of testis looks unfilled; a few inactive spermatozoa left; many stage I nests present in periphery of testis; the testicular wall is about 30 μm in thickness
Post-spawning	Spent	Same as in partly spent condition	Same as in partly spent condition

1.4.7.5 Age and size at maturity

An important parameter in fish population studies is the age and length at which the fish matures for the first time. The knowledge of this parameter is useful in the regulation of the fishery mainly from the point of view of mesh size restriction, size limits and closed areas. There are however spatial, annual and sexual fluctuations in this parameter (Table 1.11).

Rijnsdorp *et al.* (1992) reported that male dab become sexually mature at 2 years of age and at length 11 cm whilst the female matures between 2-3 years and length 14 cm in the south eastern North Sea. Earlier studies in the North Sea by Bohl (1957) showed that almost all the male dab and about 67 % of the females are mature before the fish are three years old. The smallest observed mature male and female lengths were 10.5 and 11.5 cm respectively. In the Baltic Sea the males are mature at 2 years and females at 3 years (Jonsson, 1966). Deniel (1990) estimated the length and age at first maturity for plaice and dab on the West Coast of Brittany as 40 cm and 4 years for plaice, and 27 cm and 3 years for dab. In Anglesey waters, the female dabs reach sexual maturity at lengths of no less than 13 cm and the males no less than 11 cm (Bakhsh, 1982). The age and length at 50 % maturity were also lower in male (0.86 years, 12.2 cm) than female dabs (3.06 years, 19.0 cm). In the Isle of Man and the North Sea, the age at first maturity in these areas for females is 2-3 years and 2.0-2.6 years respectively and the values for the males were 1-2 years and 1.4-1.9 years respectively (Lee, 1972; Ortega-Salas, 1980). Lozan (1992) observed that in the German Bight, dab reach sexual maturity at 10.3 cm and 1.9 years in males, and at 13.8 cm and 2.2 years in females. In Icelandic dab, males reach maturity at 2 years whilst females mature at 3-4 years. The smallest mature male was 13 cm long and the smallest mature female was 16 cm (Jonsson, 1966).

Rijnsdorp (1989) demonstrated that, in the North Sea, male plaice reached sexual maturity over a range of length between 15 and 30 cm, with 50 % reaching maturity at a length of 21.9 cm. Females attained maturity at a range of length between 31.6 and 37.2 cm, with 50 % reaching at a length of 33.9 cm. The majority of the female plaice become sexually mature as IV- and V-group. The youngest sexually mature females were of age group II. Differences were observed in the age at which plaice become sexually mature between year classes and between areas. The length and age at 50 % differed between geographical areas, increasing from south to north in the North Sea. Annual differences in $L_{50\%}$ and $A_{50\%}$ were related to annual differences in growth rate. Rijnsdorp (1989) also observed that plaice now reach sexual maturity about two to three years younger and also at a smaller size than at the beginning of the 20th century. Stearns and Crandall (1984) interpreted the variability in length

and age at maturity as a reflection of the plasticity of the reproductive strategy of fish in response to environmental stress. Seyhan (1990) showed that age at 50% maturity of male plaice in Anglesey waters has decreased from 5.06 yrs in 1970-75 to 3.0 yrs in 1987-1990. He also showed that the length at 50% maturity has declined from 22.75 cm in 1970-1975 to 19.6 cm in 1987-1990. Chuenpagdee (1990) also found a reduction in the age and length at 50 % maturity in the female between 1972-1990 on the North Wales Coast.

Table 1.11.

a) Length at 50 % maturity of the North Sea plaice (Rijnsdorp, 1989)

Areas	Male		Female	
	L _{50%} (cm)	95% C.L (cm)	L _{50%} (cm)	95% C.L (cm)
A+B	19.8	18.9-20.7	34.0	32.5-35.5
C+D	21.6	20.0-22.2	32.8	31.9-33.7
E	24.2	23.1-25.3	35.9	34.7-37.2
Average	21.9	21.1-22.7	33.9	32.6-35.2

A+B = Southern North Sea
 C+D = Central North Sea
 E = Northern

b) Age and length at 50 % maturity of male plaice in Anglesey waters (Seyhan, 1990)

Years	Age at 50 % (yr.)	Years	Length at 50 % (cm)
1970-75	5.06	1970-79	22.75
1989-90	2.1	1981-83	27.0
1977-78	3.0	1984-86	23.7
1981-83	3.0	1987-90	19.6

c) Age and length at 50 % maturity of female plaice in Anglesey waters (Chuenpagdee, 1990)

Years	Age at 50 % (yr.)	Length at 50 % (cm)
1972		29.05
1975	2.28	26.78
1978	3.99	27.27
1979	2.01	25.70
1981	1.88	24.18
1983	1.93	24.88
1984	1.48	22.56
1985	2.37	26.05
1986	1.56	25.14
1987	1.26	23.01
1988	2.06	27.11
1989	1.56	23.80
1990	2.40	23.66

d)

i) Age ($A_{50\%}$) and length ($L_{50\%}$) at 50 % maturity of dab in different localities

Sex	$A_{50\%}$ (yr.)	$L_{50\%}$ (cm)	Locality	Author
Male	0.86	12.2	Anglesey	Bakhsh (1982)
Female	3.06	19.0	"	"
All	3.0	27.0	Brittany	Deniel (1990)

ii)

Age (A) and length (L) at first maturity of dab different localities

	A (yr.)	L(cm)		
Male	1.9	10.3	North Sea	Lozan (1992)
Female	2.2	13.8	"	"
Male	2	13	Iceland	Jonsson (1966)
Female	3-4	16	"	"

1.4.8 Feeding ecology

1.4.8.1 Diet composition

Food is one of the important factors linked to fish abundance, growth and migration and information on this subject will contribute to the knowledge needed for optimum management of fish stocks. The composition of the stomach contents of a fish is indicative of the ecological niche occupied as well as its selective feeding habits, provided the composition of food is known from sampling. In addition, stomach contents may indicate the relative abundance of prey species, and to an extent, the vulnerability of each prey species to predation (Jobling, 1974). Stomach content studies are thus important in revealing interspecific and intraspecific feeding relationships between coexisting species and within a species respectively (Macer, 1967; Tyler, 1972; Basimi and Grove, 1985b; Carter, 1987; Carter *et al.*, 1991; Hoinés and Bergstad, 1999). The interrelationship between fish species is important when assessing the effects of fisheries or introducing measures for the conservation of stocks. As a consequence of competition or predator-prey relationships, conservation policy for one species may have adverse effects on other commercially important species (Gulland, 1968; Daan, 1973).

The diet of dab has been intensively investigated by earlier workers like Macer (1967), Edwards and Steele (1968), Braber and de Groot (1973) and Jobling (1974). Dab have been frequently portrayed as being a voracious and opportunistic feeder (Kaiser and Ramsey, 1997). They have well-developed eyes and are visual benthic feeders confined to food

organisms found in, on or just above the seabed (Wyche and Shackley, 1986). In Anglesey waters, dabs up to 5 cm are found to feed exclusively on crustaceans (mysids and copepods). Polychaetes are increasingly taken when they reach 6-7 cm long, eventually forming the bulk of the diet in their adult stage (Gywther, 1978). Carter (1987) concluded that dab had a more diverse diet but that the majority of the prey species were polychaetes or crustaceans. In Red Wharf Bay, the larger dab were found to eat mainly *Lagis* (= *Pectinaria*) *koreni*) while the smaller sized fish ate more varied diets which include crustaceans and echinoderms (Carter *et al.*, 1991). This trend is generally similar to the diet composition of the North Sea dab where Braber and de Groot (1973) noted that the most important food items as being crustaceans, polychaetes and a variety of other organisms including bryozoans, hydroids, siphons of molluscs, echinoderms and fish. In the North Sea, the juveniles fed more exclusively on small polychaetes and gammarids.

The diet composition and population of the juvenile stages of dab and plaice have been thoroughly investigated in various waters (Macer, 1967; Edward and Steel, 1968; Arntz, 1971; Nash *et al.*, 1992 and 1994a and 1994b; Ellis and Gibson, 1995; Bels and Davenport, 1996). Edwards and Steele (1968) studied the population of 0-group plaice and common dab in the Loch Ewe Bay, Scotland and found that the food of the two species overlap to some extent but were quantitatively different. They attributed the interaction between the two species to the change in diet of plaice from *Angulus* (= *Tellina*) siphons to *Magelona* tentacles (polychaete) in years when the abundance of the *Angulus* population has declined. Normally the tentacles of the *Magelona* formed a major source of food for the dab population in the Bay. Edwards and Steele pointed out that the plaice and dab in this Bay feed mainly on siphons and tentacles bitten off bivalves and polychaetes respectively, and later, as they get bigger, the food changes to whole polychaetes, amphipods and crustaceans. This initial period of feeding on regenerative appendages is important since at this time the fish populations are numerically much larger than later, when they will have been greatly reduced by predation. Macer (1967) also found that both the 0- and 1-groups of plaice and dab have similar diet in which polychaetes predominate, although amphipods, lamellibranchs and copepods were also important. From this analysis, these early stages of these species seem to have similar feeding habits. Detailed investigations also found that whole adult worms occur more often in the older fish than in the younger ones. The predominant polychaetes in dab diet were *Phyllodoce* and *Lagis* sp. whereas in the plaice, *Nephtys* spp. was the predominant species.

Similar diet composition in the dab was also reported by Jobling (1974), Table 1.12, in Anglesey waters. The diet consisted mainly of coastal benthic invertebrates, particularly

molluscs, polychaetes and crustaceans and there was a shift in diet composition with the size of the dab. He noted that the juvenile dab feeds upon nereid polychaetes and bivalve siphons, smaller *Crangon spp.*, whereas the larger dab take larger polychaetes such as *Arenicola spp.* and *Lanice spp.*, larger crustaceans and echinoderms, including *Ophiothrix spp* and *Echinocardium spp.*, there being a reduced dependence on bivalve siphons as a food source. Fish were also identified in the stomach of the adult dab. It was found that the bivalves, that is the siphons of *Donax spp* and *Ensis spp*, were preferred by the middle sized fish, and that the entire shells of *Angulus* and *Donax spp.* were present in the stomachs of the large fish. Complete bivalve shells were also identified in the rectum, which indicated that the jaw apparatus of the dab is not sufficient to crush the shells of the molluscs. The most frequently occurring crustaceans were *Crangon spp.* and *Portunus spp.* whilst *Carcinus spp.* predominated in the summer collection.

Studies of diet composition of dab in the Kiel Bay by Arntz (1971) showed that the polychaetes (31.1 %), crustaceans (26.3 %) and molluscs (23.7 %) were the most abundant in the diet followed by fish (11.3 %), echinoderms (3.7 %) and others (3.9 %). The diet composition of the dab population in this Bay also changes with increasing size of the fish. It was however found that this change was less pronounced in regions with low food supply than in areas with more plentiful food. Distinct annual seasonal variation in gut contents with regard to the different benthos groups was also noted. The annual cycle of the benthos biomass corresponded with the gut contents of the dab. Studies on diurnal rhythm of food intake showed that the Kiel Bay dab feed during the daytime and that feeding did not cease entirely at any season.

Sexual dimorphism in food intake was studied in the common dab from the south-eastern North Sea by Lozan (1992) and in the German Bight by Temming and Hammer (1994). The results show that the food intake of females was significantly higher than that of the males. In a tank experiment, Lozan (1992) showed that 20-cm long females consumed 73 % more food than similar sized males. Also from trawl catches, it was also found that the food intake of females was significantly higher than that of males of an equal length from the same fishing ground. Lozan found that the females have a significantly larger digestive tract than males of an equal body weight. In a 24-hour feeding study during winter, Temming and Hammer (1994) found that the female dab had significantly more food in the stomachs than males of the same size.

Ortega-Salas (1988c) observed that the food items more frequently found in the stomach of dab are those considered to be more abundant in the area rather than being of food

preference. The average weight of the digestive tract (the gut and its contents) showed that dab feeds more in summer than in winter and this reflected the growth rate between these two periods. A sequence of trawl surveys off eastern Anglesey showed that the diet of plaice was dominated by the bivalve *Abra alba* in spring and summer, and *Lagis koreni* in early spring and autumn (Basimi and Grove, 1985b) and the study also revealed that the plaice ate little food in winter. In addition, it was found that during scarcity of the preferred species (polychaetes or molluscs) in the benthos, the diet of plaice is switched to either crustaceans or echinoderms. Bels and Davenport (1996) noted that adult plaice are a more specialised feeder (on sedentary molluscs) than the dab, which feeds on any invertebrate (sedentary or mobile) that is locally common. Both species, as young animals, are often found on the same grounds, consuming similar small invertebrate prey (crustaceans, worms and young molluscs), a pattern similar to that reported by other workers above.

Tables 1.12 and 1.13 shows typical diet composition of dab and plaice from waters in North Wales and South Wales, UK.

Table 1.12. Food type and frequency of occurrence (%) of food organism in the stomachs of dab in Anglesey waters (Jobling, 1974)

Month/Year	Length Groups				
	> 11 cm	11-15.9 cm	16-20.9 cm	21-25.9 cm	≥ 26 cm
<u>October 1973</u>					
Bivalves	100	87.5	38.25	36.7	16.7
Crustaceans			26.25	33.3	16.7
Echinoderms			23.25	23.3	50
Detritus		12.5	12.25	6.7	16.5
<u>December 1973</u>					
Bivalves		50	33.7	19.6	23.4
Crustaceans			4.6	4.9	10
Polychaetes		30	21		
Echinoderms		10	40.3	59.8	43
Detritus		10	0.4	15.7	23.6
<u>February 1974</u>					
Bivalves	33	12.5		25	
Crustaceans	17	12.5			40
Polychaetes	50	50	50		
Echinoderms		25		25	60
Hydroids			50	25	
Detritus				25	
<u>Aug/Sep 1974</u>					
Bivalves		44.4	22.2		
Crustaceans		50	27.8	44.5	
Polychaetes		50	16.7		
Echinoderms			11.1	22.5	
Fish				11.1	

Table 1.13. Percentage occurrence of prey species in the gut content of plaice and dab (20-29 cm long) in April, June and October 1986 in Carmarthen Bay, South Wales, (Wyche and Shackley, 1986).

Prey	Age	April		June		October	
		Plaice (I-II)	Dab (I-IV)	Plaice (I-II)	Dab (I-IV)	Plaice (I-III)	dab (I-III)
<i>Abra alba</i>		8	0	12	10	49	47
Razor shells		15	66	18	17	4	1
Other bivalves		46	10	29	31	28	19
<i>Philine aperta</i>		0	0	5	12	2	2
<i>Lagis koreni</i>		23	0	35	7	8	7
Other polychaetes		23	14	8	10	11	8
<i>Amphiura brachiata</i>		15	10	18	24	9	5
<i>Ophiura texturata</i>		0	7	3	7	0	1
Hydroids		15	28	3	5	6	24
Amphipods		0	3	0	0	4	18
Crabs		0	3	9	5	0	2
Fish		0	17	3	5	6	3
Debris (sand, stone, etc.)		31	24	0	0	4	11

1.4.8.2 Food resource overlap

Studies on the natural diets of fishes normally indicate that the variety of prey found in stomachs very often show that fish are generalist feeders. Investigations into the feeding ecology of fish communities suggest that fishes have overlapping feeding niches only when food resources are superabundant and that niches are rather discrete when food abundance becomes reduced (Keast, 1965; Nilsson, 1967; Zaret and Rand, 1971; Specziar *et al.*, (1997). Sala and Ballesteros (1997) noted that the co-existence of similar species within the same ecosystem may occur owing to different resource use.

Resource partitioning includes food, habitat and/or time segregation (Schoener, 1974) and has been extensively documented among fishes (Ebeling and Laur, 1986 and Holbrook and Schmitt, 1986). However, food segregation seems to play a more important role than habitat or temporal separations within many fish assemblages (Ross, 1986). Carter *et al.* (1991) illustrated resource partitioning between plaice and dab in Anglesey waters and suggested that the observed patterns were due to the abundance of prey species which vary spatially and seasonally. The interspecific trophic overlap values between plaice and dab were lower in Red Wharf Bay (0.640) than in Conwy Bay (0.948). Carter *et al.* suggested that the reason might be due to the observation that the large and small *Pectinaria koreni* were separated into size categories in Red Wharf Bay in July. In the offshore area, interspecific overlap was extremely low (0.047) which indicates that the diet of the two species were completely different. The intra-specific overlaps in diets between different size categories of plaice or dab also suggested that, generally, the highest similarities were found in similar sized fish.

Horpilla *et al.* (2000) noted that competition between or within fish populations may lead to spatial segregation between the competing groups. They observed that for perch (*Perca fluviatilis L.*) and roach (*Rutilus rutilus L.*) populations in Lake Vesijarvi, Finland, as the number of preferred, large prey items in the littoral are reduced, the species better adapted in utilising smaller prey items often shifts into the open-water habitat. The species less efficient in consuming small food items may have no profit from habitat switching by following the superior competitor (Werner and Hall, 1979).

1.4.8.3 Gastric evacuation rate and food consumption studies

The modern approach to fisheries management by ecosystem modelling has prompted interest in understanding the role of fish predators within an ecosystem, which has involved the determination of feeding habits and daily ration of major commercially exploited fish species. The studies have mainly involved understanding the process of digestion and undertaking field observations of stomach contents so that daily food intake of natural populations and their effects on prey can be estimated (Daan, 1973; Swenson and Smith 1973; Elliot and Persson, 1978; Gwyther and Grove, 1981; Jobling, 1981; Majkowski and Hearn, 1984; Basimi and Grove, 1985b; Sutela and Huusko, 1997). The daily food ration has become an important component of fisheries models of individual species and groups of species (Gulland, 1970; Anderson and Ursin, 1977; Laevastu and Favorite, 1977, Sainsbury, 1986). Daily ration can influence the amount of energy available for growth in fish and also determine the effects of predator populations on the dynamics of prey and competitor populations.

Three methods have been generally used to estimate the daily food ration of fish:

- a) Laboratory experiments to measure directly the quantity of food consumed by fish and relate this to fish feeding in its natural environment (Elliott, 1972; Gwyther and Grove, 1981; Jobling, 1982; Smagula and Adelma, 1982; Basimi and Grove, 1985b).

- b) Daily ration has also been derived from total energy requirements of the fish. This method requires field measurement of growth rate and laboratory measurements of the energy added as growth, utilised by metabolism and lost through faeces and excretion (Grosslein *et al.*, 1980 and Kerr, 1982).

c) Food consumption has also been estimated from the quantity of food present in the stomach in the wild and in combination with the rate of gastric evacuation (Elliott and Persson, 1978; Gwyther, 1978; Pennington, 1985; Sainsbury, 1986; Temming and Hammer, 1994; Seyhan and Grove, 1998). Food consumption is estimated for short time intervals and the total food consumed during the 24 hr feeding cycle is obtained by summing all positive consumption estimates (Durbin *et al.*, 1983). The rate of gastric evacuation may be determined from field stomach content data (Gwyther, 1978; Seyhan, 1994) or by laboratory studies.

Sainsbury (1986) criticised methods which involved force feeding of experimental animals on the grounds that gastric evacuation rate may be underestimated. Jobling (1981) has given a detailed review of the mathematical models of estimating gastric emptying rates and feeding rates in fish. Bajkov (1935) and Daan (1973) were among the first early workers who developed models for the estimation of food consumption by fish in the wild. The main drawback about the Bajkov model was that it did not include the variable component of gastric evacuation rate. The basic assumption in commonly used methods is that food consumption is directly related to gastric capacity and thus equations for estimation of food consumption incorporate a term for gastric evacuation rate. Thorpe (1977) had noted that estimates of daily food ration which do not take into account periodicity of feeding or field rates of gastric evacuation must be misleading. Daan's (1973) model requires an estimate of the time required for complete evacuation of all food from the stomach and this is often difficult to measure.

Several studies have demonstrated that the relationship between the amount of food from a meal remaining in the stomach and time is curvilinear, rather than linear, and a number of workers have fitted their data to an exponential model (Brett and Higgs, 1970; Elliott, 1972). The models of Thorpe (1977) and Elliott and Persson (1978) for the estimation of daily food consumption of fish incorporate the assumption that the rate of gastric evacuation is exponential.

The Elliott and Persson (1978) model has been commonly used in the estimation of daily food consumption of fish in the wild (Durbin *et al.*, 1983; Sainsbury, 1986). In this model, the food consumption of wild population of fish is usually estimated from analysis of stomach contents of fish sampled at various times of the day. Gastric emptying rate together with sequential observations of stomach contents are used to estimate food intake. The following is the Elliott and Persson (1978) model:

$$C_t = \frac{(S_t - S_0 e^{-Rt})Rt}{1 - e^{-Rt}} \text{-----} (15)$$

where C_t = Food consumption at time t

S_0 = amount of food in the stomach at time t_0

S_t = amount of food in the stomach at time t

R = instantaneous gastric evacuation rate

The sampling procedure involves collecting a sample of fish at intervals of t hours for at least 24 hours. The mean stomach content weight is used to estimate S_0 and S_t for each time interval. The estimates of C_t are calculated for each time interval. These estimates (positive values) are then summed to give the total daily ration. The method assumes that:

- a) The fish feeds continuously at a constant rate within a stated period (t_0 to t_1)
- b) The cumulative amount of food consumed (C_t) therefore increases linearly during time t . Gastric evacuation rate is assumed to be exponential i.e. a constant proportion of stomach content is evacuated per unit time, and unaffected by fish size, meal size and the frequency of feeding.
- c) Gastric evacuation is assumed to begin immediately after the food is ingested, without an appreciable time lag
- d) It is also assumed that the collection of samples at short intervals should ensure that the estimates of C_t would not be seriously biased in case the assumption of continuous feeding within each period does not hold.

Basimi and Grove (1985b) derived a power model for food intake in plaice. They calculated how much of the food (S_1) present at the start should remain at the end of t hours (S_t). If this is subtracted from the observed contents at the end of the period (S_2), the residuum represents the food ingested during the short period. It was assumed that none of the new prey can undergo any digestion within the interval. Food intake (C_t) is thus given by:

$$C_t = S_2 - (S_1^b - Rt)^{1/b} \text{-----} (1.6)$$

Fange and Grove (1979) hypothesized that when fish are fed meals of a given percentage body weight, gastric evacuation time should increase in proportion to fish size to the power b (=0.33). Also, Gwyther and Grove (1981) showed that at a given temperature, gastric evacuation time (GET) of the stomach contents in dab of different weights fed to the same relative level (% bw) will vary as:

$$GET = RW^b \text{ ----- (1.7)}$$

Where b =0.33

W =Fish weight

R = Rate of gastric evacuation

1.5 Aims of present study

Chapter 2

This chapter would include the estimation of the local population abundance of dab, by size class and age, including seasonal variation and diel periodicity in catch rates. Seasonal variation in sex ratio will also be investigated. Studies on meristic counts and body proportions, including seasonal studies on length and weight relationships will be undertaken.

Chapter 3

This chapter would set out to describe growth in length and weight of dab on seasonal bases. The Von Bertalanffy Growth Model would be fitted to the observed length-at-age data by non-linear least square iterative methods. Seasonal patterns in the deposition of opaque and hyaline zones at the edge of the otolith would be followed on a monthly basis in order to determine the season of growth. Also established is the coefficient of instantaneous rate of total mortality in the male and female dab.

Chapter 4

The aim of this chapter would be to describe the reproductive biology of dab, including (a) visual and histological assessments of gonad developmental stages (b) spawning time (c) length and age at maturity (d) fecundity and (e) the annual cycle of condition, including

changes in the ovary and liver weight. An attempt is made to estimate total egg population in the survey area. Egg-size frequency distribution of various maturity stages and seasonal changes in oocyte size would also be investigated. Long-term length and age at maturity from the historical data would be estimated for both male and female dab.

Chapter 5

This chapter would seek to describe the present composition of diet of dab in the study area, based on size-specific studies. Attempts will be made to describe quantitatively intra-specific diet overlap between various size groups of dab on a seasonal basis and to study diet diversity, breadth and evenness in various size groups of dab. Sex-specific seasonal index of food ingestion (Stomach-Gut Index) is undertaken to assess feeding rate on a monthly basis. From 24-hour fishing surveys, the sex-specific and size-specific rates of gastric evacuation and food intake would be determined on seasonal bases. The study of the composition and abundance of benthic organisms in the study area will be undertaken to relate this to the diet composition of dab.

Chapter 6

This chapter will attempt to investigate the annual cyclical changes in the lipid, energy and ash composition of the gonad, liver and carcass using average 20 cm male and female dabs as examples. The metabolic energy requirements of the fish will be estimated and the possible sources of utilisable energy to meet its routine energy requirement calculated. Energy composition of some common prey items will be investigated, including ash composition of the ingested food from the stomach and intestinal regions of the alimentary canal.

Chapter 7

The findings and conclusion of the present investigation will be summarized in this chapter, including discussion on constraints and suggestions for future research.

CHAPTER TWO

The Local Population of *Limanda limanda* (L.): Population Size and Stock Identity

2.1 INTRODUCTION

In fish stock assessment, perhaps the most fundamental method is the biomass survey by trawling, which can provide an indicator of fish abundance (Charles, 2001). The estimation of the stock size of a given species (or group of species) in a given area is an essential component of fish population assessment. The most common methods are the trawl survey and hydro-acoustic methods. The bottom trawl survey (so called 'Swept Area Method') is mainly used to monitor the relative abundance of many groundfish stocks (demersal species) like cod, haddock, plaice and dab whilst the acoustic method is mainly suitable for pelagic species like herring, mackerel and sprat (Maclennan, 1990; Barange *et al.*, 1999; Hedgepeth *et al.*, 1999). The basic assumption in trawl survey methodology adapted here is that the mean catch per unit of trawled area is proportional to the stock abundance. This index of stock abundance can be converted into an absolute value by the 'swept area method' (Gulland, 1975; Sparre and Venema, 1998). A towed net samples fish in an area, which is equivalent to a long rectangular sampling unit. A trawl unit is used to estimate the mean catch at a number of trawl stations in a fish stock; the mean catch per area swept by the trawl is multiplied by the stock area to estimate the stock size or more usually the total stock weight or biomass (King, 1995). But abundance indices from these surveys often contain year effects, i.e. fluctuation in the abundance of most cohorts in one year compared to the estimates in neighbouring years (Smith and Page, 1996; Swain *et al.*, 2000).

The population numbers of dab, plaice and whiting in the survey area in previous decades have been estimated by Bakhsh (1982), Grove and Basimi (1985a) and Seyhan (1994) respectively, using the Area Density method of Everhart *et al.* (1953). This method was therefore used, for direct comparison, to estimate the current population number and biomass in this study.

2.2 MATERIALS AND METHODS

2.2.1 Study area and sampling method

For this method it is necessary to estimate the area covered during each haul. In this regard, the following was recorded:

- (i) The distance covered during the hauls was obtained from the speed of the ship and time and cross-checked with navigation positions in the ship log.
- ii) The width of each trawl was estimated as the distance between the trawl doors during fishing. The distance between the trawl doors in the School of Ocean Sciences' Research Vessels 'Prince Madog' is 31 metres (Basimi and Grove, 1985a).
- iii) The area swept is estimated from the distance trawled (speed and time) and the width of the trawled area.
- iv) The catch per unit area trawled is extrapolated to the total catch of the survey area.

The area covered in the present study is in Red Wharf Bay, Conwy Bay and the Offshore grounds on the North Wales Coast of the Eastern Irish Sea. The total survey area was estimated as about 656 Km² (Bakhsh, 1982). Seasonal dab samples were obtained from RV *Prince Madog*, University of Wales, Bangor. The vessel is 94 ft (28.4 m) long with a GRT of 182 tons. The trawl has a codend mesh size of 2.9 inches (73 mm).

Each haul was approximately of one-hour duration at a speed of about 3 knots. The samples were sorted out onboard, the length frequency of the dab was recorded in 1 cm class-intervals and a stratified subsample (chosen by length) (Henderson *et al.*, 1996 and Seyhan and Grove, 1998;) was taken for detailed analysis, including construction of the Age Length Frequency key (ALFK). Biased sampling is reduced by stratified length sampling of the catch (Henderson *et al.*, 1996). Random sampling would more often select only the most common size groups and miss out the youngest and oldest size groups which may be very small in the samples. Samples were also obtained from the commercial fishing boats in the survey area.

In the laboratory, the following measurements were made on each fish:

- a) Measurement of length and weight
- b) Measurement of head length and body depth
- c) Counting of dorsal, anal, caudal fin rays and vertebrae
- d) Removing the gonads, determining the sex, weigh the gonads

- e) Remove the gut, weigh and freeze it
- f) Remove the liver, weigh and freeze it
- g) Weigh the carcass and preserve
- h) Remove the otoliths and keep in a sealed, labelled envelope

The length/weight equation can be converted into a linear equation by log transformation of the length and weight data. Ordinary linear regression has commonly been used to estimate the regression coefficients. However, there have been criticisms of the use of linear regression to estimate the parameters of length and weight relationships (Ricker, 1973; Pauly, 1984; Basimi and Grove, 1985a) since both length and weight can vary randomly and neither is an independent variable. The linear regression technique may thus result in biased estimates (Pitcher and Hart, 1982). Thus non-linear least square method is presently used frequently to fit the length and weight data, which does not assume any causal relationship. The fitting is easily carried out iteratively on a computer with appropriate software.

For individual studies on length and weight relationship on subsamples, the total length was measured to 0.1 cm. Weight of individual fish and the carcass was measured on a *Mettler PC 24* balance to the nearest g. Weight of the liver and gonad was measured on the analytical balance *Ohaus Analytical Plus* to the nearest mg. This material was therefore available for studies described in latter chapters following the present one.

The University (School of Ocean Sciences, Bangor) conducts regular fisheries surveys in the study area. Data from these surveys date back as far as the 1960's. These data include abundance and trawl information, length and age composition, maturity, sex ratio and length/weight relationship of dab. The data have been collected in a consistent manner using the same research vessel and trawl specifications. Also, the techniques used in the treatment of the samples (e.g. subsampling procedure, length and weight measurement, determination of maturity and otolith reading) have not changed over the years. These data are currently held in the directory (M:\surveys\dab.web) of Dr. Grove. They are however being presently organised in a user-friendly format for availability on the University N: drive. These historical data were also analysed in order to put the current investigation into context.

2.2.2 Population size

Samples obtained from research surveys were used in deriving estimates of population size. Measurement of total catch on board was carried out. Then 3 or 4 fish per each cm length group were selected (length stratified subsamples) for further laboratory analysis. In the laboratory, each fish in the subsample was weighed, length measured to the nearest 0.1 cm,

determine the sex and also the age by reading the otolith. Thus for each month, using the aged length stratified subsample, an age/length matrix of total population by sex was obtained (Appendix 1).

The average population size (N) by length and age was calculated using the area-density method of *Everhart et al.*, (1953):

$$N = \frac{A}{a} \sum_{i=1}^a N_i \text{-----} (2.1)$$

Where:

- A = total survey area = 656 Km²
- a = area swept per trawl
- N_i = number of fish in the ith sample

The variance of the estimate is given by:

$$V = \frac{A^2 - aA}{a} \left[\frac{a \sum_{i=1}^a N_i^2 - \left(\sum_{i=1}^a N_i \right)^2}{a(a-1)} \right] \text{-----} (2.2)$$

The standard error is:

$$\frac{\sqrt[3]{V}}{\sqrt[3]{N}} \text{-----} (2.3)$$

The estimated number at length was converted to weight at length using the length/weight relationship. The number at age was converted to the weight at age (W_t) using the length/weight relationship in combination with the Von Bertalanffy growth function:

$$W_t = a \left(L_\infty (1 - e^{-K(t-t_0)}) \right)^b \text{-----} (2.4)$$

Where a and b = fitted constants of the length/weight data (See below)

L_∞, K and t₀ = parameters of the Von Bertalanffy equation (See Chapter 3)

2.2.3 Meristic and morphometric studies

The head length was measured from the tip of the mouth to the farthest posterior margin of the right operculum. The deepest part of the body from the base of the dorsal fin to the base of the anal fin was taken as the body depth. The measurements were taken with a divider and an electronic vernier-sliding calliper to the nearest 0.1 cm. The dorsal, anal and caudal fins and the vertebrae were counted using a hand held counter. The vertebrae were counted including the urostyle. The fish was carefully filleted dorsally to expose the skeleton. The results were complemented by X-ray photography.

The length and weight relationships for a range of fish sizes were fitted by non-linear least square iterative method (Microsoft Origin 5.0) since both length and weight are considered as dependent variables.

2.2.4 The X-ray technique and the film processing protocol

A portable X-Ray machine (Model: PRI 10/III) was used. The objects (dead fish) were placed on a cassette (AGFA) containing a screen (Curix Blue C2) and film (Curix RP1 Plus 100 NIF or Curix Blue HC-S Plus 100 NIF, 18 x 24 cm) 30-31 cm from the X-ray source. Exposure times 0.2-0.3 seconds produced satisfactory images of the skeleton. Films were developed as follows:

- i. G150 Agfa developer (1.1 litre diluted in 5.6 litre distilled water). Immersion and agitation time 50 sec to 60 sec under red light
- ii. Kodak Max Stop Bath Solution (1.3 litre diluted in 5.4 litre of distilled water). Immersion and agitation time 15 sec under red light
- iii. Agfa G350 fixer solution (1.3 litre diluted in 5.4 litre of distilled water). Immersion and agitation time 1 min under red light. Immersion and agitation time for 15 min in the normal light
- iv. Rinse bath and air dried

2.3 RESULTS

To indicate the population size and its structure, collected data on length and age structure were combined. The number and weight of the dab in the study area is about 2.34×10^6 and 146.8 tonnes respectively (Table 2.1). The age/length matrix used for the males and females is given in Appendix 1. Females are more abundant, contributing about 57 % by number to the total population. The male population is dominated by fish belonging to the 16-20 cm length groups (58 %) and age groups 1-2 years (77% by number). Similarly, the 16-20 cm size and 1-2 age classes dominate the female population by number, respectively contributing 56 % and 82 %. The contribution of 3-year old fish is also significant but there is a rapid decline in population abundance after that age. In view of the size (73 mm) of the codend mesh, it is likely that fish ≤ 15 cm may be greatly under represented (Basimi and Grove, 1985a). Thus comparison with other estimates obtained for dab in the survey area will be done with full consideration of this phenomenon.

Table 2.1. Estimated population size ($\pm 5.E$) of dab on the North Wales Coast by sex, length group and age, from 1999-2000 fishing surveys.

A. Male

a) Number at length (cm)		b) Number at age (yr.)		c) Weight at age	
Length Class	Number	Age	Number	Age	Weight (Kg)
≤ 10	47211	0	47747	0	340.16
11-15	261039	1	389107	1	10911.91
16-20	581789	2	386017	2	20484.47
21-25	108555	3	113465	3	8704.06
26-30	1122	4	50478	4	4850.69
≥ 31	0	5	12902	5	1428.41
Total	999716 ± 73859	Total	999716	Total	46719.70 Kg

B. Female

a) Number at length (cm)		b) Number at age (yrs)		c) Weight at age (yrs)	
Length Class	Number	Age	Number	Age	Weight (Kg)
≤10	24844	0	37159	0	382.90
11-15	117742	1	499483	1	18313.77
16-20	742735	2	583454	2	47389.79
21-25	387598	3	151406	3	20031.48
26-30	60173	4	31766	4	5822.20
≥31	3261	5	21550	5	4965.13
		6	9885	6	2666.17
		≥7	1650	≥7	509.99
Total	1336353 ±100511	Total	1336353	Total	100082.43 Kg

Seasonal effects were observed in the catch rates. There were significant differences ($F=2.42$; $P=0.012$) in seasonal catch rates (number hr^{-1}), with catch rates generally higher in autumn and summer (Table 2.2), and significantly lower in winter and spring. The peak rate occurred in October 2000, with a catch rate of 228 hr^{-1} . The lowest catch rate was in the winter month of February 2000 (42 hr^{-1}). The catch per area trawled in 24-hour fishing survey is shown in Appendix 2. The average number caught km^{-2} in winter (February 2000) varied between $94 - 1168 \text{ km}^{-2}$ whilst in the summer (July 2000), the catch rate varied between $374-5977 \text{ km}^{-2}$.

Table 2.2. Seasonal variation in abundance index of dab (average number hr^{-1}) on the North Wales Coast, (Day time catches only between 10.00-14.00 hr) by size group.

L cm	Month and year											Avg.
	Feb '99	Mar '99	Sep '99	Oct '99	Nov '99	Feb '00	Mar '00	Apr '00	May '00	Jul '00	Oct '00	
≤ 10	0.00	16.2	0.0	1.0	0.0	0.8	2.1	0.90	2.6	0.4	3.8	2.5
11-15	7.2	19.5	15.2	25.5	8.2	7.6	20.3	4.4	16.4	47.9	62.1	21.3
16-20	69.2	34.1	31.0	73.1	55.0	24.3	35.9	24.4	23.7	45.2	122.2	48.9
21-25	14.4	3.2	16.0	31.8	37.7	8.4	6.8	13.3	17.3	30.8	35.5	19.6
26-30	0.8	0.0	2.2	4.2	2.7	0.4	0.4	3.6	8.6	15.2	4.7	3.9
≥31	0.2	0.0	0.0	0.2	0.0	0.0	0.4	0.9	1.3	1.2	0.2	0.4
Total	91.7	73.0	64.3	135.7	103.6	41.5**	66.0	47.6**	69.9	140.6	228.4**	96.6

** Significantly different ($P<0.05$) from average (Tukey-Kramer pairwise multiple comparison test for equal size data sets). Original data was Square Root Transformed to reduce variance.

There is some evidence of diel periodicity in apparent abundance in Table 2.3 from the 24-hour fishing studies. It was observed that the catch rates during night-time (between 22.00-02.00 hr) were significantly higher ($P<0.05$) than day-light (10:00-18:00 hr). The maximum catch rate at night was $1549 \text{ dabs hr}^{-1}$. The minimum catch rate was in day-light

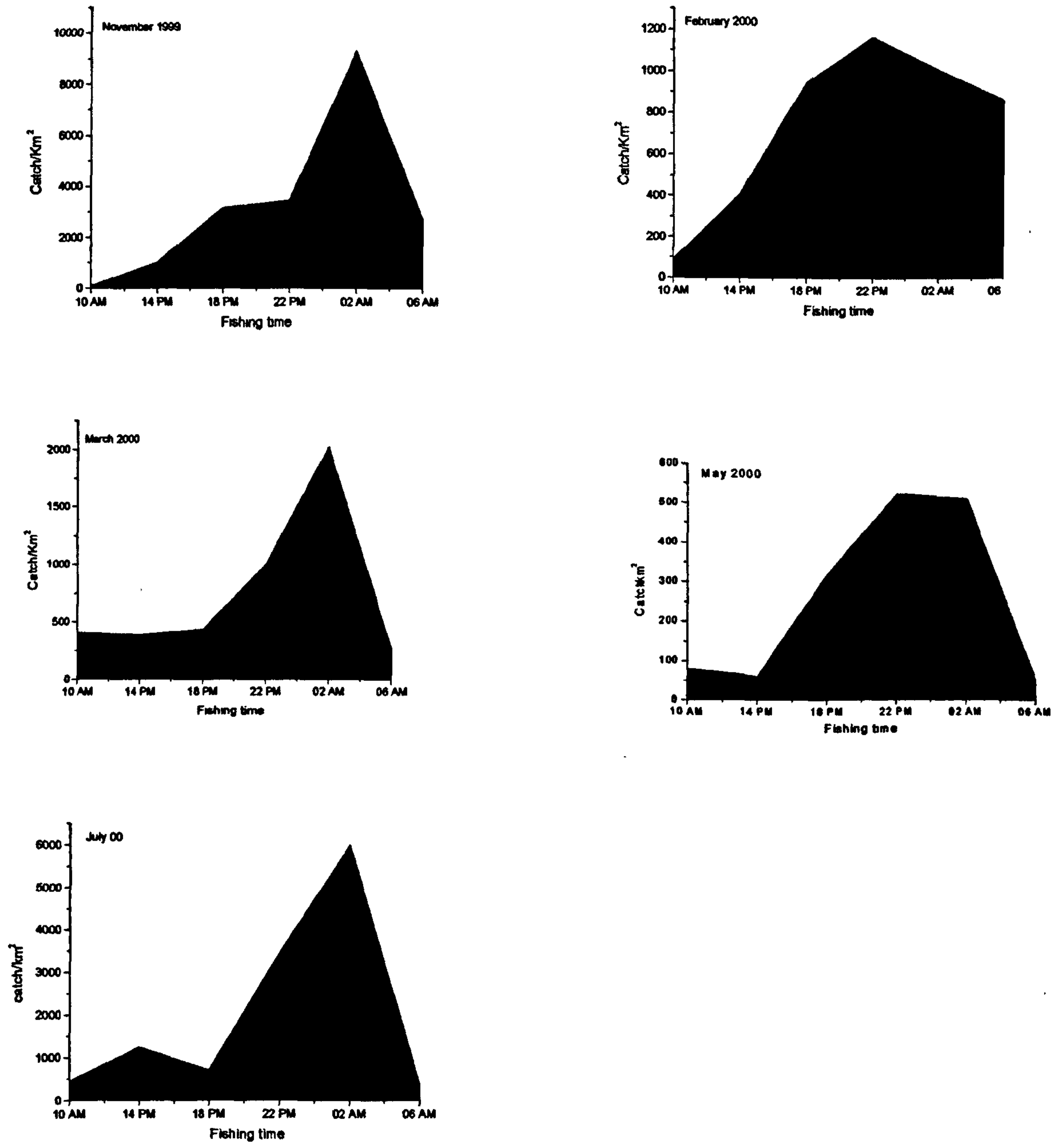
(16 dabs hr⁻¹). The catch rates in number (km⁻²) peaked during night-time in a 24-hour fishing cycle (Figure 2.1). In November 1999, for example, the catch rate varied between 103-1003 km⁻² during daylight (10:00 -18:00 hr) and between 3448-9287 km⁻² at night (22:00-02:00 hr).

Table 2.3. Catch rate of dab (number hr⁻¹) in monthly 24-hour fishing surveys, 1999-2000, on the North Wales Coast, by time of day.

Fishing Time (hr)	Nov99	Feb00	Mar00	May00	Jul00
10:00	17.1	15.6	68.5	81.6	76.5
14:00	167.4	68.6	65.6	60.0	209.8
18:00	527.5	158.5	72.5	320.4	119.2
22:00	575.3	197.8**	167.3	523.8**	576.5**
02:00	1549.1**	168.7	337.6**	511.3**	996.9**
06:00	450.0	144.0	45.3	52.5	62.4

** The mean catch rate at night (22:00-02:00 hr) was significantly higher ($p < 0.05$, Tukey-Kramer pairwise multiple comparison) than during daylight (10:00-18:00 hr).

Figure 2.1. Catch rate (number km⁻²) of the dab in the 24-hour fishing surveys on the North Wales Coast, 1999-2000



The percentage length frequency distribution (Figure 2.2) showed some seasonal fluctuations in the modal length, ranging from 16 cm to 21 cm. The lowest values were found in March 1999 (17 cm), February 2000 (17 cm) and October 2000 (16 cm). The highest was in November 1999 (21 cm) and July 2000 (21 cm). In general the length ranged between 10-

30 cm but occasionally, length groups < 10 and > 30 cm did appear in the catches. The minimum observed length in samples from the present study was 5 cm and the maximum was 37 cm. An examination of the progression of modes in the length frequency distribution indicates a possible seasonal occurrence of juveniles and period of recruitment into the fishery. Juveniles (between 5-10 cm in length) were found in depths ≥ 10 m in March and April, which is also the spawning period. This appears to be followed by the gradual movement of new 'recruits' (about 15 cm in length) into the fishery between July and November, indicated by the presence of modes about the 15 cm length in July, September, October and November size frequency polygons. The percentage composition of trawl catches of dab in the study area between 1966 to 2000 (Figure 2.3) also showed that the sampled population mainly consisted of fish in length group 10-30 cm, with the dominant size at around 20 cm. However, in some years, there appeared to be stronger recruitment probably indicated by the appearance of strong modes at 10-15 cm. This pattern was also observed in the latest year (2000) when the 15 cm fish dominated the catch. This observation is further supported by the percentage composition by length groups, between 1966-2000, which confirmed that the population has been dominated by fish populations in the length group 15-24 cm (Figure 2.4). Between 1970-1980s, dab with length < 15 cm contributed significantly to the total percentage composition of the samples. The proportion of the very large fish has remained comparatively small since nearly four decades ago.

Figure 2.2. Percentage monthly length composition of dab in trawl survey catches on the North Wales Coast, 1999-2000

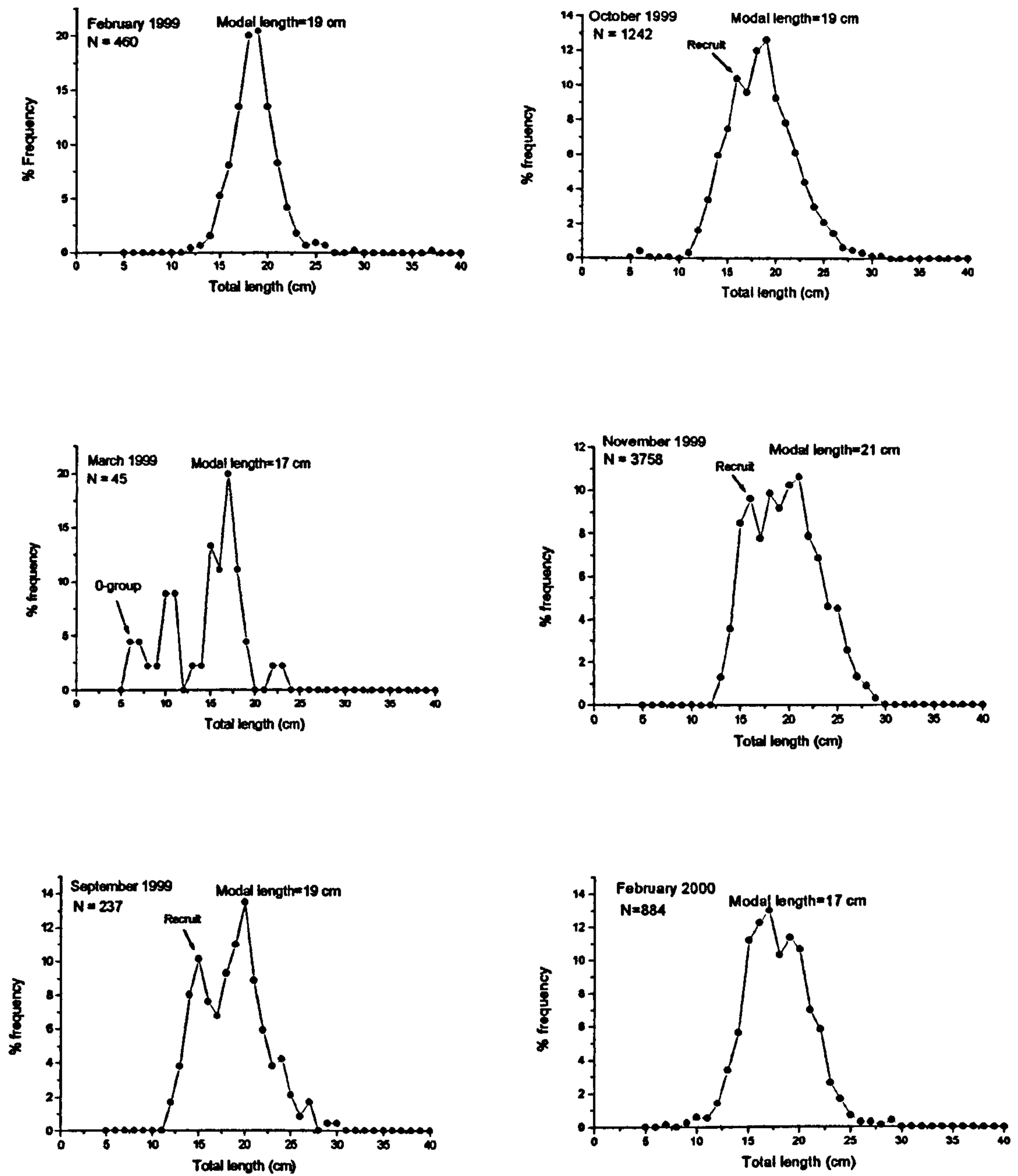


Figure 2.2 continued.

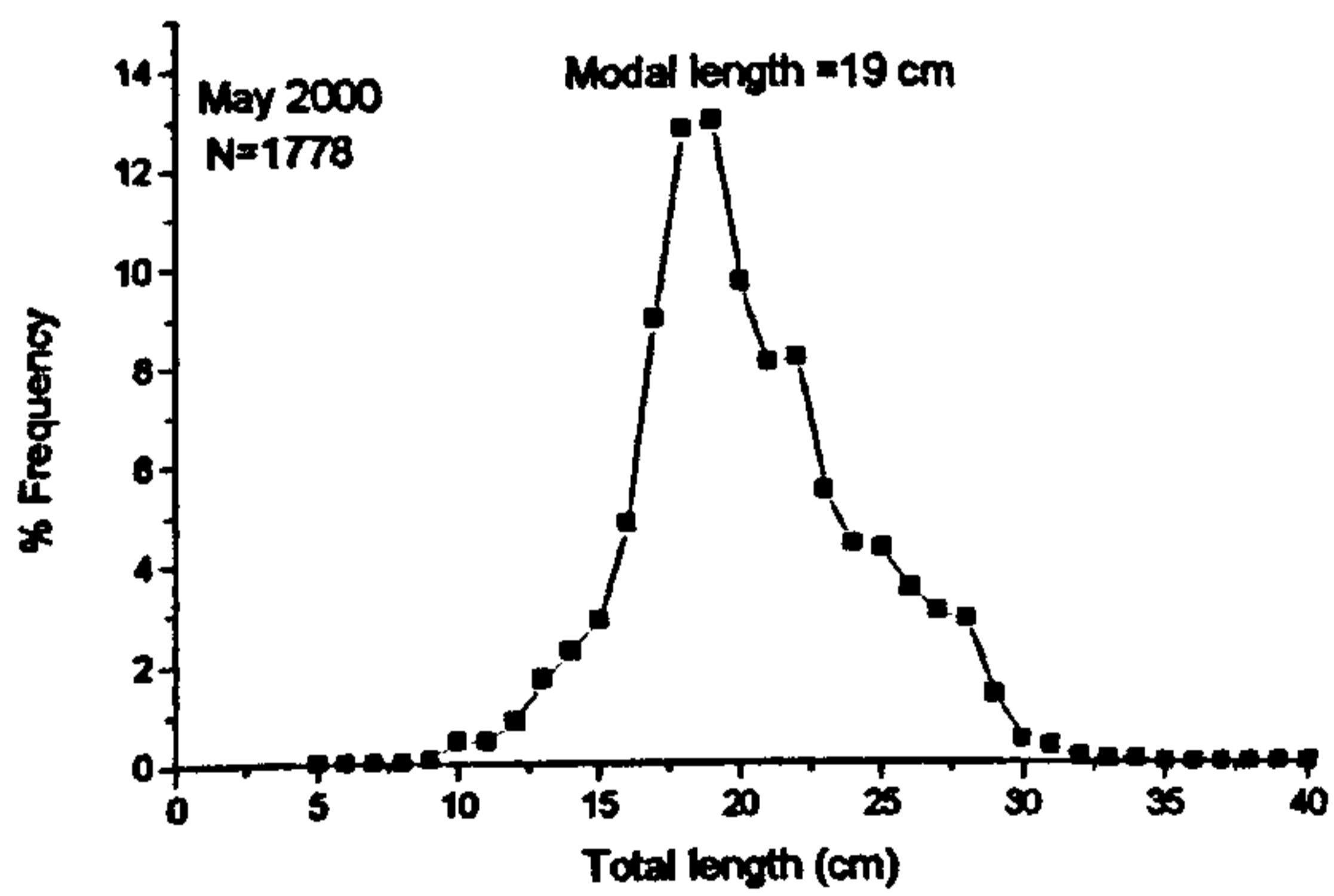
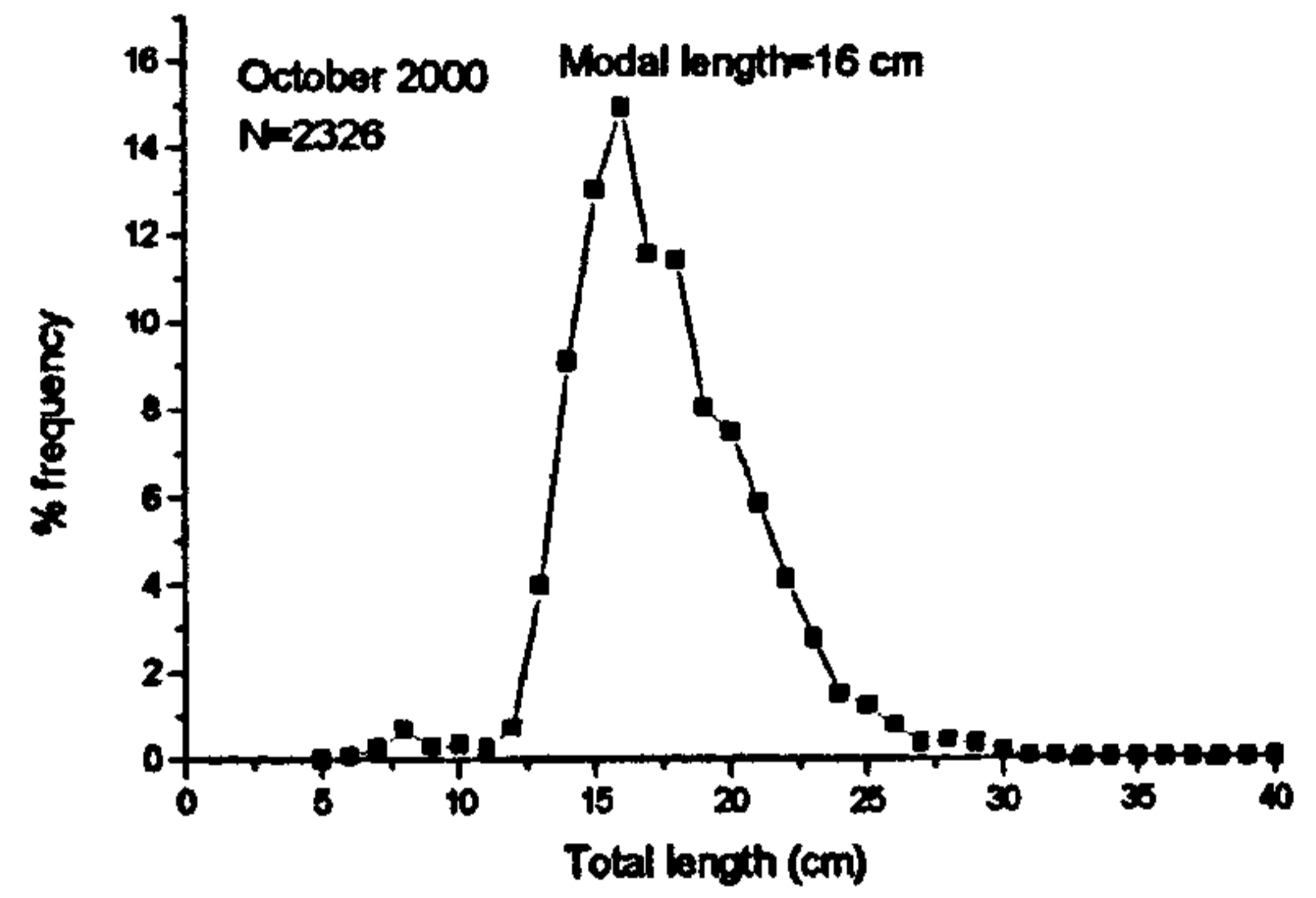
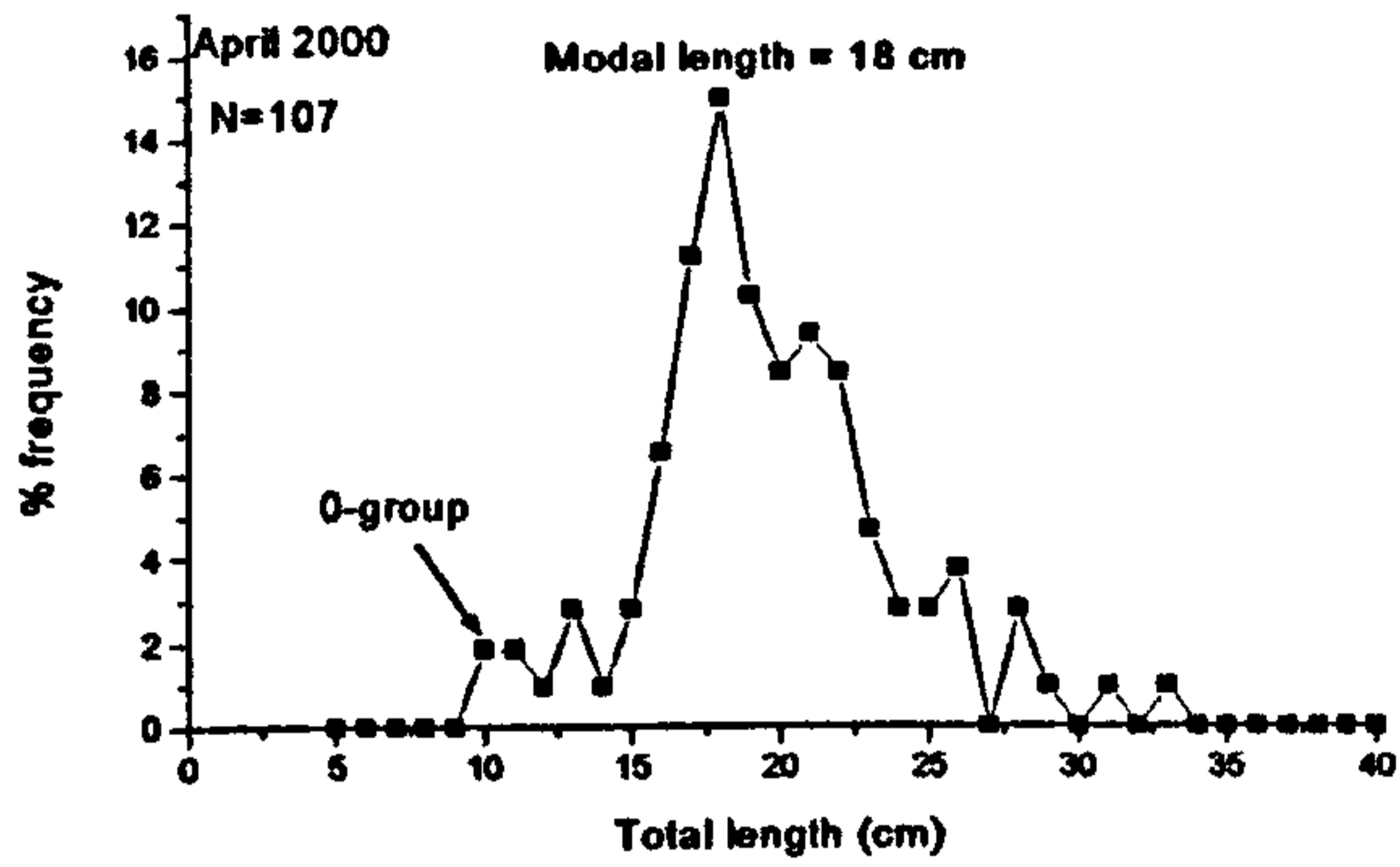
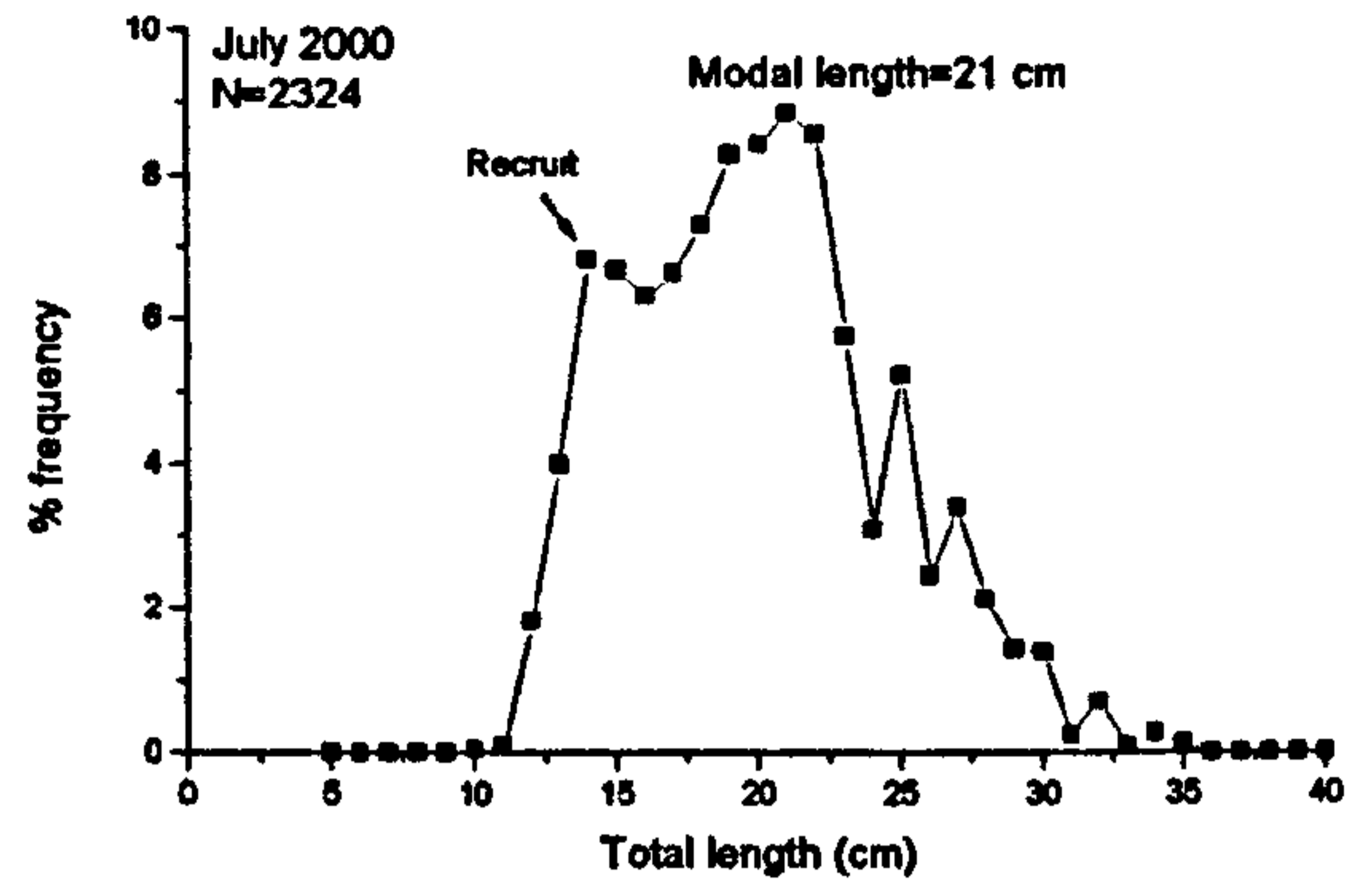
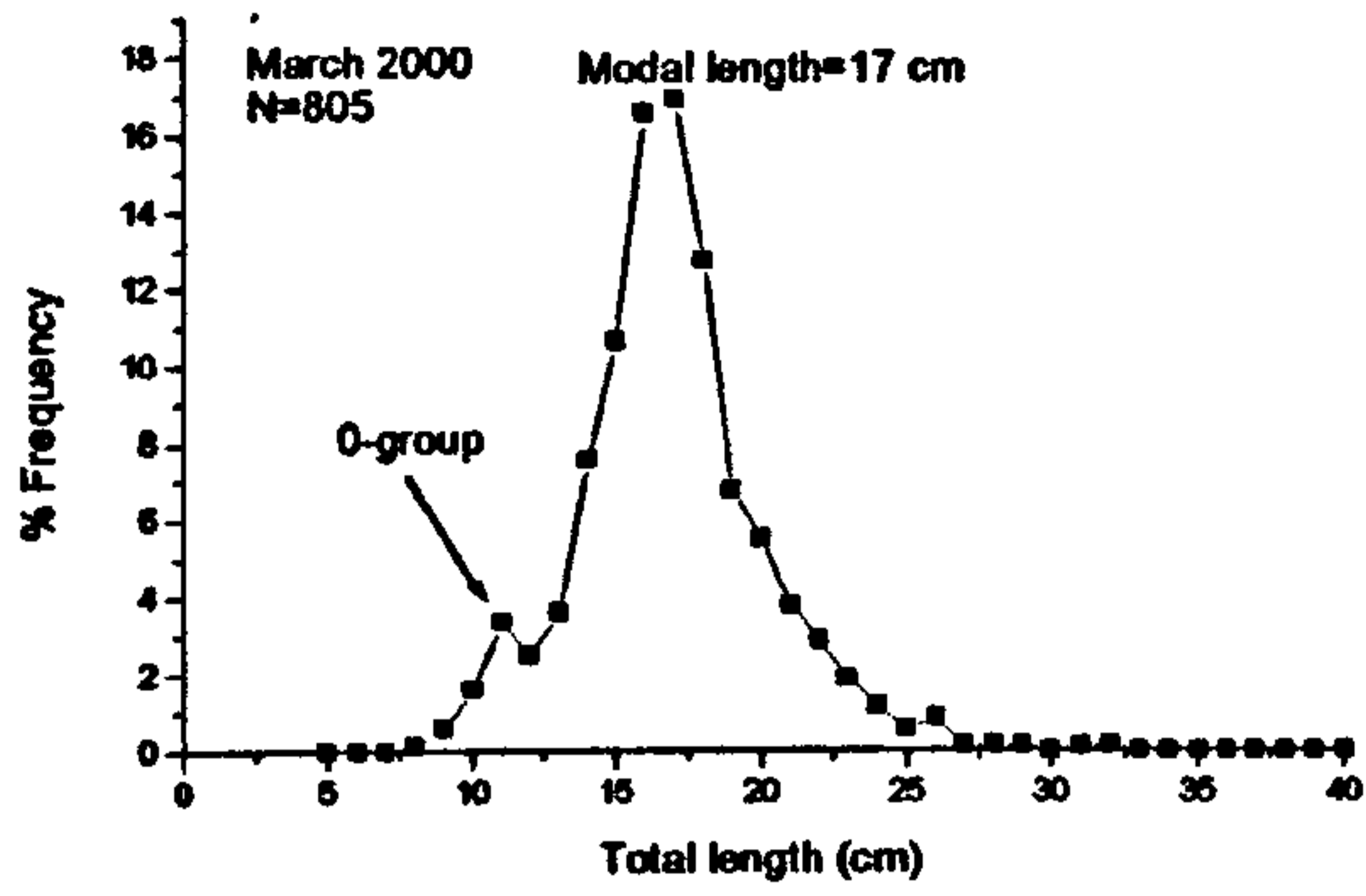


Figure 2.3. Percentage composition by length of dab on the North Wales Coast over the 34-year period, 1966-2000. The earliest samples are at the top and each curve is displaced downward by a distance proportional to the date of capture to allow ease of comparison. Dotted lines show sample size (number of dabs caught) was less than 500. Solid lines show sample size was more than 500. The two dashed vertical lines show the length composition of dab samples between the length range of 10 and 30 cm. Data were not available for 1967, 1968 and 1971, therefore the percentage catch compositions for these years are not included in the Figure.

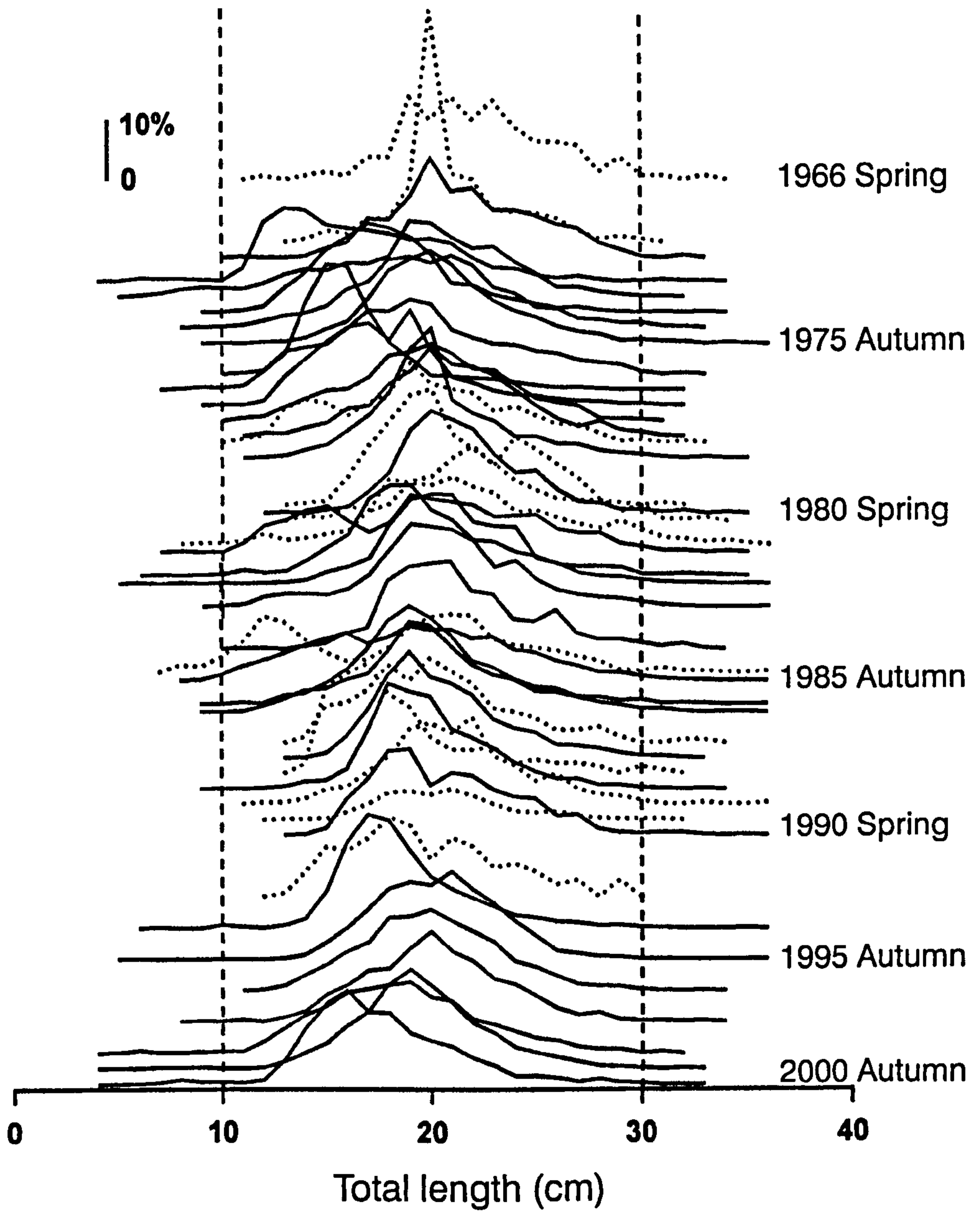
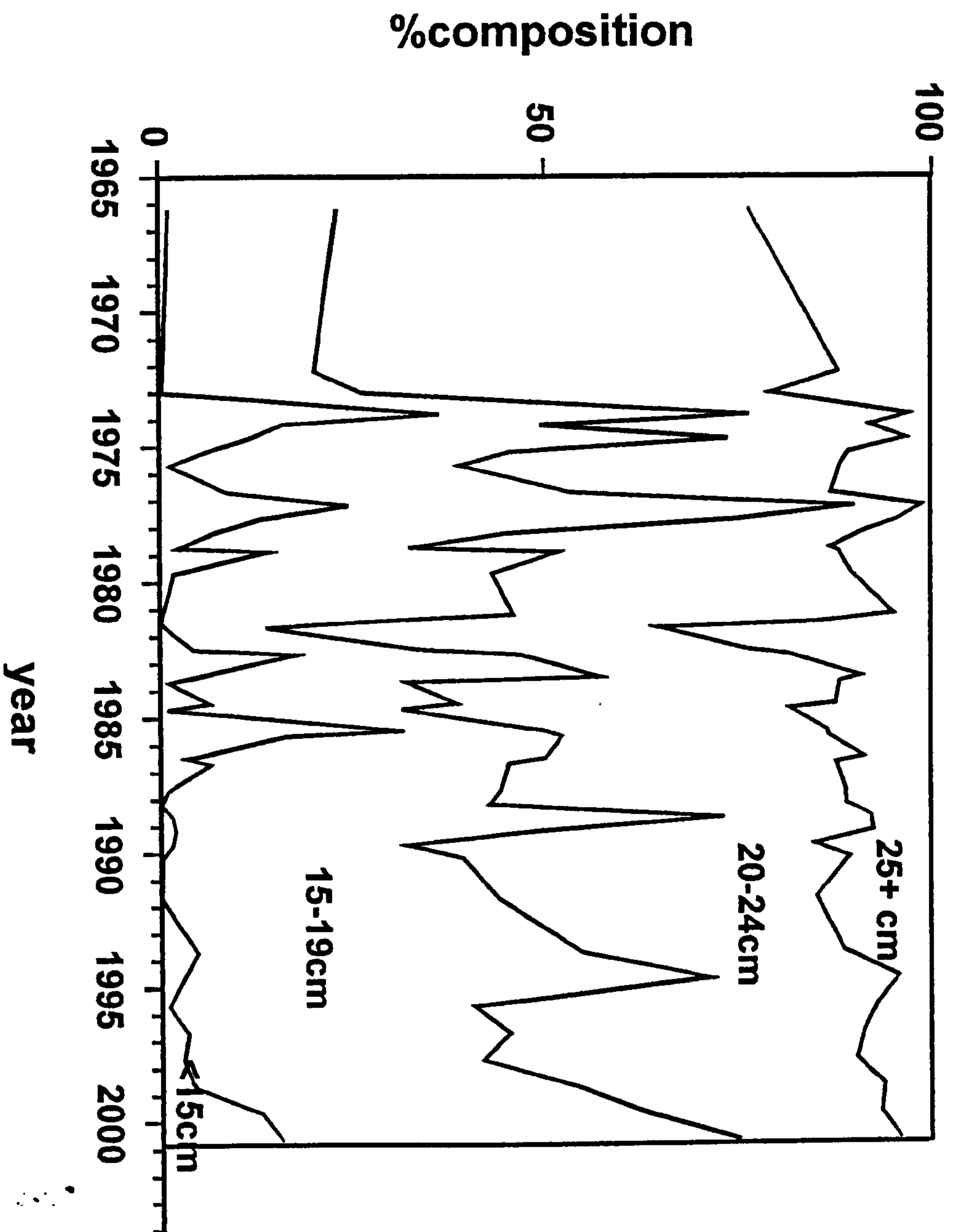


Figure 2.4. Percentage composition of dab (by length groups) on the North Wales Coast, 1966-2000.



There was a high seasonal variability in the distribution of sex ratio in the study area (Table 2.4). This was partly due to the monthly variation in sample sizes (number of fish caught). However, the females dominate the inshore dab populations and there is a significant departure ($P < 0.05$) from the 1:1 sex ratio. There appears to be a tendency for the male contribution to increase in the summer and also with increasing depth, from 10 to 18.5 m (Tables 2.5 and 2.6). Beyond 19 m, females dominate the small catches. The females become more abundant in the spawning season (autumn-winter). These observations are illustrated graphically in Figures 2.5 and 2.6. The distribution of the sex ratio in the historical data also supports this observation (Figure 2.7): prior to 1990, the male contribution was highest in April-June and lowest late in the year. In the historical data, the long-term averages of the ratio of female to male (1.829:1) in the autumn and 1.153:1 in the spring were significantly different.

Table 2.4. Average monthly variation in sex ratio by depth and season on the North Wales Coast, in 1999-2000 fishing surveys

MTh/yr.	Depth m	Sex ratio Female : Male	Total Number	Chi- squared- χ	Significance **
Feb99	19.5-39	1.7 : 1.0	460	31.3	HS
Mar99	8-18	1.9 : 1.0	46	4.3	S
Sep99	14-18	1.6 : 1.0	245	11.5	HS
Oct99	11-17	1.5 : 1.0	1538	64.1	HS
Nov99	11-20	2.5 : 1.0	3746	685.1	HS
Feb00	9-18	10.0 : 1.0	889	594.5	HS
Mar00	8-18	4.0 : 1.0	806	285.9	HS
Apr00	11-13	11.5 : 1.0	108	78.4	HS
May00	9.5-14	2.2 : 1.0	1788	259.2	HS
Jul00	11.5-18	2.7 : 1.0	2326	488.6	HS
Oct00	10-25	1.7 : 1.0	2329	156.1	HS

Chi-squared test to assess deviation from 1:1 sex ratio. **There is a significant departure ($P < 0.05$) from the sex ratio (1:1) in all months. HS implies that the departure from the 1: 1 sex ratio of females to males was highly significant. S implies the departure was significant in March 1999 (probably due to small sample size) but less so than the other months.

Table 2.5. Variation in daily trawl catch rates and sex ratio of dab at various depths, 1999-2000

Average Depth (m)	Range Depth (m)	Male No.	Female No.	Trawl Duration (Min)	Catch rate No.hr ⁻¹
11.5	11-12	195	439	134	283.88
14.0	13-15	68	100	96	105.47
14.5	11-21	69	112	58	187.24
14.5	13-16	123	193	80	237.00
15.5	10-21	117	148	110	144.00
17.5	13-22	168	147	108	175.00
18.5	17-20	99	175	98	167.75
19.3	14-25	33	173	109	113.42
33.0	30-36	0	0	60	0
37.5	35-42	0	11	103	6.41
40.0	36-41	0	0	60	0
40.0	39-41	0	0	60	0

Table 2.6. Summary of the variation in sex ratio with depth

Depth (m)		Male No.	%	Female No.	%	Total
10-15	Inshore	456	35.08	844	64.92	1300
≥16.0	Offshore	417	39.94	654	61.06	1071

Figure 2.5. Seasonal variation in sex ratio (Female: Male, with Male=1), on the North Wales Coast, 1999-2000.

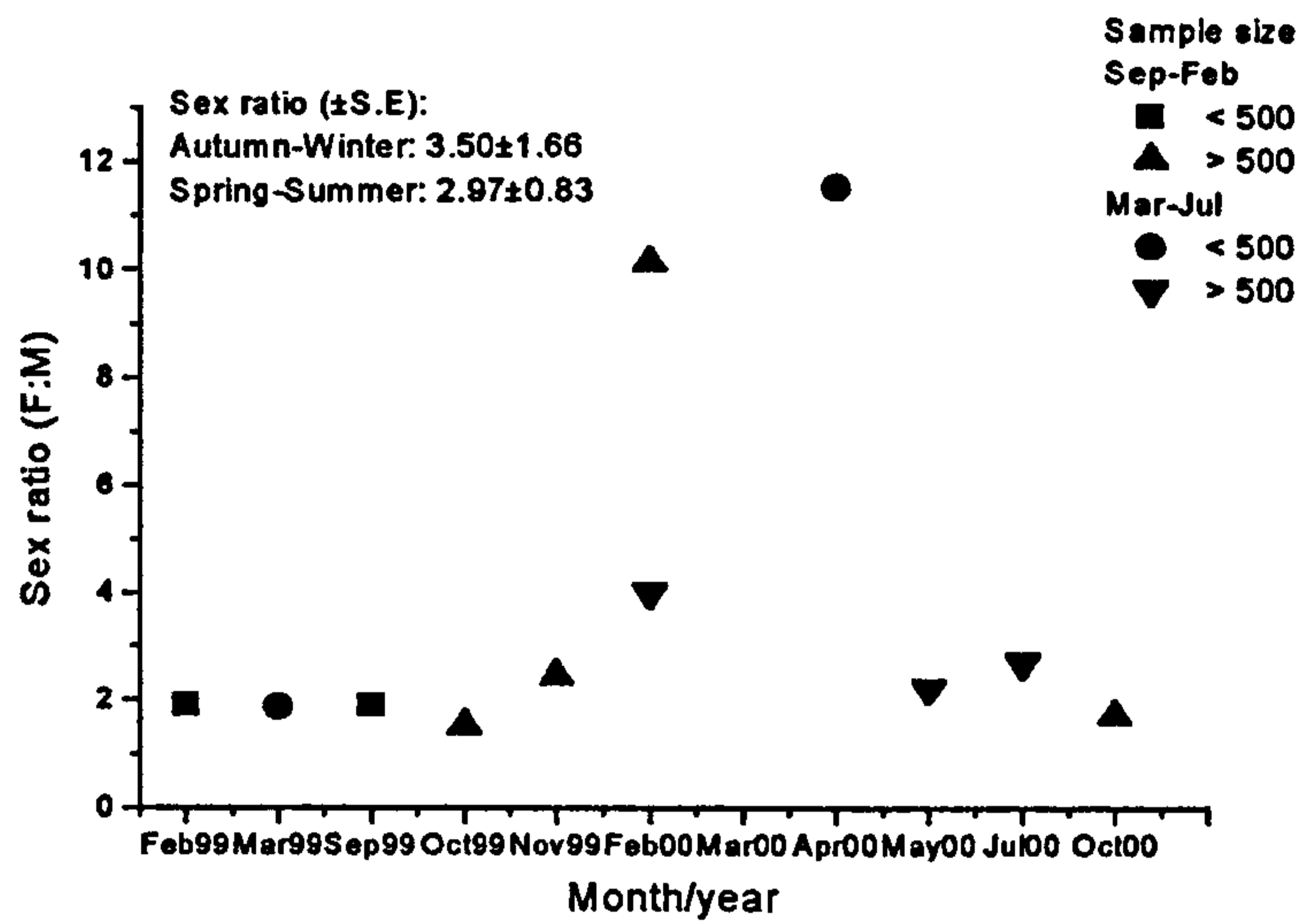


Figure 2.6. Variation in sex ratio (Female: Male, with Male=1), with depth on the North Wales Coast, 1999-2000.

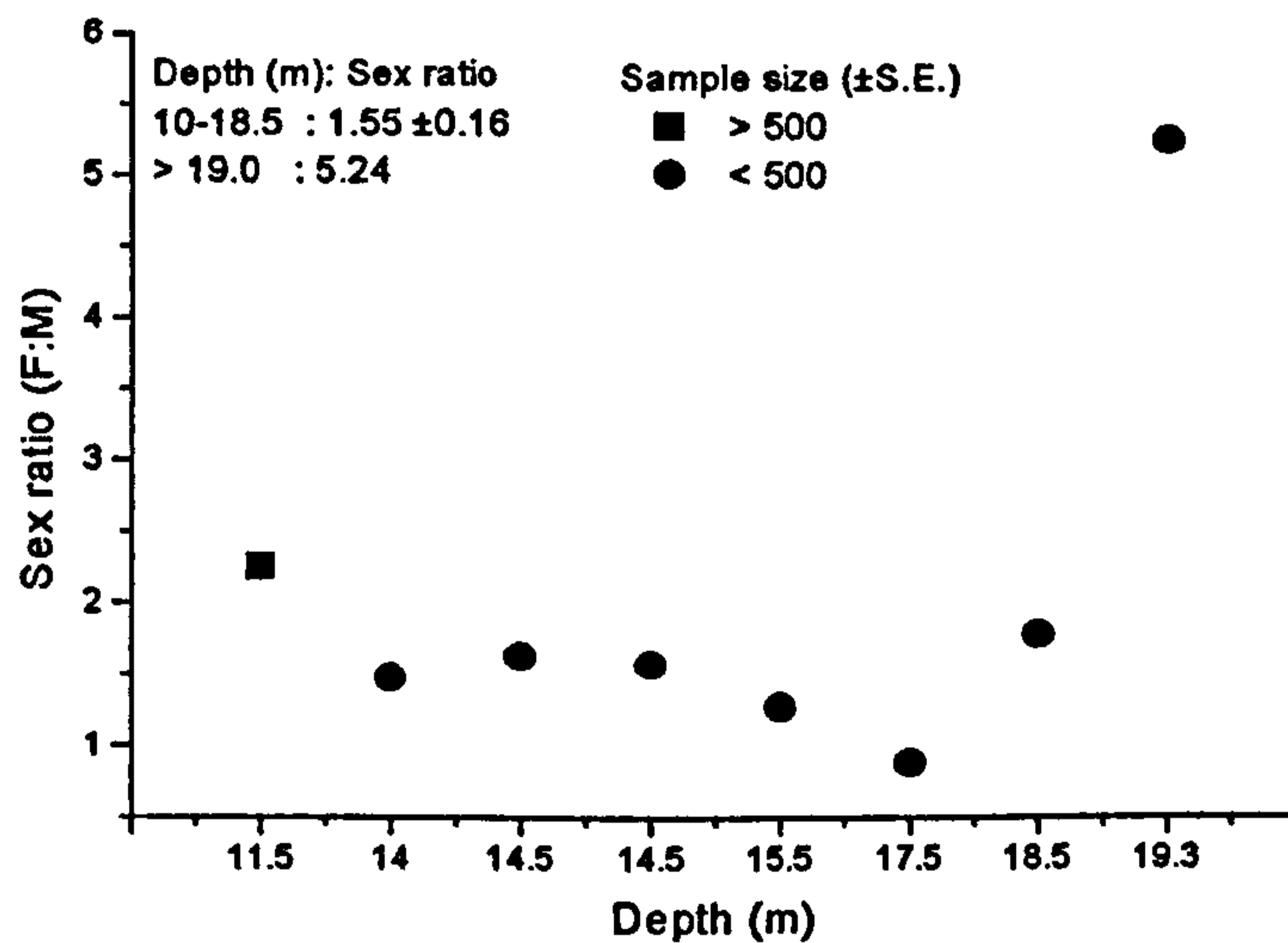
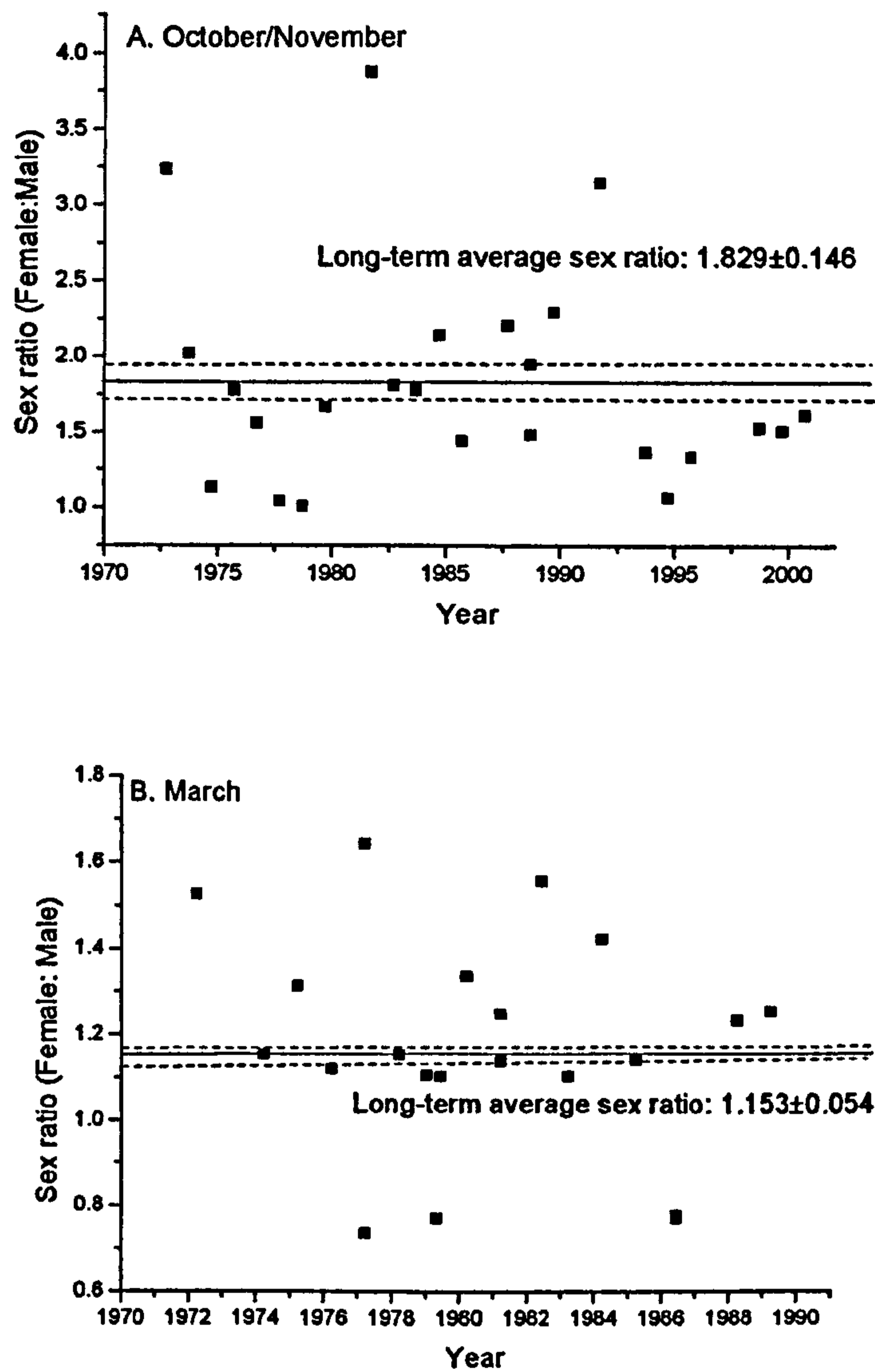


Figure 2.7. Long-term seasonal variation in the sex ratio of dab on the North Wales Coast, 1970-2000. The estimated average sex ratio is \pm S.E.



The seawater temperature measurements within the vicinity of the survey area show considerable monthly variation (Table 2.7).

Table 2.7. Average seawater temperature in the Menai Strait (Courtesy of Dr. Des Barton, School of Ocean Sciences, University of Wales)

Month	Mar	Apr	May	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Year	00	00	00	00	00	00	00	00	00	01	01	01	01
Temp °C	8.02	10.12	12.19	15.79	17.53	15.68	12.42	9.04	8.77	4.99	6.26	6.82	8.09

Meristic analyses (Tables 2.8 and 2.9) showed no significant difference ($P>0.05$) in anal fin rays, dorsal fin rays, caudal fin rays and vertebral median counts between the male and female dab. The result of the X-ray photography is shown in Figure 2.8.

Table 2.8. Mean count of meristic characters in male and female dab on the North Wales Coast, 1999-2000

Female

Characters	N	Mean \pm 95%CL	Median	Min	Max
Dorsal fin	567	73.61 \pm 0.26	74	64	83
Anal fin	567	56.74 \pm 0.06	57	48	64
Caudal fin	567	17.71 \pm 0.20	18	16	19
Vertebrae*	508	40.12 \pm 0.10	40	39	41

Male

Characters	N	Mean \pm 95%CL	Median	Min	Max
Dorsal fin	203	73.53 \pm 0.43	74	63	81
Anal fin	203	56.76 \pm 0.31	57	51	63
Caudal fin	203	17.74 \pm 0.20	18	16	19
Vertebrae*	173	40.33 \pm 0.16	40	37	44

*Vertebral counts include Urostyle

Table 2.9. Kruskal-Wallis non-parametric test of meristic count between male and female dab

Meristics	P-value	Significance level
Dorsal fin	0.949	NS
Anal fin	0.849	NS
Caudal fin	0.505	NS
Vertebrae	0.084	NS

NS= No significant difference ($P>0.05$) in median values between the sexes

In the linear regression analyses between head length and also body depth versus total length, the intercepts were not significantly different from zero (Tables 2.10 and 2.11). A constrained linear regression (with intercept $a=0$) was therefore used. The study shows strong correlation between total length and head length in both sexes (Figure 2.9), although the male head length was greater in relative size. The same was true between total length

against body depth (Figure 2.10). The results suggest that the total head of male and female dab can be predicted by multiplying the total length by the multiplicative factors 0.214 and 0.210 respectively. The body depth length can also be predicted by multiplying the total length by 0.366 and 0.378 in male and female respectively.

Table 2.10. Relationship between Head length (HL in cm) and Total length (TL in cm) (with $\pm 95\%$ CL) in male and female dab on the North Wales Coast, 1999-2000.

	Female:	Male:
Equation	HL =0.210(± 0.001) x TL	HL =0.214 (± 0.001) x TL
r	0.981	0.979
N	567	203
P	<0.0001	<0.0001

The result suggests significant difference in the multiplicative factor for the head length/total length relationship between the two sexes.

Table 2.11. Relationship between Body depth (BD in cm) and Total length in male and female dab on the North Wales Coast, 1999-2000.

	Female:	Male:
Equation	BD =0.378(± 0.001) x TL	BD =0.366 (± 0.002) x TL
r	0.984	0.979
N	565	203
P	<0.0001	<0.0001

The result suggests significant difference in the multiplicative factor for the body depth/total length relationship between the two sexes.

Figure 2.8. X-ray photography of dab to show the skeleton with the vertebrae, ribs, neural spines and "intercalated supports".

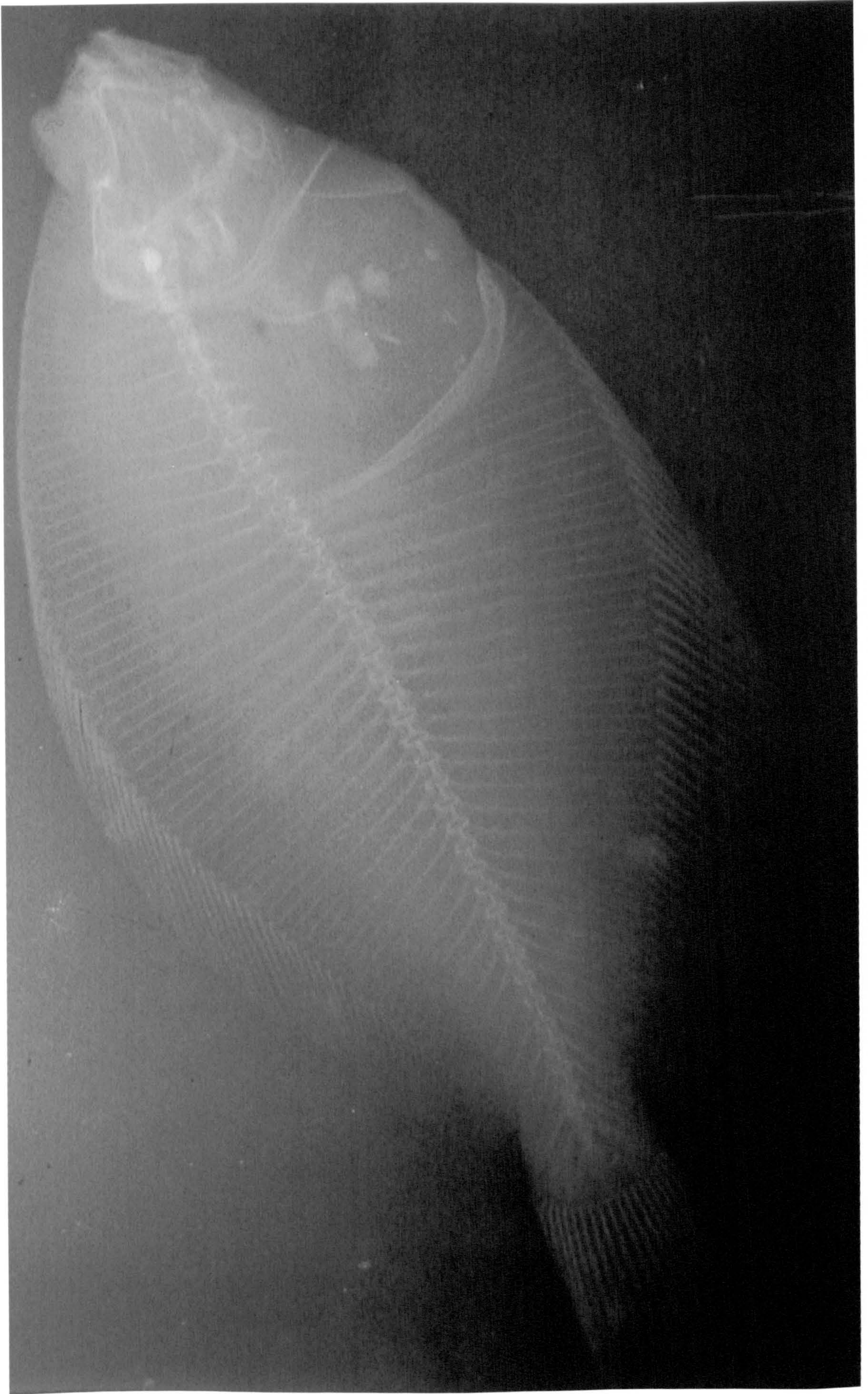


Figure 2.9. Relationship between head length and total length in male and female dab on the North Wales Coast, 1999-2000

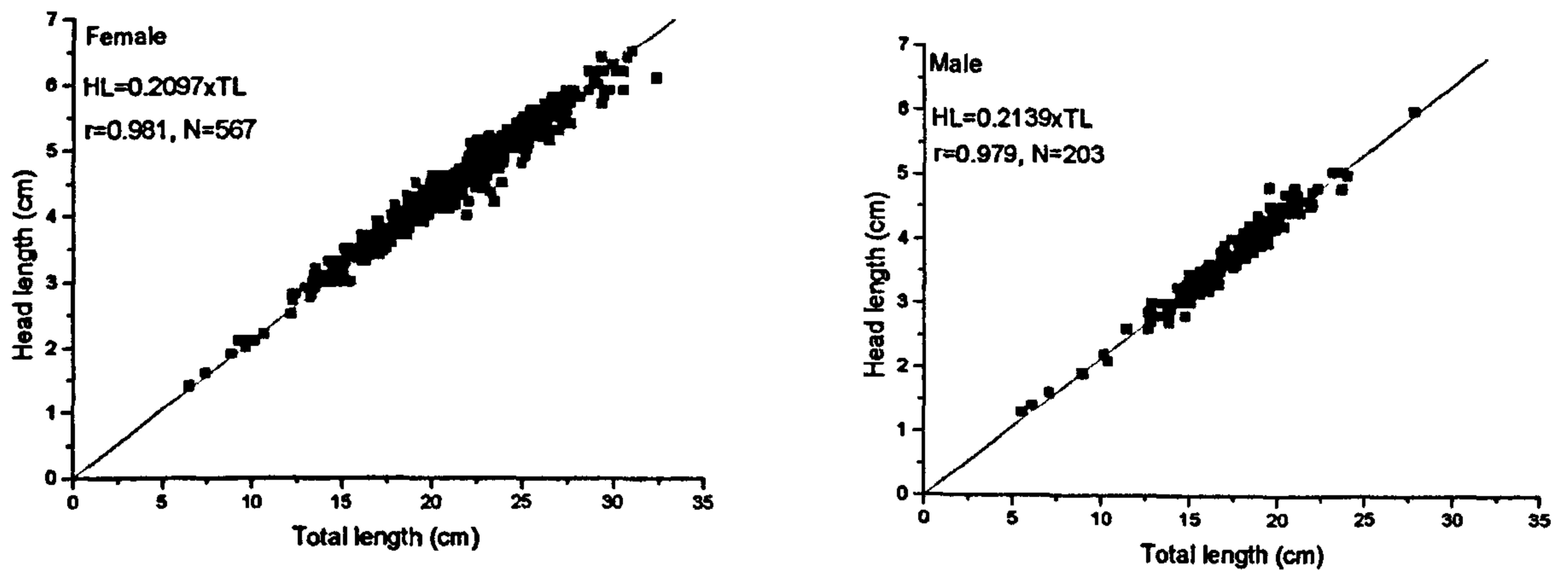
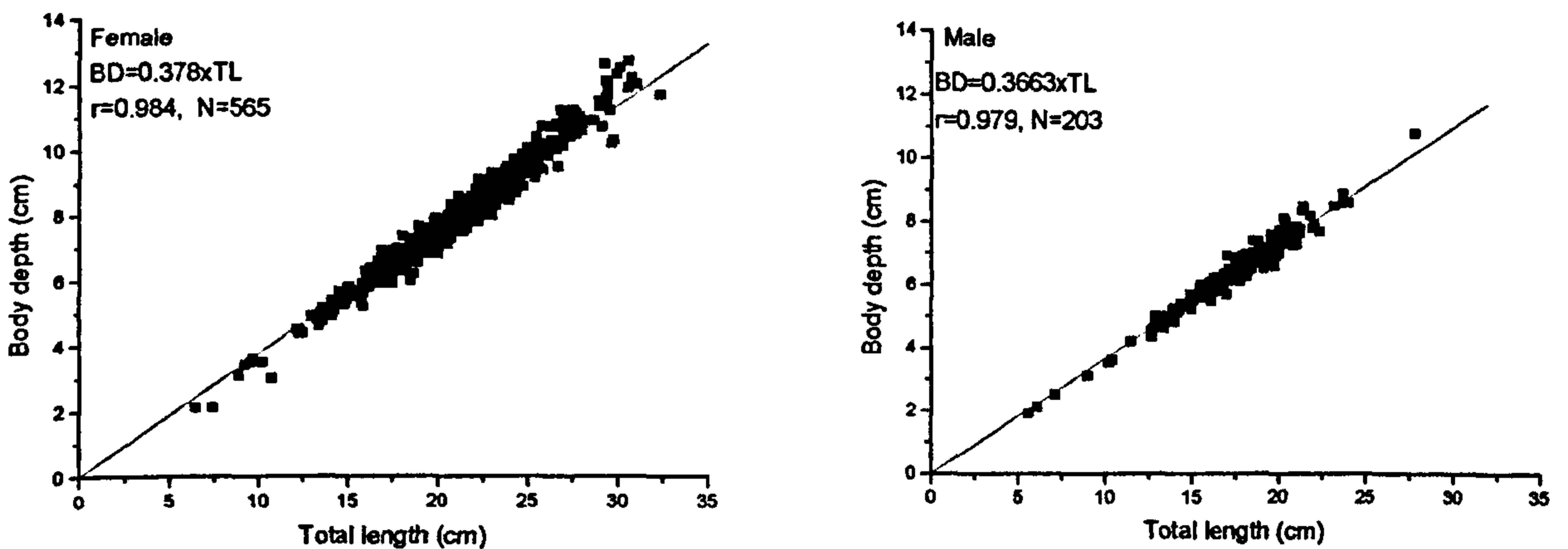


Figure 2.10. Relationship between body depth and total length in male and female dab on the North Wales Coast, 1999-2000



Results of monthly studies on length and weight relationship in both males and females are given in Table 2.12. Covariance analysis across all months for each sex shows significant differences in some of the fitted constants ($P < 0.05$). The growth in weight in relation to length is approximately isometric ($b \approx 3.0$) for most of the year in each sex. After spawning, the value of the power declined significantly ($b \ll 3.0$) in March and April 2000, which suggested negative allometric growth. This relationship becomes either isometric or positively allometric ($b \geq 3.0$) in the summer (July-September) and during the peak spawning season

(February) when the bigger fish gained weight possibly due to heavy feeding in summer and autumn and the massive increase in the weight of gonads in females (February).

Table 2.12. Length and weight relationship (fitted constants $\pm 95\%$ CL) of dab on North Wales Coast, 1999-2001.

$$\text{Weight} = a(\text{Total Length})^b$$

A. Female:

Month	Year	a	b	Growth	r	n
Feb	1999	0.004 \pm 0.002	3.356 \pm 0.110**	+	0.996	25
Mar	1999	0.012 \pm 0.098	2.947 \pm 0.292	Isometric	0.971	34
Apr	1999	0.005 \pm 0.005	3.176 \pm 0.308	Isometric	0.938	55
May	1999	0.027 \pm 0.103	2.702 \pm 1.131	Isometric	0.903	10
Jun	1999	0.037 \pm 0.046	2.624 \pm 0.392	Isometric	0.970	16
Jul	1999	0.004 \pm 0.003	3.329 \pm 0.257	+	0.942	65
Aug	1999	0.008 \pm 0.005	3.096 \pm 0.177	Isometric	0.961	89
Sep	1999	0.004 \pm 0.004	3.336 \pm 0.106**	+	0.978	155
Oct	1999	0.003 \pm 0.002	3.363 \pm 0.148**	+	0.968	118
Nov	1999	0.009 \pm 0.004	3.053 \pm 0.1300	Isometric	0.978	167
Dec	1999	0.007 \pm 0.004	3.147 \pm 0.185	Isometric	0.944	137
Feb	2000	0.006 \pm 0.002	3.233 \pm 0.108**	+	0.967	240
Mar	2000	0.017 \pm 0.005	2.791 \pm 0.085**	-	0.974	212
Apr	2000	0.022 \pm 0.007	2.688 \pm 0.087**	-	0.986	98
May	2000	0.010 \pm 0.004	3.000 \pm 0.108	Isometric	0.970	231
July	2000	0.007 \pm 0.002	3.161 \pm 0.073	+	0.984	302
Oct	2000	0.010 \pm 0.004	3.042 \pm 0.119	Isometric	0.981	109
Jan	2001	0.017 \pm 0.006	2.859 \pm 0.103	-	0.965	55

Growth in weight is isometric when $b=3.0$

+ = Growth in weight and length is positively allometric ($b>3.0$)

- = Growth in weight and length is negatively allometric ($b<3.0$)

Covariance analysis

ANOVA

Common fitted constants:

Exponents	Values
a	0.009
b	3.036

Common equation: $W = 0.009 \cdot TL^{3.036}$

** = Exponents (b) significantly different ($P<0.05$, $F_b=12.98$, $F_a=10.30$) from the average fitted power ($b=3.036$).

Table 2.12 continued.

B. Male:

Month	Year	a	b	Growth	r	n
Feb	1999	0.012 ±0.020	2.913 ±0.541	Isometric	0.960	18
Mar	1999	0.011 ±0.016	2.926 ±0.511	Isometric	0.994	12
Sep	1999	0.015 ±0.008	2.857 ±0.185	Isometric	0.962	78
Oct	1999	0.020 ±0.017	2.733 ±0.285	-	0.921	65
Nov	1999	0.020 ±0.010	2.774 ±0.169	-	0.976	66
Dec	1999	0.006 ±0.012	3.158 ±0.634	Isometric	0.984	12
Feb	2000	0.008 ±0.009	3.064 ±0.395	Isometric	0.968	30
Mar	2000	0.042 ±0.028	2.430 ±0.240**	-	0.947	56
Apr	2000	0.043 ±0.020	2.406 ±0.337**	-	0.994	8
May	2000	0.028 ±0.017	2.631 ±0.205	-	0.948	101
July	2000	0.015 ±0.007	2.867 ±0.162	Isometric	0.968	105
Oct	2000	0.028 ±0.015	2.644 ±0.172	-	0.981	44

Growth in weight is isometric when $b=3$

+ = Growth in weight and length is positively allometric ($b>3.0$)

- = Growth in weight and length is negatively allometric ($b<3.0$)

Covariance analysis

ANOVA

Fitted constants

Exponents	values
a	0.012
b	2.913

Common equation $W = 0.012 \cdot TL^{2.913}$

** = Exponents (b) significantly different ($P<0.05$, $F_b=2.74$, $F_a=2.91$) from average fitted power ($b=2.913$)

Monthly comparison of the coefficients of length/ weight relationship between male and female dab shows that these coefficients differ significantly between October and November (beginning of the spermatogenesis and oogenesis in males and females respectively), and in February (the peak spawning month for the female); Table 2.13. The females are heavier than the males during the breeding season since they carry hydrated oocytes. In late winter and early spring, both sexes are in emaciated condition after spawning (and with low stomach contents); thus there is no significant difference in their weights. For stock assessment purposes, therefore, the length/weight data of both sexes may be combined in March-September (spring and summer) but treated separately between October-February (autumn and winter). Table 2.14 shows that the coefficients of length and weight relationships estimated in previous student survey (October1995-1998). In these years, the length and weight relationships are isometric or nearly isometric. Significantly however, the estimates for the power (b) in the males and females are not significantly different from the

October estimates derived in this study. Figure 2.11 also showed that the coefficients of the length/weight relationships in the female dab in October 1979 are not significantly different from the 1999 and 2000 estimates obtained from the present study.

Table 2.13. Monthly statistical comparison (covariance analysis) of the length/weight relationship between male and female dab in different months

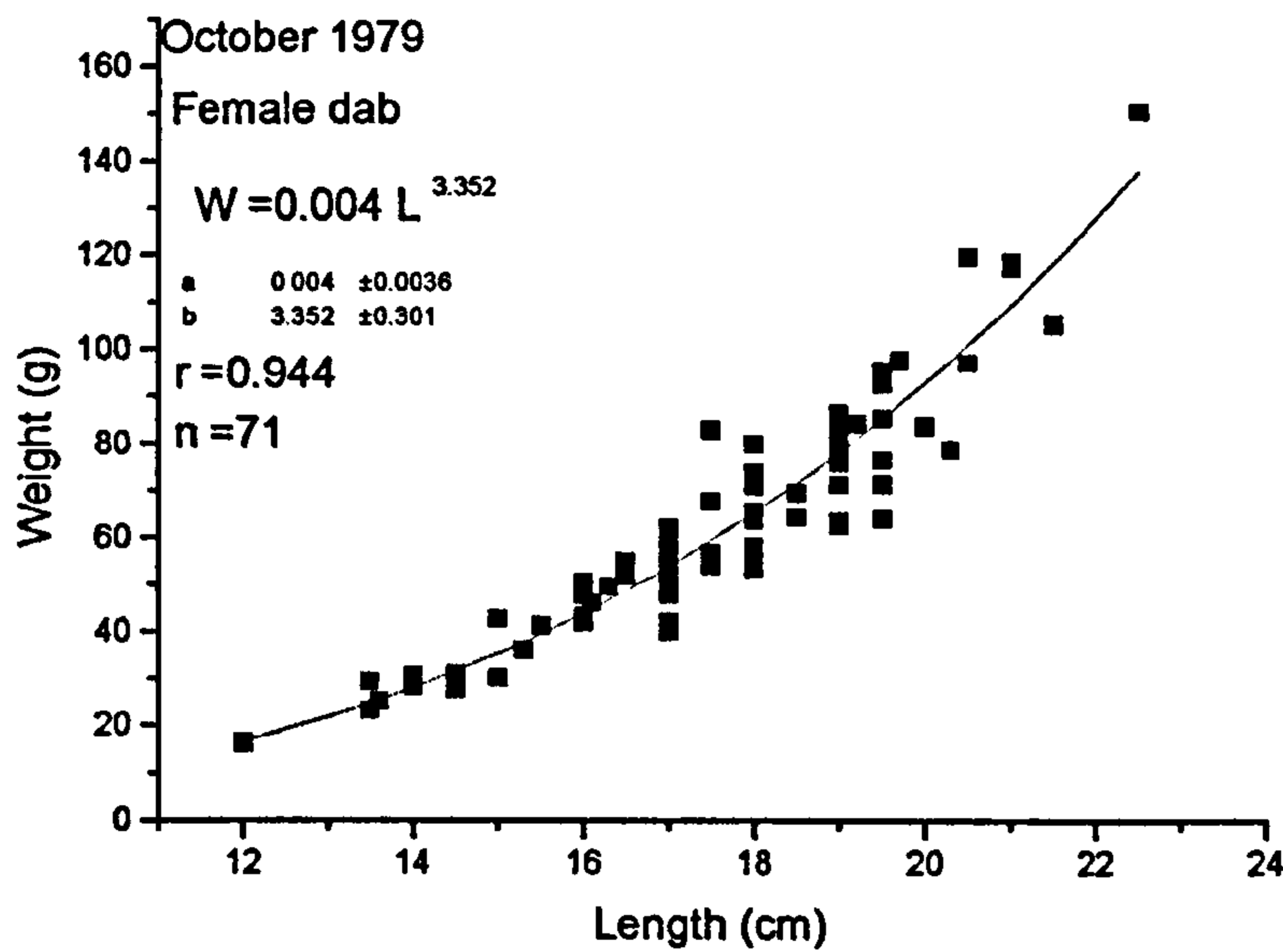
Month/year	Common b	F-Ratio	P-value	Common a	F-Ratio	P-Value
Feb99	3.135	3.43	0.072	0.007	2.63	0.113
Mar99	3.191	0.39	0.414	0.006	0.16	0.306
Sep99	3.027	3.80	0.052	0.009	3.05	0.082
Oct99	2.884	7.24	0.008**	0.013	6.60	0.011**
Nov99	2.984	6.14	0.014**	0.011	5.49	0.020**
Dec99	3.202	0.05	0.827	0.005	0.23	0.634
Feb00	3.108	11.63	0.001**	0.005	8.60	0.004**
Mar00	2.824	0.39	0.535	0.015	0.16	0.306
Apr00	2.608	0.24	0.624	0.026	0.04	0.847
May00	2.887	2.44	0.120	0.014	1.28	0.259
Jul00	3.084	4.33	0.038**	0.008	3.07	0.081
Oct00	3.033	5.08	0.026**	0.009	4.71	0.032**

** The fitted constants significantly different at $P < 0.05$. The weights differ in the spawning period (October, November and February 2000) because the females are ripening or ripe with eggs and thus heavier. Both sexes are in emaciated condition after spawning March 2000 and April 2000 and therefore there is no significant difference in weight between the two sexes.

Table 2.14. Length and weight relationships for dabs from surveys on the North Wales Coast (fitted by FIGP software computer programme, BioSoft)

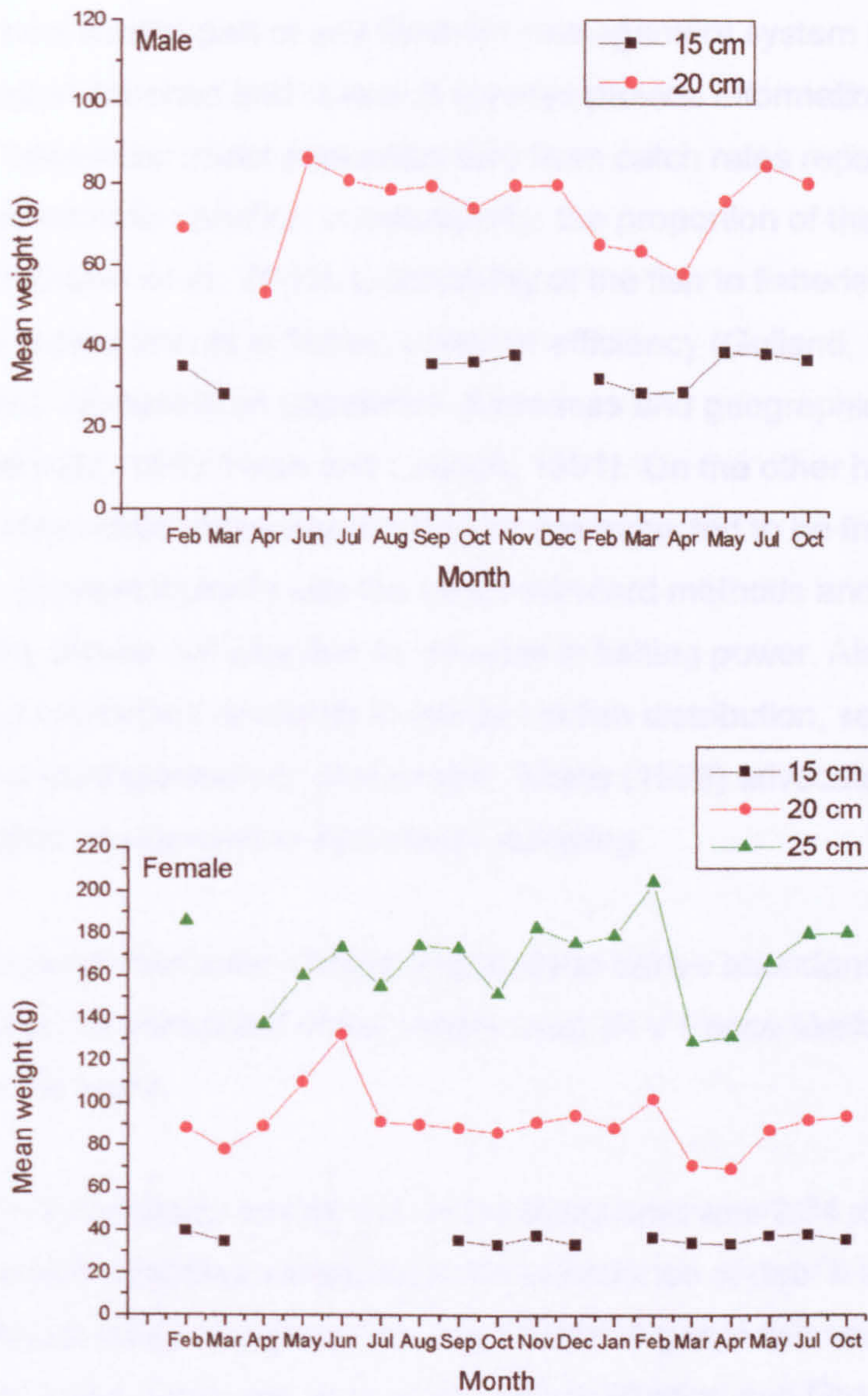
Year	Sex	a	b
1995	Male	0.016	2.890
	Female	0.014	2.916
	All sex	0.015	2.901
1996	Male	0.009	3.055
	Female	0.008	3.0990
1997	Male	0.006	3.160
	Female	0.013	2.940
	All sex	0.009	3.060
1998	Male	0.011	2.960
	Female	0.012	2.990

Figure 2.11. Length and weight relationship in female dab on the North Wales Coast, October 1979.



Seasonal changes in the mean weight of both male and female dab are represented in Figure 2.12 for three sizes of fish. It can be observed that there is a significant decline in weight in the bigger, larger fish (20 and 25 cm) after spawning between February and April. These variations are not distinct in the 15 cm females since immature fish that do not exhibit seasonal cycles in gonad condition dominate this size group. In males, however, comparatively significant numbers are mature at 15 cm and thus show a decrease in weight at this time.

Figure 2.12. Seasonal variation in the mean weight of different sizes of male and female dab on the North Wales Coast, 1999-2001



2.4 DISCUSSION

One of the central problems in fishery stock assessment is to obtain an abundance index that is proportional to stock size and which will reflect stock trends and longer term responses to changing management regimes. Deliberate surveys aimed at measuring relative abundance patterns should be a central part of any fisheries management system (Hilborn and Waters, 1992). Catch rates in fisheries and research surveys provide information on variation in fish population size. Inferences about population size from catch rates reported from fisheries are complicated by systematic variation in catchability, the proportion of the population captured by a unit of effort (Swain *et al.*, 2000). Catchability of the fish to fisheries usually increases over time due to improvements in fishing power or efficiency (Gulland, 1983); it can also be density dependent, increasing as population decreases and geographic range contracts (Crecco and Overholtz, 1990; Rose and Leggett, 1991). On the other hand, abundance indices inferred from research survey catch rates are expected to be free of these difficulties (Gulland, 1983). Surveys typically use the same standard methods and gear each year, so survey catchability should not vary due to changes in fishing power. Also, fishing during surveys is usually conducted randomly in relation to fish distribution, so catchability should not vary due to range expansion or contraction. Krebs (1989) advocated random sampling within a survey area as opposed to systematic sampling.

Such a fisheries survey has been used in this study to derive abundance estimates. The survey method and the particulars of the vessel used (R.V Prince Madog) have not altered significantly over 29 years.

The total estimated population size of dab in the study area was 2.34×10^6 . There are however considerable seasonal variations in the abundance of dab. It should also be noted that this estimate includes the 0-group fish and smaller 1-group fish which may have been underrepresented in the catch due to mesh selectivity (Basimi and Grove, 1985a). Indeed, Basimi and Grove showed that these sizes of plaice are not fully represented in the catches due to mesh selection. An earlier population estimate of dab, in the same area, had been made by Bakhsh (1982) as 1.20×10^6 . This suggests an increase in population number of about 95 %. It should however be noted that Bakhsh omitted the 0-group and 1-year old fish from his estimate because of the problems of mesh selectivity. Thus, when 0-group and 1-year old fish are also omitted from the present estimates, the total population number will be 1.36×10^6 which agrees closely with Bakhsh's estimate. This observation suggests that the dab population in the survey area has remained relatively stable over the past 20 years.

A study by Rijnsdorp *et al.* (1992) showed that the average catch rate was 2943 dabs hr^{-1} in the Southeast North Sea. This is almost twice as much as the peak nightly catch rate in this study (1549 dabs hr^{-1}). Lozan (1988) also found that in winter, the density of dab in the North Sea was 50 kg hr^{-1} (equivalent to about 180-200 dab hr^{-1}). In Icelandic waters, the catch per hour varies from 14 to 122 dab hr^{-1} between stations (Jonsson, 1966).

The present study appears to suggest seasonal variation in local catch rates, with the peak catch rates occurring in autumn-summer, whilst lower catch rates were observed during winter and spring. It is thus likely that temperature may have an effect on the abundance and distribution of this species. Also, in the commercial fishery in the survey area, catches were so poor during the winter period that extra supplementary samples were difficult to obtain. Jonsson (1966) observed that in, winter, the Icelandic dab seeks deeper waters. Bohl (1957) and Lee (1972) also observed that, as winter approaches, the North Sea dab move away from rapidly cooling coastal waters towards the open seas. Campos *et al.* (1994) and Bolle *et al.* (1994) observed that in the North Sea, the flatfish larvae abundance become relatively low during winter.

Other factors, which affect the abundance of dab, have been reported. Power *et al.* (2000) investigated the factors affecting flatfish abundance and found that dab abundance was significantly related to seasonal environmental variables such as suspended solids, oxygen, and the abundance of the prey, *Crangon crangon*. Tidal levels have also been noted to exert marked effects on the catch rates of dab (Hempel, 1964). Hempel observed that trawling during flood-tides gives higher catch rates of *Limanda limanda* in inshore waters. Rijnsdorp *et al.* (1992) attributed fluctuation in abundance levels to seasonal migration of adult dab between offshore waters and coastal spawning grounds in the North Sea. They observed increased catch rates in the coastal waters but the catch rates decreased further offshore. This concept is also supported by Ortega-Salas (1988b) for the Irish Sea dab. Dabs were mostly found to be non-existent in offshore waters ≥ 30 m in the present study. Htun-Han (1978b) stated that North Sea dabs are greatest in numbers in sand banks at depths of 20-40 m but Lee (1972) reported that its range can extend up to 200 m in the North Sea.

It has been reported that dab larvae are the most abundant among the flatfish larvae in the North Sea (Campos *et al.*, 1994). Surveys to determine larval abundance have not yet been carried out in the project area and therefore comparison could not be made with the North Sea. In order to determine the annual recruitment of this species in the study, a young fish survey might be an area worthy of future investigation.

There is evidence of diel periodicity in abundance in this study. The catch rate was significantly higher at night (22.00-02.00 hr) than day-time. This finding supports the observation made by Parrish *et al.* (1964) that the catches of dab were higher in the Moray Firth in darkness than by day. Woodhead (1964) observed that greater number of dabs were caught during the first haul after sunrise in the North Sea. The increased catch rate at night might also be explained on the opportunistic feeding habit of dab (Kaiser and Ramsay, 1997). Kaiser and Spencer (1996) and Ramsay *et al.* (1996) have demonstrated that dabs migrate into areas of sea bed that have been disturbed by trawling activity.

There is also a decline in catch rates in dab number with increasing length in males (> 20 cm) and females (> 25 cm). This observation is consistent with the historical data (Figure 2.4). The decline in catch rates with increasing length of dab (> 15 cm) in the North Sea was attributed to size-selective mortality (Rijnsdorp *et al.*, 1992). The absence or poor representation in catches of the smaller dab (< 10 cm) was also reported by Bohl (1957) for the North Sea. Mesh-size selection was partly responsible for this. The modal length for the dab populations in the study area fluctuates within a narrow range of 16-21 cm between 1999-2000. This agrees well with the results of Bakhsh (1982). The presence of modes at 15 cm between July and November probably indicates the arrival of 'New Recruits' into the fishery from the nursery groups. Campos *et al.* (1994) also found that dab spawn during the winter and spring months in the southeastern North Sea, showing a peak in late April. They noted that juvenile dabs are dependent on coastal nursery areas, but metamorphosing dab are known to settle in deeper waters and begin entering the coastal areas only as juveniles in summer and autumn. Rijnsdorp *et al.* (1992) concluded that the majority of the dab of length 6-16 cm that settled in the open seas in the North Sea are recruited from coastal nursery grounds. In the present study, the length distributions in all months were dominated by size groups of 16-20 cm and few dab smaller than 10 cm or bigger than 30 cm were caught. This structure is reflected in the historical data on length composition of dab in the study area, possibly suggesting there may not have been any serious perturbation of the dab population over this time. This size distribution is also similar to that reported by Rijnsdorp *et al.* (1992) for the North Sea dab population. In the historical data, the proportions of size groups > 15 cm increased dramatically in the populations sampled between 1975 and 1985. The contribution however declined significantly afterwards. These observations could be attributed to 1) either a beam trawl was used in the 1980s in the survey area or 2) strong recruitment pulses during this period or 3) sampling artefact due to varying "patchiness" of size groups. The argument in favour of recruitment is not likely to be substantiated since the proportion of the adult dab population, which could have benefited from such recruitment

pulses, in the proceeding years in early-1990s to mid-1990s did not subsequently reflect that (Figure 2.4).

Sexually matured dab can be observed at a length of 11 cm and 15 cm in male and female dab respectively, thus the catches represent mainly the mature part of the recruited population. There are monthly variations in sex ratios. The long-term trend in the variability in sex ratio in the study area showed that the male proportions increase in spring and summer but decline significantly during the cold season and this was in agreement with the present study and studies in the North Sea. Seasonal variations in sex ratios have been reported by Bohl (1957) and Saborowski and Buchholz (1997) for the North Sea dab. Saborowski and Buchholz, 1997 also observed reduced number of males in autumn and winter. They attributed the reason to seasonal migrations towards the coast and back to offshore areas for feeding and spawning purposes. After spawning, the females return to the coastal areas whilst the males remain in deeper waters. Simpson (1959a) suggested that the influx of large number of juveniles from the adjacent nursery area into the sampling area may alter the sex ratio substantially in flatfish populations. Another important factor is differential mortality of the sexes due to their distribution in the sampling area. However, in the summer flounder, no segregation of sexes was observed during any phase of their annual or seasonal cycle of distribution (Morse, 1981). Morse however maintained that the paucity of males in the larger size groups was the result of differential growth rate and a greater maximum age of the females. It was also observed that the natural mortality rates of the males increase 'dramatically' after ages 4 and 5 years.

The present study found no significant difference ($P>0.05$) in the median anal fin count and the dorsal fin count between samples of male and female dab. There were also no significant differences ($P>0.05$) in the dorsal fin and anal fin counts between the present study and the earlier study by Bakhsh (1982). Comparison of meristic characters between different dab populations shows that the mean dorsal fin ray count in the South and Southwest Icelandic waters (higher) and the Baltic Sea (lower) differ significantly ($P<0.05$) from the dorsal fin counts in the present study. The mean dorsal fin count in the North Icelandic waters and North Sea is not significantly different from that of the present study. The mean anal fin counts in the Icelandic waters (higher) and the Baltic Sea (lower) differ significantly ($P<0.05$) from the anal fin count in the present study. However, the anal fin counts in the North Sea are not significantly different ($P<0.05$) from the anal fin count in the present study. The mean vertebral counts in the adult dab population in Icelandic waters and the North Sea are not significantly different ($P>0.05$) from the present study. Jonsson (1966) found that the meristic counts in Icelandic dab were generally higher than the North Sea and Baltic Sea dabs. He

made the observation that the fishes in the northern regions differ from the more southern fishes of the same species, in having higher numbers of vertebrae, dorsal fin and anal fin rays. The results of these comparisons should be treated with caution since the data in the present study were not normally distributed and thus valid comparison should be made with the median and not means. But the use of comparison using the mean counts is necessitated by the fact that only mean counts of meristic racial characters were available for the Icelandic waters, Baltic Sea and the North Sea dab populations. Environmental factors like temperature, light, density of water column, salinity and current have been claimed to influence the racial characters in fish populations (Jensen, 1937, 1939; Nikolsky, 1963). Rasmussen *et al.* (1999) found that interannual variability can be significant for vertebral numbers and concluded that sampling year could have a pronounced effect on meristic characters. A study of meristic characters was made by Lozan (1988) in different areas of the North Sea. He found that significant fluctuations in the number of fin rays can occur from year to year, whilst there was little or no variation in the vertebral count.

The studies of body proportions indicate a linear relationship between total length against head length or body depth and that the multiplicative factors used to predict head length from the total length in male and female are significantly different ($P < 0.05$). Similarly, the multiplicative factors for predicting body depth from total length are significantly different ($P < 0.05$) between the sexes. Bakhsh (1982) however used an inappropriate power model and could find no significant difference in the slopes and intercepts of the regression of body depth and fish length between the sexes and claimed that growth in body depth was isometric with growth in fish length. He also showed that the dabs in Anglesey waters were found to have a relatively longer head length than those of the Baltic Sea; and that the body depth in this area was intermediate in value between those for the Belt Sea and Western Baltic (Jensen, 1937).

The common exponent of the length/weight relationship is 2.911 and 3.036 for male and female dab respectively, indicating that growth of dab in the Anglesey waters is nearly isometric. Monthly values could therefore be taken as a measure of the condition of the fish (Basimi and Grove, 1985a). As the spawning season progressed, running and spent fish become significantly different in condition in March and April from other groups ($P < 0.05$) since they lost extra weight as a result of spawning. Fully ripe females could also become significantly heavier in weight as a result of adding extra weight due to increased ovary weight and as a result of increased oocyte diameter. Thus fluctuation in the weight changes in the female component is principally due to changes in the mature females. There is a drastic reduction in weight in the mature female after spawning in March and April (Figure

2.12). On the contrary, there is little or no weight change in the immature female. The male dab also gained weight between December and January, when they are fully ripe, with increased size of testes as a result of milt formation. The mature male also suffers weight loss in the postspawning period in March and April. Statistical comparison in the exponents of the length/weight relationship between the male and female dab shows that they differ significantly ($P < 0.05$) in condition between October 1999, November 1999 and February 2000. Growth in weight was either isometric or positively allometric in October, November and February in the female dab but growth was isometric or negatively allometric in the male during this period. This observation is possibly due to different timing of the gonad development, spawning time and feeding rate (as will be demonstrated in Chapters 4 and 5) in the male and female dab in autumn and winter. Growth in weight in relation to length was negatively allometric in both sexes in the postspawning period in spring (March and April). This seasonal variation has also been demonstrated by workers like Chuenpagdee (1990) for the Irish Sea female plaice and Ortega-Salas (1980) for the Isle of Man dab. Ortega-Salas showed that the maximum value of the condition of dab was obtained around August-September and minimum after spawning in May. Basimi and Grove (1985a) noted that the loss in individual body weight in plaice which occurs in winter is caused by decreased feeding rate, loss of body reserves for maintenance requirements and the loss of reproductive products during spawning. These conditions thus lead to considerable changes in condition factors. Bagenal (1957b) conducted length and weight studies on the long rough dab, *Hippoglossoides platessoides* (Fabr.), and also showed monthly variations in the condition of the fish. He observed that all groups of the fish tend to be in good condition in November and December but the condition declined in spawning time in March and April, and after which there was a recovery. Monthly length/weight relationships of juvenile plaice were examined by Nash *et al.* (1992) and they found the relationships were fairly stable through September 1989 to March 1990. However there was a decline in weight-per-unit length from December to March. Detailed studies on the seasonal variation in condition factor (in relation to spawning activity) in male and female dab are undertaken in Chapter 4.

Seasonal and long-term variation in growth and mortality rates in dab are examined in the next chapter.

CHAPTER THREE

Growth and Mortality Rates of *Limanda limanda* L.

3.1 INTRODUCTION

The analysis of the population structure of species is of primary importance in developing an optimal strategy for its efficient management (Coyle, 1998). Growth in size is a major component of biological production and the problem of 'growth overfishing' (taking too many fish when they are too small) cannot be ignored in many fisheries. Information on body size might contain useful information about longevity, mortality and variation in recruitment rates (e.g. presence of strong modes in the length frequency distribution); see Hilborn and Waters (1992).

Accurate age determination and reliable validation techniques are important components of growth studies in fish populations (Joyeux *et al.*, 2001). Growth models form a central part of population models for stocks where growth is a major component of production. Prediction of growth in a natural population of fishes is an important facet of many applied problems in fisheries management. As a first approximation it might be expected that age would be an adequate criterion of size and growth potential. However, the rates of growth of fishes are influenced by environmental conditions such as relative abundance of food, relative density of population and temperature (Fonds *et al.*, 1992) as well as by sex. Age is thus only a relative index of size or growth rate in relatively constant environments.

Mathematical models have been used to describe the growth pattern of fish. These have involved finding out the expression that best describes age versus length and age versus weight data. Annual growth rate decreases with increasing fish size and this relationship of juvenile and adult flatfish growth (both in weight and length) can be described by the Von Bertalanffy growth equation (e.g. Beverton and Holt, 1957). The non-seasonal Von Bertalanffy growth function (Von Bertalanffy, 1938) has regularly been used to describe growth in fishes, crustacean and molluscs. The parameters of the models are easily incorporated into models of stock assessment. The size L_t of the fish at any time t is given by:

$$L_t = L_\infty(1 - \exp^{-K(t-t_0)}) \text{-----}(3.1)$$

Where:

L_∞ = asymptotic size of the fish if it grows indefinitely

K = instantaneous growth constant or curvature parameter and is the rate at which L_∞ is approached

t_0 = theoretical age at zero length of the fish

Thus, the Von Bertalanffy growth function contains these three parameters which must be estimated to be able to fit the model of age/length data. There are various ways of fitting the model to age/length data.

i. Graphical methods

The commonly applied graphical methods include the Ford-Walford plot (Ford, 1933 and Walford, 1946), the Gulland and Holt plot (Gulland and Holt, 1959) and Von Bertalanffy plot (Von Bertalanffy, 1938). The Ford-Walford method is a plot of fish length at the end of the incremental period plotted against the length at the beginning of the corresponding incremental period. The Gulland and Holt plot is based on the observation that the annual increment in length declines linearly with increasing age of fish. Fish increase in length as they grow older, but their growth rate declines. This means that their increment in length per unit time decreases when they get larger, approaching zero when they become old (Sparre and Venema, 1998). The Von Bertalanffy plot method however requires an initial input of L_∞ which can be obtained from the Powell-Wetherall plot (Powell, 1979; Wetherall *et al.*, 1987) or, in fish under low exploitation, from the observation of the largest fish in the sample.

The above graphical methods have often been criticised since they do not take into account seasonal growth and also they mostly involve manual fitting of the data. Bias is also caused during transformation of the original data sets.

ii. Non-linear least square method of fitting Von Bertalanffy growth equation

In the graphical methods, growth parameters are normally estimated by converting the VBG equation to a linear form and frequently using linear regression analysis. A more direct technique can, however, be used such as the non-linear curved regression method wherein the growth parameters are estimated in a way so that the sum of squares of deviation

between the model and the observation (that is between the data points and the resultant growth curve) is minimised (Hilborn and Waters, 1992; King, 1995; Sparre and Venema, 1998). That is the sum is minimised with respect to the parameters L_{∞} , K and t_0 . The mathematical expression is illustrated below (Sparre and Venema, 1998).

$$\sum_{i=1}^n [L_i - L_{\infty}\{1 - \exp(-K(t_i - t_0))\}]^2 \text{ -----(3.2)}$$

Where:

n =Number of observations

L_i =Length of fish number i

t_i = Age of fish number i

$i = 1, 2, 3, \dots, n$

This robust and objective method for growth parameter estimation in fish has been widely acclaimed and is now in greater use in fish growth estimations (Gayanilo *et al.*, 1996; Sparre and Venema, 1998; Grove, pers. comm.). It is iterative and can only be handled conveniently with the aid of a computer. The technique avoids the necessity of using simple algebraic formulae to estimate the VBGF parameters, and based on a direct search for the parameters that best fit length-at-age data; that is the values of K , L_{∞} and t_0 that best fit the curve. A computer is thus best suited for such trial in locating the best fit.

iii. Mortality rates

One of the most commonly used methods in temperate waters for the estimation of total mortality is the catch curve analysis (Beverton and Holt, 1956; Chapman and Robson, 1960; Robson and Chapman, 1961; Ricker, 1975; Pitcher and Hart, 1982; Pauly, 1984). The catch curve is a graphical representation of the logarithm of numbers N_t in various age groups plotted against their corresponding age t .

The most useful way of expressing the decrease in number through time is by means of the exponential decay model of the type:

$$N_t = N_0 \cdot \exp^{-Zt} \text{ ————— (3.3)}$$

Where:

N_0 = initial number of fish at time $t = 0$

N_t = number of fish remaining at time t

Z = instantaneous coefficient of total mortality rate (time^{-1})

The relationship conforms to a simple linear regression of the form when transformed logarithmically:

$$\ln N_t = \ln N_0 - Z t \text{ ————— (3.4)}$$

Z is estimated from the slope, with sign reversed, from the descending right arm of the plot.

The following assumptions are made in the catch curve analysis:

- a) Z is constant for all selected age groups in the regression
- b) There is minimal or no recruitment fluctuation for the recruited age groups. This means that they have the same abundance at the time of recruitment
- c) All recruited age groups are subject to the same catchability by the gear used for sampling
- d) The sample is representative of the average population

Some of these assumptions are clearly unrealistic. In view of these, it is normal in catch curve analysis to exclude those age groups which are suspected of not being under full exploitation due to either i) mesh selectivity ii), they are still in the nursery grounds and not fully recruited to the fishable population and/or (iii) a previously poor year-class. The older fish may also be excluded since the estimated abundance is normally subject to great uncertainty; there may be fewer of them due to fishing and natural mortality and older fish may become less vulnerable to one or more gears. For instance, they may swim faster so that they can easily escape the trawl (Sparre and Venema, 1998).

As with growth curves, a catch curve is best analysed by non-linear methods.

The total mortality can be broken down into mortality due to fishing (F) and mortality due to natural causes (M). However, differential movement of fish by age into and out of the study area can distort the estimate of Z independently of the M and F .

$$Z = F + M \text{ ————— (3.5)}$$

Estimates of natural mortality rates are essential for the management of commercial fisheries. Among the standard techniques requiring M as input parameters are yield per recruitment analysis (Beverton and Holt or Thompson and Bell analytical methods) and Virtual Population (or Cohort) Analysis), both of which are sensitive to errors in M . The value of M greatly affects the behaviour of the yield function of an exploited fish population (Beverton and Holt, 1957). Overestimating M will underestimate the fishing mortality and overestimate stock sizes. Conversely F is overestimated if M is underestimated. In view of this, whenever possible, M is estimated using several methods.

3.2. MATERIALS AND METHODS

3.2.1 Age determination

The age of individual fish was determined from the alternating opaque and hyaline bands on each otolith pair. Saggital otoliths were removed from the sacculus after making a transverse incision behind the skull. Fibrous material was removed from otoliths, which were cleaned in distilled water and dried. Otoliths with very rough surfaces were gently rubbed on a hard and clean surface. This is intended to remove any debris settling on the surface of the otolith. Each otolith was immersed in a 'histo-clear' solution in a solid watch glass and viewed under transmitted and/or reflected light under a low power microscope. Age determinations are based on a 1 April hatch date with first year fish designated as age 0 and second year as age 1, up to eighth year as age 7 (Ortega-Salas, 1980; Bakhsh, 1982; Basimi and Grove, 1985a). Ages were determined on two separate occasions, and ages were selected that were consistent on both occasions. The consistency was over 95 %. An age-length frequency key was used to estimate age composition from length frequency data.

3.2.2 Otolith accretion and seasonal growth

The aim of this study was to determine the time of year in which otolith growth zones were laid down. The study was thus focussed on the edge of the otolith. In this regard, otolith pairs were allocated to one of four classes every month (Basimi and Grove, 1985a):

- Stage I: The first faint traces of new opaque material was visible on the tip of the otolith
- Stage II: The opaque material was noticeable but made a fine, incomplete ring

- Stage III: The opaque ring was complete and extensive
 Stage IV: The otolith had an extensive hyaline outer layer

3.2.3 Estimation of growth rate

3.2.3.1 Seasonal growth in length and weight

Study of seasonal growth in length and weight was limited to cohort components I-IV since these comprise the vast majority of the populations in both sexes and also because of their comparatively high growth rates. Also there are considerable fluctuations in the estimated mean length at age in the older cohorts.

The seasonal growth of dab was fitted to the formula (Basimi and Grove, 1985a):

$$L_t = L_n - G'e^{-K't} \text{-----}(3.6)$$

Where:

- L_t = Total length in cm on day t after 1 April in the nth year of life (otolith age)
- L_n = Asymptotic length in cm for that age group
- G' = Total increment in length for that age group from the previous year
- K' = Instantaneous seasonal growth rate

The seasonal growth in weight by a cohort group was determined from the seasonal growth in length from the equation above and using the seasonal length/weight relationships, described in Chapter 2. The number of days (t) was computed from 1st April (as birthday of the fish).

3.2.3.2. Annual growth rates

The parameters of the Von Bertalanffy Growth function of male and female dab were estimated by non-linear least square method (Microsoft Origin 5.0 Software).

The annual growth in weight is obtained from the relationship between length and weight, modified by substituting L_t of the VBGF. This involves combining the VBGF with a power model for length and weight relationship, $W_t = aL^b$ to obtain the VBGF curve for growth in weight:

$$W_t = a \left[L_{\infty} (1 - \text{Exp}^{-K(t-t_0)}) \right]^b \text{-----}(3.7)$$

Where *a* and *b* are parameters of the length/weight relationship

The annual instantaneous rate of growth (*G*) in weight of each age group (taken as 1 stanza) was calculated from the following formula:

$$G = \text{Log}_e \left(\frac{W_{t+1}}{W_t} \right) \text{-----}(3.8)$$

Where W_t = weight at *t* years
and W_{t+1} = weight at *t*+1 years

3.2.4 Estimation of mortality rates

The instantaneous rate of total mortality coefficient (*Z*) for each sex was estimated from the exponential model, using the catch curve analysis. The estimation was based on 'pseudocohort' analysis (one-sample analysis including several cohorts). Total mortality rate in the historical data was estimated by progressively following the fate of a cohort over its life span in successive surveys. The instantaneous rate was converted, for illustration, into percentage mortality (*P*) from the following formula (King, 1995):

$$P (\%) = 100(1 - \text{exp} (-Z)) \text{-----}(3.9)$$

Because no data was available to relate *Z* to total fishing effort in the local area, the rate of natural death (natural mortality, *M*) suffered by the dab, other than fishing, was estimated by following empirical methods:

a) Pauly (1980) related *M* to growth parameters (L_{∞} and *K*) and the ambient temperature ($T^{\circ}\text{C} = 8^{\circ}\text{C}$) of the water column.

$$\text{Ln } M = -0.0152 - 0.279 \text{Ln} L_{\infty} + 0.6543 \text{Ln} K + 0.463 \text{Ln} T^{\circ}\text{C} \text{-----}(3.10)$$

b) Gunderson and Dygert (1988) related M to the gonadosomatic ratio:

$$M = 0.03 + 1.68 \left(\frac{\text{Gonad wt.}}{\text{Somatic wt.}} \right) \text{-----} (3.11)$$

An evaluation of the various methods of estimating M has been carried out by Gunderson and Dygert (1988) and they have concluded that gonad-somatic weight was superior to any of the life history parameters (K , L_{∞} , $L_{50\%}$ or $A_{50\%}$) in predicting natural mortality rates. The precision could be improved by using dry weight of gonad and somatic tissues and also by selecting fish with fully developed gonads. Gonad samples were therefore taken during the breeding season and dried.

c) Beverton and Holt (1959) demonstrated that the ratio of natural mortality rate to growth rate in flatfish is given by the relationship:

$$1.5 < M+K < 2.5$$

This relationship could therefore be considered as an indicator of the reliability of the method used. The biological interpretation is that high natural mortality rates are normally associated with higher initial growth rate (K).

Fishing mortality is estimated from:

$$F = Z - M \text{-----} (3.12)$$

and Exploitation rate (E), that is rate of capture, from:

$$E = F+Z \text{-----} (3.13)$$

This is the proportion of death due to fishing. When $E \geq 0.5$, then the stock is considered likely to be overexploited (Gulland, 1984). But there should be cautious application of this interpretation since the estimate of Z may likely include emigration from our coastal (nursery) zone, thereby overestimating the rate of capture (E) in the fisheries.

3.3 CURVE FITTING

Non-linear curve fitting was carried out using the computer software Microsoft Origin v.5.0 and Biosoft (FigP v. 2.7) based on the Levenberg-Marquardt Algorithm and, where necessary, the Simplex minimisation method as well.

3.4 RESULTS

Figure 3.1 shows growth zones on the otoliths of dab. The four otolith conditions, depicting seasonal deposition of the opaque zones are shown in Figure 3.2. Fully and partially crystalline otoliths are illustrated in Figure 3.3. Studies of the seasonal occurrence of the four otolith conditions in this study show that growth in dab in our area starts in February, with the appearance of first traces of the opaque zones. By April, over 70 % of the fish have either started deposition of the opaque zones or increased the extent of the opaque zones. By May, the majority of the fish (about 64 %) have extensive opaque material (Figure 3.4).

Figure 3.1. Growth zones on the otoliths of dab, aged between 0 to 8 years, on the North Wales Coast (A, C-I: 12.5 x Magnification; B: 11.5 x Magnification)

- A. Age group 0**
- B. Age group 1**
- C. Age group 2**
- D. Age group 3**
- E. Age group 4**
- F. Age group 5**
- G. Age group 6**
- H. Age group 7**
- I. Age group 8**

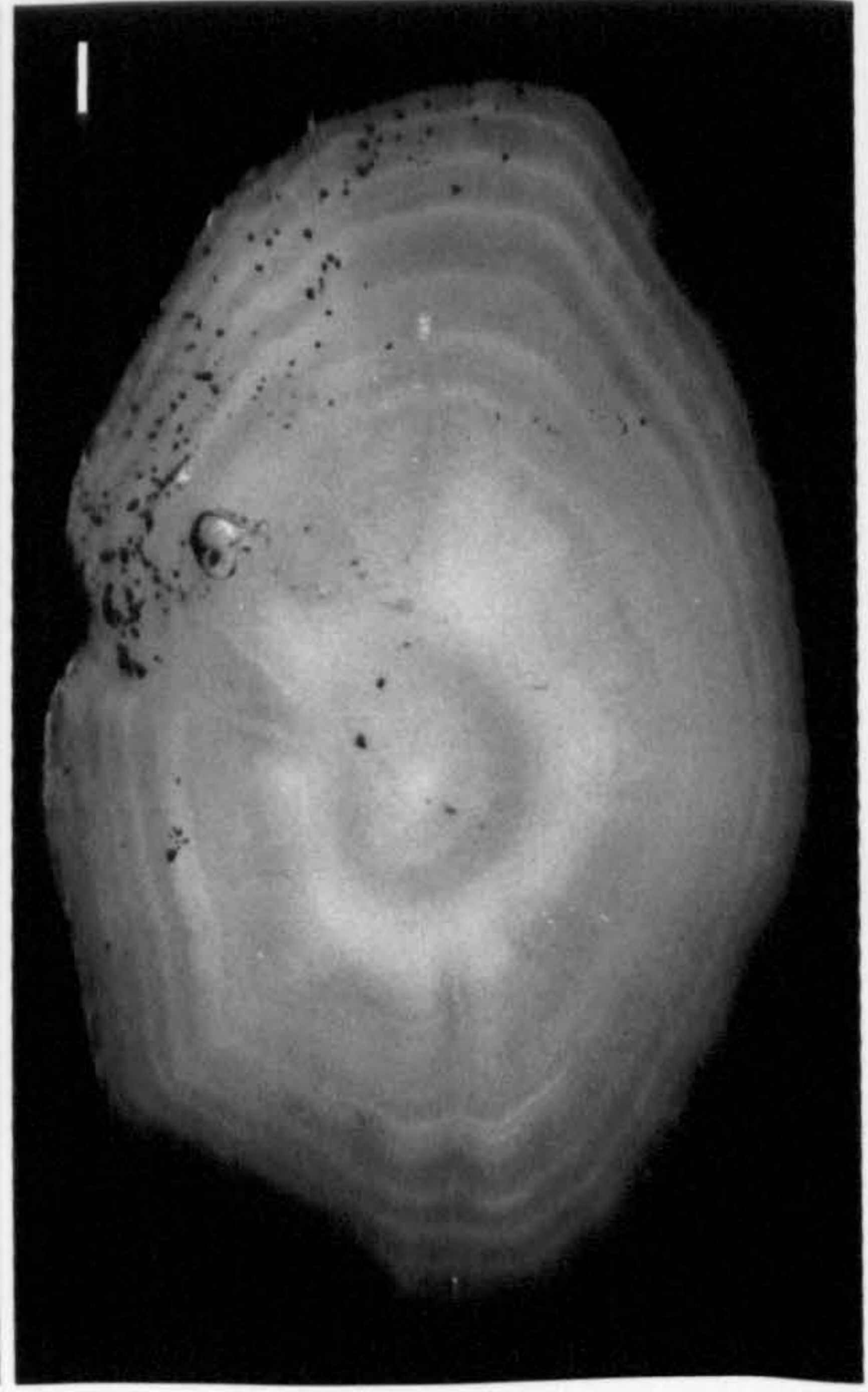
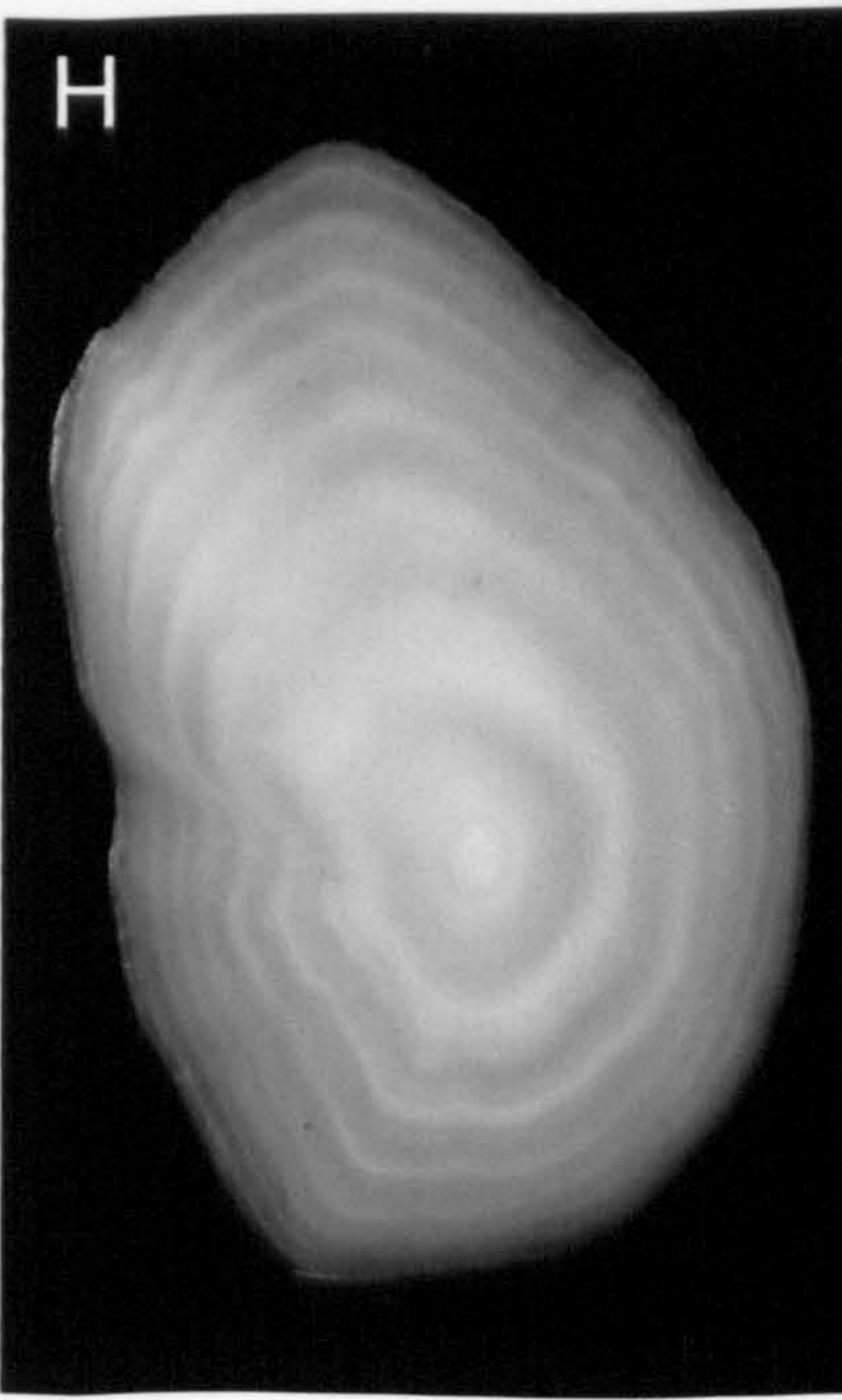
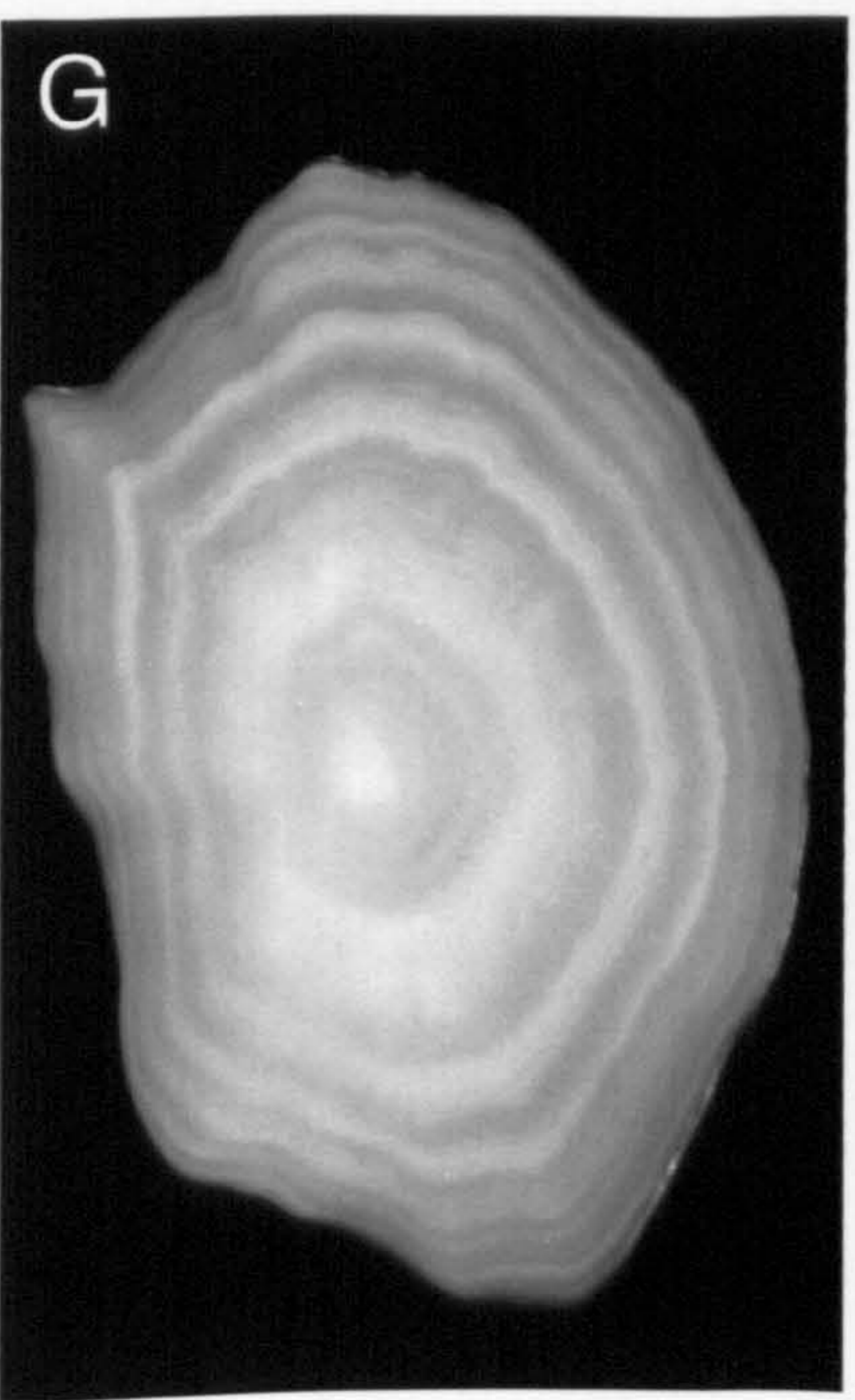
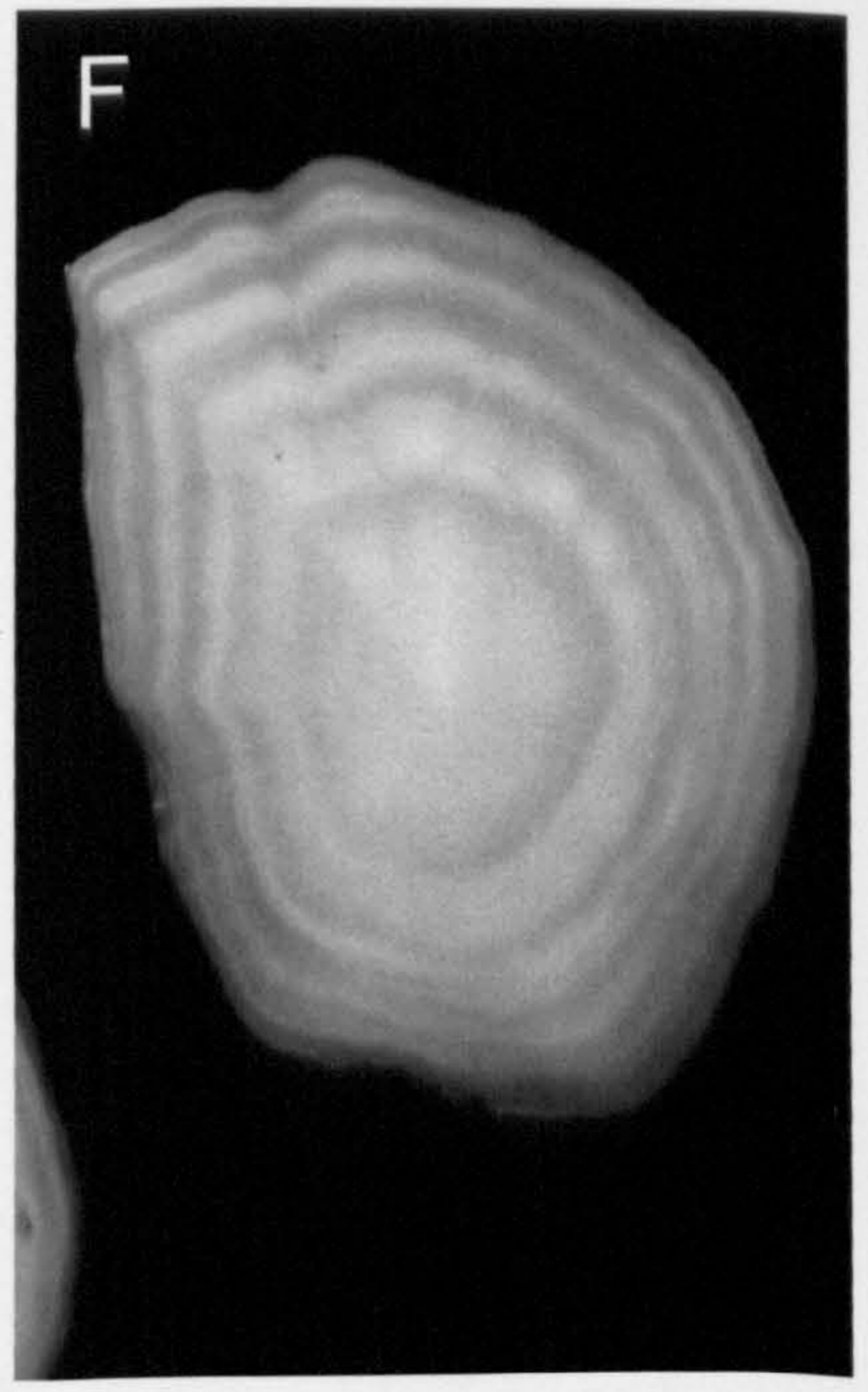
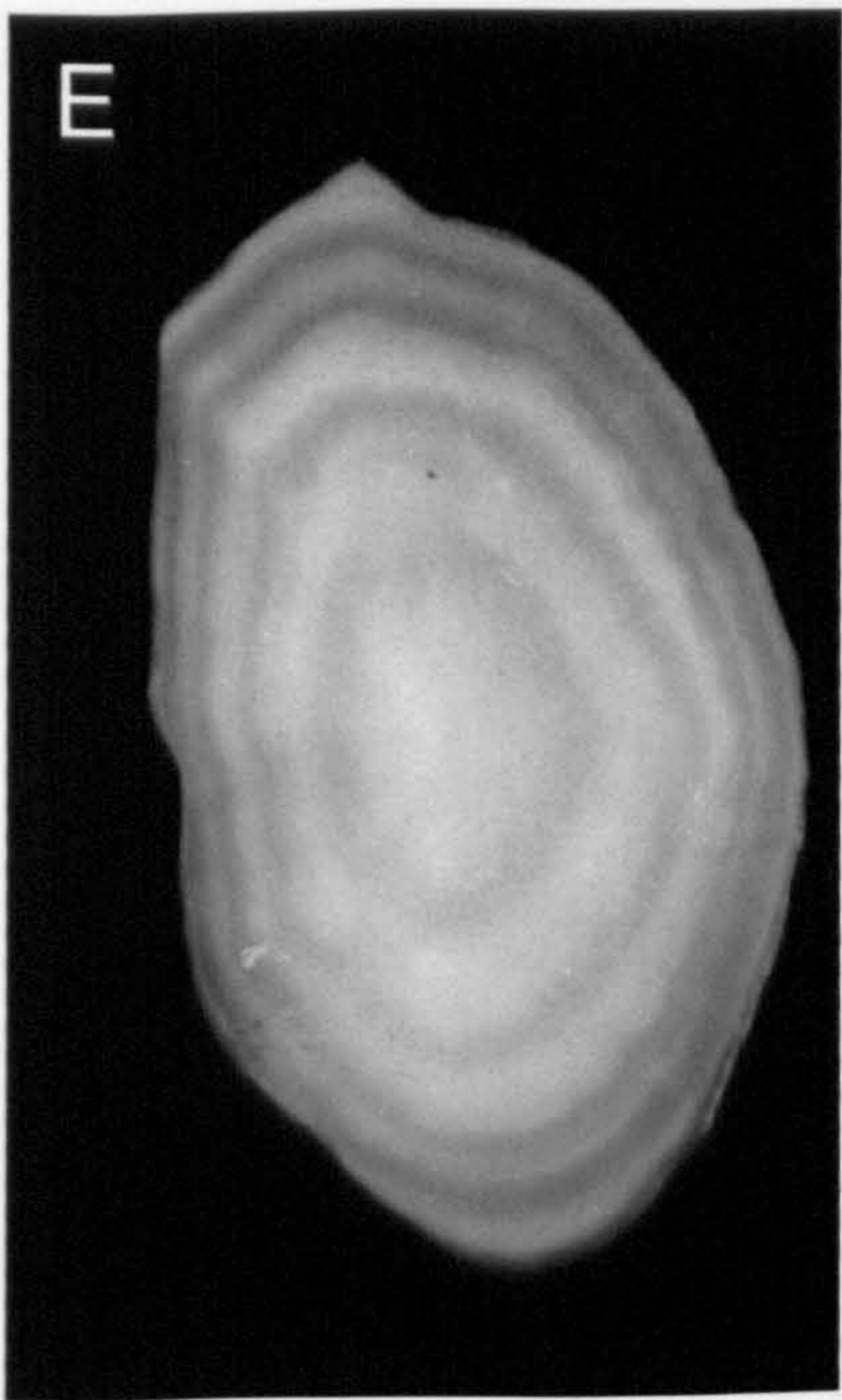
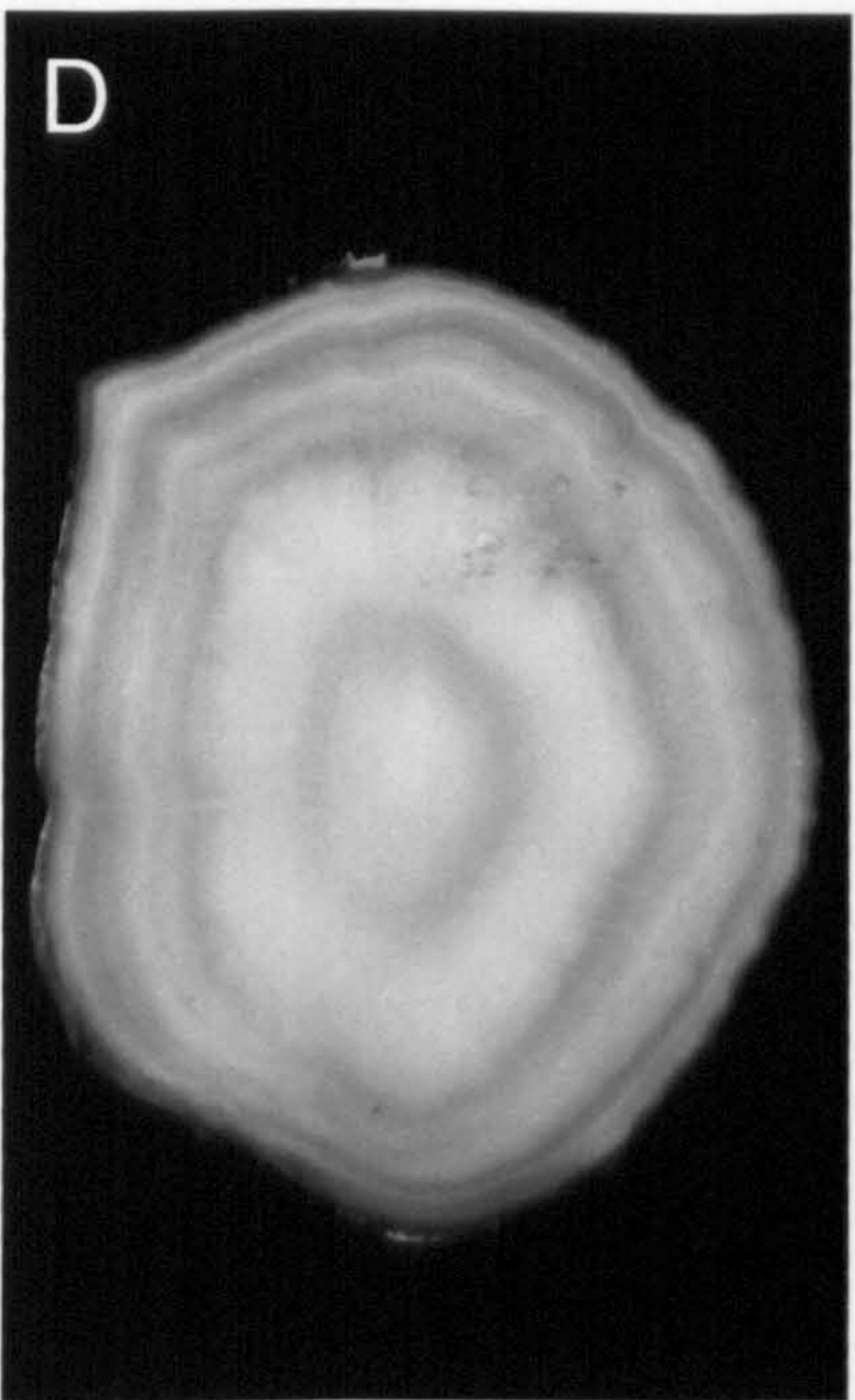
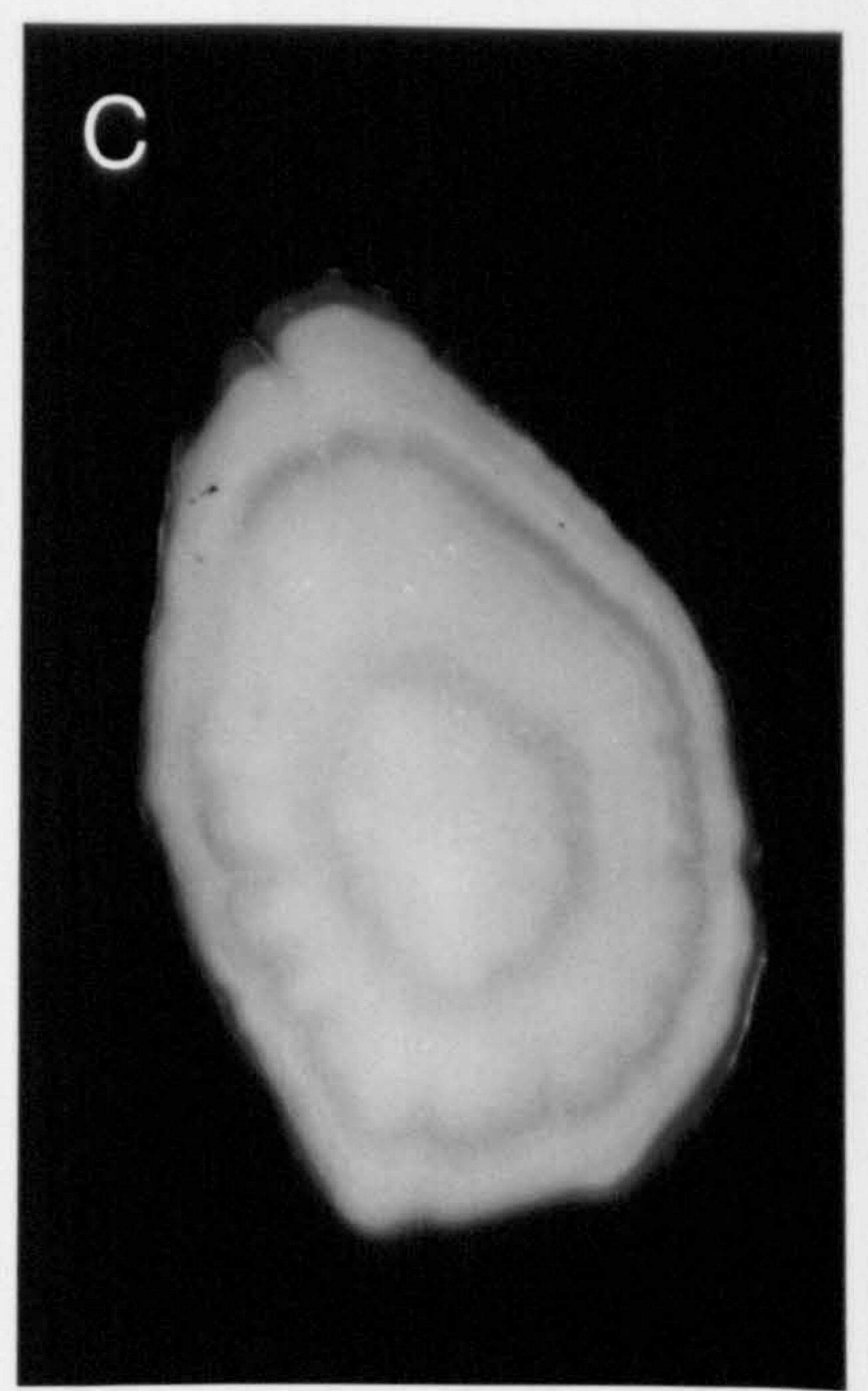
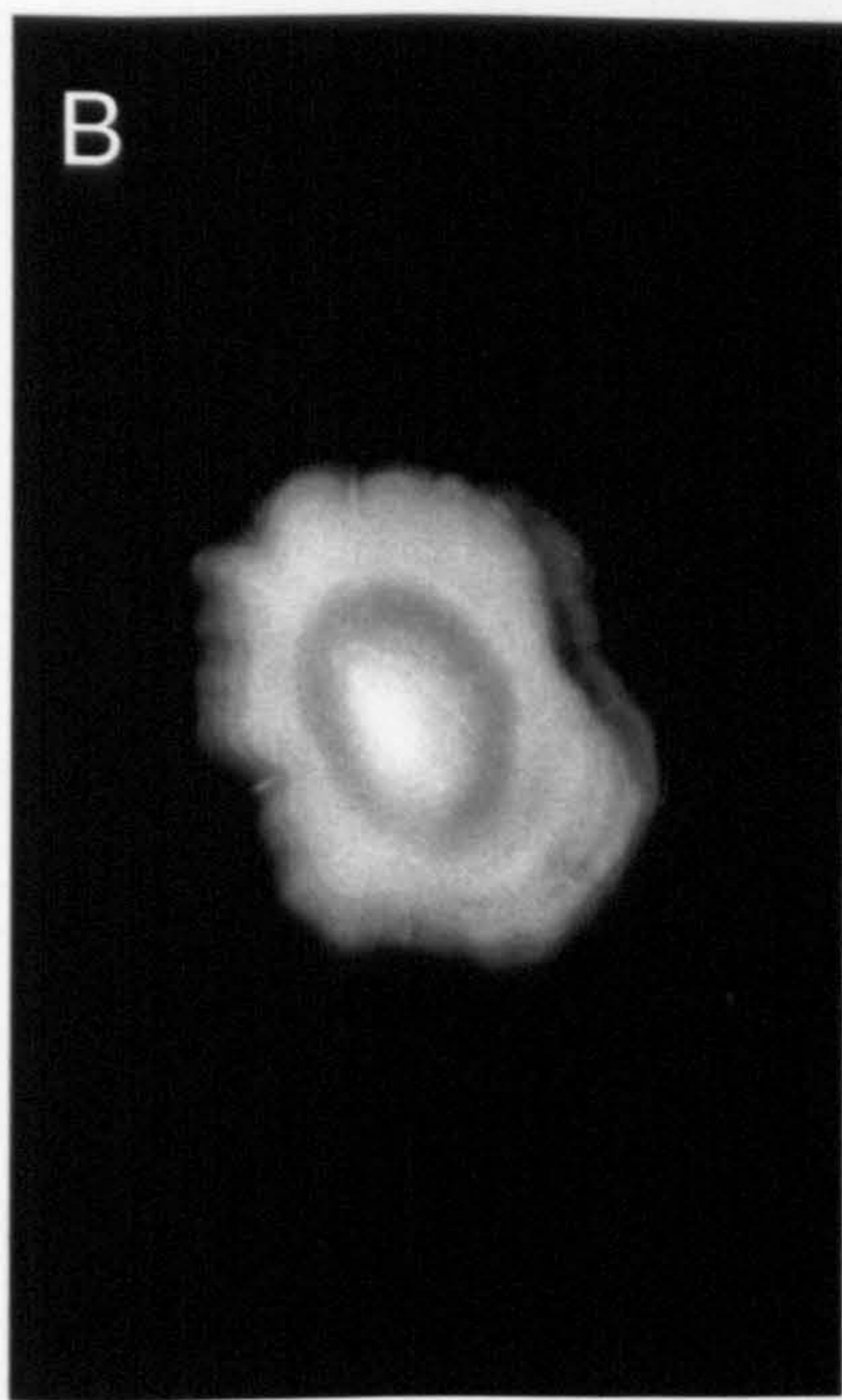
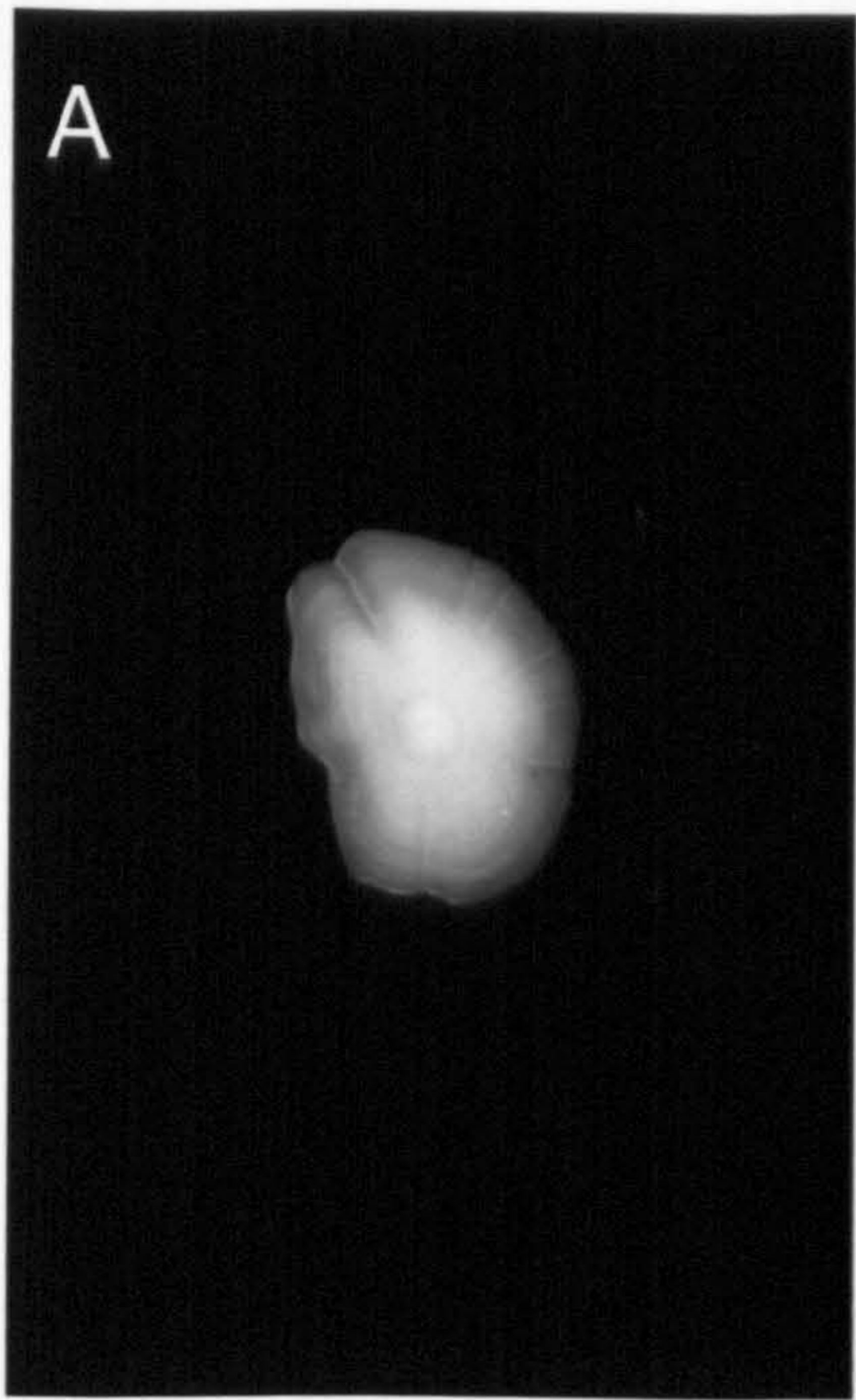


Figure 3.2. The Four otolith conditions to determine growth seasons in dab (I-IV: 16.5 x Magnification)

- I. First development of an opaque layer at the top edge of the otolith in February 1999, approaching 5th growth season.**
- II. The opaque layer has become more extensive as a thin layer round the edges of the otolith in April 1999. The fish has started its 4th growth season.**
- III. An extensive layer of opaque material is at the edge of the otolith in a fish in its 3rd growth season in May 1999.**
- IV. An extensive hyaline layer is formed at the edge of the otolith, in November 1999 in a fish, which has completed its 3rd growth season.**

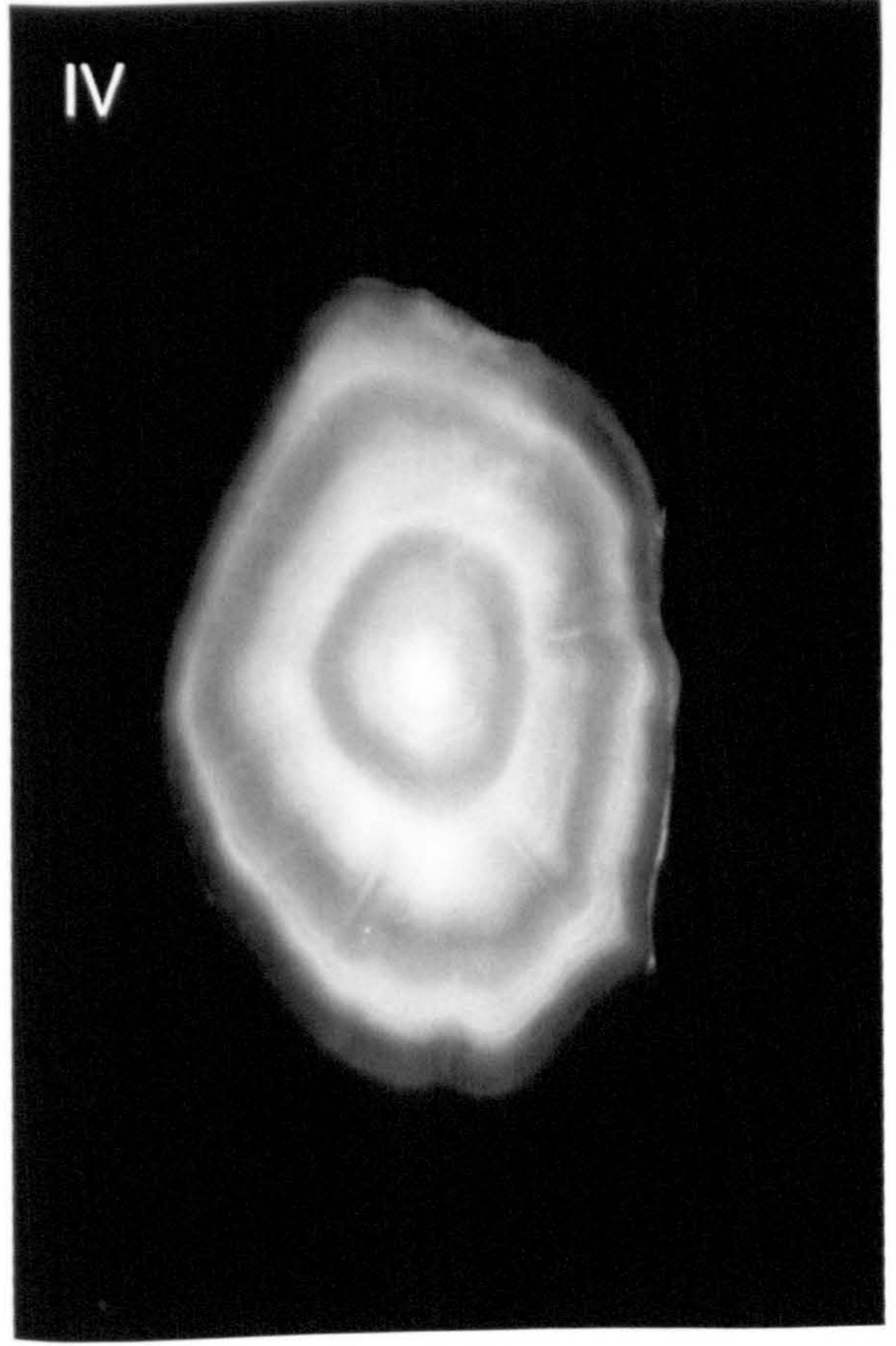
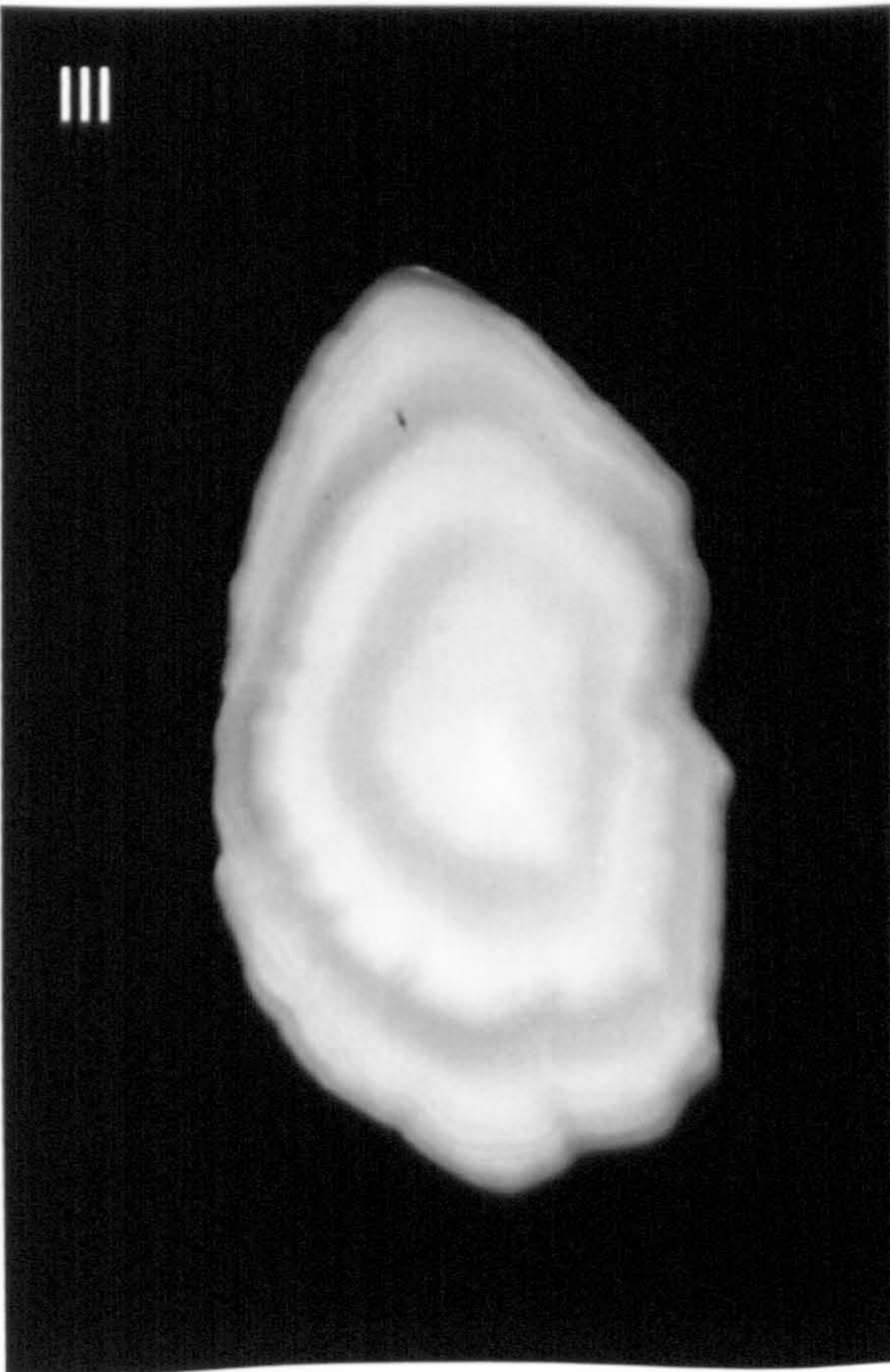
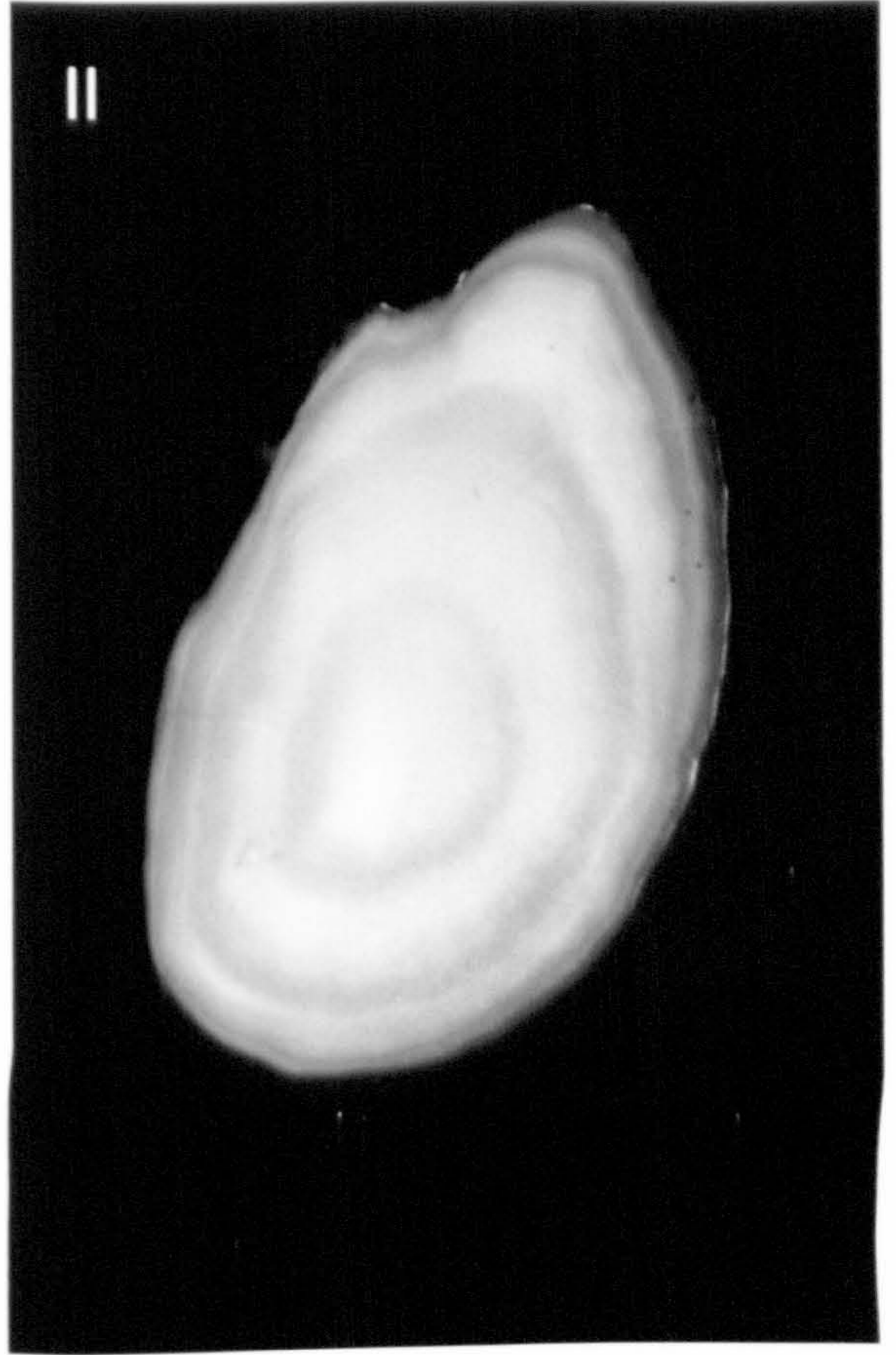
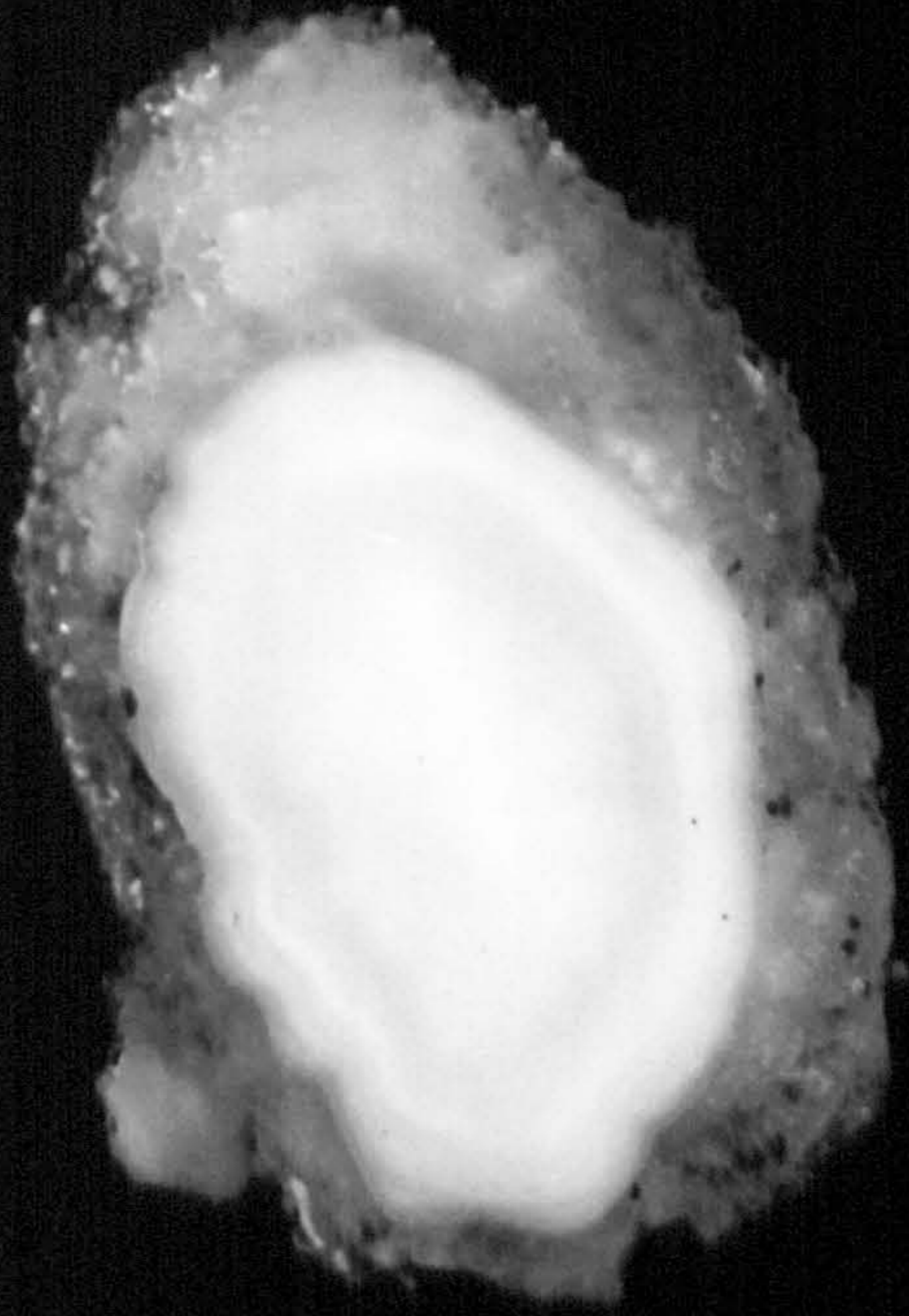


Figure 3.3. Crystalline otoliths in dab (A-B: 17 x Magnification)

A. Partially crystalline

B. Fully crystalline

A



B

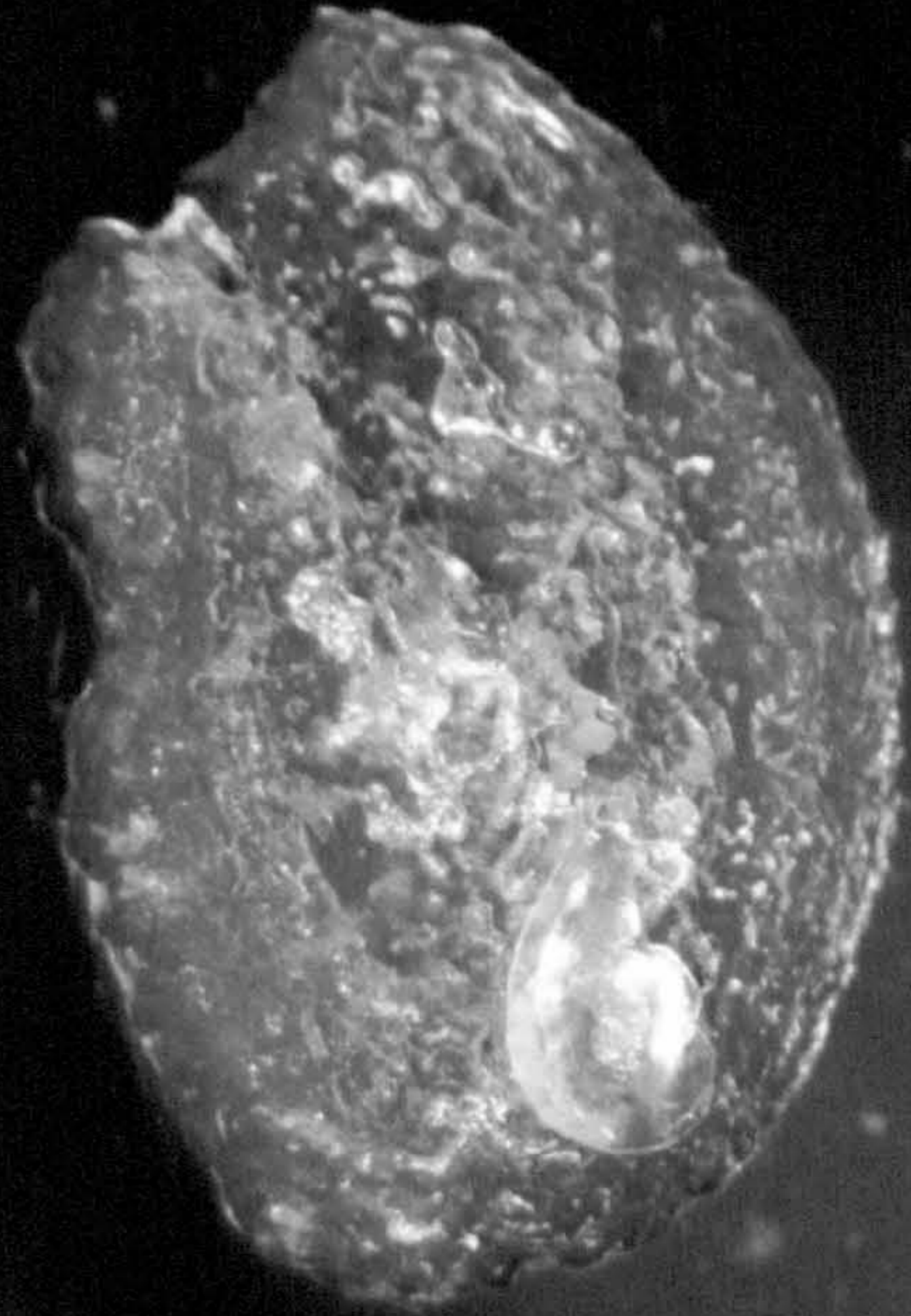
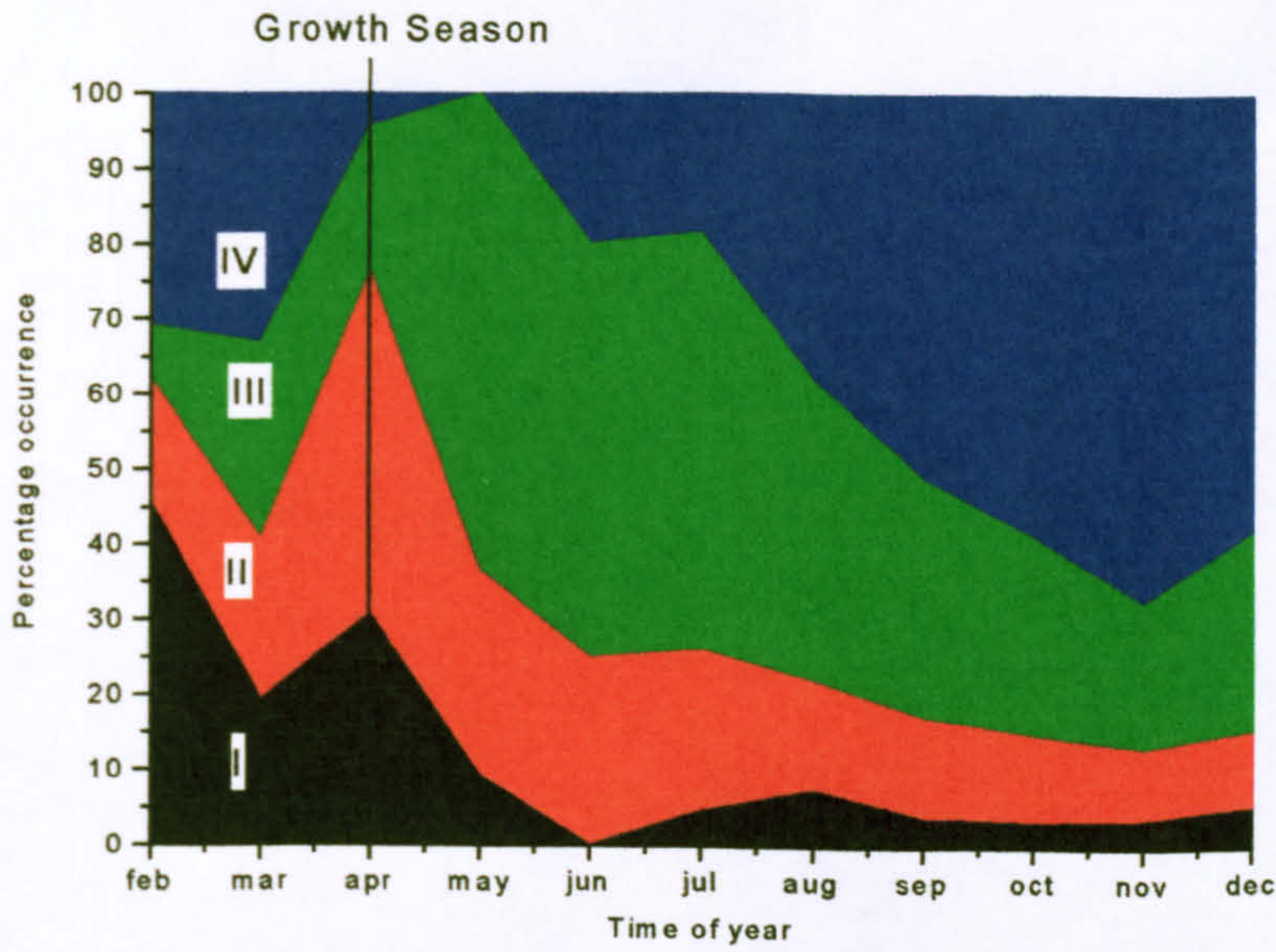


Figure 3.4. Percentage occurrence of the four otolith conditions based on seasonal surveys, 1999-2000



The study also shows that there is a relatively sharp increase in average total length (Figure 3.5) of the dab as extensive deposition of the growth zone occurs between May and July. Fitted curves were made to describe the average seasonal growth patterns in length for each cohort and sex of dab, taking 1st April as the onset of seasonal growth in length. These curves, for growth in length, when combined with a known condition (seasonal length and weight relationships), allowed construction of the curves for seasonal change in weight (Figure 3.6).

Figure 3.5. Seasonal changes in mean length of male and female dab, 1999-2000

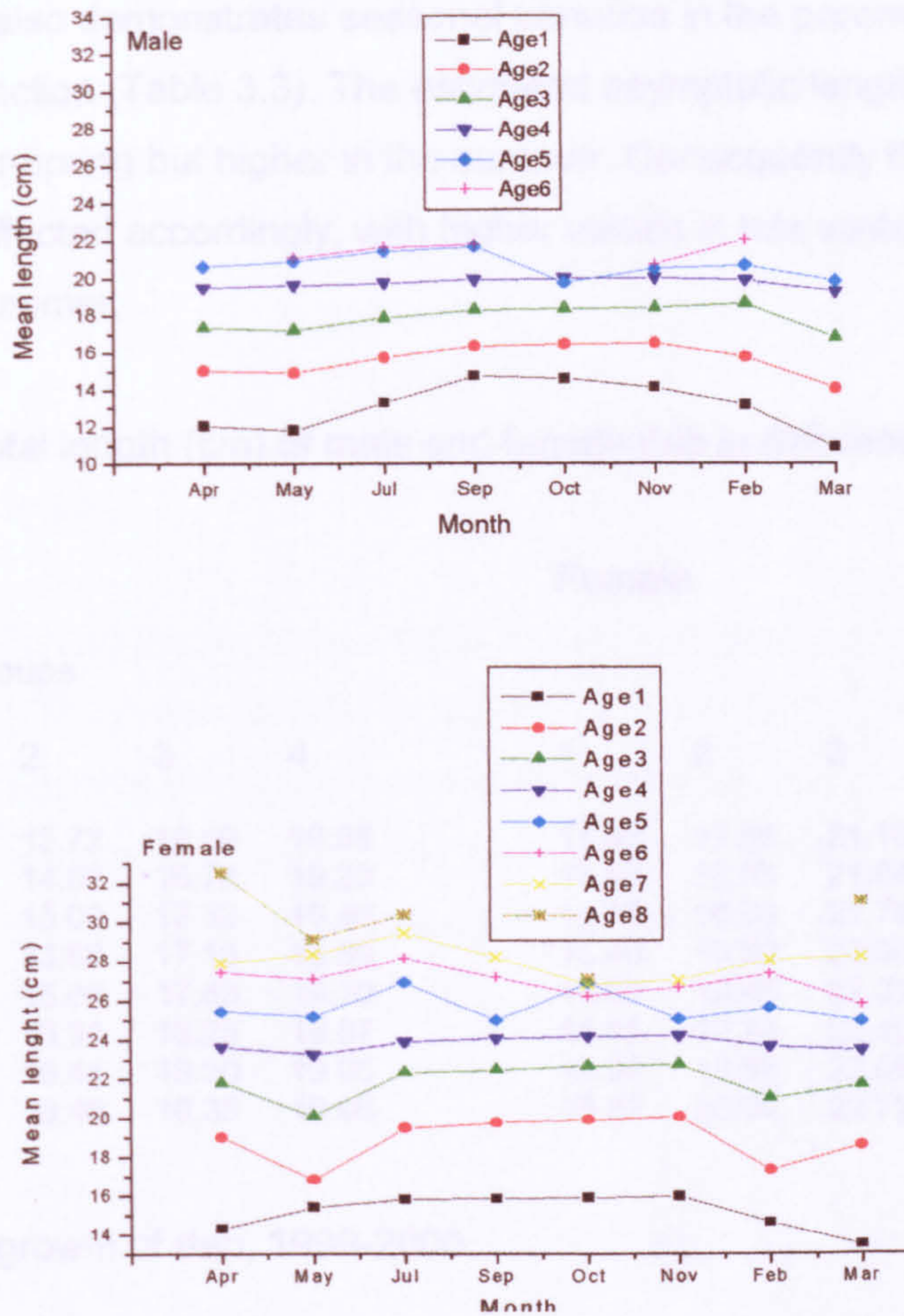
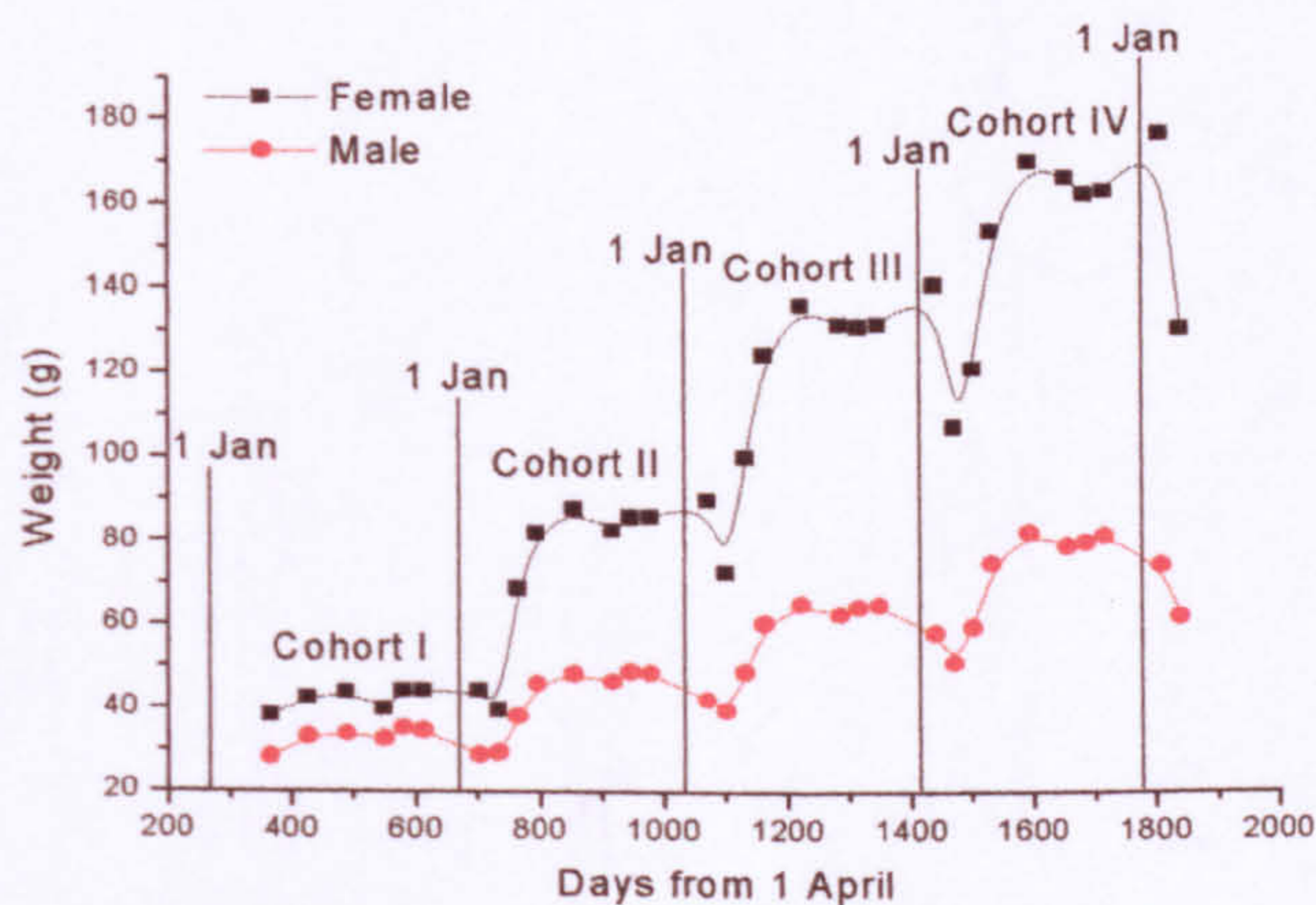


Figure 3.6. Seasonal changes in weight of male and female dab between their 1st and 5th birthdays on the North Wales Coast, 1998-2000



The seasonal variation in mean length at age, for four age groups, for male and female dab is shown in Table 3.1. The computed asymptotic lengths, seasonal growth rates and length increments between cohort components are shown in Table 3.2. In both males and females, the results show that seasonal growth rates slow down with increasing age of the cohort as expected. The study also demonstrates seasonal variation in the parameters of the Von Bertalanffy growth function (Table 3.3). The estimated asymptotic length generally appears to be lower late winter-spring but higher in the summer. Consequently the estimated parameters (K) are affected accordingly, with higher values in late winter and spring but lower values in the summer.

Table 3.1. Average total length (cm) of male and female dab in different months during 1999-2000

Months	Male				Female			
	Age groups							
	1	2	3	4	1	2	3	4
Feb	13.12	15.72	18.59	19.86	14.62	17.56	21.10	23.63
Mar	10.89	14.02	16.78	19.20	13.45	18.56	21.64	23.45
Apr	12.03	15.00	17.32	19.46	14.29	18.98	21.78	23.59
May	11.80	13.88	17.18	19.59	15.40	16.80	20.08	23.23
Jul	13.26	15.68	17.83	19.70	15.80	19.45	22.31	23.86
Sep	14.70	16.31	18.23	19.87	15.85	19.74	22.45	24.03
Oct	14.56	16.45	18.30	19.95	15.90	19.88	22.66	24.15
Nov	14.10	16.48	18.35	19.96	15.97	20.04	22.72	24.19

Table 3.2. Seasonal growth of dab, 1999-2000

Cohort	Male			Female		
	Ln cm	G'	K' mth ⁻¹	Ln cm	G'	K' mth ⁻¹
I	14.81	6.14	0.0122	16.04	6.30	0.0201
II	16.71	1.90	0.0118	19.94	3.88	0.0163
III	18.53	1.82	0.0106	22.94	2.84	0.0082
IV	20.07	1.54	0.0098	24.72	1.78	0.0042

Table 3.3. Seasonal variation in Von Bertalanffy Growth Parameters (\pm SE) in dab, 1999-2000

	Male			Female		
	L_{∞} cm	K yr ⁻¹	t_0 year	L_{∞} cm	K yr ⁻¹	t_0 year
Feb	24.16 \pm 1.36	0.31 \pm 0.07	-1.48 \pm 0.45	34.33 \pm 2.44	0.20 \pm 0.04	-1.65 \pm 0.39
Mar	23.80 \pm 2.57	0.31 \pm 0.11	-0.93 \pm 0.46	29.67 \pm 1.55	0.32 \pm 0.07	-0.92 \pm 0.37
Apr	25.78 \pm 1.56	0.25 \pm 0.04	-1.51 \pm 0.28	30.94 \pm 2.21	0.27 \pm 0.08	-1.33 \pm 0.52
May	24.95 \pm 3.27	0.28 \pm 0.12	-1.22 \pm 0.73	35.46 \pm 1.59	0.20 \pm 0.03	-2.04 \pm 0.34
Jul	25.53 \pm 2.04	0.25 \pm 0.07	-1.93 \pm 0.58	38.81 \pm 5.69	0.14 \pm 0.05	-2.48 \pm 0.78

**** See below (Table 3.4) for illustrative analysis of autumn surveys data (1999 and 2000) for comparison with other studies.**

The annual values for mean length at age in the autumn between 1975 and 2000 are shown in Figures 3.7 and 3.8. The mean lengths for the 1 and 2 year old fish for both sexes fluctuate only within narrow limits over the years. The older fish exhibit more annual variability in estimated mean length, but these were based on smaller samples. For males (Figure 3.7), no consistent change for size-at-age in autumn is apparent from the samples over the 25 year study period. In females (Figure 3.8), most age groups above 4 years of age may have decreased in size after 1985.

Figure 3.7. Annual variation in mean length at age in the male dab, 1975-2000. Age groups (0++, 1++, etc.) indicate that the group have laid down both opaque and hyaline rings for the current year but will not achieve their next birthday for a further six months.

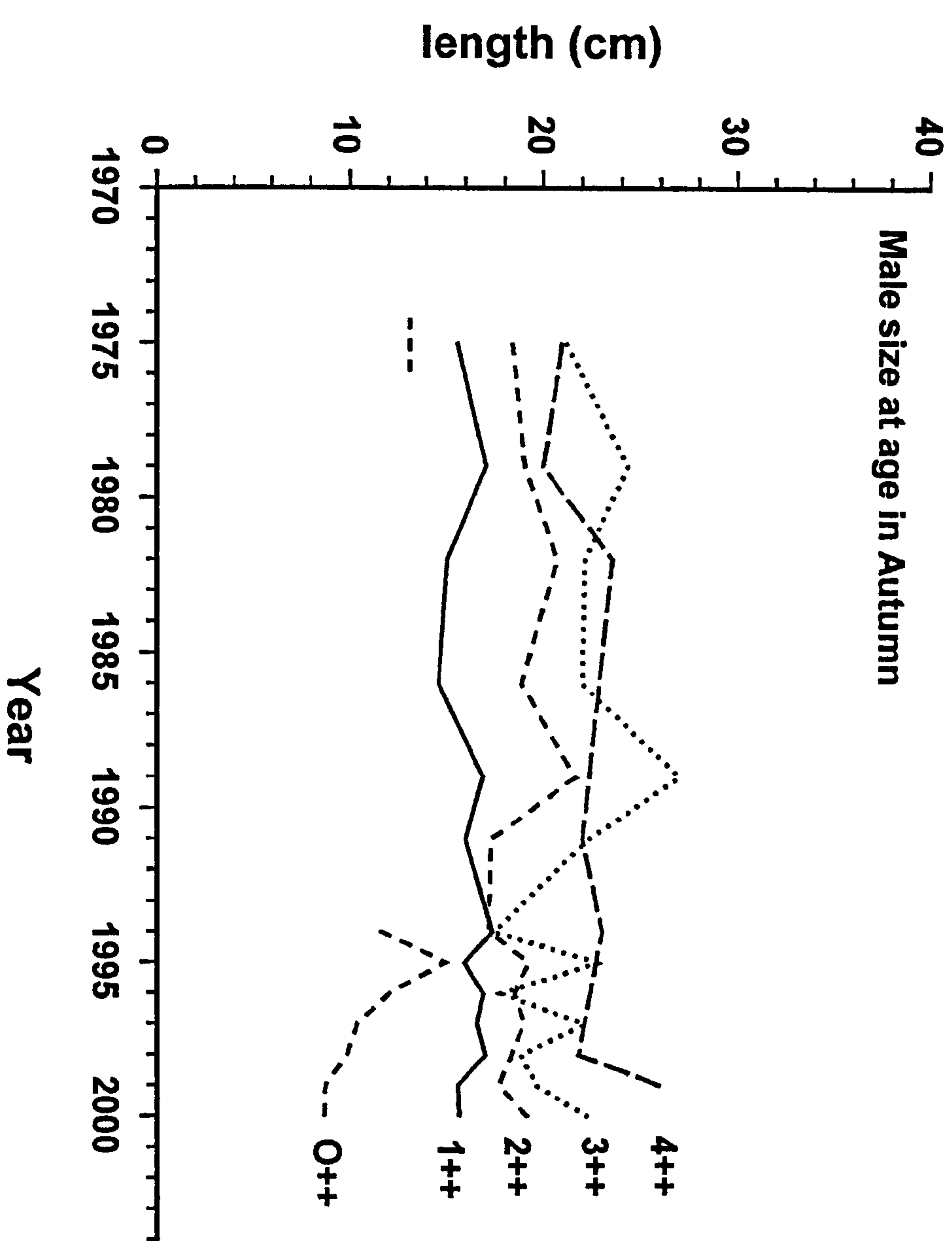
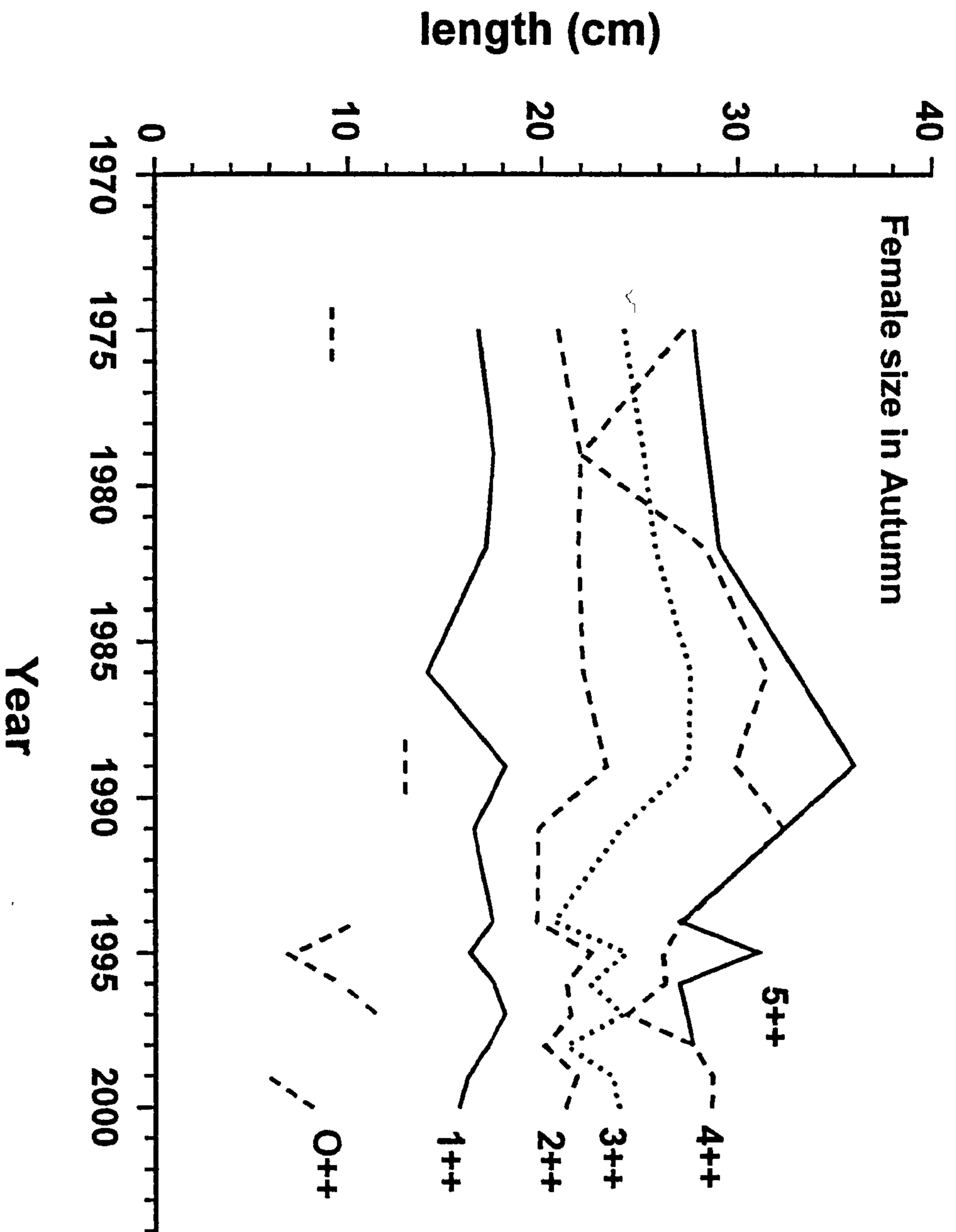


Figure 3.8. Annual variation in mean length at age in the female dab, 1975-2000. For symbols see Figure 3.7.



The major annual surveys in the 1990-2000 period have been carried out in autumn. At this time, the dab they have attained a particular size at the end of the growing season and have also not begun full gonad development. The autumn period is thus a fairly conservative time to express size. Von Bertalanffy Growth parameters were estimated for autumn samples separately for 1999 and 2000. The present study was able to identify 6 and 8 age groups in the male and female dab populations respectively. In both 1999 and 2000 (Tables 3.4 and 3.5), the numerically low older age groups (≥ 7 years) of females could not easily be used in the estimation of population parameters. The estimated annual growth parameters in (Table 3.6) show that the female dab grows to a larger length than the male. The maximum observed length in the field was 36.7 cm for female and 26.0 cm for male. The growth constant (curvature parameter K) is significantly higher in the male than the female because of the difference in the L_{∞} values. The annual (autumn) growth parameters from past surveys (1994-1998), Table 3.7, show a similar trend, with the male dab having higher relative growth rates but lower asymptotic lengths than the female dab. However, the estimated length at infinity (L_{∞}) for the females in 1995 is much higher than in other years. But since the standard deviation of size at age is usually large by several cm, the size of one or two older fish can easily be well above (or below) the true mean for that group. The mean length at age is higher in the females than the males (Figure 3.9). The annual growth in weight and the annual instantaneous rate of growth in weight (G) at age are shown in Figures 3.10 and 3.11 respectively.

Table 3.4. Annual growth rate of male and female dab

Mean length (cm) \pm std, weight (Wt) and instantaneous growth rate (G) at age, based on autumn surveys, 1999 and 2000

1999 Age Yr.	Male			Female		
	Mean length (cm)	Wt (g)	G	Mean length (cm)	Wt (g)	G
0.5	8.67 \pm 1.78	7.82	1.28	9.73 \pm 1.60	8.38	1.49
1.5	15.19 \pm 1.38	28.19	0.64	16.72 \pm 2.07	37.08	0.80
2.5	17.53 \pm 1.96	53.32	0.37	20.29 \pm 2.09	82.32	0.49
3.5	20.18 \pm 1.09	77.24	0.23	22.81 \pm 1.85	134.94	0.33
4.5	21.50 \pm 1.17	97.37	0.15	25.54 \pm 1.20	187.38	0.23
5.5	24.05 \pm 1.08	113.18		27.94 \pm 1.20	235.12	0.16
6.5				29.29 \pm 1.60	276.15	0.12
7.5				35.33 \pm 1.53	310.09	

2000 Male				Female		
Age Yr.	Mean length (cm)	Wt (gm)	G	Mean length (cm)	Wt (gm)	G
0.5	11.57 ±1.22	15.67	0.79	13.49 ±1.26	24.09	0.87
1.5	15.76 ±1.12	34.33	0.47	17.84 ±1.80	57.32	0.54
2.5	17.70 ±1.06	54.91	0.31	21.35 ±1.37	98.05	0.36
3.5	19.75 ±1.10	74.48	0.21	23.76 ±1.52	140.66	0.25
4.5	21.94 ±0.62	91.59	0.14	26.39 ±1.78	181.35	0.18
5.5	22.45 ±0.50	105.81		27.43 ±1.76	218.01	0.14
6.5				28.84 ±1.75	249.77	0.10
7.5				31.01 ±2.01	276.56	

Table 3.5. Number at age (N_t) and $\text{Log}_e(N_t)$ in male and female dab, based on autumn surveys, 1999 and 2000

1999	Male		Female	
	N_t	$\text{Log}_e(N_t)$	N_t	$\text{Log}_e(N_t)$
0.5	18	2.89	12	2.48
1.5	392	5.97	502	6.22
2.5	380	5.94	570	6.35
3.5	116	4.75	147	4.99
4.5	49	3.89	34	3.53
5.5	12	2.48	27	3.30
6.5			11	2.40
7.5			3	1.10

2000	Male		Female	
	N_t	$\text{Log}_e(N_t)$	N_t	$\text{Log}_e(N_t)$
0.5	92	4.52	527	6.27
1.5	744	6.61	1450	7.28
2.5	530	6.27	1044	6.95
3.5	345	5.84	522	6.26
4.5	72	4.27	264	5.57
5.5	27	3.29	154	5.04
6.5			83	4.47
7.5			53	3.96

Table 3.6. Comparison of growth parameters (\pm SE) between 1999 and 2000 in male and female dab from autumn samples

Growth parameters 1999		Growth parameters 2000	
Male		Male	
L_{∞}	= 26.17 ± 2.31 cm	L_{∞}	= 25.73 ± 1.74 cm
K	= 0.36 ± 0.11 yr ⁻¹	K	= 0.30 ± 0.07 yr ⁻¹
t_0	= -0.66 ± 0.31 yrs	t_0	= 1.53 ± 0.37 yrs
r	= 0.993	r	= 0.997
Growth parameters 1999		Growth parameters 2000	
Female		Female	
L_{∞}	= 33.23 ± 1.79 cm	L_{∞}	= 33.44 ± 0.81 cm
K	= 0.29 ± 0.05 yr ⁻¹	K	= 0.25 ± 0.02 yr ⁻¹
t_0	= -0.77 ± 0.19 yrs	t_0	= -1.55 ± 0.13 yrs
r	= 0.995	r	= 0.999

Table 3.7. Von Bertalanffy Growth Parameters of dab on the North Wales Coast from past students' autumn surveys, (data fitted by FIGP computer software, Biosoft).

Year	Sex	L_{∞} cm	K yr ⁻¹	t_0 yr	No. of age groups
1994	Male	22.61	0.43	-1.361	5
	Female	29.69	0.32	-0.910	8
1994	Male	23.00	0.43	-1.350	5
	Female	30.61	0.29	-1.020	8
1995	Male	22.79	0.71	-0.281	4
	Female	54.53	0.102	-1.460	8
1996	Male	23.53	0.78	-0.060	6
	Female	25.53	0.71	-0.170	6
1997	Male	21.35	0.89	-0.309	4
	Female	25.44	0.81	-0.494	8
1998	Male	22.00	0.62	-0.490	6
	Female	26.20	0.55	-0.110	8

Figure 3.9. Annual growth in length of male and female dab, autumn 1999 and 2000 based on autumn samples when fish are 6 months beyond their birthday. The oldest fish in the samples were few in numbers; data points for this age group were not used in the estimation of growth parameters.

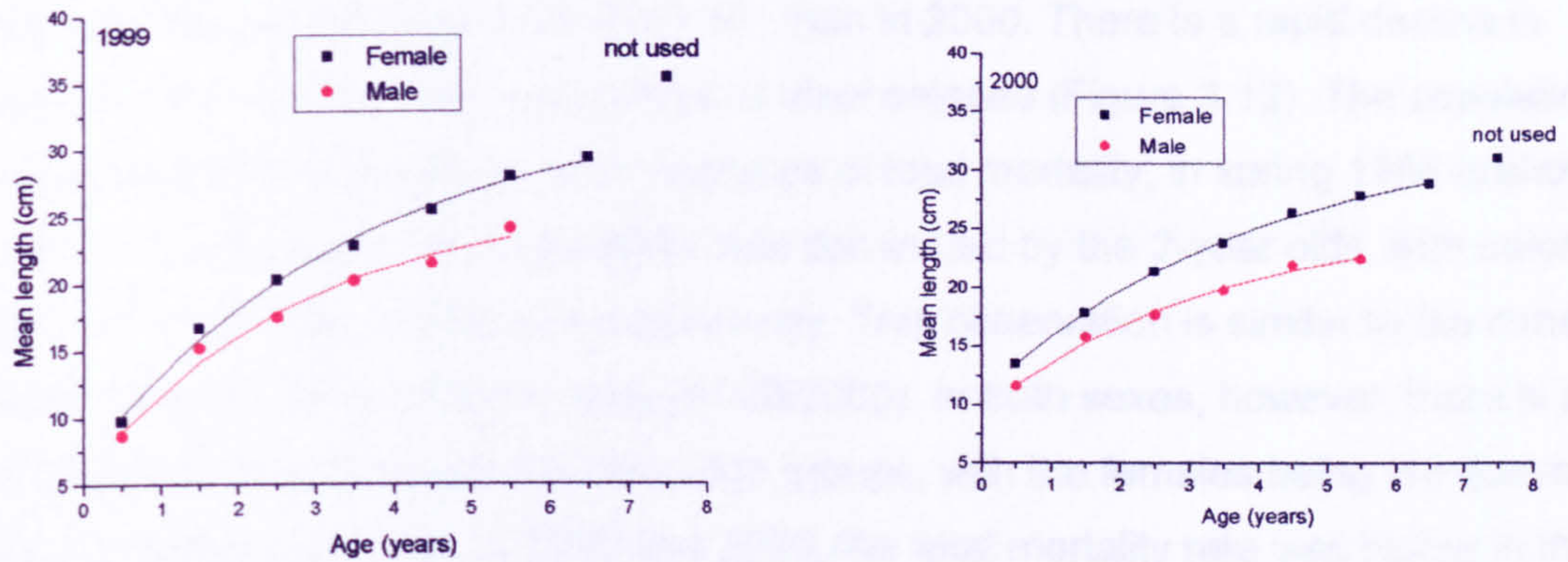


Figure 3.10. Annual growth in weight in male and female dab, autumn 1999 and 2000

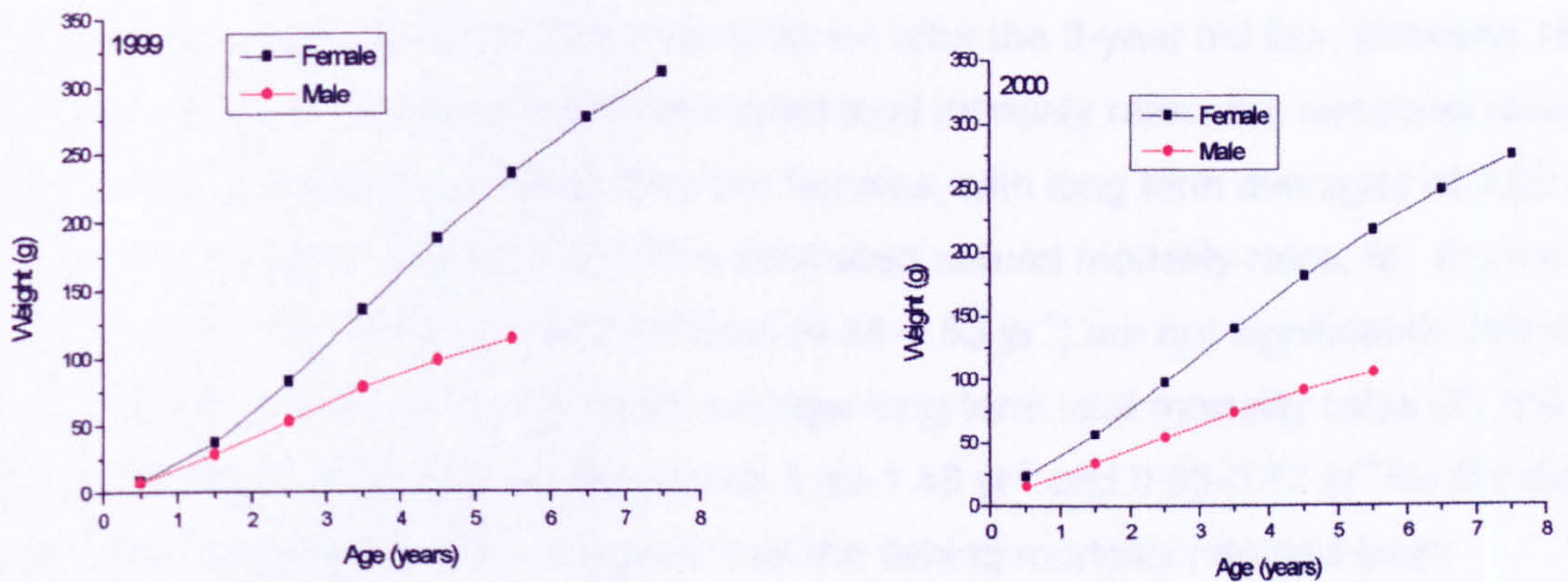
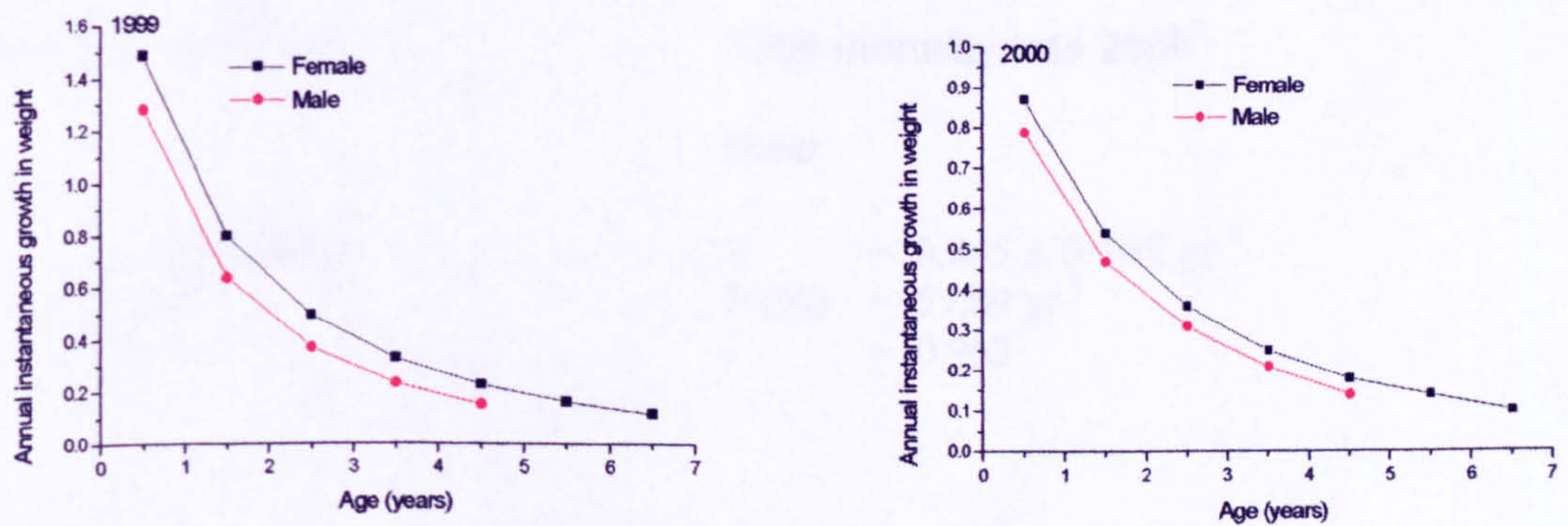


Figure 3.11. Instantaneous growth in weight in male and female dab, autumn 1999 and 2000



The calculated total mortality rates (Table 3.8) between the male and female dabs in 1999 were not significantly different ($P > 0.05$). The mortality for the male dab in 1999 was not significantly different ($P > 0.05$) from that in 2000 whilst in the case of the female, the death rate was significantly higher in 1999 ($P < 0.05$) than in 2000. There is a rapid decline in population number for the older age groups in trawl catches (Figure 3.12). The population structure of male and female dab, with estimates of total mortality, in spring 1966 is shown in Figure 3.13. In both sexes, the population was dominated by the 2-year olds, with catches of 7.5 and 12.5 hr^{-1} in male and female respectively. This observation is similar to the current population structure in the present study (1999/2000). In both sexes, however, there is a gradual decline in abundance in the older age groups, with the females being the dominant sex in these age groups. Like in 1999 and 2000, the total mortality rate was higher in the male ($Z=0.62 \text{ yr}^{-1}$) than the female ($Z=0.54 \text{ yr}^{-1}$) in 1966. This pattern in abundance index and mortality between the sexes is also observed between 1972-2000 in different seasons (Figure 3.14), which indicates no significant change in the age distribution of the population in the study area for nearly four decades. The dominant year-class has been the 2-year old fish in both sexes, with a rapid decline in abundance after the 3-year old fish. Between 1966-2000, there were large variations in the estimated total mortality rates, but remained usually higher and more variable in the males than the females, with long term averages of 1.95 yr^{-1} and 1.16 yr^{-1} respectively (Figure 3.15). The estimated natural mortality rates, M , (by the two methods) in males (0.47-0.53 yr^{-1}) and females (0.39-0.53 yr^{-1}) are not significantly different (Table 3.9). Thus, based on the estimated average long-term total mortality rates (Z), the fishing mortality rates (F) can be worked out as 1.42-1.48 yr^{-1} and 0.63-0.77 yr^{-1} for the male and female dab respectively. This suggests that the fishing mortality rate had been significantly higher on the male population than the females.

Table 3.8. Comparison of instantaneous rate of total mortality coefficients (Z) in male and female dab between 1999 and 2000 (by 'pseudocohort' analysis)

Total mortality rate 1999		Total mortality rate 2000	
Male		Male	
Z	$= 0.903 \pm 0.134 \text{ yr}^{-1}$	Z	$= 0.865 \pm 0.139 \text{ yr}^{-1}$
P (%)	$= 59.47 \text{ yr}^{-1}$	P (%)	$= 57.89 \text{ yr}^{-1}$
r	$= 0.969$	r	$= 0.963$

Total mortality rate 1999

Female

$$Z = 0.891 \pm 0.079 \text{ yr}^{-1}$$

$$P (\%) = 58.98 \text{ yr}^{-1}$$

$$r = 0.981$$

Total mortality rate 2000

Female

$$Z = 0.582 \pm 0.019 \text{ yr}^{-1}$$

$$P (\%) = 44.12 \text{ yr}^{-1}$$

$$r = 0.997$$

Statistical comparison of mortality rates between males and females, 1999

ANOVA:

Source	DF	SS	MS	F	P
Combined regression	1	31.312	23.717	133.88	< 0.001
Between slopes	1	0.001	0.001	0.010	0.941**
Between intercepts	1	0.201	0.017	0.100	0.762**
Residual (Error)	8	1.417	1.417		
Total	11	32.931			

Common slope and intercept:

Term	Coefficients	S.E
Intercept	8.3288	0.2506
Slope	-0.8970	0.0548

** No significant difference ($P > 0.05$) in the slopes and intercepts of the regressions for the males and females. Common equation: $\ln(N) = 8.3288 - 0.8970 * \text{Age}$; $Z = 0.8970 = 59.22 \%$.

Figure 3.12. Estimation of total mortality rate in male and female dab, 1999 and 2000. Please refer to section 3.1 (iii) for explanation of 'not used' in the figure.

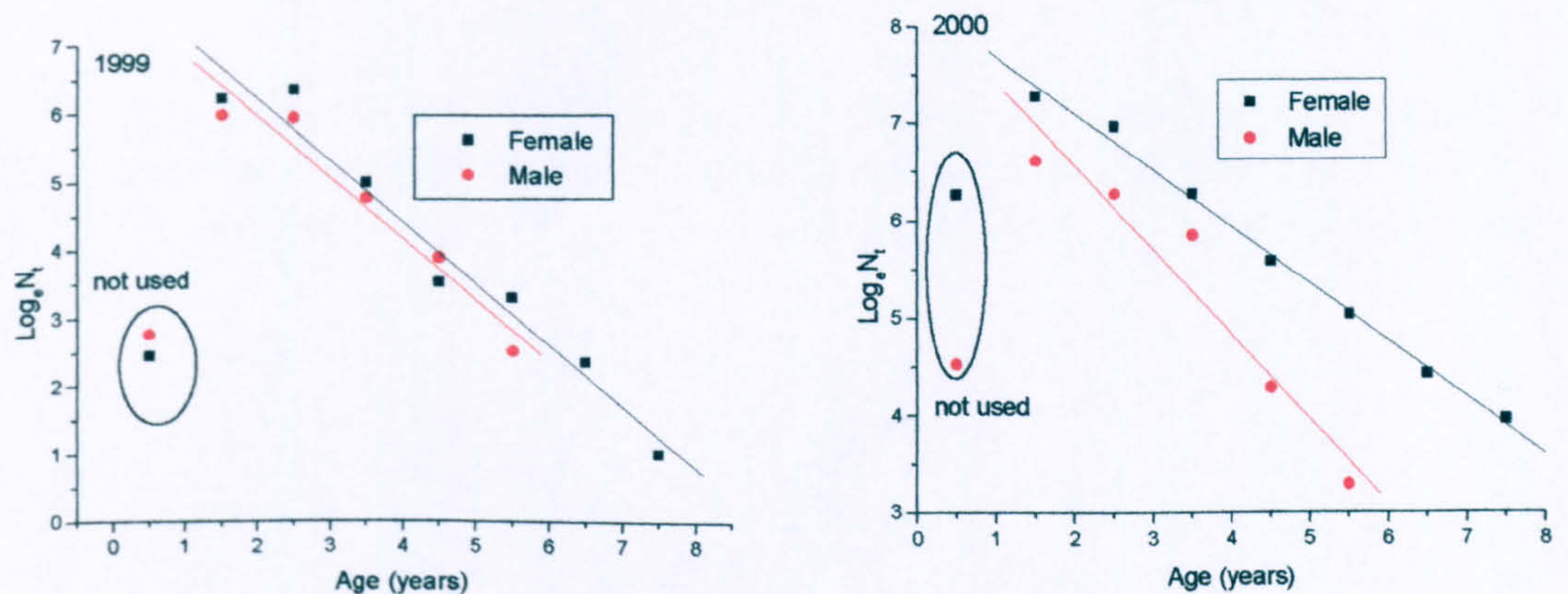


Table 3.9. Estimates of Natural Mortality Rate ($M \text{ yr}^{-1}$), Fishing Mortality Rate ($F \text{ yr}^{-1}$) and Rate of Capture ($E \text{ yr}^{-1}$) of dab, 1999 and 2000.

a) Male					
	yr^{-1}		yr^{-1}		
	M	M/K	Z	F	E
1999					
Pauly	0.532	1.48**	0.903	0.371	0.411
Gunderson and Dygert	0.045	0.12*	0.903	0.858	0.950
2000					
Pauly	0.474	1.58**	0.865	0.391	0.452
Gunderson and Dygert	0.054	0.18*	0.865	0.811	0.938
b) Female					
1999					
Pauly	0.432	1.49**	0.891	0.459	0.515
Gunderson and Dygert	0.453	1.56**	0.891	0.438	0.492
2000					
Pauly	0.391	1.57**	0.582	0.191	0.328
Gunderson and Dygert	0.528	2.11**	0.582	0.054	0.093

**** inside the range $1.5 < M/K < 2.5$**

*** outside the range $1.5 < M/K < 2.5$**

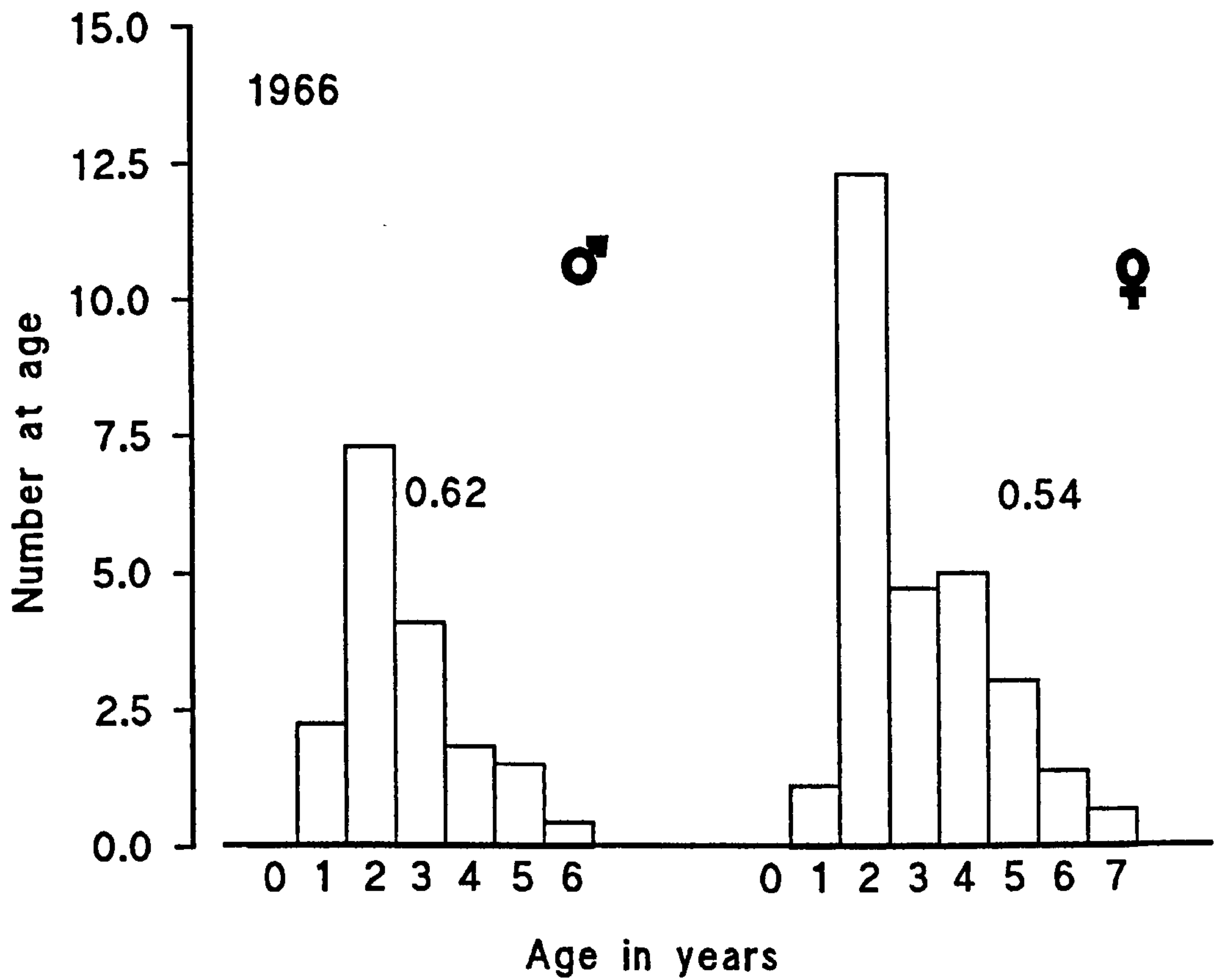
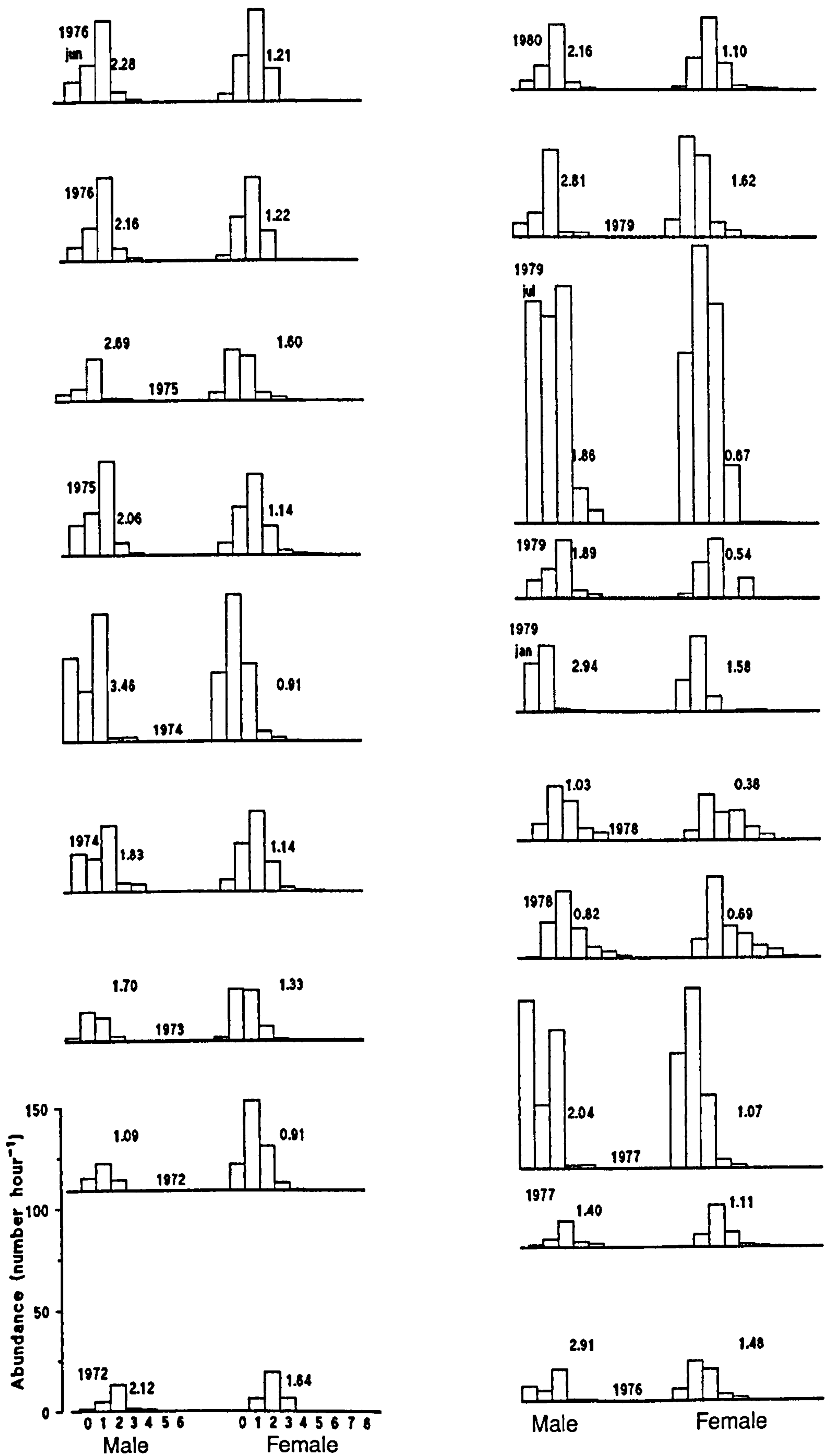
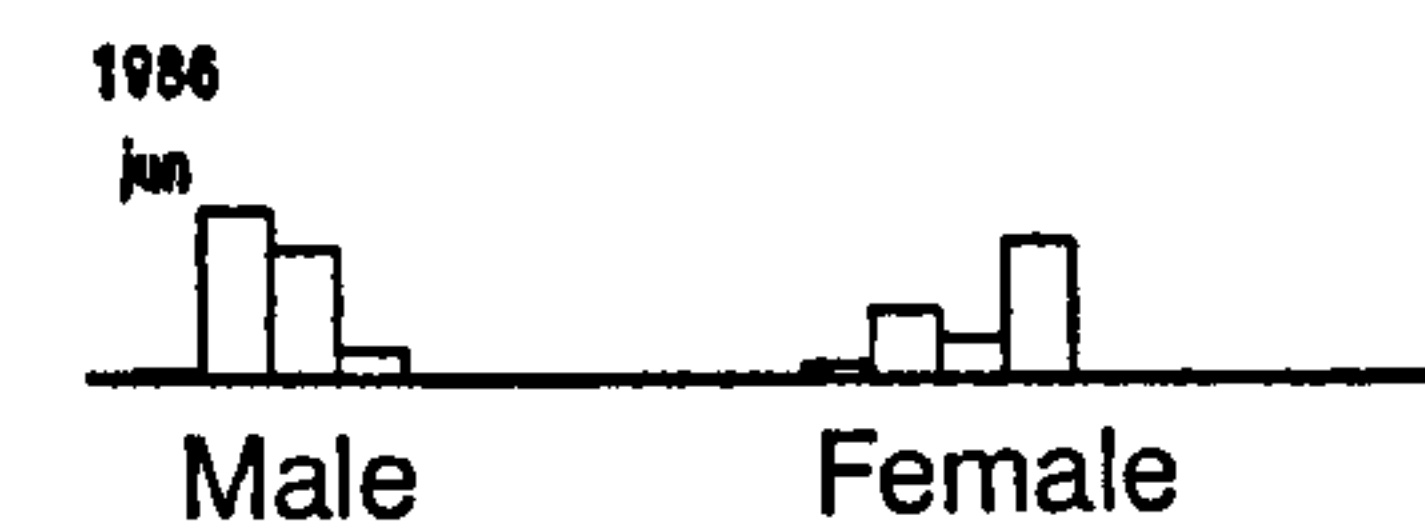
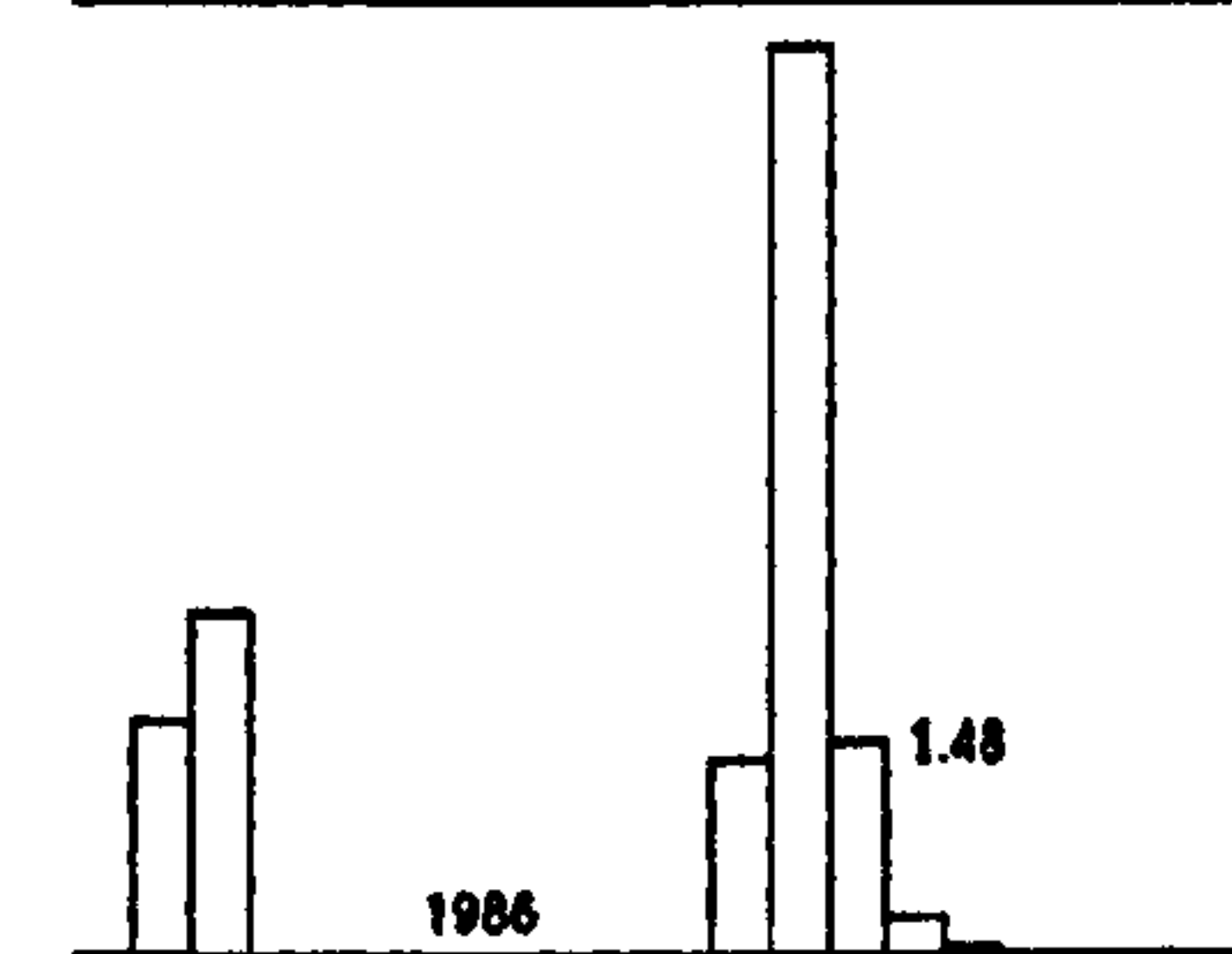
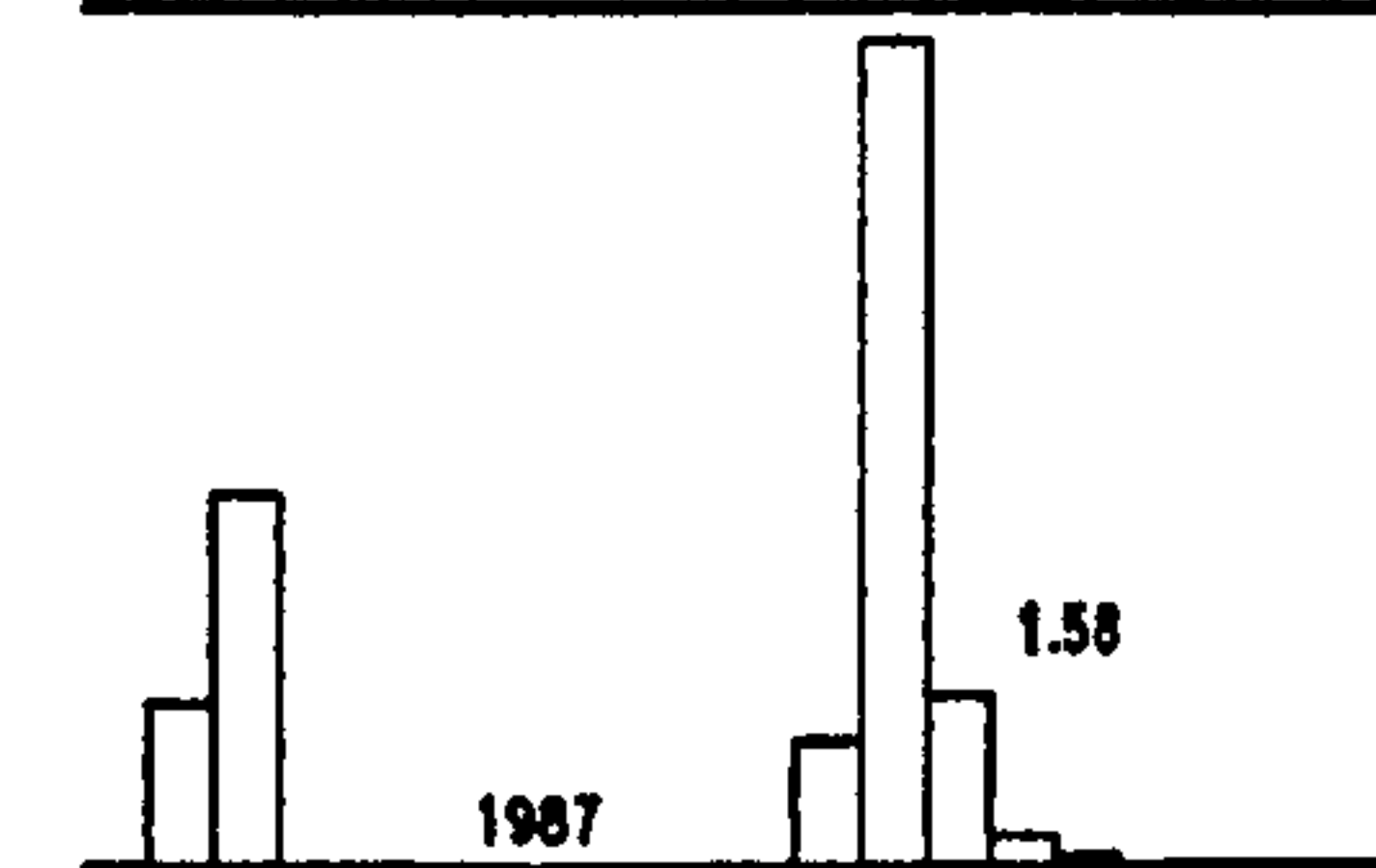
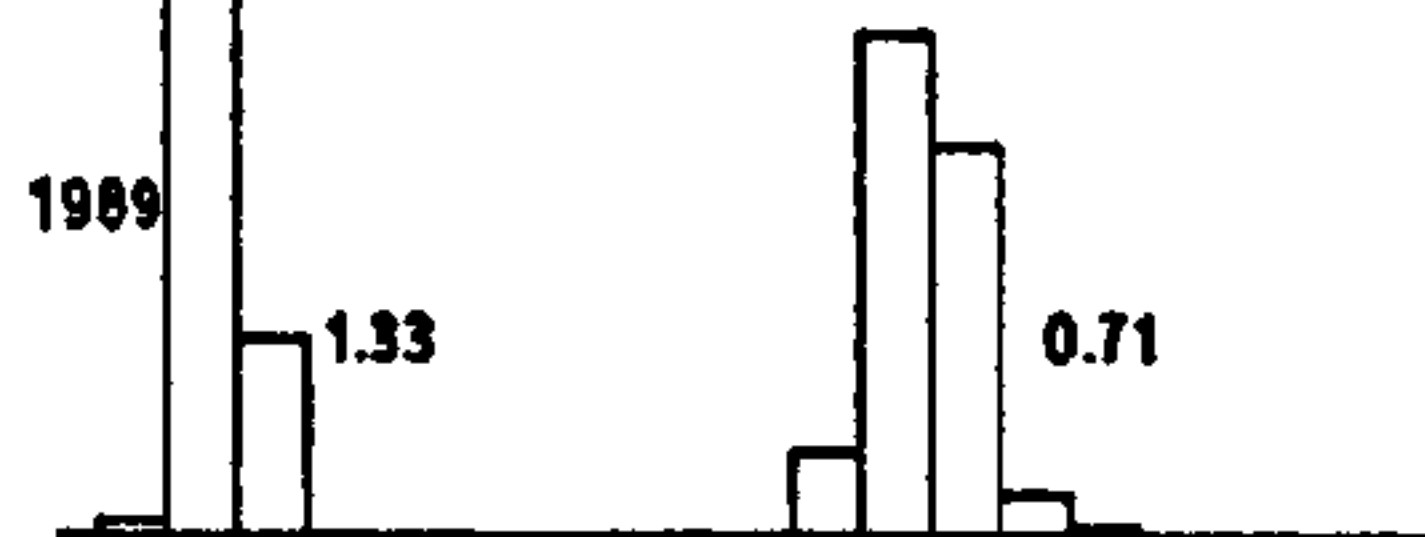
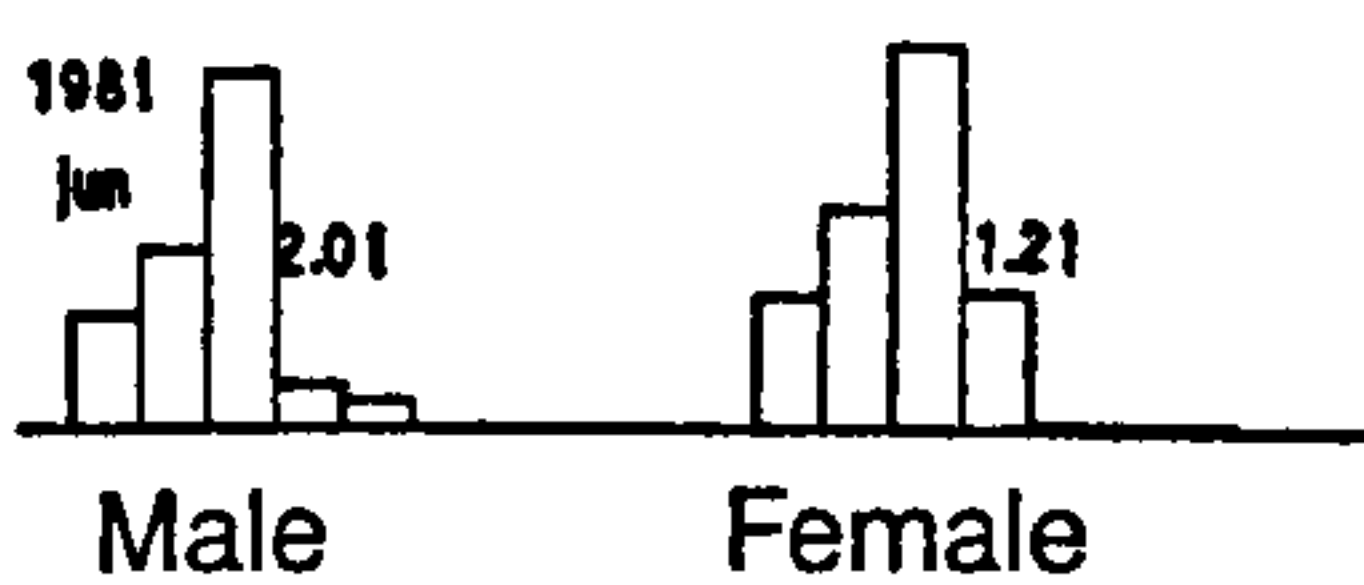
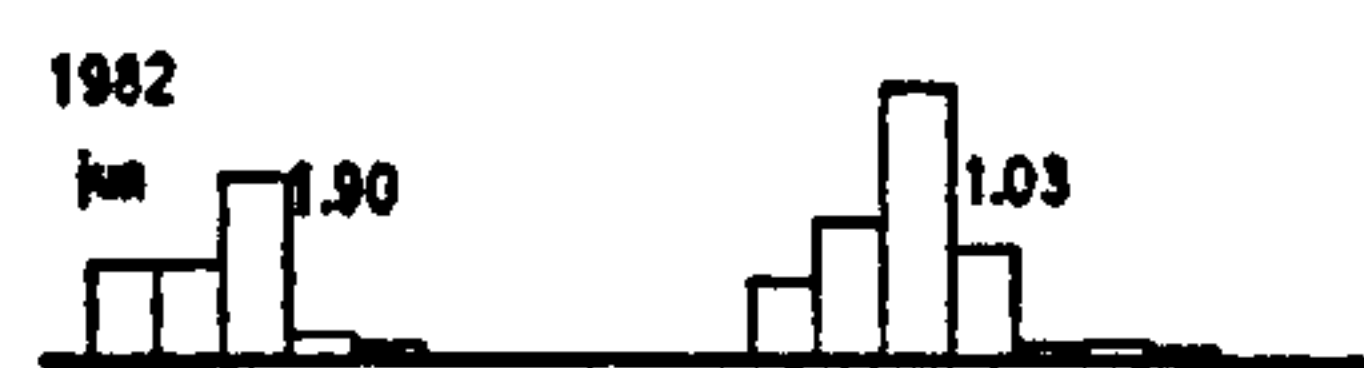
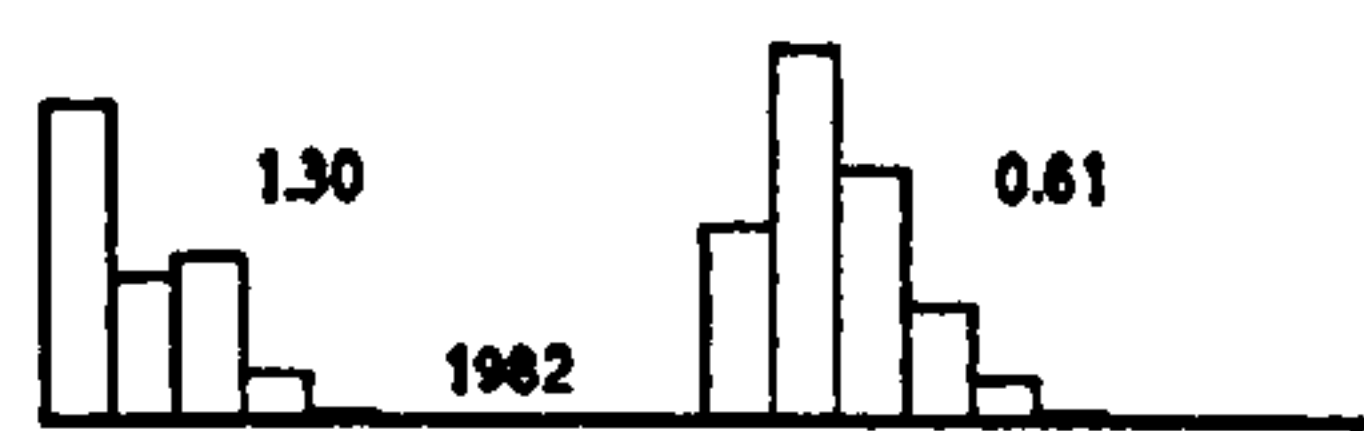
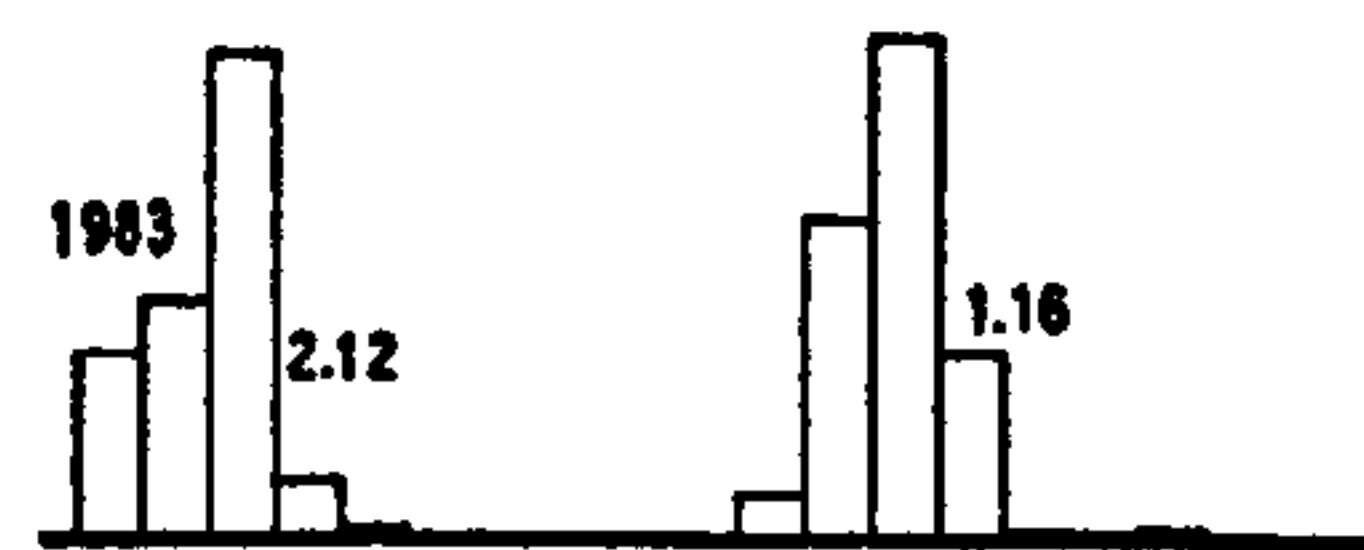
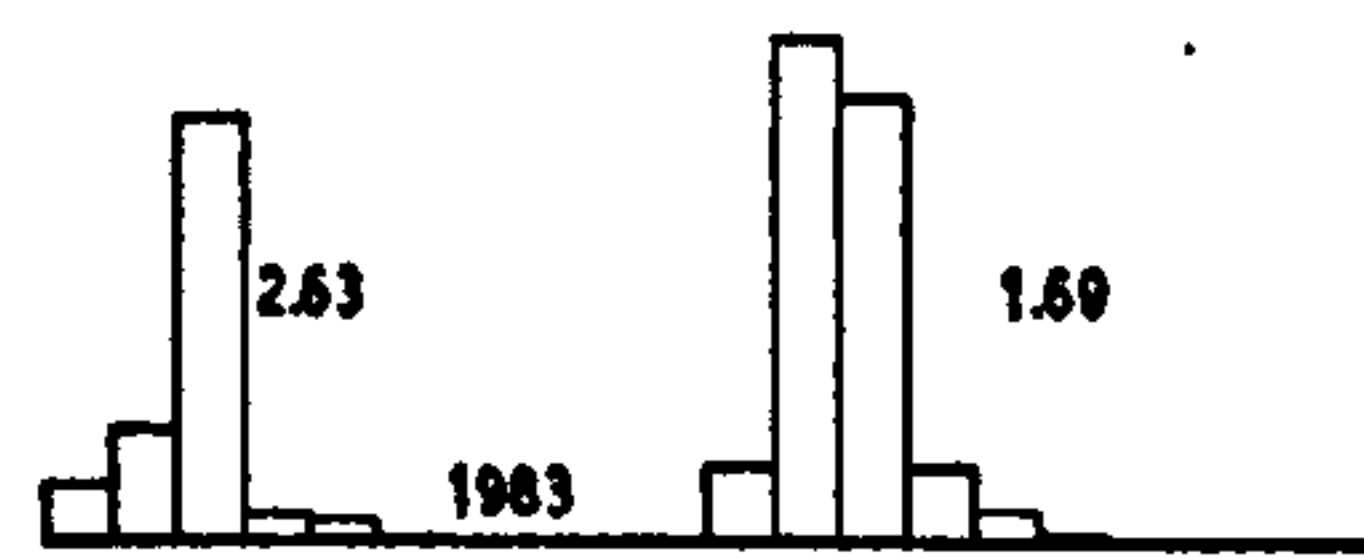
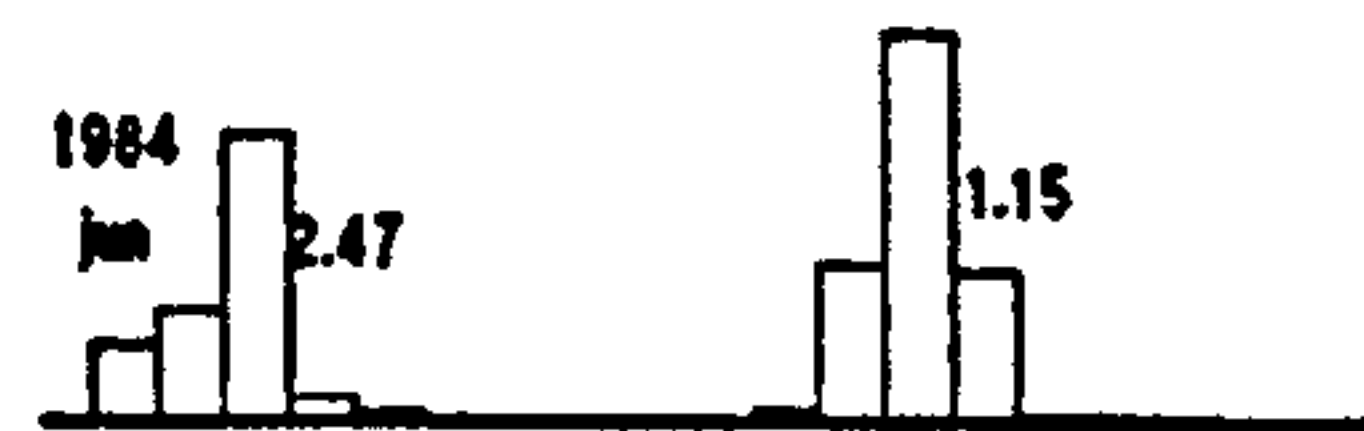
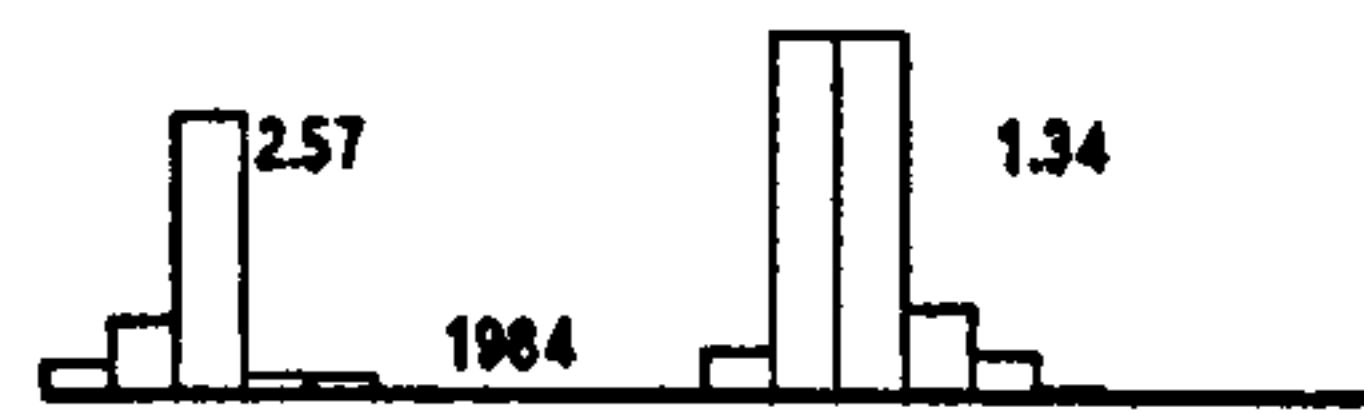
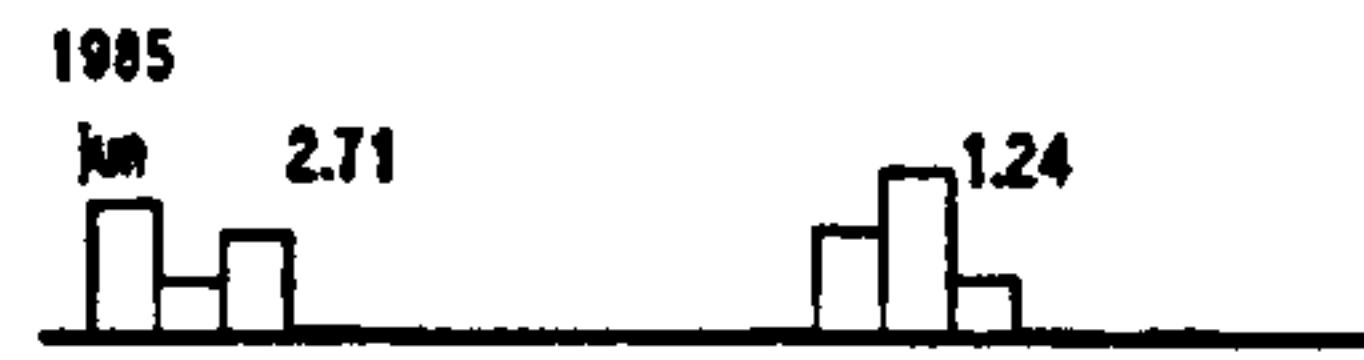
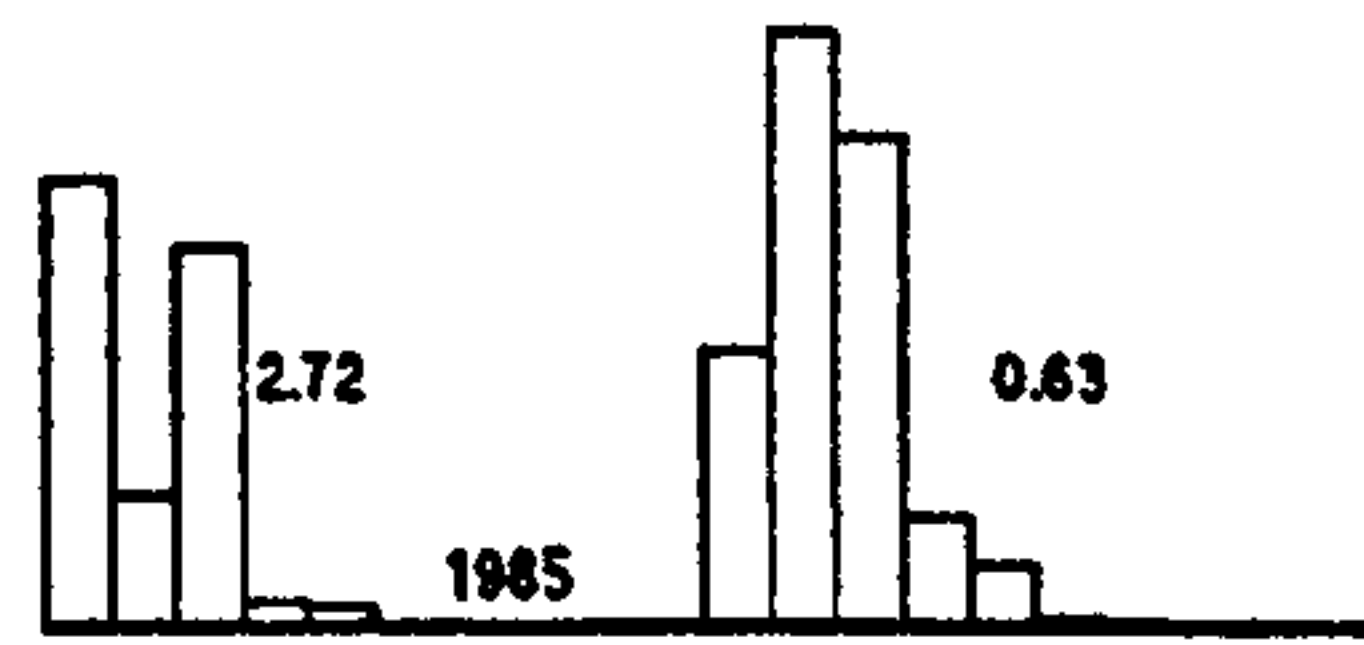
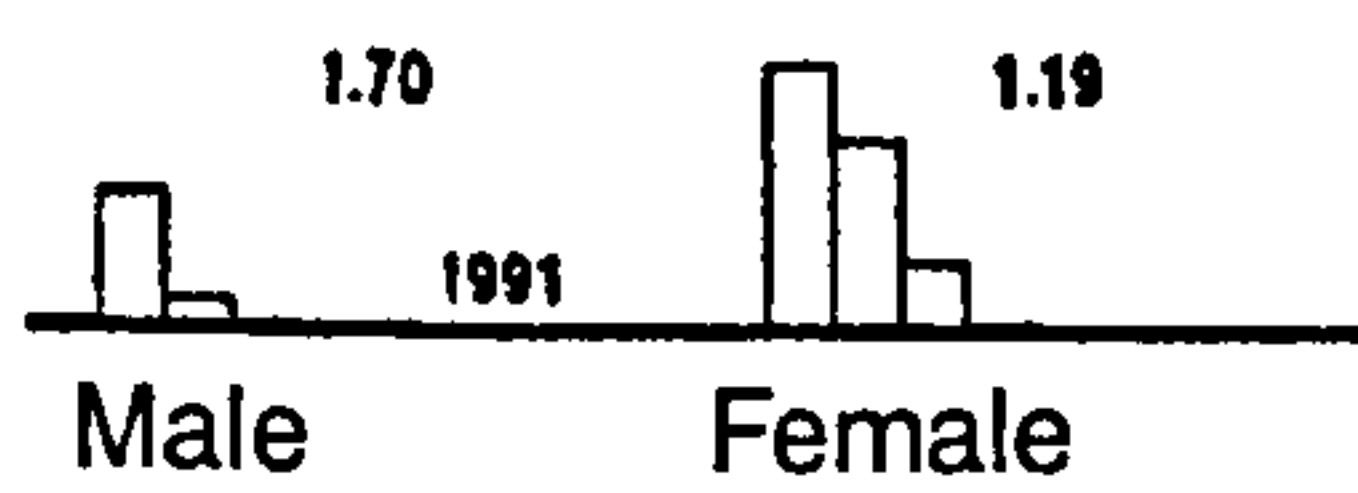
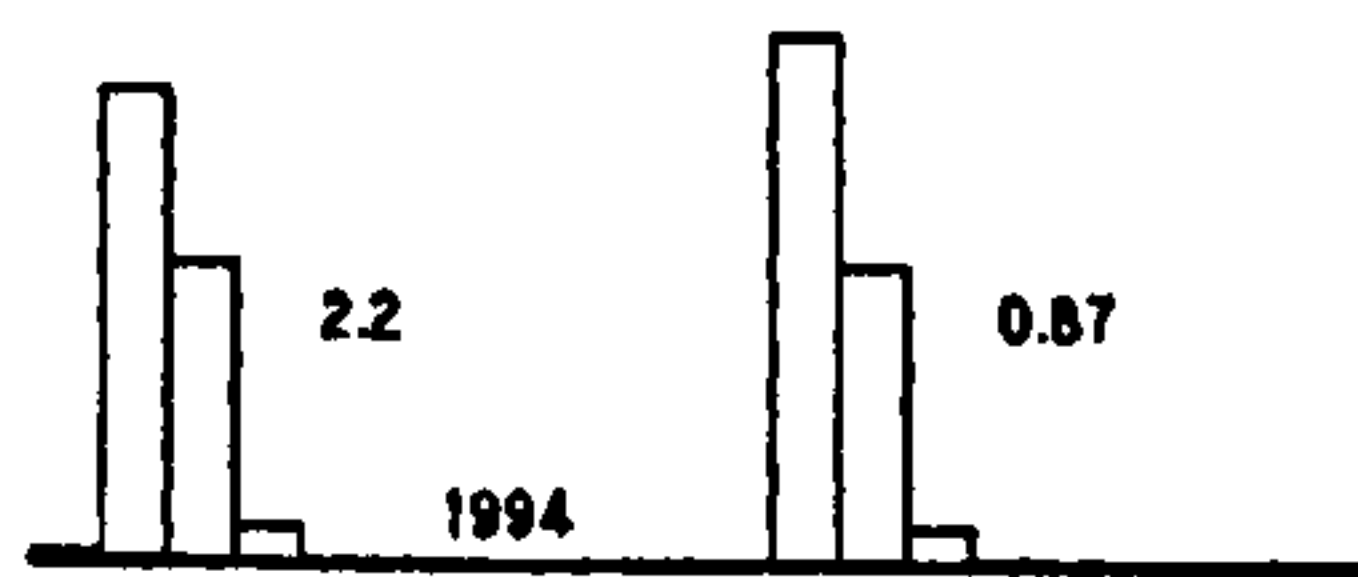
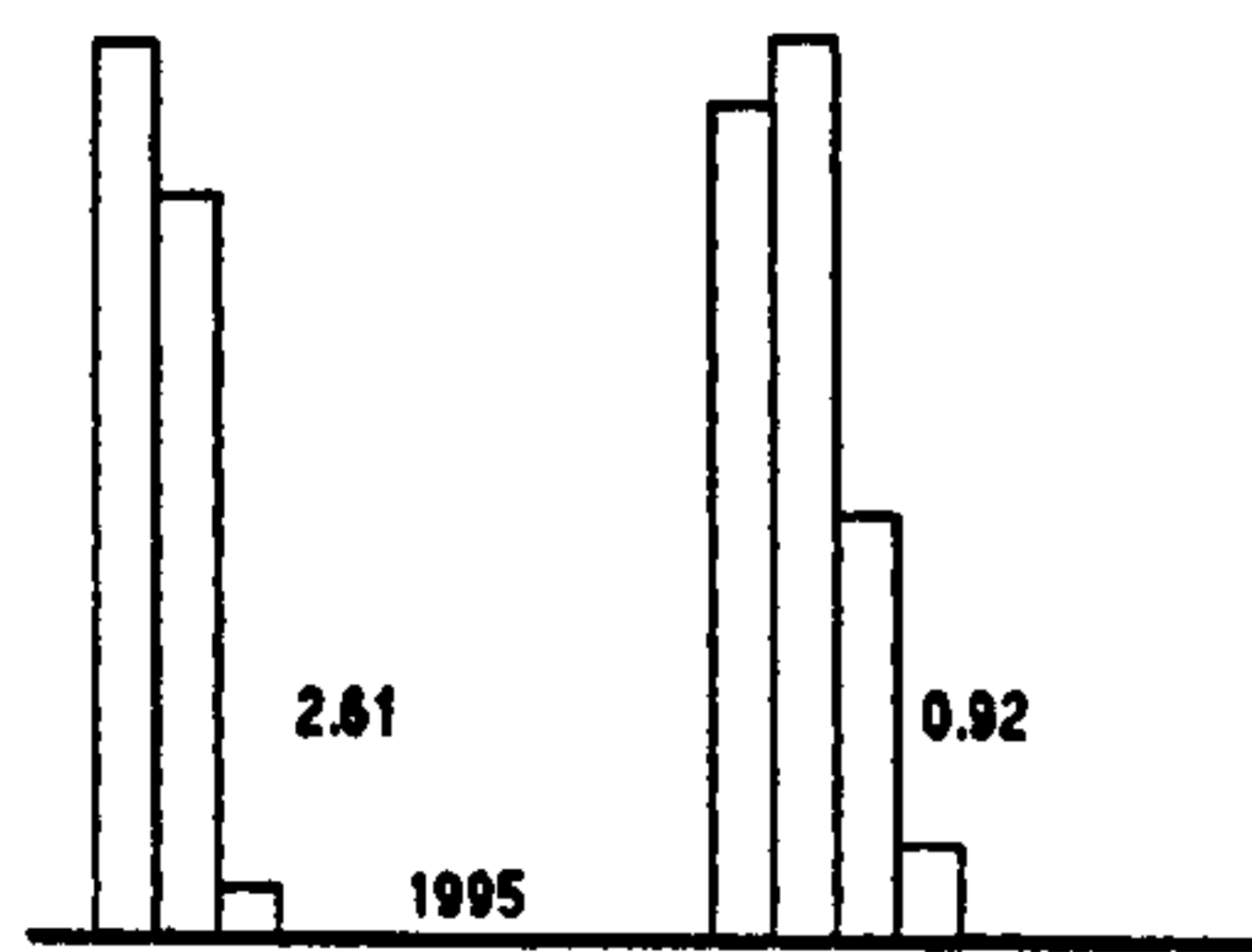
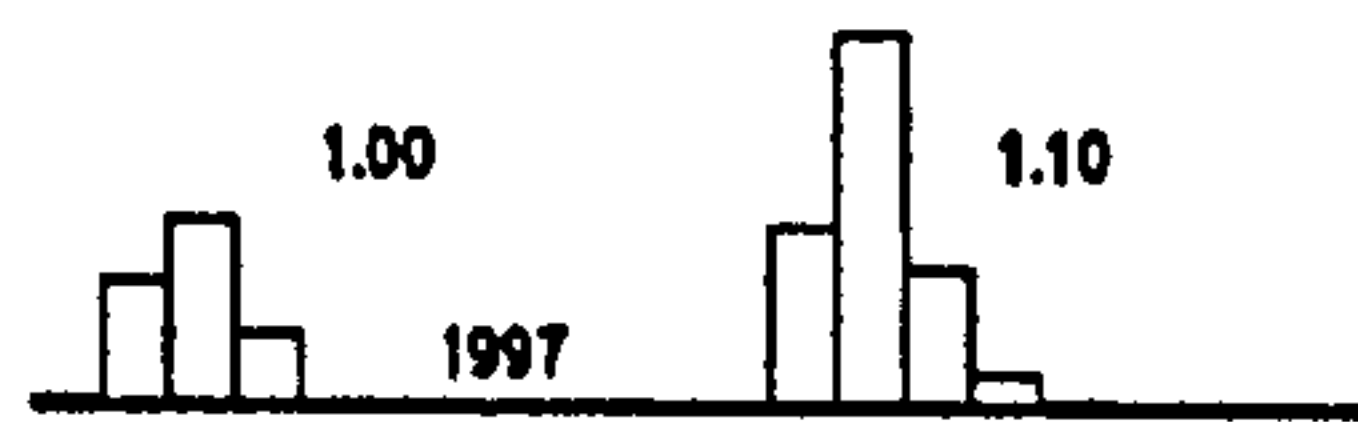
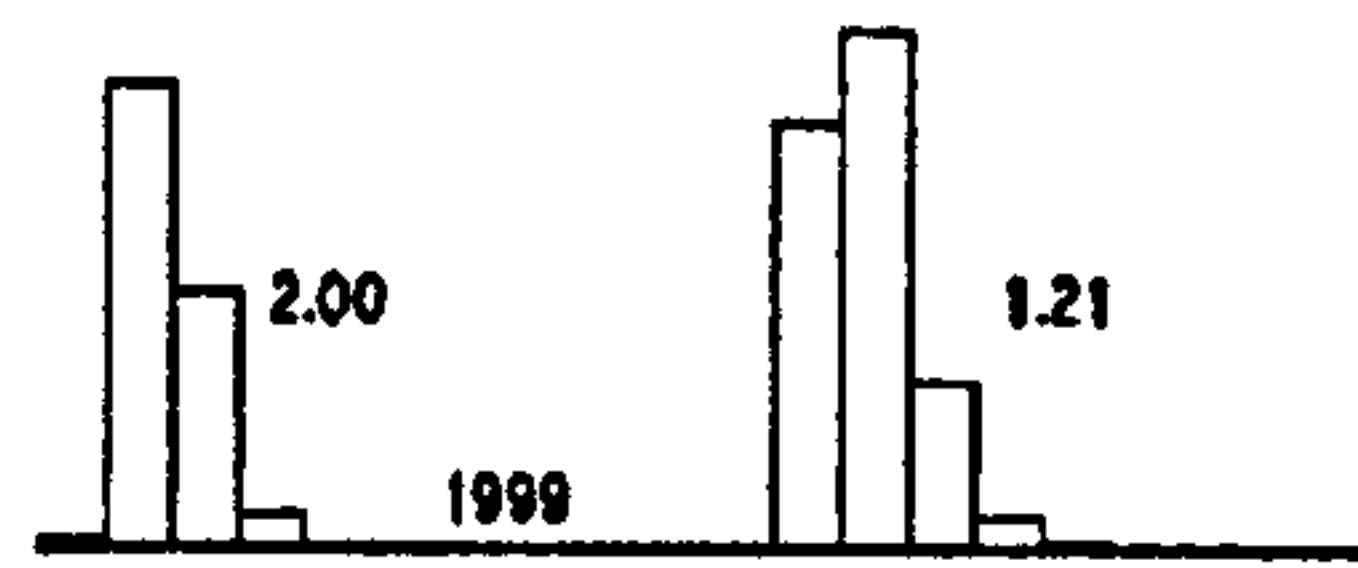
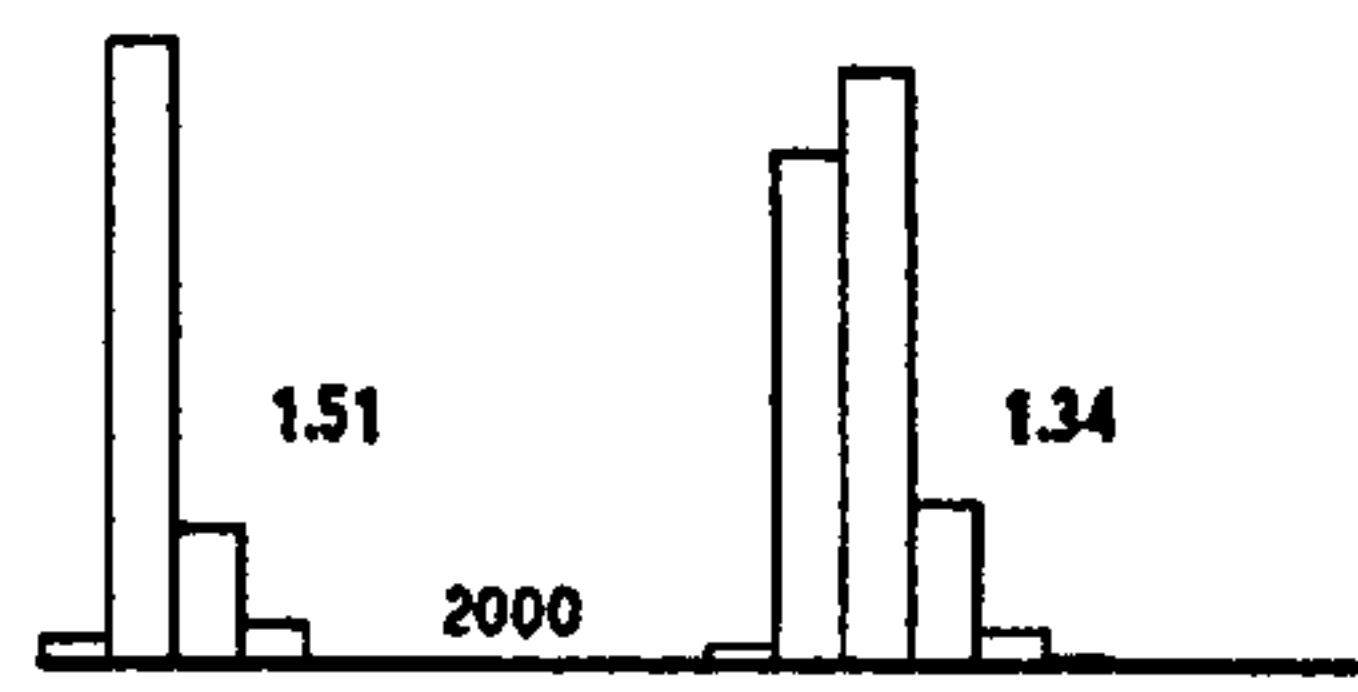


Figure 3.13 Age structure of *Limanda limanda* caught by FV "Shamrock" in Spring 1966. Sexes are shown separately and instantaneous coefficients of mortality for fully exploited year classes are shown (yr^{-1}). X axis: age in years; Y axis: numbers caught per hour.

Figure 3.14 (represents graphs on the next three pages). Catch rates (Number caught hr^{-1}) on Y-axis and Age in years on X-axis, and the instantaneous rate of total mortality of male and female dab ('pseudocoHORTS') between 1972 and 2000 on the North Wales Coast. Vertical separations are proportional to the time between successive samples and the year date is to the left of a figure for spring samples and in the centre for autumn samples.



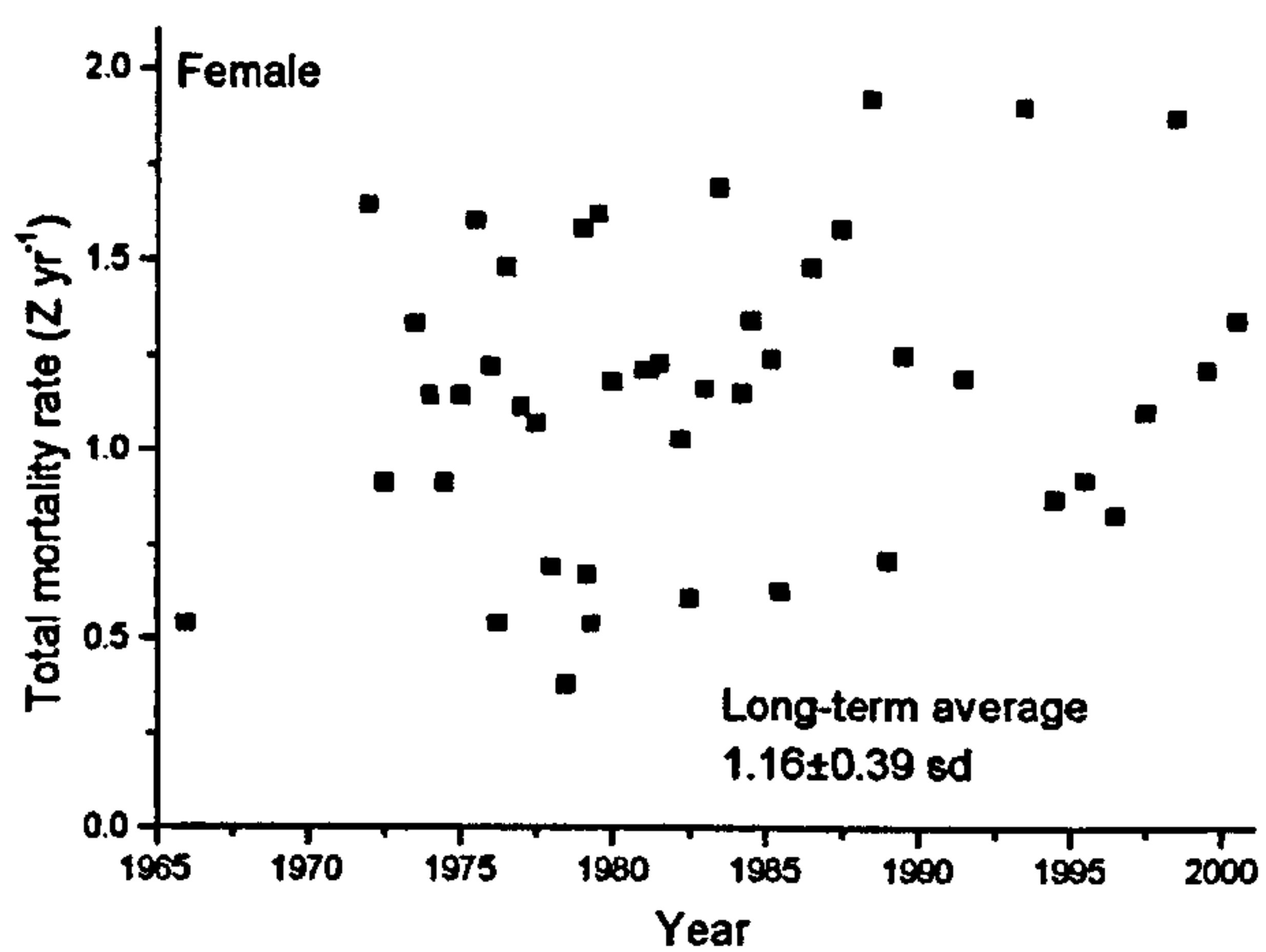
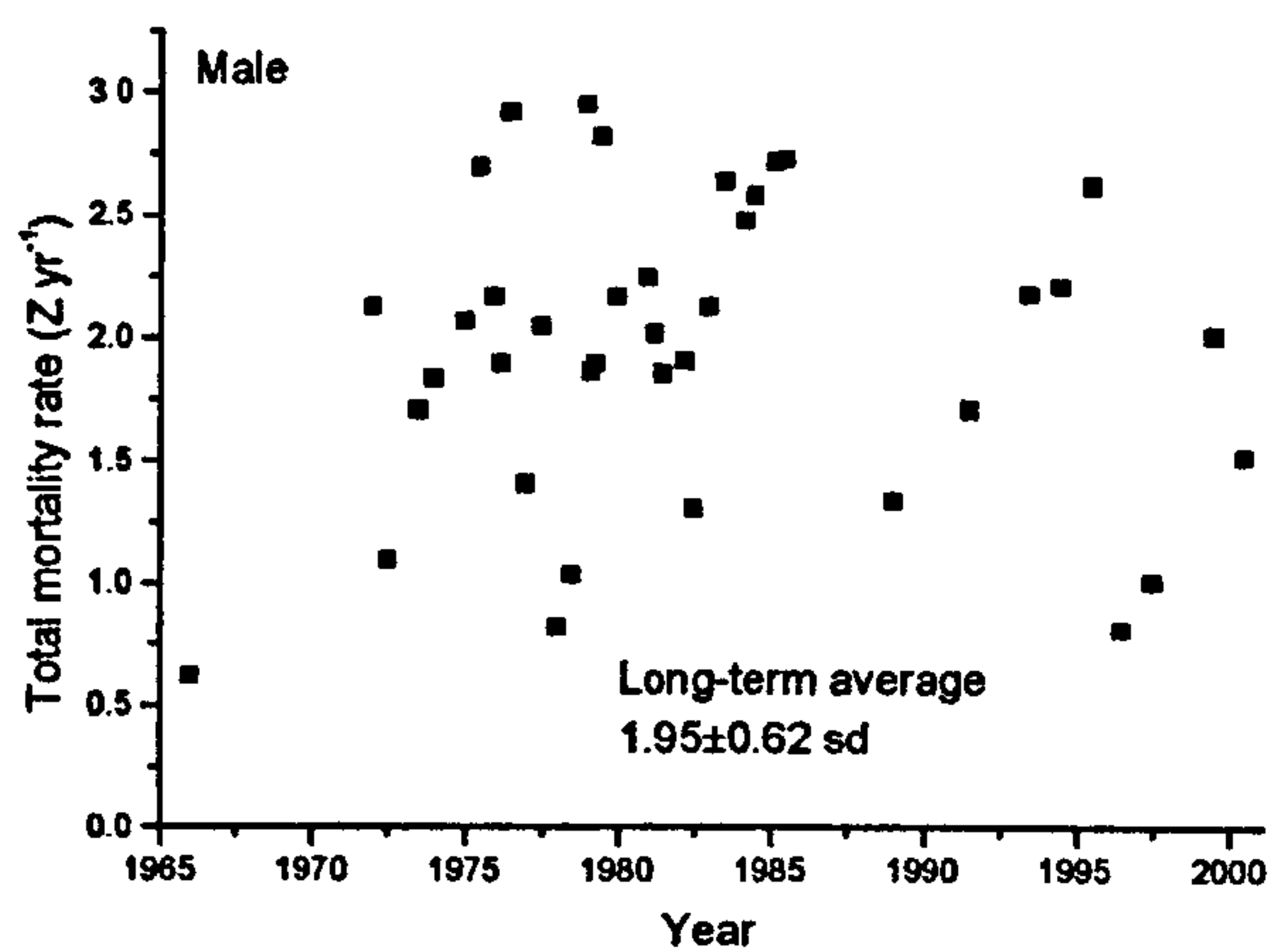




Male

Female

Figure 3.15. Estimated long-term total mortality rate in male and female dab by catch curve analyses of 'pseudo-cohorts', 1966-2000

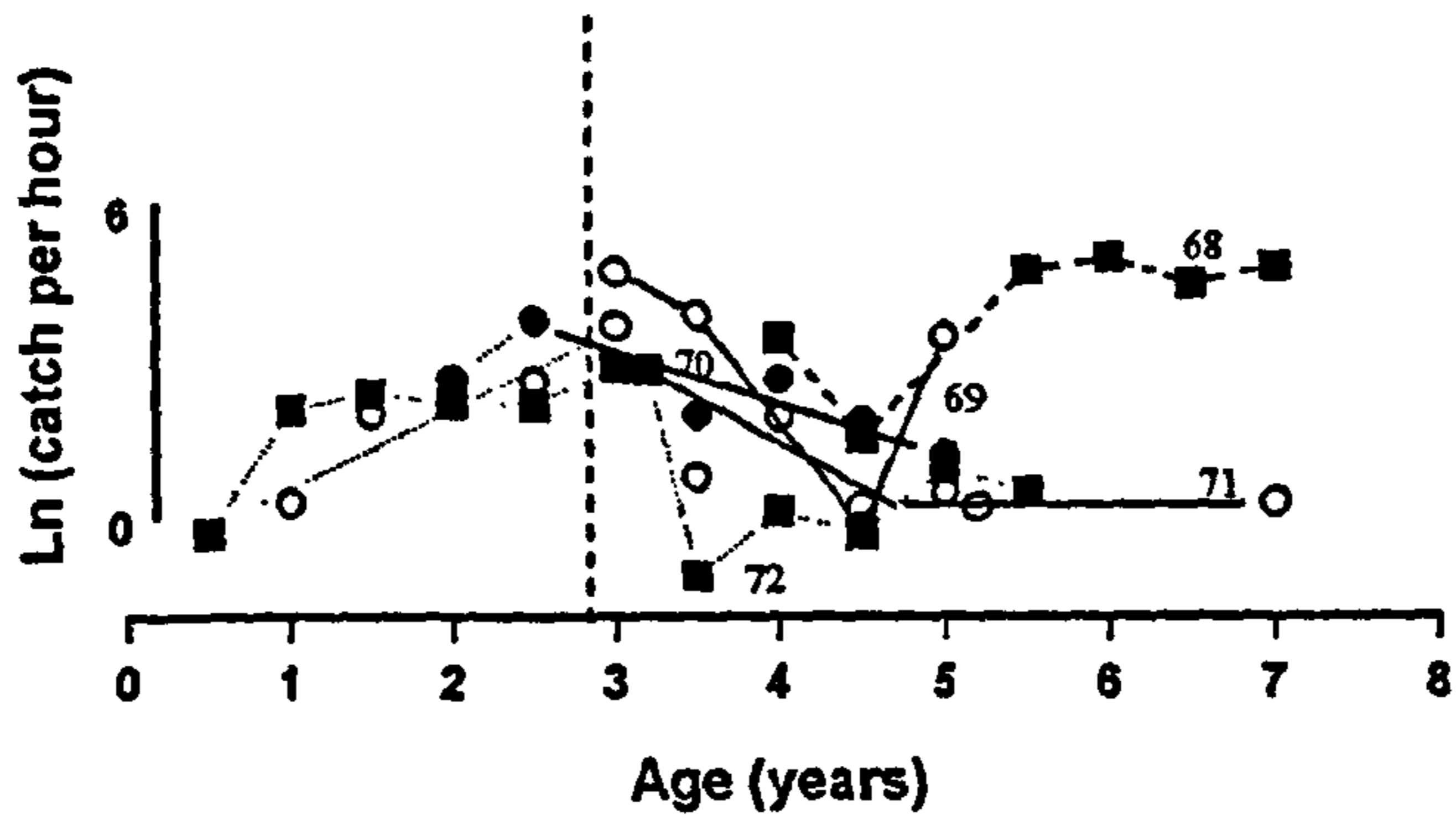


The abundance index (Figure 3.16) and total mortality rate (Figure 3.17) were also estimated by following the fate of individual cohorts through time between 1968 and 1996. This analysis was deemed necessary in order to assess the accuracy of the earlier mortality rates (in Figure 3.15) obtained by analysis of 'pseudocoHORTs' (one-sample analysis including several cohorts). The result in Figure 3.16 showed that a decline in the abundance of year-classes ≥ 3 years old in all cohorts of males and females. After 1972, the male dab older than 5 years were generally not available in the catches whilst catches of females with year classes 6 or more years were frequent. The estimated total mortality rates (Z) based on year of cohort birth (Figure 3.17) showed that Z in males (1.51 yr^{-1}) is 20.8 % higher than Z in Females (1.25 yr^{-1}). This trend is similar to that obtained by the analyses of 'pseudocoHORTs' in Figure 3.15 and there are no significant differences between these two sets of estimates.

Figure 3.16 (represents male and female cohorts respectively on the graphs in the next two pages). The abundance of cohort components by year-classes (age groups) on the North Wales Coast, 1968-1996. Earliest cohorts (e.g. 1968) are at the top and each subsequent cohort is displaced downward by one log unit for ease of comparison.

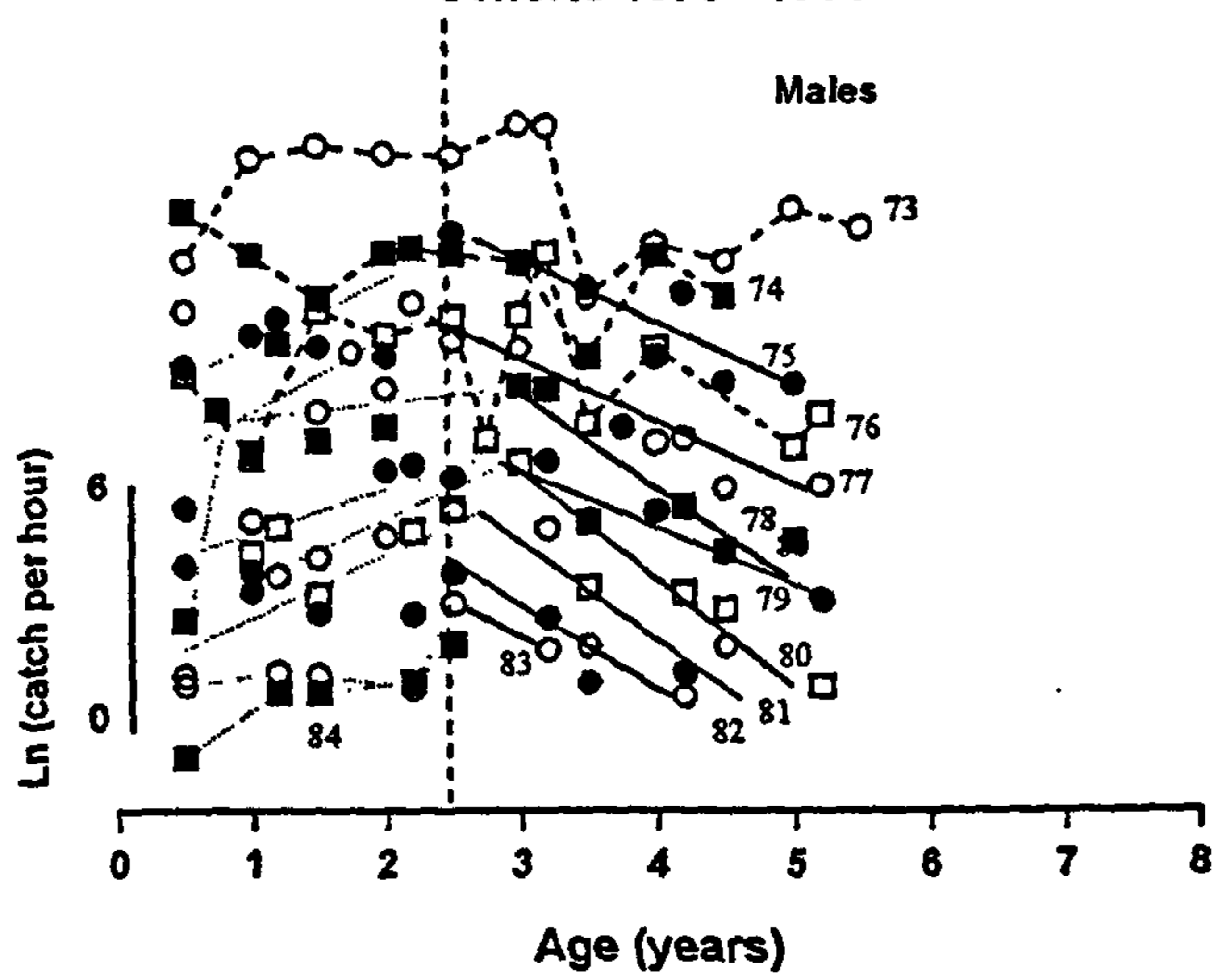
Cohorts 1968 - 1972

Males



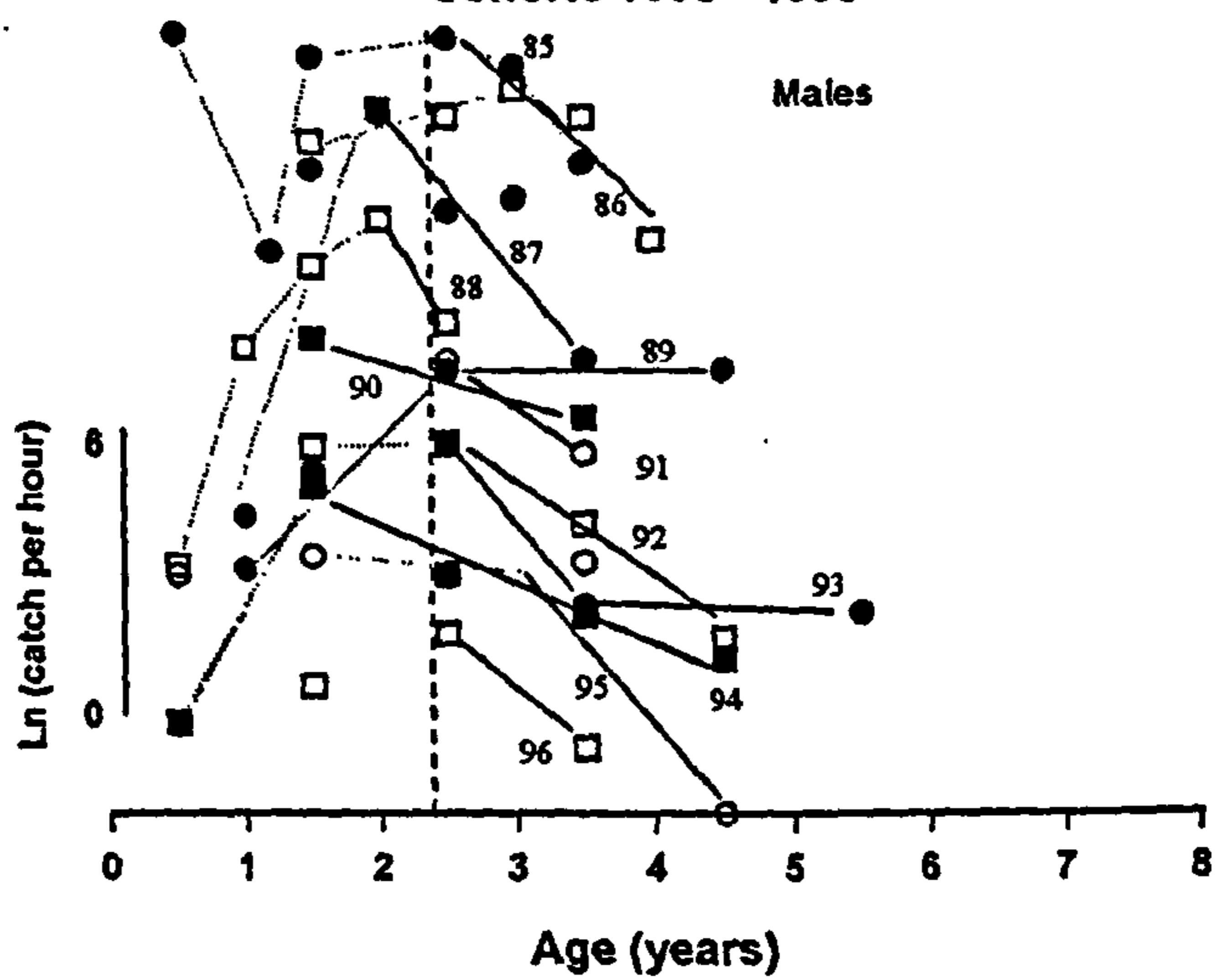
Cohorts 1973 - 1984

Males



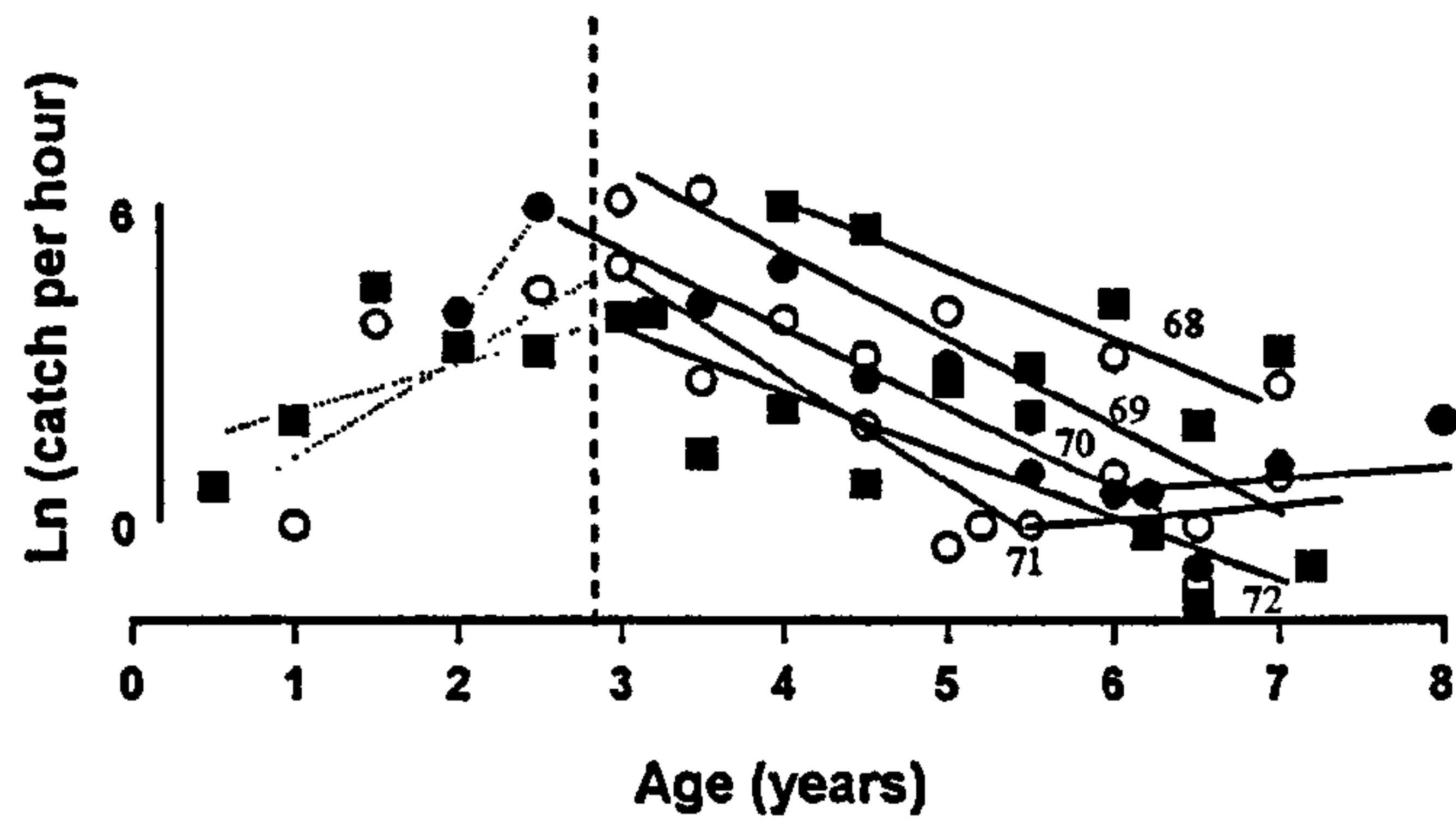
Cohorts 1985 - 1996

Males



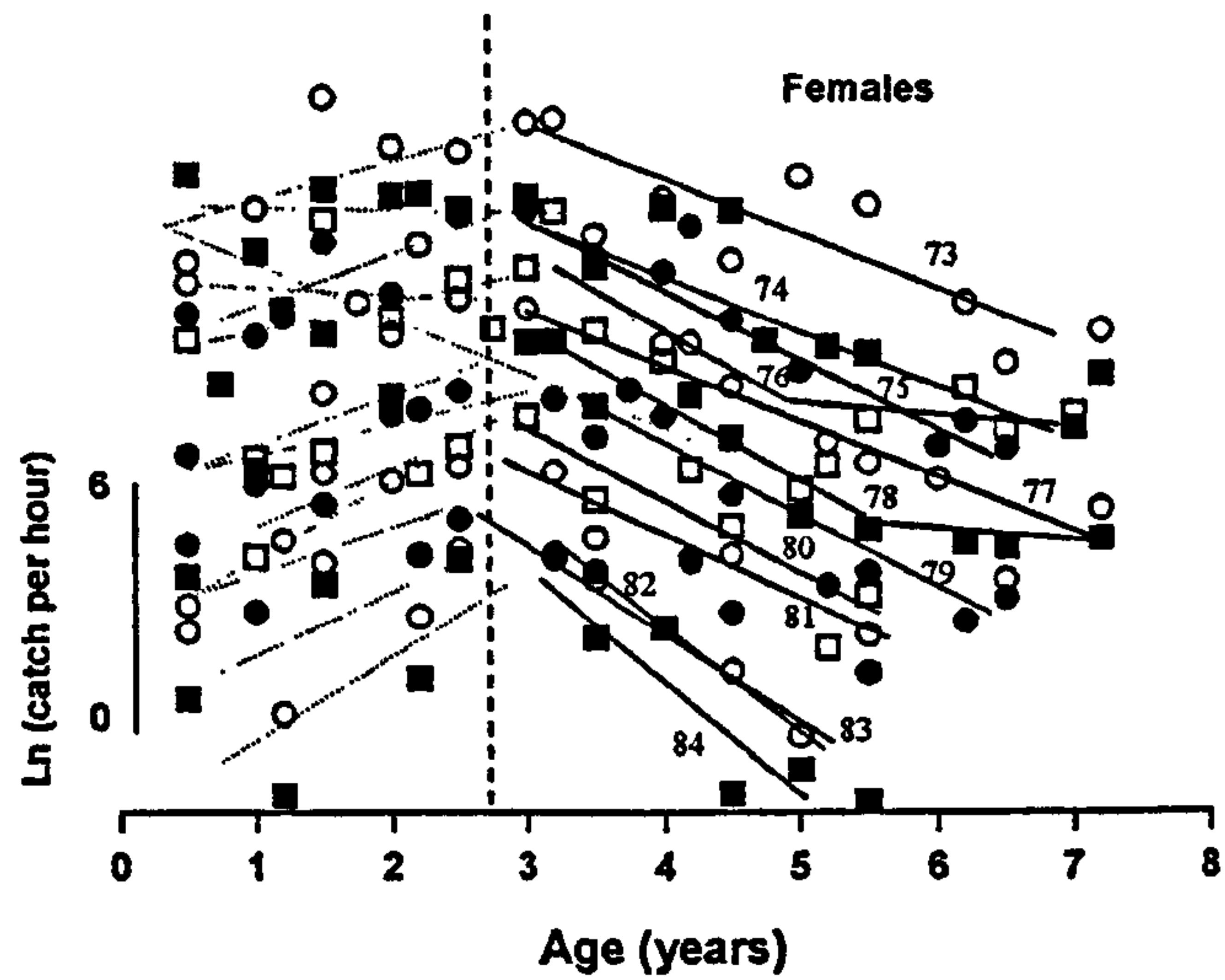
Cohorts 1968 - 1972

Females



Cohorts 1973 - 1984

Females



Cohorts 1985 - 1996

Females

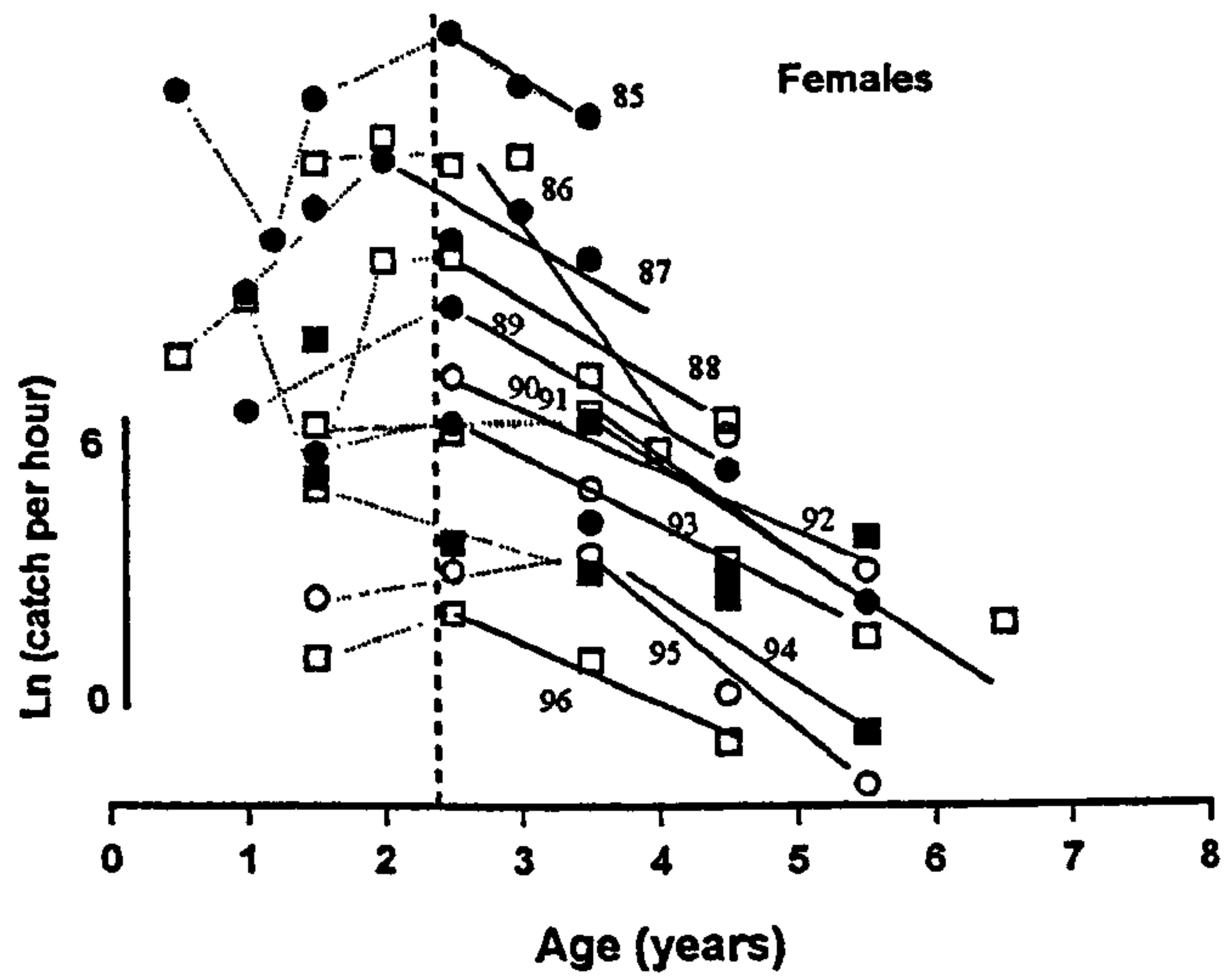
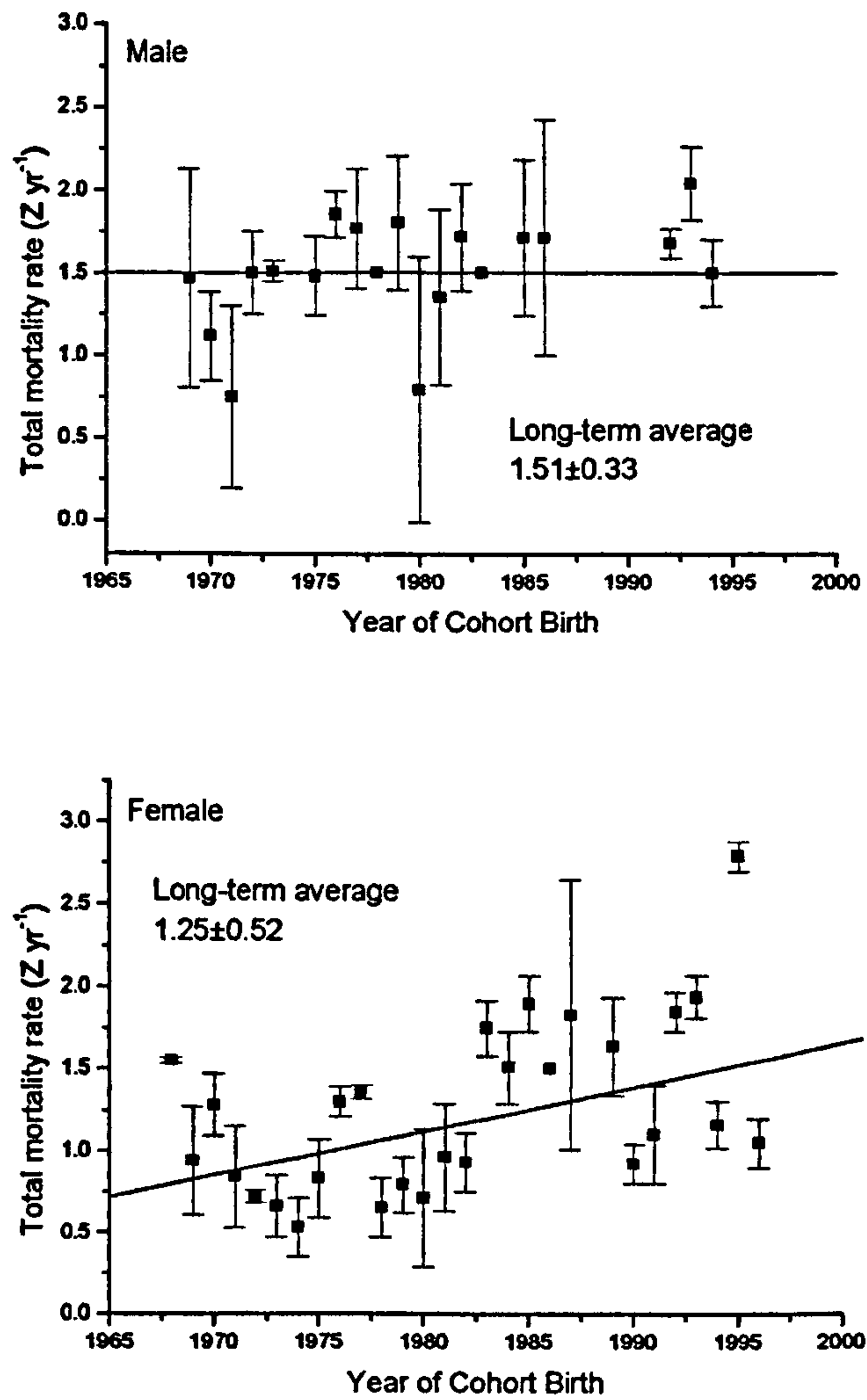


Figure 3.17. Estimated long-term average mortality rate of male (n=19) and female (n=28) dab obtained by analyses of cohorts, 1968-1996: male mortality trend line is not significant but female trend is significant (0.03 ± 0.02 95%CL). Vertical bars are standard errors.



The seasonal occurrence of crystalline otoliths is shown in Table 3.10. The maximum occurrence was in July and the minimum in August. Chi-squared test however suggests that there were no significant differences ($P>0.05$) in their seasonal occurrence.

Table 3.10. Seasonal occurrence of crystalline otoliths in dab, 1999/2000

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
%	2.38	4.76	8.70	9.09	5.00	13.85	2.11	5.09	9.95	7.34	4.27

There are no significant differences (Chi-square $\chi^2=16.832$, $df=10$, $P=0.078$) in the occurrence of crystalline otoliths between the months.

3.5 DISCUSSION

This study shows the opaque zone in the otoliths starts appearing in February (stage I) and gradually gets thicker in relatively large number of fish by April. The choice of April 1st as the start of the growth season suggested by Bakhsh (1982) is supported by this finding. Similarly, Basimi and Grove (1985a) found the date appropriate for the local plaice population. The maximum deposition (stage III) occurs in the majority of the fish between May and July, giving credence to the widely held view of summer growth in this species. Ortega-Salas (1980) and Bakhsh (1982) also noted that otolith accretion was greatest in summer when opaque bands were greatest and slowest in winter when hyaline rings were formed. An earlier study by Bohl (1957) on dab otoliths also noted that opaque zone was deposited in most otoliths between May and October, and the hyaline ring between November and April, with some variations with age and between individuals of the same age. These variations are also observed in the dab otolith conditions in this study. Basimi and Grove (1985a) observed that the opaque zone begins to appear in the majority of plaice in March whilst the onset of hyaline zone in most fish occurs in June and July. Ortega-Salas (1980) associated rising sea temperature with opaque band formation and falling sea temperature with hyaline rings. This observation might be true in this study since the period of intensive deposition of the opaque and hyaline layers respectively coincides with high and low seasonal seawater temperatures respectively. The study suggests about 6.6 % of annual occurrence of crystalline otoliths in the local populations of dab. The reasons for the occurrence of crystalline otoliths have not yet been established, though pollution effects might not be ruled out.

The study shows dramatic seasonal changes in weight in the dab. The seasonal changes in weight can be related to reproductive and feeding activities. The fish have lost considerable weight after spawning in March and April. With the resumption of active feeding in late spring and early summer, the fish steadily gain weight rising to a peak in the summer. There is a slow down in growth in weight again with the onset of gametogenesis (and declining feeding rate) in the autumn. As the gonads develop and massively increase in weight at the peak of spawning season in winter (January and February), the female dab increased in condition. The male dab also exhibit similar pattern at the height of the spawning season in December and January but the seasonal changes in weight are less dramatic compared to the female dab. Basimi and Grove (1985b) observed that, in plaice, daily feeding rate varies with season and fish size, with the greatest food intake in late spring and early summer. This pattern, combined with winter fasting and spawning, leads to considerable changes in condition factors. This study indicates that the increase in the frequency of deposition of opaque otolith material coincides with a significant increase in mean length and weight of fish between May and July. There are however variations in the mean length at age, with observed mean length of fish getting smaller between February and April. This might partly be explained on the migratory element of the larger fish to spawn further offshore and the arrivals of the 1 and 2 year old recruits between February and April. This behaviour temporarily lowers the mean length of the cohort, until the surviving spawners return. Ortega-Salas (1988a) noted that the mean weight and mean lengths at age of the Irish Sea dab varied throughout the year. He observed they are higher in the summer and hence result in higher estimated growth rate. In winter, the dabs apparently decrease in weight and length. He attributed this observation to the movement (emigration) of the larger fish from the sampled area probably for overwintering and spawning. The seasonal growth rates in the younger age groups were higher than the older age groups in the present study. Under laboratory conditions, Fonds *et al.* (1992) also found that juvenile plaice and flounder eat more food and grow faster at higher temperature than do larger older fish.

In general, size at age has been rather constant. Analysis of historical data shows noticeable variation only in the mean length of the 4- and 5-year old female fish between 1989 and 1998. This pattern was evident in the 3-year male dab. This observation might be attributed to size selective mortality on the older age groups during these years or seasonal migrations to and from the shallow coastal or deeper waters for feeding or spawning purposes (Saborowski and Buchholz, 1997).

The higher rate of fishing mortality in the males could be explained on their behaviour. The male dabs usually remained in deeper waters and could be vulnerable to fishing whilst the females move frequently between offshore and coastal areas for reproductive and feeding purposes. Sexual differences in total mortality rates have also been observed by Beverton (1964) and Basimi and Grove (1985a) for plaice. This observation was also made by Ortega-Salas (1988b) for the Isle of Man dab population, where the Z is 1.39 y^{-1} for male and 1.04 y^{-1} for females. Emigration was also given as a reason for this difference. Bohl (1957) reported that males disappeared from the catches at an earlier age than females. The unavailability of male dab older than 5 years in catches was also observed when the fate of the cohort was progressively followed from birth between 1973-1996 (Figure 3.16). This observation reinforces the explanation on the offshore distribution of the old mature males in deeper waters, which made them unavailable to the sampling gear in use. The sexual distribution of dab in the southern North Sea has been characterised by a reduced number of males during autumn and winter (Saborowski and Buchholz, 1997). However immigration of large females was also evident in autumn. This pattern of distribution may result in sexual differences in both real and estimated mortality rates. In comparison with the historical data, the age structure of the dab population in the present study has not changed significantly. This may be attributed to the fact that this species is normally taken as a fisheries bycatch in bottom trawls and is not really targeted in the same way as plaice. As a result, fishing pressure has not been intensively high on this species to cause any major perturbation in the population abundance and age composition. The maximum observed age in the population in the 1966 samples was 7++ years, which compares favourably with the current age-structure. The decline in abundance after 3 years may suggest size-specific mortality (Ricker, 1969). Causes of size-selective mortality may be related to differences between slow- and fast-growing individuals in metabolism, age at maturity, and predator-prey interaction (Fossen *et al.*, 1999). They argued that if maturation and spawning result in increased mortality, then maximum age will be higher for slow-growing individuals than for the faster growing conspecifics. The increased abundance levels of the 0-group fish in both sexes in the autumn of 1974, 1977, 1994 and 1995 may indicate strong recruitment in these years or patchiness in juvenile distributions.

Though the range of estimated natural mortality rates for the male and female dab was closer by the two methods used in this study, Pauly's method however suggests that M may be slightly higher in the male dab. This pattern is similar to the finding by Lee (1972) and Bakhsh (1982). Lee estimated M as 0.49 yr^{-1} for male and 0.31 yr^{-1} for female and Bakhsh estimated M as 0.69 yr^{-1} for male and 0.52 yr^{-1} for female for North Sea and North Wales Coast dab populations respectively. In the North Sea plaice, Bannister (1977) also postulated

higher natural mortality rates and higher fishing mortality rates on males than females. The Gunderson and Dygert (1988) method clearly appears to be suitable for female dab in ripe condition. Its application is restricted to within the breeding season and totally unsuitable for the male dab due to its relatively small gonad throughout the year. The natural causes of death in fish populations could be predation, diseases or senescence. Rijnsdorp (1994) stated that stress due to spawning may increase mortality from diseases and predation. However, these factors can be difficult to quantify. Not surprisingly the accurate assessment of natural mortality and recruitment has remained an intractable problem in fisheries ecology. Reviews in fisheries biology referred to recruitment as the '*last unsolved problem in fish population dynamics*'. The reliability of the estimates of natural mortality should be taken more as '*an article of faith than a proven fact*' (Pitcher and Hart, 1982). Ironically these two input parameters are central to dynamic pool sustainable fisheries exploitation and management with regard to fish yield forecasting, setting catch quotas or total allowable catch (TAC). The shift in emphasis to ecosystem-based fisheries management modelling, largely involving stomach content analysis, appears promising (Pitcher, 2000; Jennings *et al.*, 2001). Bailey (1994) proposed that density-dependent predation mortality in juvenile flatfish may either dampen or generate variability in recruitment and thus considered it a regulatory process. Macer (1967) and Gibson *et al.* (1993) have reported several potential piscivorous predators of larvae and juvenile flatfishes. Macer (1967) observed that the high mortality rate of 0-group plaice and dab was due to predation. He found 0-group dabs in the stomachs of 1-group plaice, and 1-group dab (cannibalism). This study also found 0-group dab in the stomach of whiting and grey gurnard. Langton and Bowman (1980) noted that Bothidae and Pleuronectidae comprised by weight between 0.3 and 2.5 % of the diet of cod and 0.5 and 1.0 % of the diet of hake in the Georges Bank.

Annual growth studies show that females attain greater ultimate size than males, and the oldest specimens were also females. Males grow relatively faster than females, and are the first to approach their asymptotic length. This observation is in conformity with the life-history theory of longevity (Deniel, 1990; Jobling, 1995) and similar to observations for the North Sea (Lozan, 1989; Rijnsdorp *et al.*, 1992), Coast of Brittany (Deniel, 1990) and Isle of Man (Ortega-salas, 1988a). The theory states that species reaching their asymptotic length rapidly have shortest life spans and also highest values of K (growth rate) and M (natural mortality). Comparison of the growth estimates for male and female dab in this study with Bakhsh (1982) shows no significant difference in the growth rates of dab between 1978-80 and 1999. There has however been an increase in the asymptotic lengths for the male and female dab by 25 % and 19 % respectively during this period. Lozan (1989) also observed an improvement in the asymptotic length in the German Bight between 1955, 1969 and 1986.

There are variations in the growth parameters of different populations of dab. Inspection of Table 1.5 (Chapter 1) will reveal that the asymptotic lengths of the female dab in this study are not significantly different from the dab populations in the offshore area in the south-eastern North Sea (Dogger Bank) and the Isle of Man. It was however higher than the dab populations around the Wadden Sea in the coastal area of the North Sea (Rijnsdorp *et al.*, 1992). The dab population in the coast of Brittany (Deniel, 1990) has the highest asymptotic length in both males and females. Sparre and Venema (1998) have shown the Growth Performance Index (Φ)

$$\Phi = \ln K + 2 * \ln L_{\infty}$$

to be remarkably constant between different populations of the same species, as long as similar units (e.g. cm) and definitions (e.g. total length) are used. An average growth performance index ($\Phi \pm SE$) was calculated for the different growth parameters of dab in Table 1.5 as $\Phi = 5.75 \pm 0.15$ and $\Phi = 5.45 \pm 0.17$ for female and male respectively. The growth parameters of the dab population from the coast of Brittany ($\Phi = 6.85$ and $\Phi = 6.72$) for male and female respectively are shown to be significantly different from the other populations. The primary environmental factors that have been considered to be responsible for the observed regional differences are temperature, salinity, depth, population density, and the amount and quality of the food available, Lozan (1989); Rijnsdorp and van Leeuwen, (1992, 1996); Nash *et al.* (1994a). Temming and Hammer (1994) suggested that growth variation between sexes might result from energy intake or metabolic expenditure. Lozan (1989) studied the growth rates of dab in eight areas of the North Sea and observed fish growth depends not only on the temperature and salinity but also on the population density, the food supply, and the water depth. He noted that the generally poor growth of the dab in the Dogger– and Fisher Banks may have to do with the low temperature and the available food in those regions, which is poor in calories. The increase in growth of juvenile plaice in the 1950s was related to an increase in the availability of food in the coastal waters of the southern North Sea (Rijnsdorp and van Leeuwen, 1992). Rijnsdorp *et al.* (1991) and Nash *et al.* (1994a) found evidence of density–dependent effects on the somatic growth of juvenile plaice in the North Sea and Isle of Man respectively. Sogard and Able (1992) noted that water temperatures are beneficial to growth but only up to an optimum level. They reported that at higher temperatures young plaice display stress responses and stop foraging activity. Purchase and Brown (2001) observed that growth rates increase with increasing temperature in the Atlantic cod. Karakiri *et al.* (1989) found that the mean size and hence the growth rates of plaice is affected by food availability. Jonsson (1966) pointed out that growth conditions

were favourable for dab with plentiful food supply and a less crowded environment. As a result of intensive removal of competing species, the dab in western Baltic have higher growth rate than their counterparts in the North Sea where the population density is higher, and with consequently greater competition for food. Growth changes in the plaice have been significantly correlated with indices of plaice density, eutrophication, and seabed disturbance by beam trawling in the North Sea (Rijnsdorp and van Leeuwen, 1996). Dreves *et al.* (1999) illustrated spatial growth differences between subpopulations in the Baltic flounder (*Platichthys flesus*) in the Gulf of Finland, with mean age for the same length varying by 1 or 2 years. They observed a significant decrease in length at age in the flounder populations from the southwestern to the northeastern areas. Fishing intensity will also affect the growth characteristics of fish and thus the life history trait (Beverton and Holt, 1957; Ricker, 1981; Jennings and Kaiser, 1999). It may be suggested from this study that the relatively constant population structure of dab observed between 1966-2000 may be due to only moderate fishing pressure on this species. This may not be surprising as dab is not regarded as a prime commercial fish and there is therefore little fishing on this species; most of it is incidentally taken as by-catch in trawlers. A possibility exists also that dab populations are now benefiting from ecosystem overfishing (or a combination of growth and/or recruitment (Pauly, 1984)) of the plaice populations; this means that plaice (the main competitor) population may have been reduced through intensive fishing in the Irish Sea and thus creating less competition for dab for food and habitat. Unpublished historical data on plaice (from MSc student surveys in the survey area) showed that the abundance, average size range, size and age at maturity of plaice has declined. Also, the total mortality rate of this species has increased. It may be worth noting that there is intraspecific diet overlap between the two species (Carter *et al.*, 1991). This phenomenon has been reported elsewhere (Pauly *et al.*, 1998 and Rodhouse *et al.*, 2001). Rodhouse *et al.* (2001) reported that globally, as groundfish landings have decreased, landings of cephalopods, which are short-lived trophic opportunists, have increased in some fisheries suggesting overfishing of their predators and, or competitors, may have positively affected cephalopod populations. Pauly *et al.* (1998) found, for species that have been exploited by fisheries between 1950-1994, a transition from long-lived high trophic level species to short-lived low trophic level species in the global marine ecosystems.

The next chapter will examine the reproductive biology of dab, including maturation, fecundity, variation in egg size, seasonal changes in gonad, liver weight and condition factors.

CHAPTER FOUR

Reproductive Biology of *Limanda limanda* L.: Maturation, Fecundity, Seasonal Changes in Egg Size, Ovary, Testes and Condition Factor

4.1 INTRODUCTION

The objective of this chapter was to describe the reproductive biology of dab, including (a) visual and histological assessments of gonad developmental stages (b) spawning time (c) length and age at maturity (d) fecundity and (e) the annual cycle of condition, including changes in the ovary and liver weight. An attempt is made to estimate total egg population in the survey area. Egg-size frequency distribution of various maturity stages and seasonal changes in oocyte size are also determined.

4.2 MATERIALS AND METHODS

4.2.1 Gonad maturity staging

The stages of gonad maturation were classified based on a combination of scales described by Htun-Han (1978b,c) and Rijnsdorp (1989) for the North Sea dab and plaice respectively, a standard key used in the School of Ocean Sciences, Bangor and from personal observations. The classifications were based on both external appearance and histological sections of the gonad. The gonads of all fish sampled were assigned to maturation stages so that spawning time and associated cycle in gonad maturation could be determined. Ovaries were assigned a maturity code based on an 8-point maturity classification for macroscopic examination (described below). These assignments were verified with histological evaluation.

4.2.1.1. Visual Assessment:

IMMATURE

A. Female dab

The ovaries in a dab are conical. The base lies at the back (posterior) of the body cavity and the apex extends backwards towards the tail, the degree of the extension depending on the maturity stage of the dab. This structure is similar to that of plaice.

Stage I:

The ovaries are thin, slender, glassy and translucent in appearance and underdeveloped. The length is about 10-15 mm for a fish of length between 11-15 cm. The average weight of ovaries for immature fish between 11-15 cm is 0.08 g and the gonadocarcass ratio (GCR), ratio of gonad weight to carcass weight, is about 0.39 %. This stage is present all year round.

Stage II:

This is a maturing stage. The ovaries are slightly larger, translucent, glassy and grey in colour intermediate in size between stages I and III. The pre-vitellogenic oocytes are still invisible to the naked eye. The average ovary weight for maturing fish between 16-20 cm is about 0.60 g and the GCR is about 0.68 %. The stage is classified as being immature and such a fish can be present all year round.

RESTING

Stage III: Mature and pre-spawning.

The stage belongs to mature dab outside the breeding season (resting period). The ovaries are slightly reddish (pale), flat and slack. They protrude into the body cavity and average length is about 80 mm for a 20 cm fish. The eggs are not visible to the naked eye. The average ovary weight is 0.76 g for a 20 cm fish and the GCR is about 0.92 %. The average oocyte diameter is 0.15 mm. The main external difference from stage II is that the ovaries are not firm and do not appear glassy. This maturation stage is dominant between July to October.

PRE-SPAWNING

Stage IV: Ripening

The ovaries are slightly swollen, pinkish and granular. Very few eggs are beginning to be transparent and just visible to the naked eye in November but most eggs become visible as the season progresses in December and January. Most eggs are still however opaque. The average ovary weight is about 3.22 g and the average GCR is about 4.15 % for a 20 cm fish. The average egg diameter is about 0.49 mm. This maturation stage is dominant from November and early December.

Stage V: Ripe

This is the beginning of the hyaline stage. Eggs are larger, yolky and less than 50 % of the eggs are transparent and now have a speckled appearance. The average ovary weight is 14.19 g for a 20 cm fish. The average egg diameter is 0.57 mm. The GCR is about 18.52 %. This condition dominates in January and early February.

Stage VI: Fully ripe

Eggs are larger, yolky and more than 50 % of the eggs are transparent. The ovary is full and the egg sizes are irregular. The average ovary weight is 21.61 g for a 20 cm fish. The average egg diameter is 0.58 mm. The GCR is about 27.72 %. This condition persists between February and early March.

SPAWNING

Stage VII. Running

The ovary is reddish, flabby and may be partly spent. Only a small amount of opaque eggs are present. The opaque eggs give the ovary a granular appearance. Hyaline (transparent) eggs predominate, producing a speckled appearance. Eggs running freely in ovarian cavity and run from vent on slight pressure. The ovary weight is 6.33 g and the GCR is about 9.48 % for a 20 cm fish. The average egg diameter is 0.36 mm. This dramatic reduction in average egg size indicates that the larger eggs are being spawned in batches. This condition dominates in March.

POST-SPAWNING

Stage VIII. Spent

The ovary is mainly empty, resembling an empty bag and is blood shot. The ovary weight is 0.95 g and the GCR is about 1.76 % for a 20 cm fish. The average egg diameter is 0.13 mm. Very few large eggs may remain, which may be resorbed. The ovary is approaching stage 3. This stage dominates between April and May.

B. Male dab

The testes of a dab are elongate bodies situated ventral to the kidney with the long axes lying dorso-ventrally against the posterior wall of the body cavity. They are attached to the body wall by mesenteries. The main difference from the ovary is that the testes do not penetrate towards the tail end of the male dab. This structure is similar to that of plaice.

IMMATURE

Stage 1.

Testes are very small and barely visible. The average weight of both testes is 0.07 g for an immature fish between 11-15 cm and the GCR is about 0.27 %. This stage is present all year round.

Stage II.

This is a maturing stage. Testes slightly bigger and visible. The average testes weight is 0.09 g for a maturing fish between 11-15 cm and the GCR is about 0.52 %. This stage is present all year round.

RESTING

Stage III: Mature and pre-spawning.

Testes slightly bigger, colour grey but no milt present. Lobed and slack. The average weight is 0.14 g and the GCR is 0.18 % for a 20 cm mature fish. This stage dominates between June and September.

SPAWNING

Stage IV: Ripe/Running

Lobed appearance, white and flat. Soft to the touch. The average weight is 1.39 g and the GCR is 1.87 % for a 20 cm fish. Brownish and, if running ripe, white milt runs out of genital pore on slight pressure. This stage starts appearing in the population in October. This condition is dominant among mature males between November and January, but few running fish could be identified as late as May-June

POST-SPAWNING

Stage V: Spent

Small, form of half moon, colour brown and shrunken. Often going back to stage 2. The average weight is 0.14 g and the GCR is 0.17 % for a 20 cm fish. This condition starts appearing in February and becomes dominant between March to June. The vas deferens is generally empty but may contain some milt.

4.2.1.2 Histological classification

This study was carried in order to confirm some ovary maturation stages based on visual examination. The main focus of the histological studies was on the progressive development of the ovary. It was intended to show the stages in the development of the oocytes from the immature (oogonia) stage to the tertiary vitellogenic stages (hyaline oocytes) and finally to the spent stage when the vitellogenic oocytes are degenerating and conspicuous spaces (septa) are present in the lumen of the ovary.

For this study, the gonads of freshly killed specimens were used. For the females, the ovary being conical, a small piece was cut from the fore and middle parts. The fixative used was either Bouin's or Susa (Disbrey and Rack, 1970; Dr. G. Walker, pers. comm.). The gonads were then dehydrated in ethanols and toluene and embedded in paraffin wax. Slides were prepared from histological sections of approximately 7-10 μm thickness, cut from paraffin wax using a microtome. The sections were mounted onto slides on a hot plate (operated 2-5 $^{\circ}\text{C}$ below the melting point of the wax). Glycerine albumin was used as adhesive. The sections were de-waxed in 'histo-clear' solution, dehydrated in ethanol and stained with mercuric Bromophenol Blue (Mazia *et al.*, 1953). The stained sections were dehydrated in

ethanol, cleared in 'histo-clear' and mounted in D.P.X. The classification of gametogenesis was accomplished with reference to Tong (1967), Jones, (1974); Htun-Han, (1978b and c); Yoneda *et al.* (1998) and Bromley *et al.* (2000).

It was also important to show the histological appearance of the testes in the spawning season and the postspawning season. In the males, the testis is elongate and lobed; the piece of tissue was from the middle section.

A. Female

Oogenesis

A. Stage I (Immature) – Pre-vitellogenesis (Oogonia)

Only pre-vitellogenic oocytes are present. The oogonia are small (average less than 0.20 mm in diameter) and appear spherical.

B. Stage III (Mature and resting)- Primary oocyte

The oogonia grow into the primary oocytes, which are larger. In the resting stage, post-ovulatory follicles are present. The nucleus in the cytoplasm is visible. The stage III oocytes in the resting stage are irregular in shape. There are still some pre-vitellogenic oocytes.

C. Stage IV (Pre-spawning) – Primary and Secondary Vitellogenesis

The oocytes have reached the primary and secondary yolk stages. The oocytes are characterised by the presence of yolk droplets. Yolk globules are present throughout the cytoplasm. The oocyte nucleus is clearly distinguishable at this stage. The dark stained cortical alveoli granules occur around the periphery of the cytoplasm (Bromley *et al.*, 2000).

D. Stage V-VI (Spawning) – Tertiary Vitellogenesis (Hyaline stage)

The oocyte swells as it becomes hydrated. The yolk appears as a homogenous mass filling the interior of the oocyte (coalescence of yolk), leading to the disappearance of the nucleus. The oocytes become irregular in shape.

E. Spent stage (VIII):

Vitellogenic oocytes are degenerating and conspicuous spaces (empty follicles) are present in the septa. When the ovary wall extends into the lumen of the ovary, it forms a septum (Jones, 1974).

B. Male

Spematogenesis

A. Spawning stage

The lumina of the lobules are filled with spermatozoa and a few cysts containing spermatids are also present (Tong, 1967). The ripe spermatozoa remained unattached in the lumen and vas deferens of the testes, active and move freely.

B. Spent stage

The lumen of the testes looks empty, with hardly any spermatozoa remaining.

4.2.2 Length and age at maturity

The maturity data were analysed by taking into account the distribution of mature and immature dab for each sex. The proportion of mature dab was determined by length and age (Appendix 3). The length and age at 50 % maturity ($L_{50\%}$ and $A_{50\%}$ respectively) were determined from the iterative statistical logistic sigmoidal curve (Microsoft Origin 5.0 and Biosoft FigP 2.7), based on the following model:

$$Y = a / (1 + \text{Exp}(-K(X - X_c))) \text{-----} (4.1)$$

Where:

Y = % maturity at length or Age

X_c = Fitted length (or age) at 50 % maturity

X = Total length in cm or Age in years

a = is set at 100

K = Fitted constant

4.2.3 Determination of fish fecundity

There are two widely used methods of determining fish fecundity:

4.2.3.1 Volumetric method

The method involves preserving the ovaries in a modified Gilson fluid (Simpson, 1951). The fluid not only preserves and harden the eggs but also help to liberate them by breaking down the ovary membranes (Bagenal, 1966). The jars containing the ovary should be shaken intermittently. The eggs are separated from the ovarian tissue using a sieve and a stream of water. The eggs are then diluted to a known volume, stirred and three 1ml or more aliquots extracted by pipette. The presence of yolk indicates that the eggs are ripening and are part of the spawning season stock. Therefore, eggs with predetermined diameter in each sample are counted and the mean count of three or more aliquots times the ratio of: total suspension/aliquot volume is used to estimate fecundity. The chemical composition of modified Gilson fluid (Bagenal, 1966) is given below:

100 ml	60 % Alcohol
15 ml	80 % Nitric acid
18 ml	Glacial acetic acid
880 ml	Water
20 g	Mercuric chloride

4.2.3.2 Gravimetric method

The gravimetric method has also been frequently used to estimate fecundity in fish (Burd and Howlett, 1974; Fleming and Gross, 1990; Jonsson and Jonsson, 1999) by a subsampling procedure. The sub-sample could either be wet or dry.

The dry method involves making a slit in the ovaries to open them, followed by preservation of the whole ovary in Gilson's fluid. The jars are shaken at intervals to help remove the ovarian tissue from the eggs. After careful decanting, the eggs are washed in an evaporating basin and any remaining pieces of ovarian tissues are removed . The washed eggs are then poured through a funnel containing a small piece of plankton silk. Excess water is removed by a vacuum connected to the funnel or drying the eggs on a filter and blotting paper. The eggs are now referred to as dry eggs and these are weighed immediately. The subsampling involves selecting a random of 300–400 eggs and weighing this sample. The eggs in this

random sample are counted under a lens. The fecundity estimate is obtained by multiplying the number of eggs in the subsample by the ratio:

$$\frac{\text{Wt. of all eggs}}{\text{Wt. of eggs in sample}}$$

If the eggs in various parts of the ovary are of different sizes, it is necessary to take several subsamples from different parts of the ovary and to calculate the average from them (Nikolsky, 1963).

Fecundity is estimated as wet weight by counting the number of eggs per 10 g or smaller portions. The estimate is obtained by taking a subsample of eggs suspended in fluid, using a pipette. Morse (1981) used both volumetric and gravimetric methods to determine fecundity in the summer flounder, *Paralichthys dentatus* L. Baxter (1959) used Simpson's (1959a) dry weight method to estimate fecundity in the North Sea herring.

In recent years, other methods have been used to estimate fish fecundity. Kraus *et al.* (1999) used the automatic counting and gravimetric method to estimate the fecundity of the Baltic cod (*Gadus morhua*). Ovary samples were hardened in boiling water and the ovarian tissues were dis-aggregated with Trypsin solution. The estimates of fecundity of lesser Sandeel, *Ammodytes marinus* Raitt, in the north western North Sea were derived by Gauld and Hutcheon (1990) using a photoelectric egg counter and the number of eggs (F) were fitted against fish length (L) using the model:

$$\text{Log } F = a + b \log L.$$

There are however concerns as to the choice of ovary for the determination of fecundity in fish. These concerns have been due to the difficulty in distinguishing between eggs that will be laid in the next spawning and those that will be laid in later years. The selection of fish with the appropriate maturation stage is therefore very crucial to the accurate determination of fecundity. Simpson (1951) suggested the following guidelines in the selection of fish for fecundity estimation:

a) to select fish which will spawn within 2 to 3 months, because the eggs which are about to be spawned are large with considerable amount of yolk.

b) to ignore fish whose eggs will be spawned in future years since these eggs will be considerably smaller and white.

c) to avoid selecting fish whose ovaries contain transparent eggs, indicating that spawning may have started. In the North Sea, Burd and Howlett (1974) proposed to use only filling fish and to avoid using fish with fully ripe gonads since some eggs may have been shed. Nichol and Acuna (2001) noted that the fecundity of fish species which spawn their eggs in batches may be underestimated if the ovaries of partially spent females are selected for fecundity estimation.

Fecundity may be overestimated if the eventual loss of oocytes due to atresia (oocyte resorption) is not taken into account. Oocyte atresia can occur in varying degrees throughout the spawning season, depending on the species and environmental conditions (McFarlane and Saunders, 1997). Nichol and Acuna (2001) suggested that this bias can be minimised if ovaries chosen for fecundity estimations are developed and near spawning condition.

Fecundity was estimated in this study by the volumetric method. A total of 74 fresh ovaries of maturity (ripening) stage were used during the breeding season (December-January). The ovaries containing fully 'ripe' transparent eggs (with hyaline eggs) were not used because some eggs could already have been spawned. Before counting, the eggs were separated from the ovarian tissues by preserving fresh ovaries in Gilson's fluid. To ensure effective penetration of the fluid, the bottle containing the ovary was stirred vigorously periodically for about a week. The fluid was decanted off and the ovary washed several times with tap water. The solution was filtered through a fine sieve to remove any remaining ovarian tissue into a flask. This method ensured that all the eggs were freed from the connective tissue. The eggs were suspended in tap water and made up to 3.0–4.0 litre (depending on ovary size), agitated to ensure uniform distribution, and five 1 ml samples extracted for counting individually on a partitioned petri dish (Bogorov tray) under a low power dissecting microscope. The overall coefficient of variation of the mean count was 15.34 %. Bohl (1957) excluded small eggs in his dab samples less than 0.153 mm whilst Lee (1972) estimated fecundity in dab by excluding small eggs with diameter below 0.12 mm. Bakhsh (1982) excluded eggs less than 0.12 mm. In the present study, it was found from the oocyte size frequency distribution that about 60 % and 70 % of the eggs in the resting and spent stages respectively have diameter ≤ 0.14 mm. Thus on the basis of the size frequency distribution and histological studies, eggs less than 0.15 mm were excluded from the fecundity estimate.

For each female, total body weight, somatic weight (body weight minus the gonads), total length, age, total ovary weight and the fecundity were recorded (Ricker, 1979). Kraus *et al.* (2000) noted that as growth in length and weight are variable and may show deviations, data had to be transformed to common logarithms to linearize the relationships between variate and covariate and to achieve normal distribution in variation. Thus to obtain a straight-line relationship for fecundity and length, both variates were transformed to logarithms and the relationship expressed by the equation:

$$\text{Ln Fecundity} = \text{Ln } a + b (\text{Ln Length})$$

This transformation was done also for fecundity versus somatic weight and fecundity versus ovary weight relationships.

4.2.4 Egg production

Average egg production (E_i) per female in the study area i was estimated from the following modified equation by Marteinsdottir *et al.* (2000):

$$E_i = \frac{\sum (N_i \times P_i \times F_i)}{\sum (N_i \times P_i)} \text{-----(4.2)}$$

Where N_i =total number of females at age i
 P_i =proportion of mature females at age i
 F_i =potential fecundity at age i

4.2.5 Seasonal changes in egg size

For each pair of ovaries from a 20 cm fish, the diameter of randomly selected eggs were measured using a calibrated eye piece micrometer. The ovaries at various maturity stages were preserved in Gilson's fluid. About 20 random measurements were made for each individual ovary. If the cell was spherical, the diameter was measured; if oval, the mean of the longest and shortest axes was taken. Additional random measurements were carried out for size frequency distribution of egg size from various stages of maturity.

4.2.6 Cyclical changes in gonad, liver weight and condition factor

Samples of mature dabs, between February 1999 to January 2001, with a length of 11 cm and above were collected monthly and sorted by sex. Normally, the samples were treated the same day they were caught by the otter trawl. When this was not possible, due mainly to the late return from survey grounds, the samples were frozen overnight and excess water and slime removed the following morning. For each sex, the samples were grouped into the following sizes: 11-15 cm, 16-20 cm, 21-25 cm, 26-30 cm and ≥ 31 cm. Fish were weighed to the nearest g whilst gonads and liver were weighed to the nearest mg. The gut was also removed and the carcass weighed.

The following parameters were estimated:

a) Gonadocarcass ratio:

$$\text{GCR} = \frac{\text{Gonad weight}}{\text{Carcass weight}} \times 100 \text{ -----(4.3)}$$

b) Hepatocarcass ratio:

$$\text{HCR} = \frac{\text{Liver weight}}{\text{Carcass weight}} \times 100 \text{ -----(4.4)}$$

c) Condition factor:

$$K = \frac{\text{Carcass weight}}{(\text{Total length})^3} \text{ ----- (4.5)}$$

4.3 RESULTS

The results of visual assessment of gonad developmental stages in female and male dab are shown in Figures 4.1 and 4.2 respectively. The histological classifications of key maturity stages in female and male gonads are also given in Figures 4.3 and 4.4 respectively.

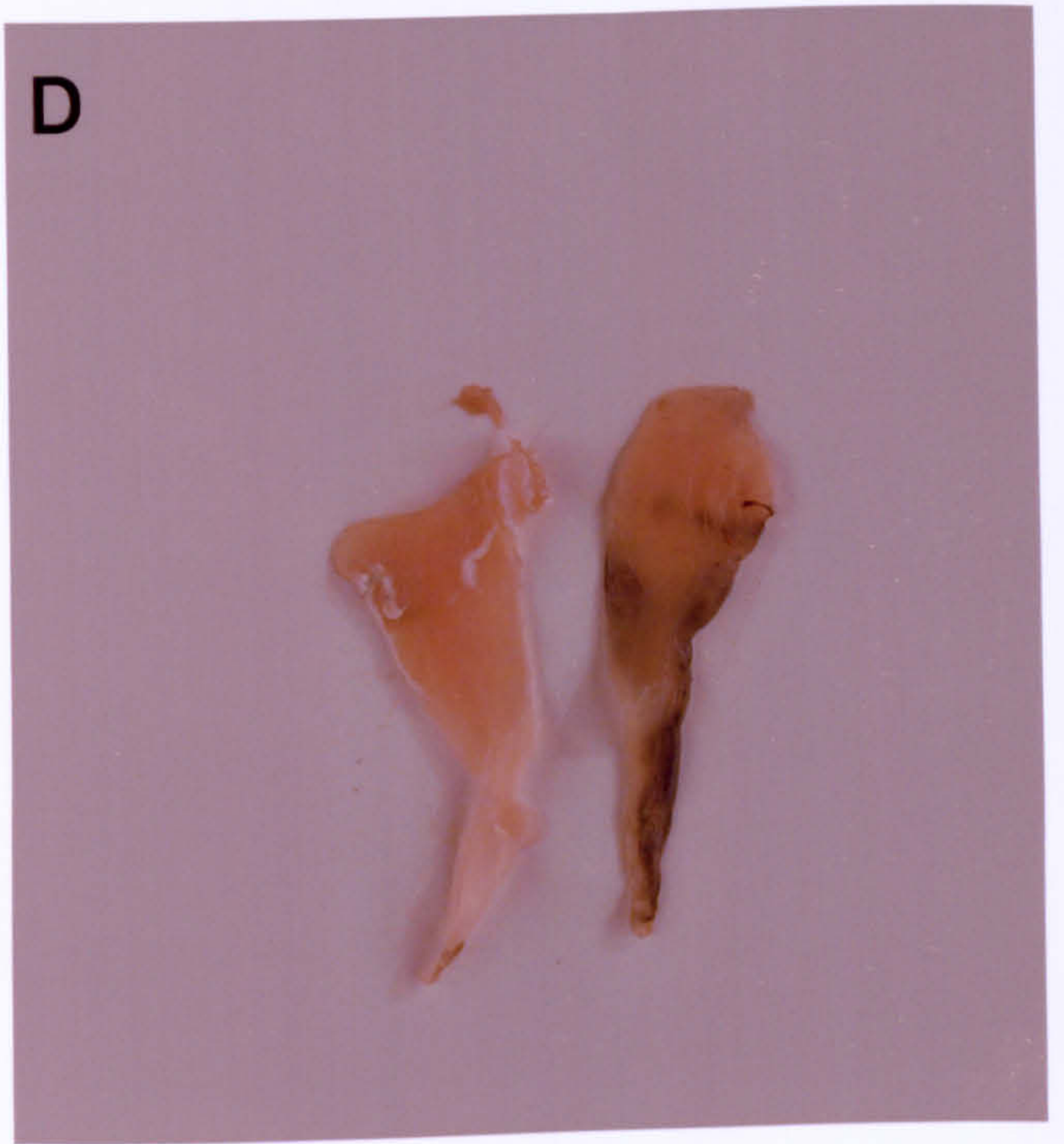
Figure 4.1. Ovaries of 20 cm dab showing different maturity stages (See text for detailed description)

A. Immature ovaries

B. Ripe ovaries at the height of spawning in February

C. Running ovaries (partially spent) in early March

D. Resting ovaries in July



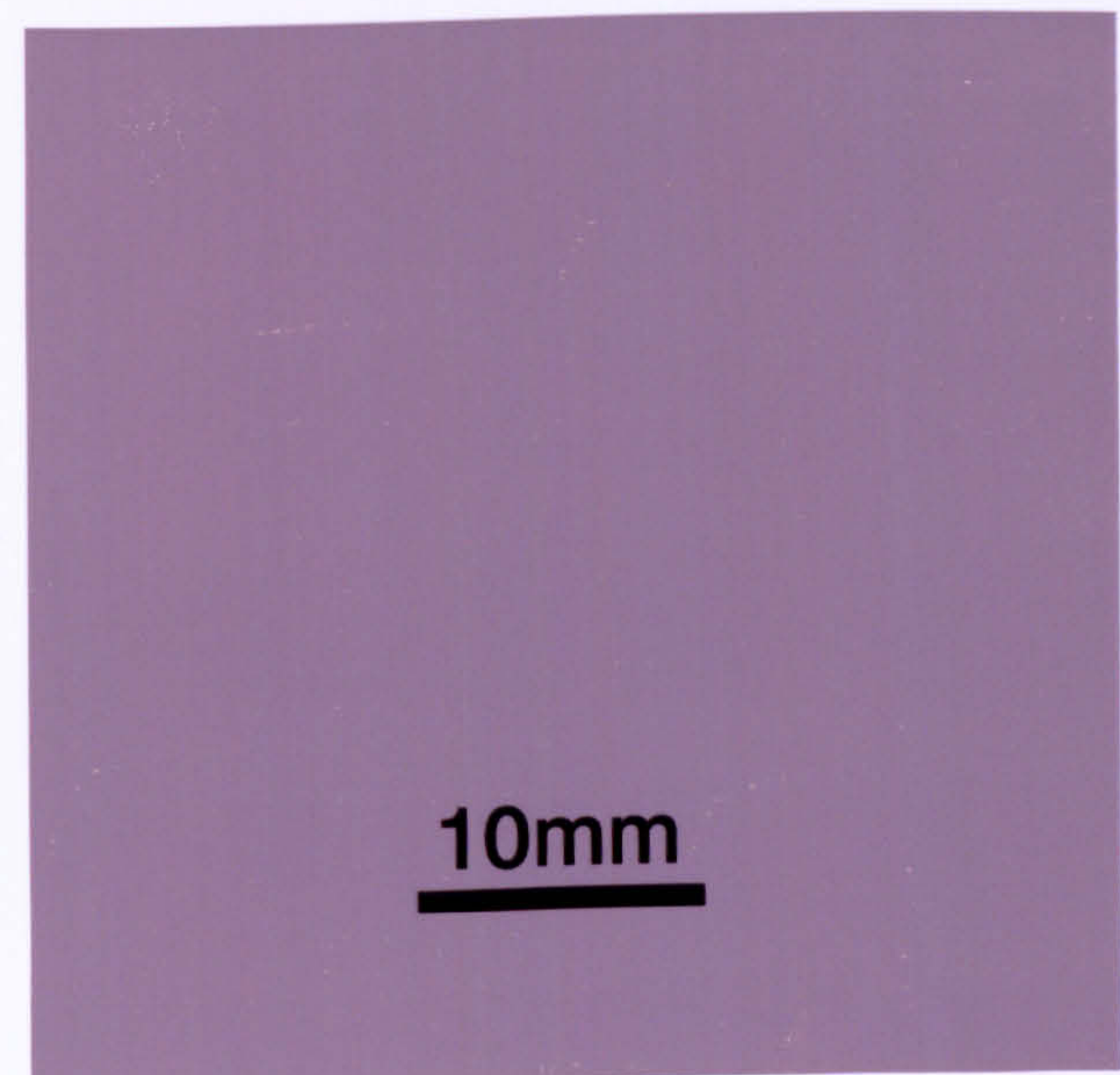
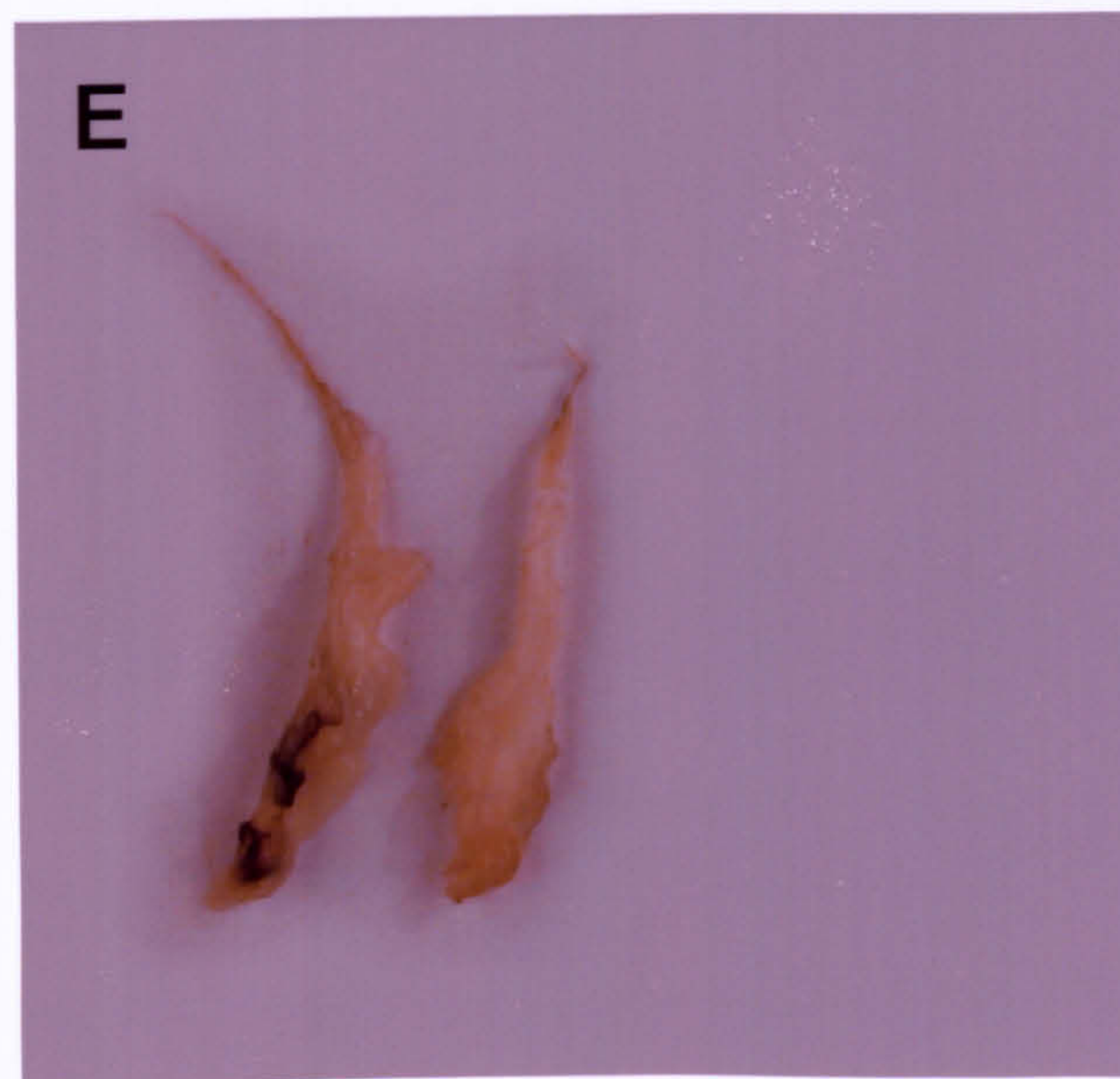
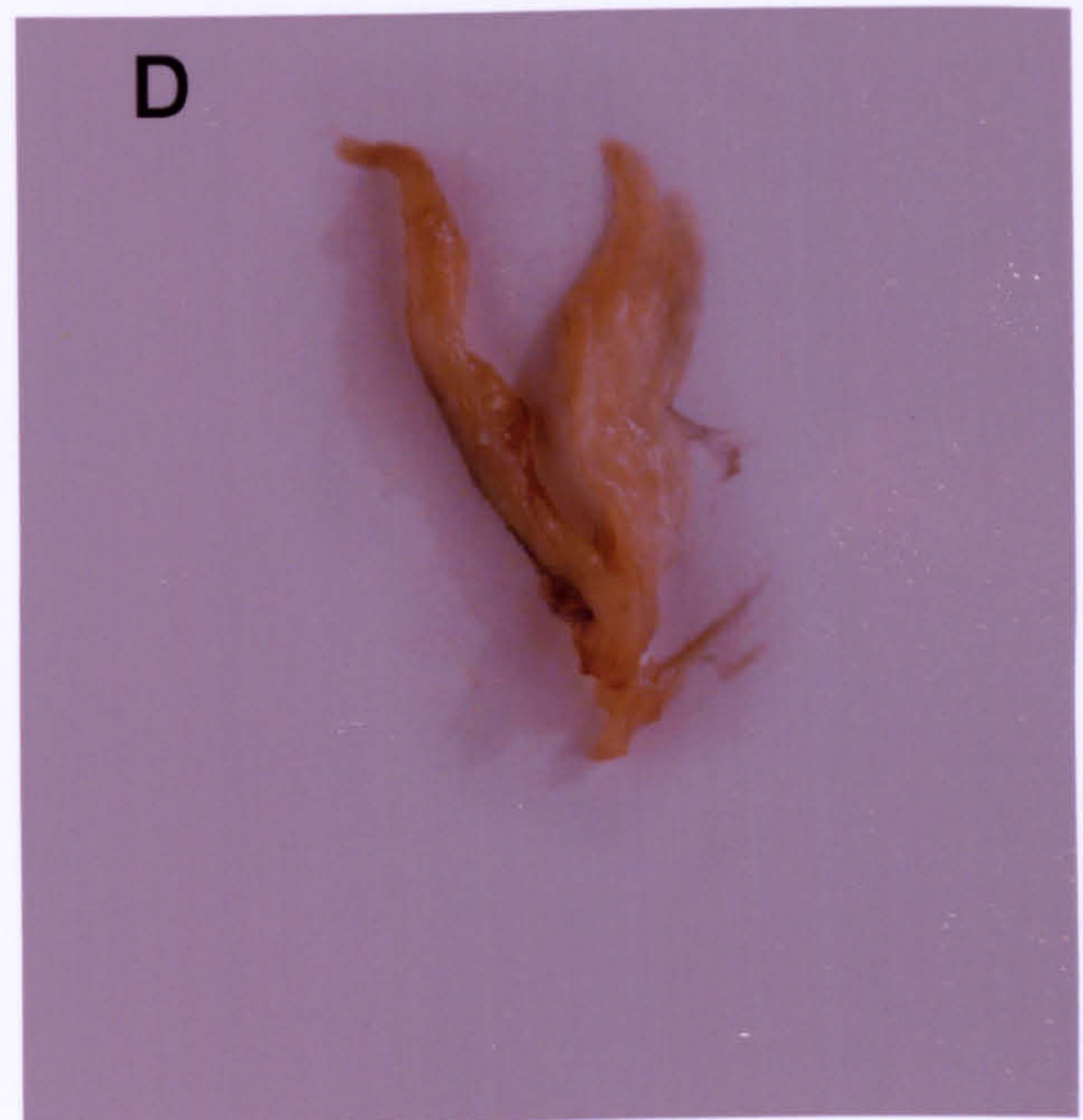
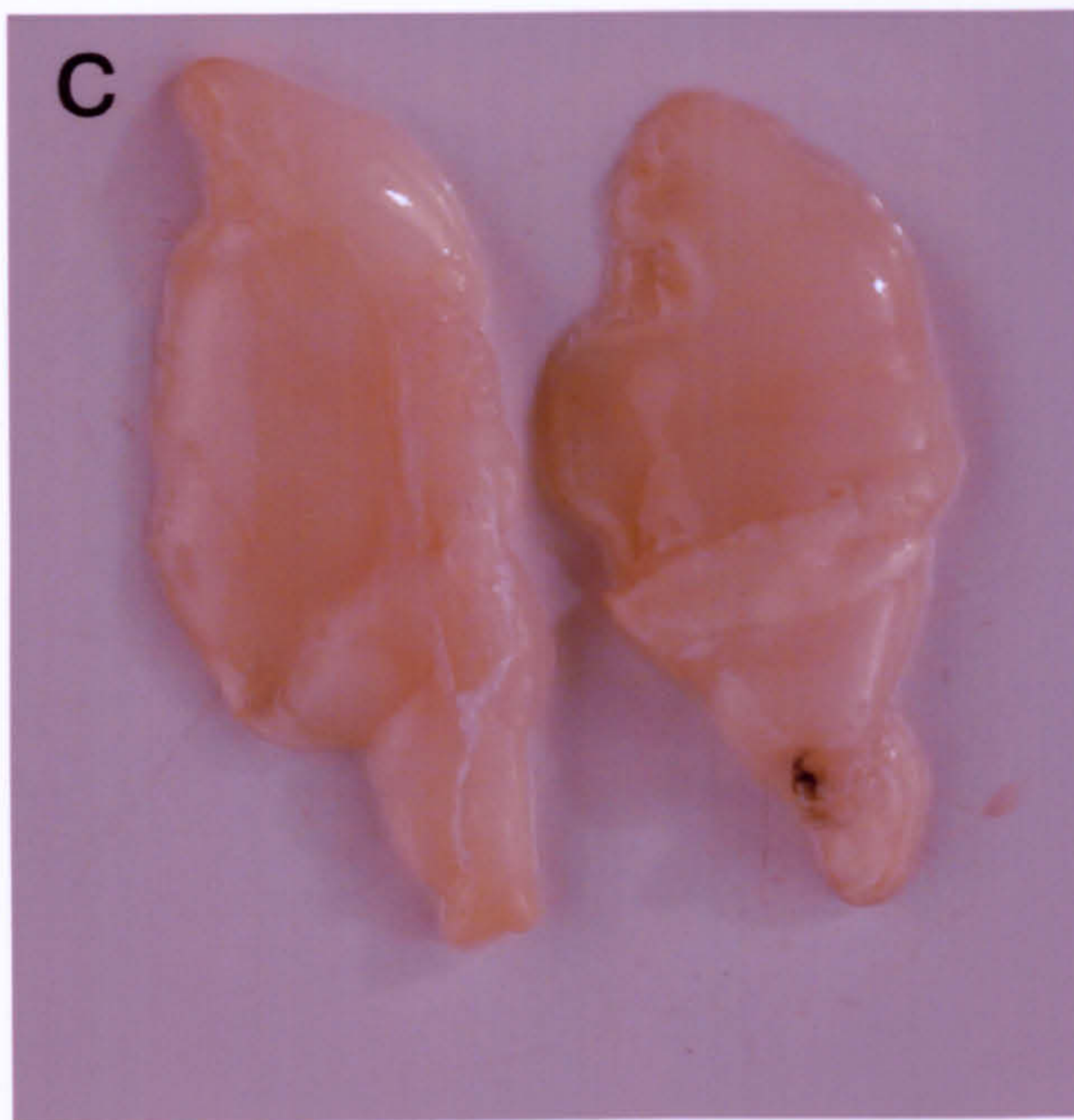
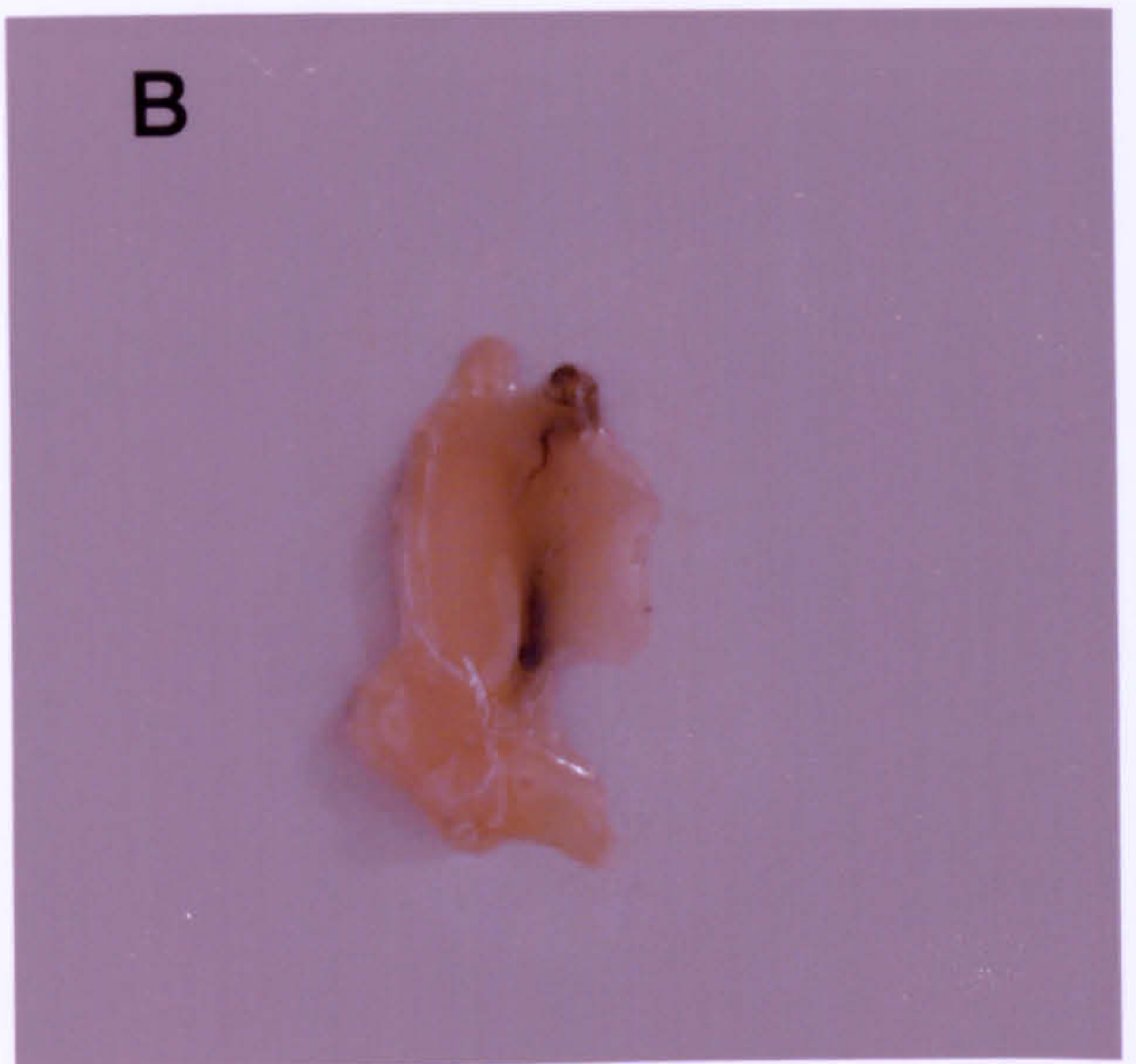
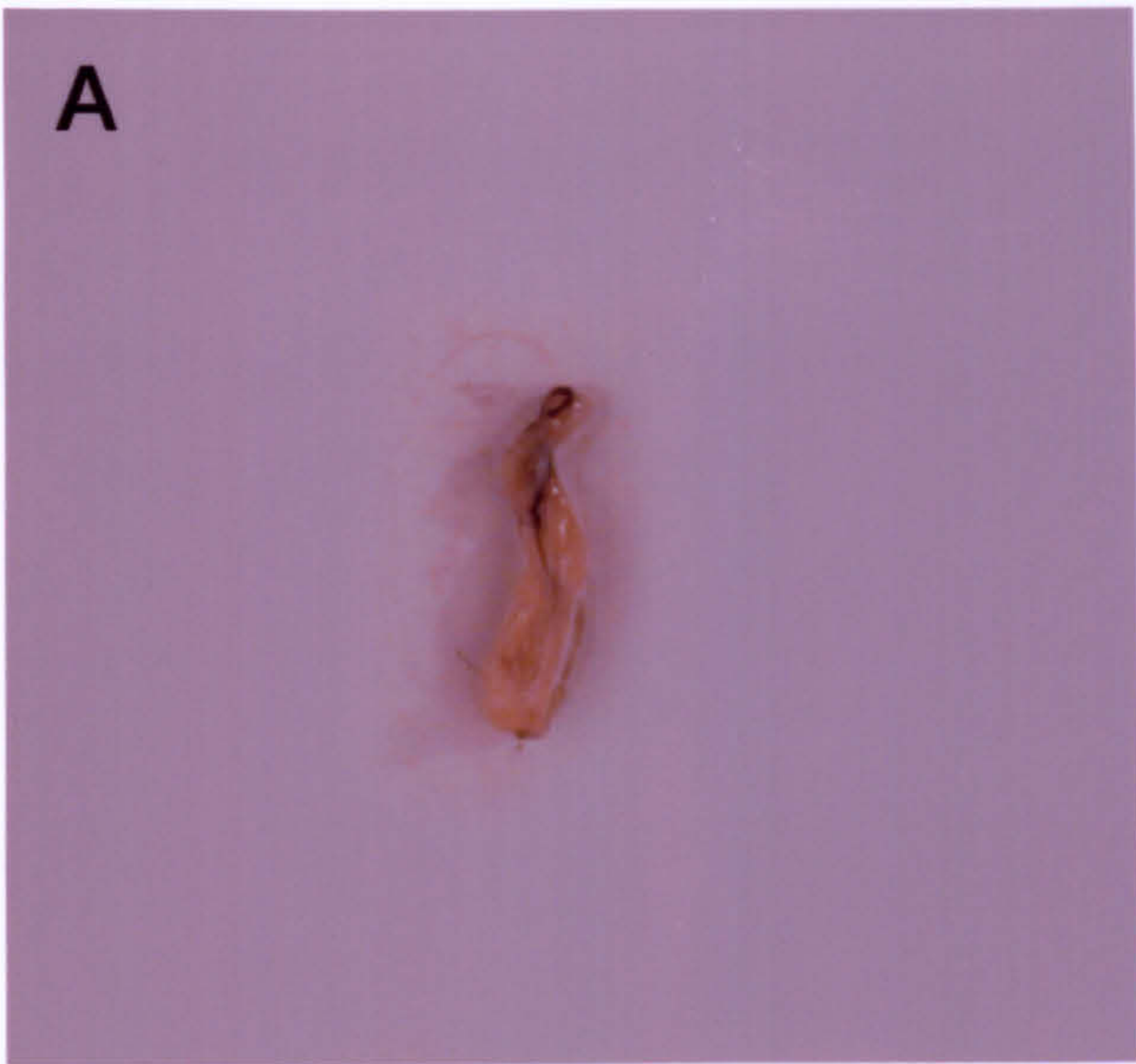
10mm



A horizontal scale bar located below the specimens in panel C, indicating a length of 10 millimeters.

Figure 4.2. Testes of 15 and 20 cm dab showing different maturity stages (See text for detailed description)

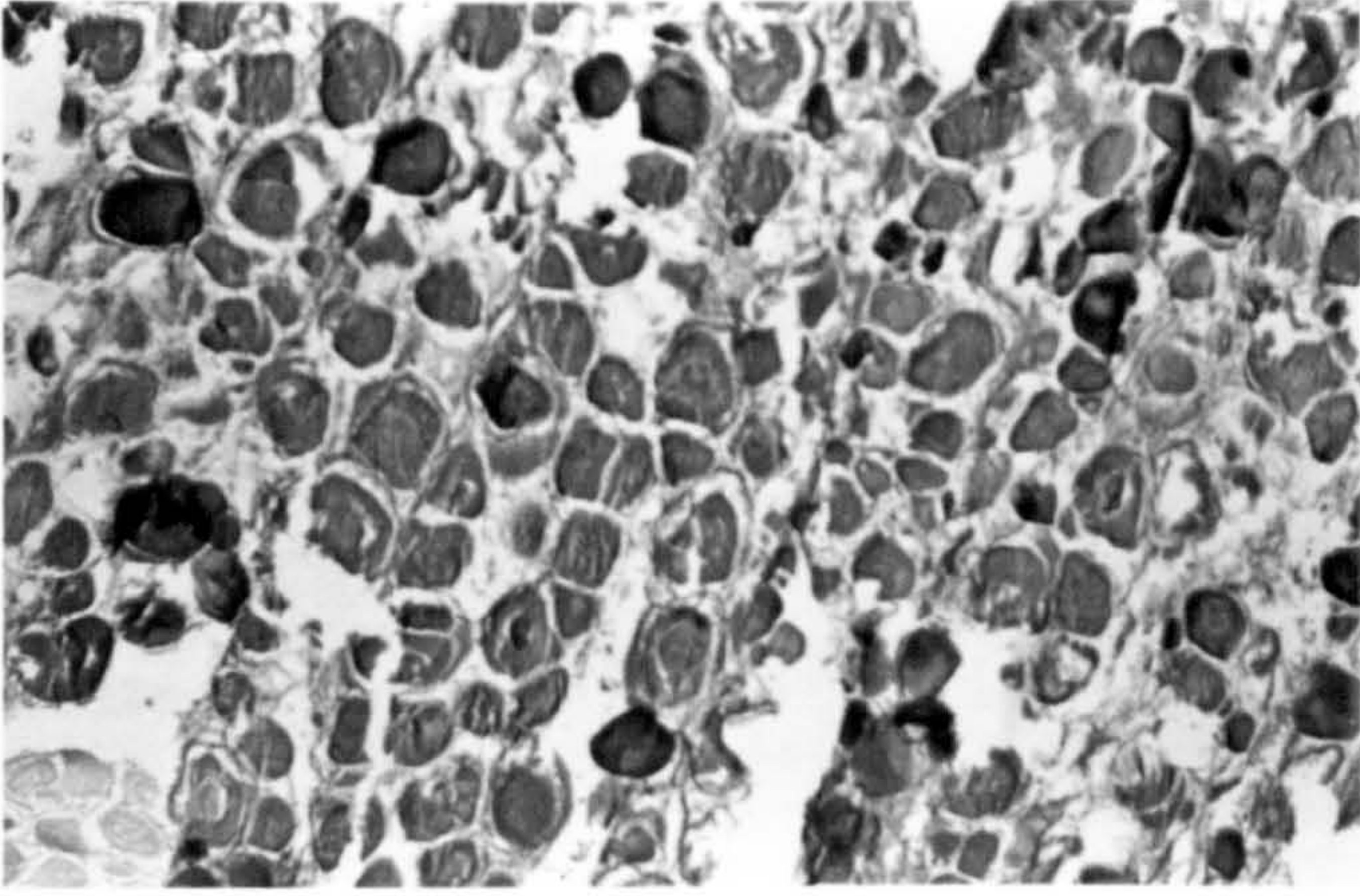
- A. Immature testes (of a 15 cm fish)**
- B. Ripening testes at the onset of spermatogenesis in October**
- C. Ripe testes at the height of spawning in January**
- D. Spent testes in February**
- E. Resting testes in July**



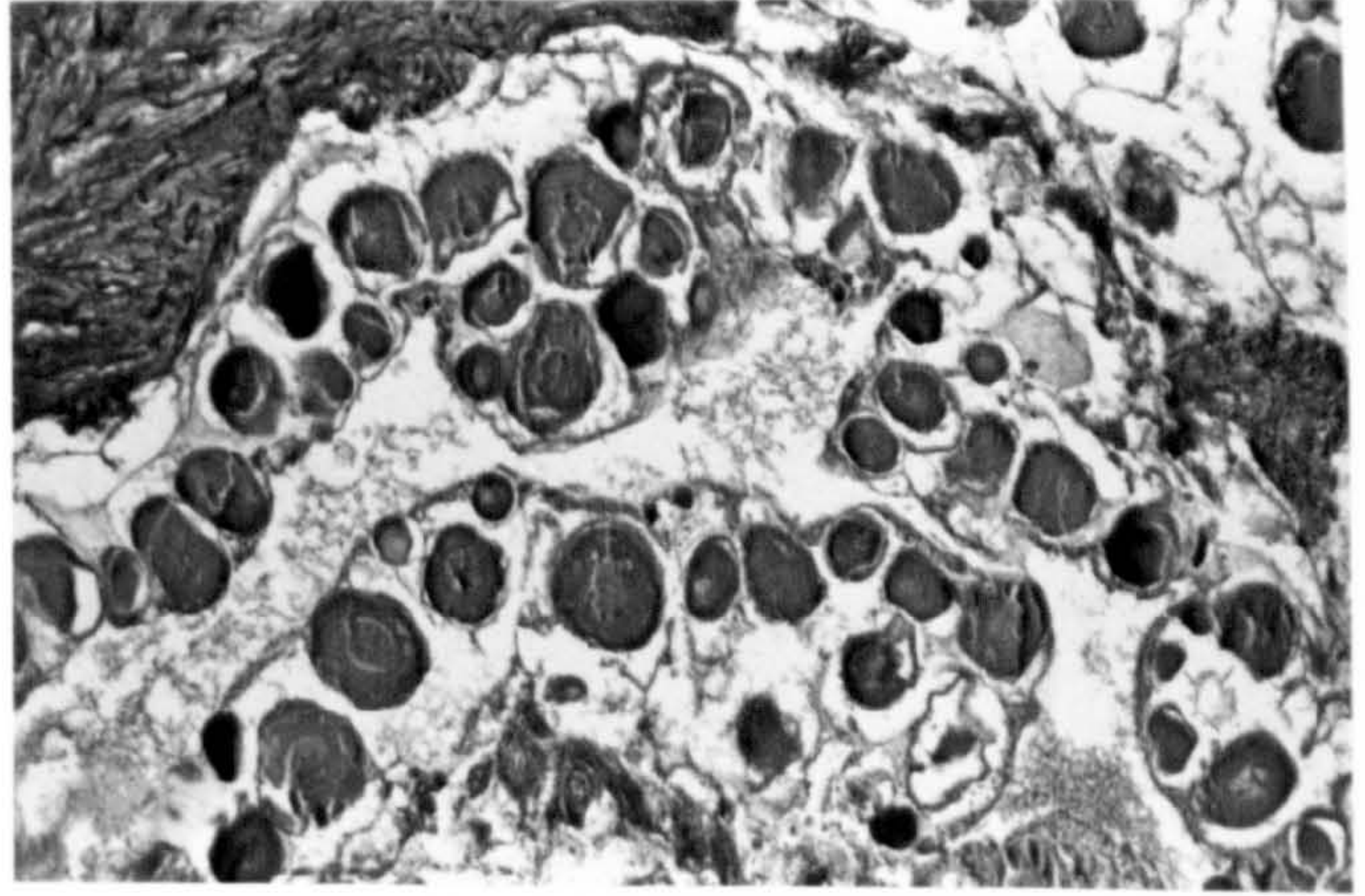
**Figure 4.3. Histology of ovaries of 20 cm dab (See text for detailed description).
(A-B: 82 x Magnification; C-D: 80 x Magnification)**

- A. Pre-vitellogenic stages (immature), showing pre-vitellogenic oocytes.**
- B. Resting stage- showing primary oocytes and post-ovulatory follicles. The nucleus is visible.**
- C. Ripe (secondary yolk stages). The oocytes are much larger and are characterised by the presence of yolk droplets. The oocyte nucleus is clearly distinguishable at this stage.**
- D. Fully ripe (Hyaline, tertiary vitellogenic stage). The oocyte swells as it becomes hydrated. The nucleus disappears. The oocytes become irregular in shape.**
- E. Spent stage. Vitellogenic oocytes are degenerating and conspicuous spaces (empty follicles) are present in the septa.**

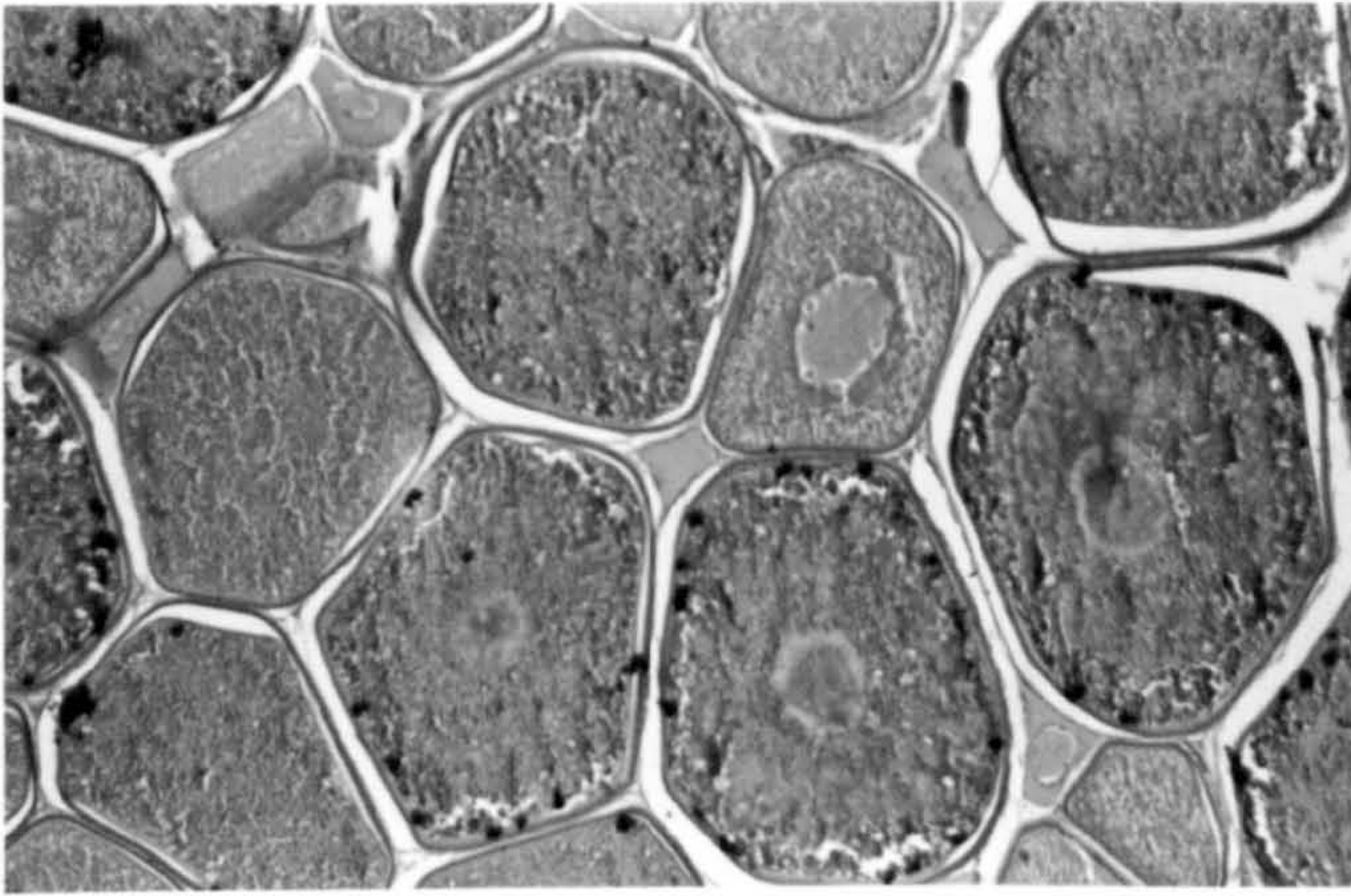
A



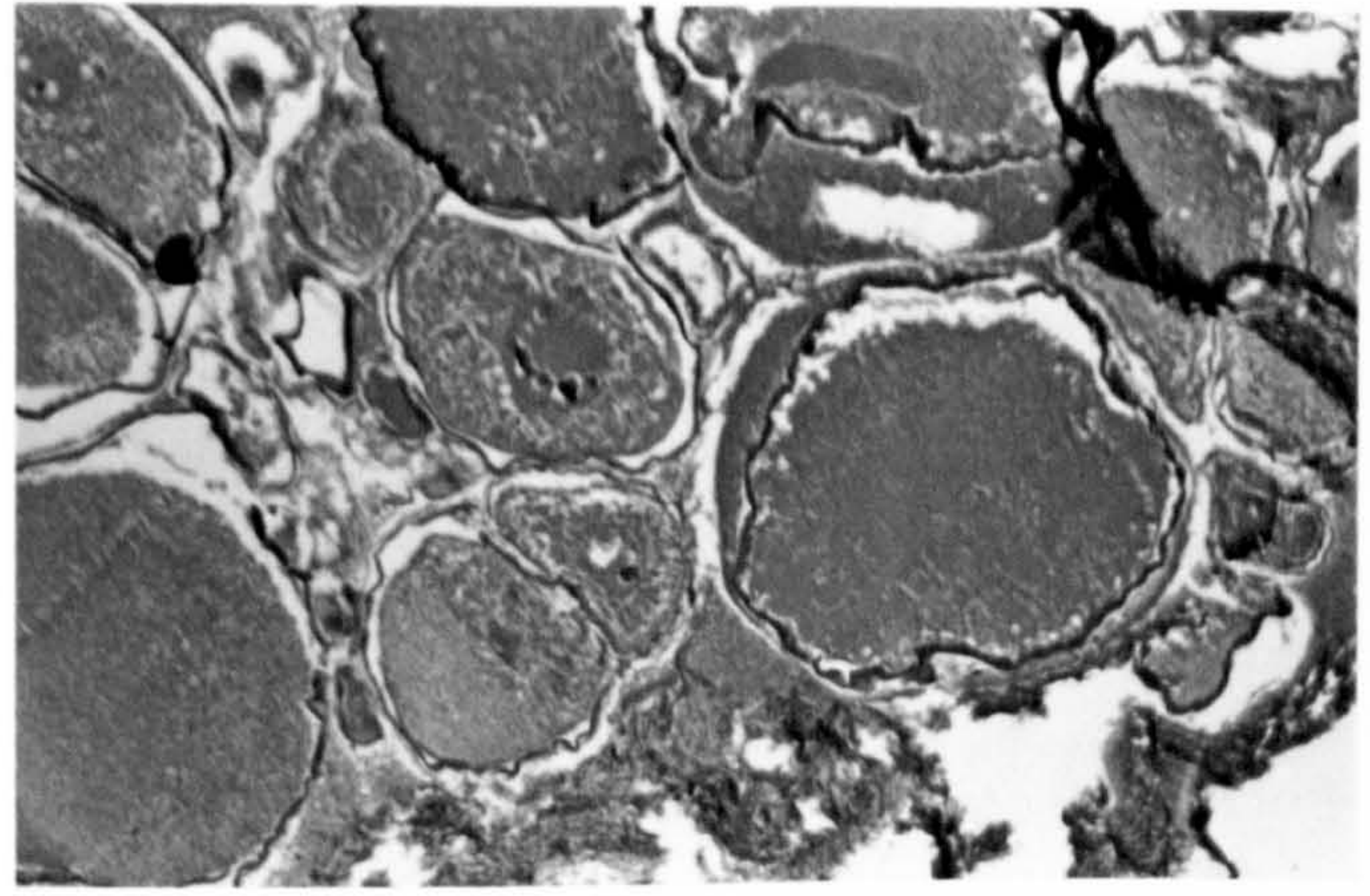
B



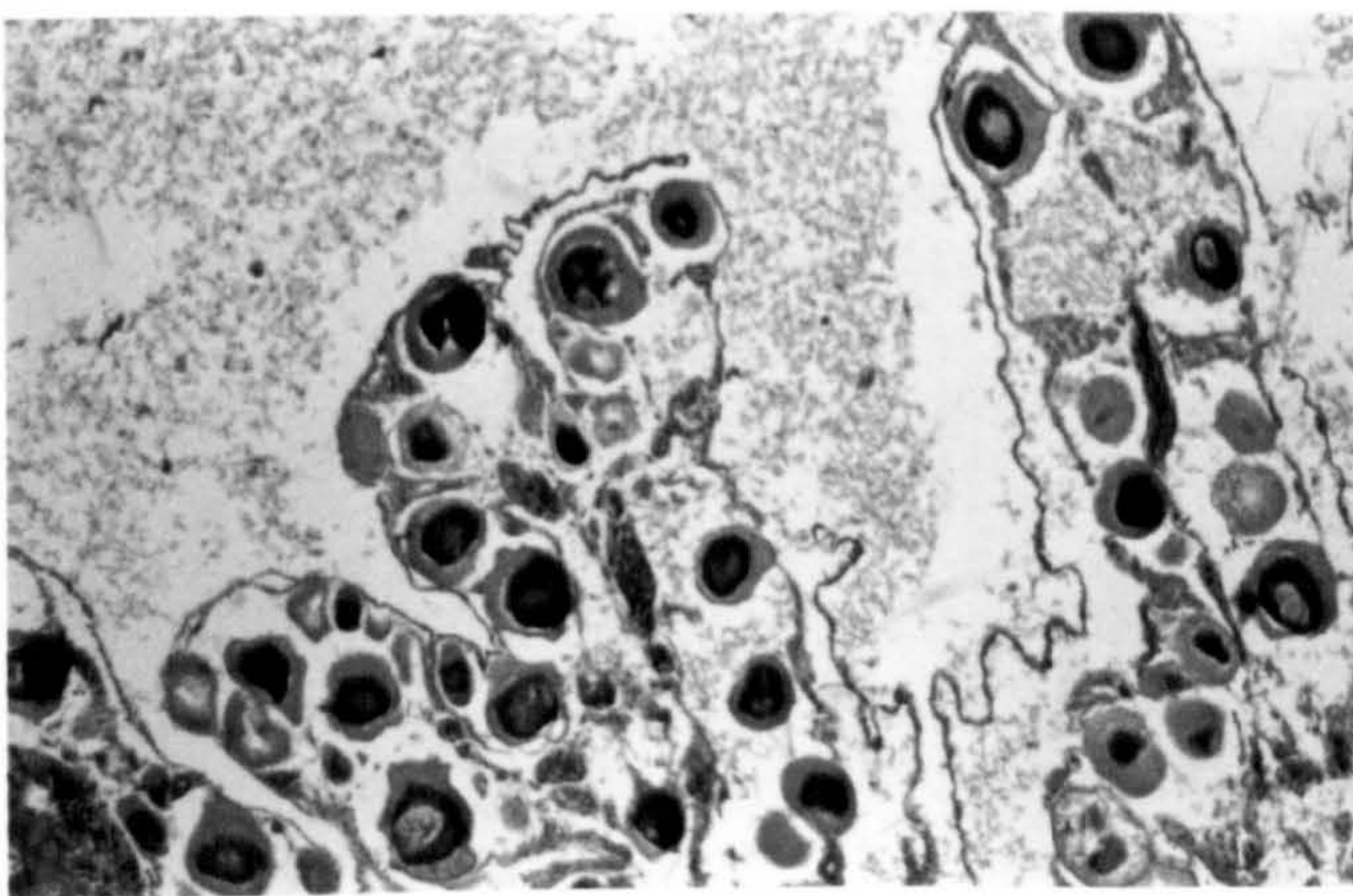
C



D



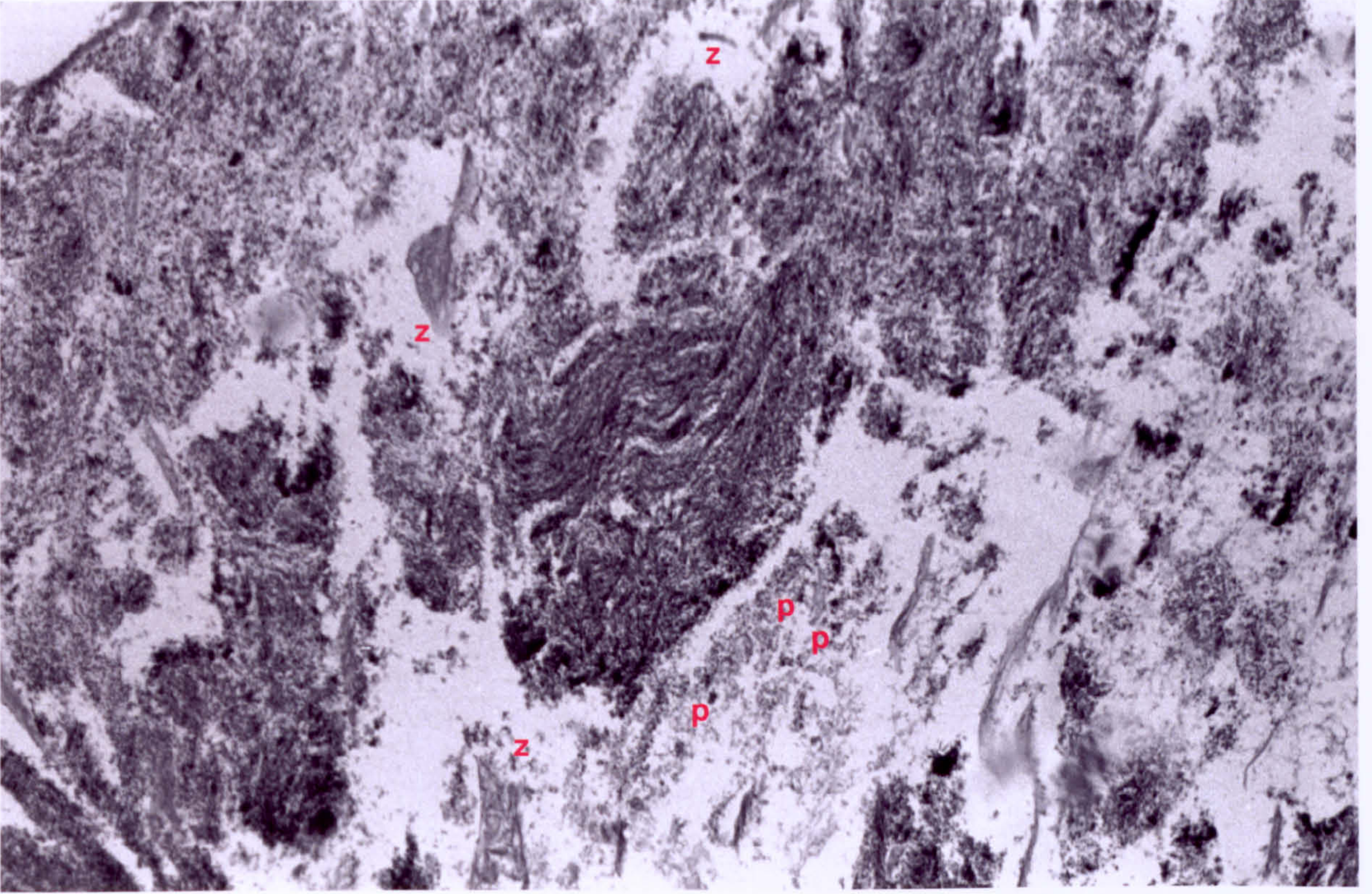
E



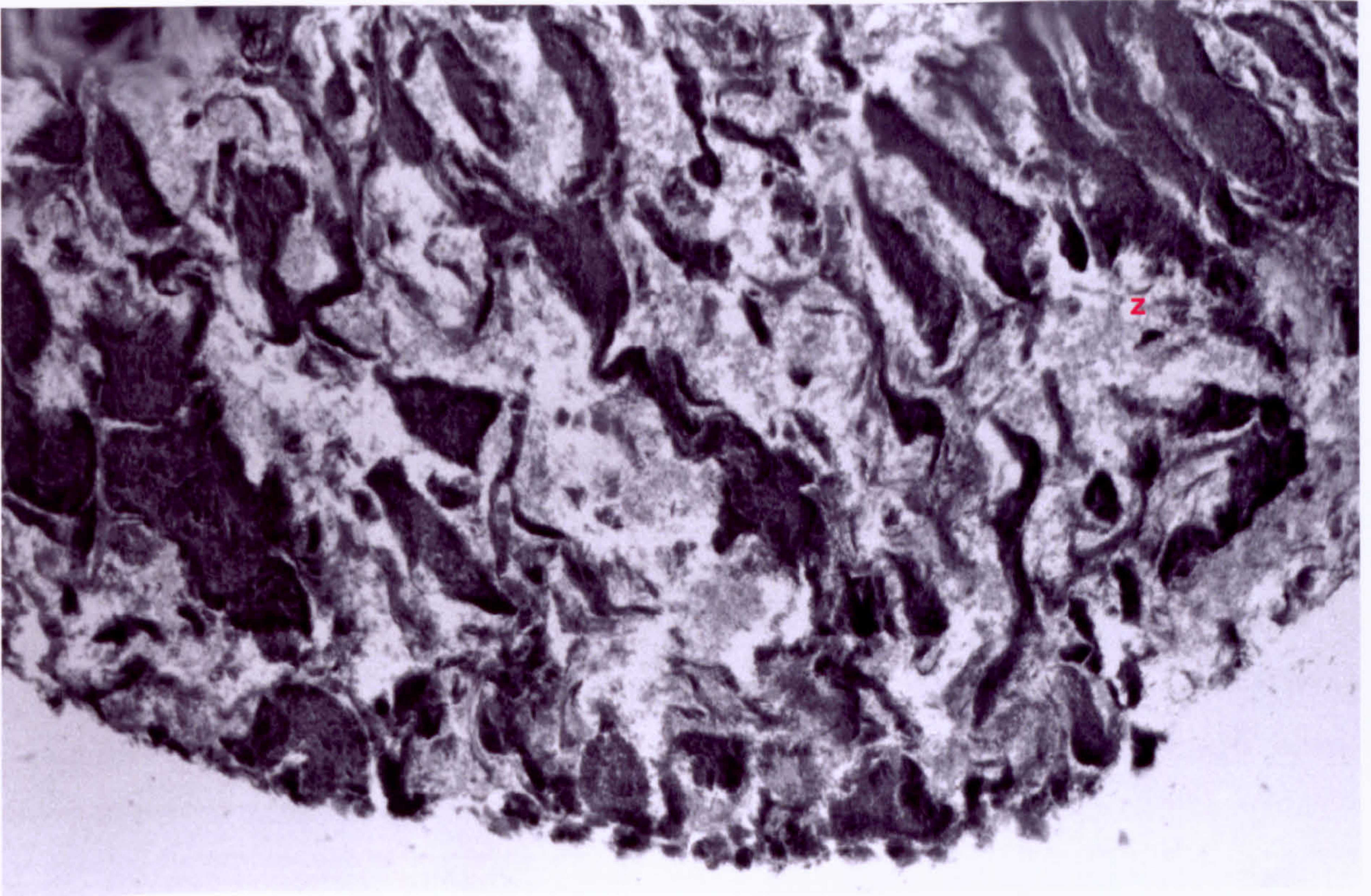
**Figure 4.4. Histology of testes of 20 cm dab (See text for detailed description).
(A-B: 150 x Magnification)**

- A. Ripe (Spawning). The spermatozoa and spermatids exist in the lumen of the testes. (See diagrams: p = spermatids: z = spermatozoa).**
- B. Spent stage (Postspawning). The lumen of the testes looks empty, with few spermatozoa remaining.**

A



B



The study shows that the onset of gonad development starts earlier in the male than female. By October 1999 spermatogenesis has started in about 10 % of the mature male population and in October 2000 over 80 % of the mature male population had ripening testes (Figure 4.5). On the other hand, the onset of oogenesis was in November, in 67 % of the mature female. The peak spawning activity is in December - January for the male whilst is in January-February for the female; these are periods when the testes and ovary attained maximum reproductive sizes in the spawning season. Most of the mature male populations (over 74 %) were in either spent or running condition by February 2000. But 77 % of the mature females were in similar condition by March. It is shown further in Figure 4.5 that some males were in running condition up to the beginning of July 2000 in contrast to the females, which were in either spent or resting condition by May 2000.

There is therefore a one-month difference in the timing of gametogenesis between males and females in the study are, with the male initiating gonad development early in October. This observation thus suggests that the complete resting period (inactive gonad) for the males runs from the end of July to September, but from June to October for the females. There appears however to be annual variations in the process of gametogenesis in the dab populations. This is based on the observations that a significant proportion of the male dabs were in ripening condition (>80%) in October 2000 whilst only comparatively few (about 10 %) were in similar condition in October 1999. Also, in March 1999 most female dabs (66.67 %) were in either ripe or running condition but in March 2000, about 50 % were in the spent condition. Based on the results of this study, however, the reproductive season for dab on the North Wales Coast could be classified as follows:

Period	Stages	Females	Males
Pre-spawning*	Ripening	November-December	October-November
Spawning	Ripe/full	January-March	December-January
Post-spawning	Spent	April-May	February-June
Resting	Inactive	June-October	July-September

* Onset of gametogenesis

Figure 4.5. Seasonal occurrence of various maturity stages in male and female dab, 1999-2001

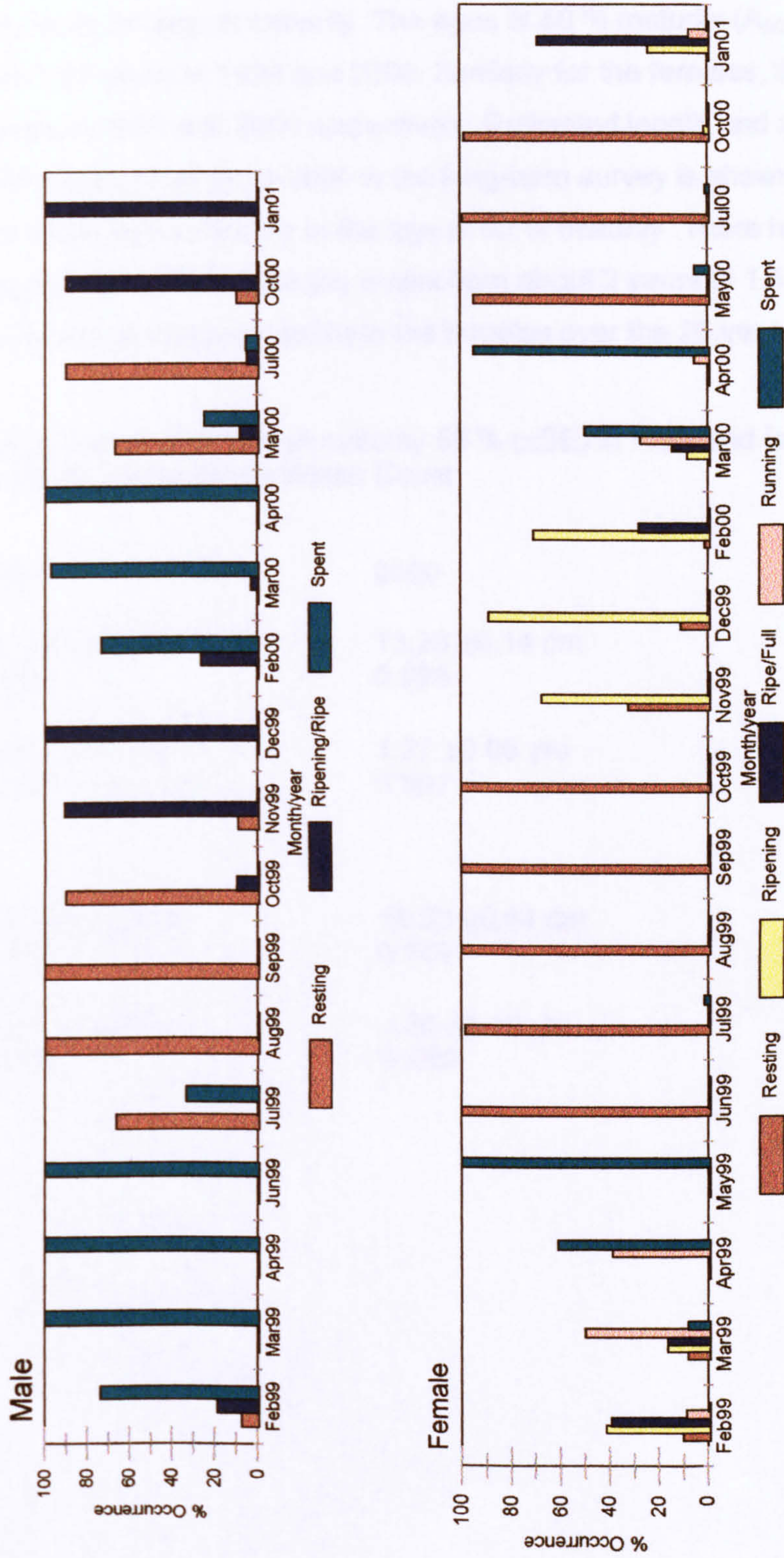


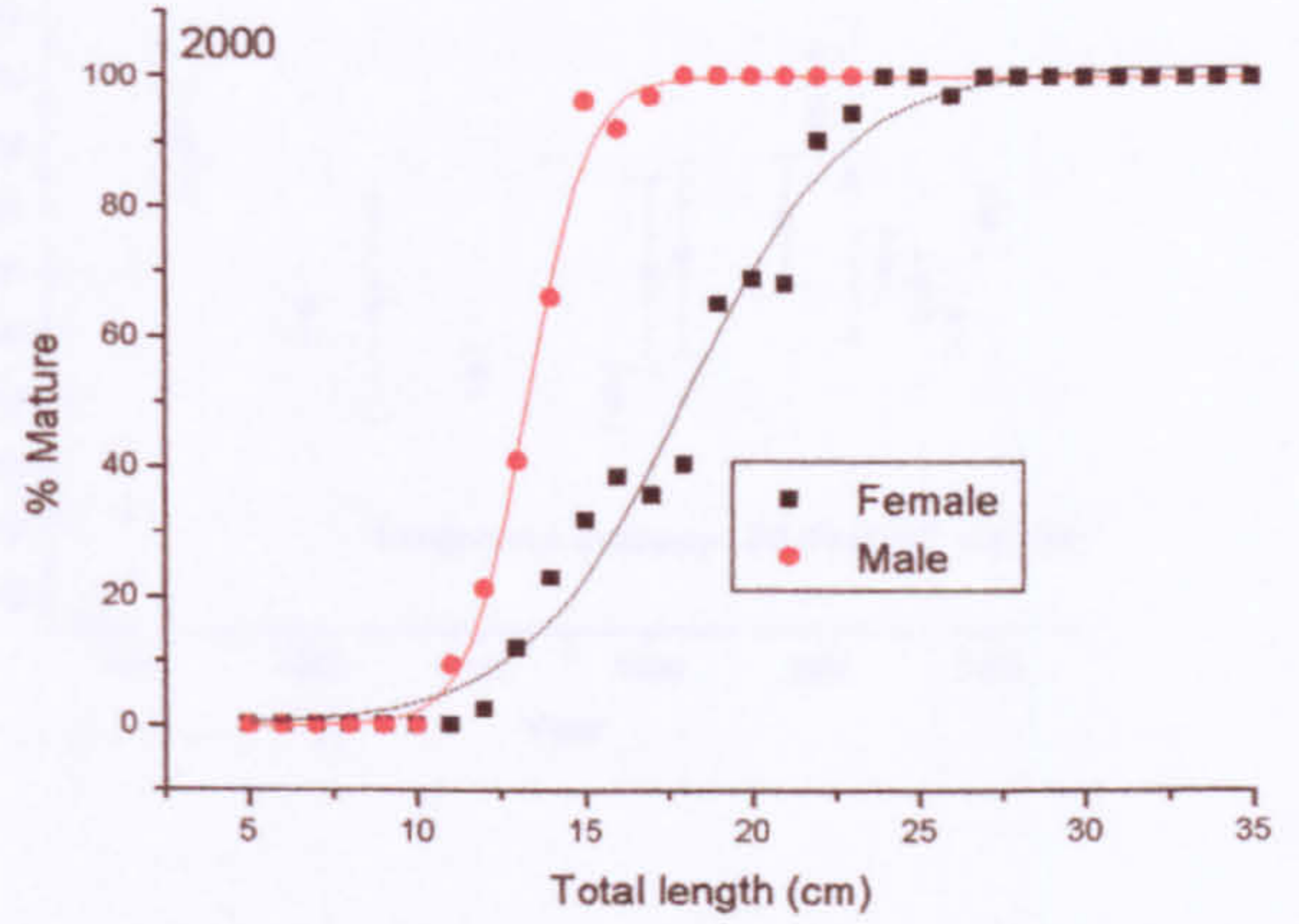
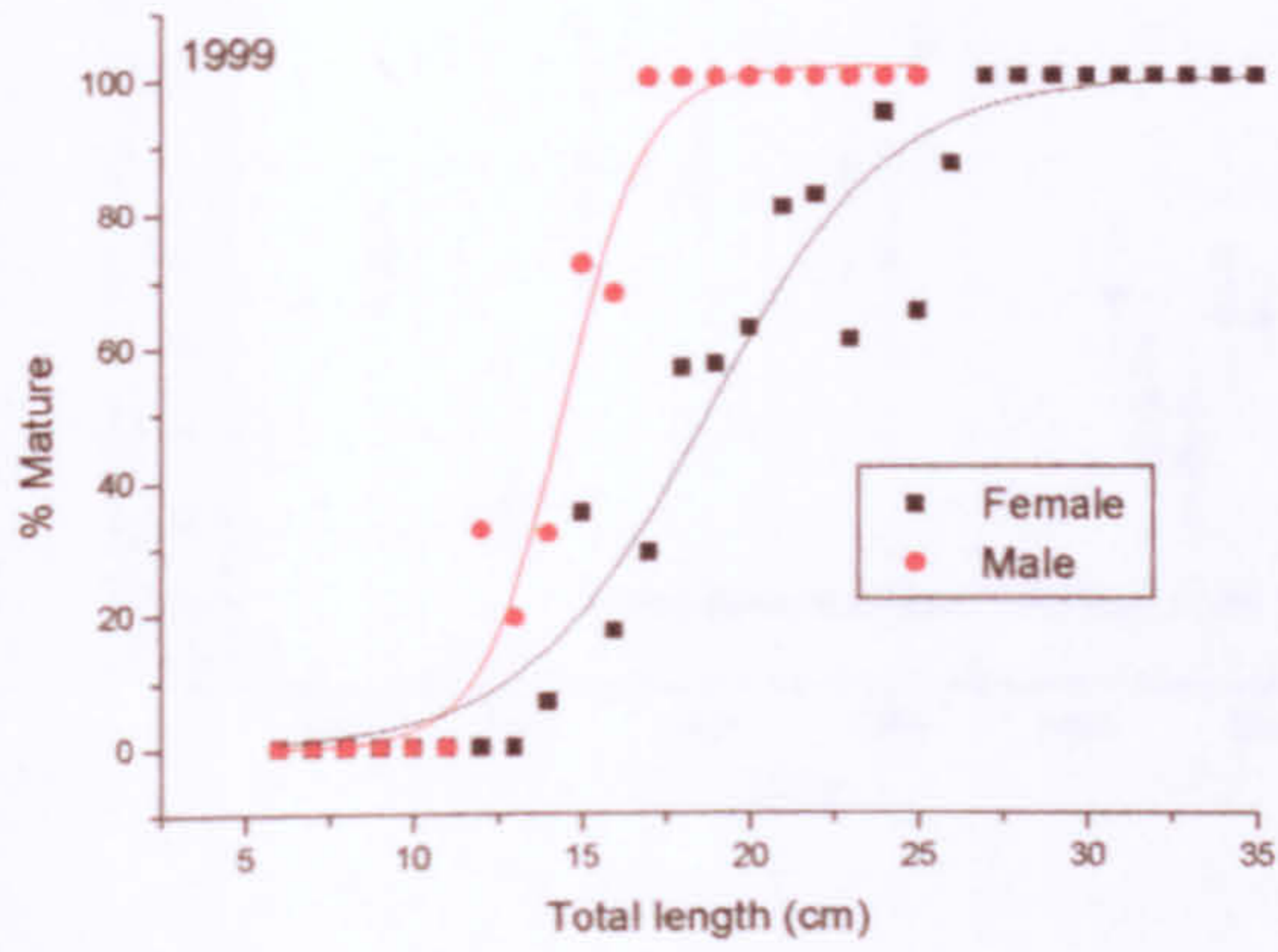
Table 4.1 also showed that the males mature at a smaller length and earlier age than the females. It was observed in the present study that the smallest mature male was not less than 11 cm and the female not less than 12 cm. In 1999 and 2000 the estimated $L_{50\%}$ values were 14.43 cm and 13.28 cm respectively for the males whilst the comparable values were 18.33 cm and 18.03 cm for the females (Figure 4.6). There were no significant differences between the length at 50% maturity between 1999 and 2000 in the same sex but there were significant differences in the age at maturity. The ages at 50 % maturity ($A_{50\%}$) in the male dab were 1.42 and 1.27 years in 1999 and 2000. Similarly for the females, the $A_{50\%}$ was 2.14 years and 2.36 years in 1999 and 2000 respectively. Estimated length and age at 50 % maturity between the autumn of 1976-2000 in the long-term survey is shown in Figures 4.7 and 4.8. The plots show high variability in the age at 50 % maturity. There had been a decrease in the age at 50 % maturity in the males from about 2 years to 1.5 years. But these parameters have remained relatively stable in the females over the 25 years.

Table 4.1. Estimated Length and Age at maturity 50 % (\pm SE) in male and female dab, autumn 1999 and 2000, on the North Wales Coast

Male	1999	2000
$L_{50\%}$	14.43 \pm 0.54 cm	13.28 \pm 0.14 cm
r	0.988	0.998
$A_{50\%}$	1.42 \pm 0.11 yrs	1.27 \pm 0.08 yrs
r	0.995	0.997
Female		
$L_{50\%}$	18.33 \pm 0.93 cm	18.03 \pm 0.44 cm
r	0.973	0.989
$A_{50\%}$	2.14 \pm 0.09 yrs	2.36 \pm 0.19 yrs
r	0.995	0.989

Figure 4.6. Maturity curves for male and female dab, autumn 1999 and 2000

A. Length at maturity



B. Age at maturity

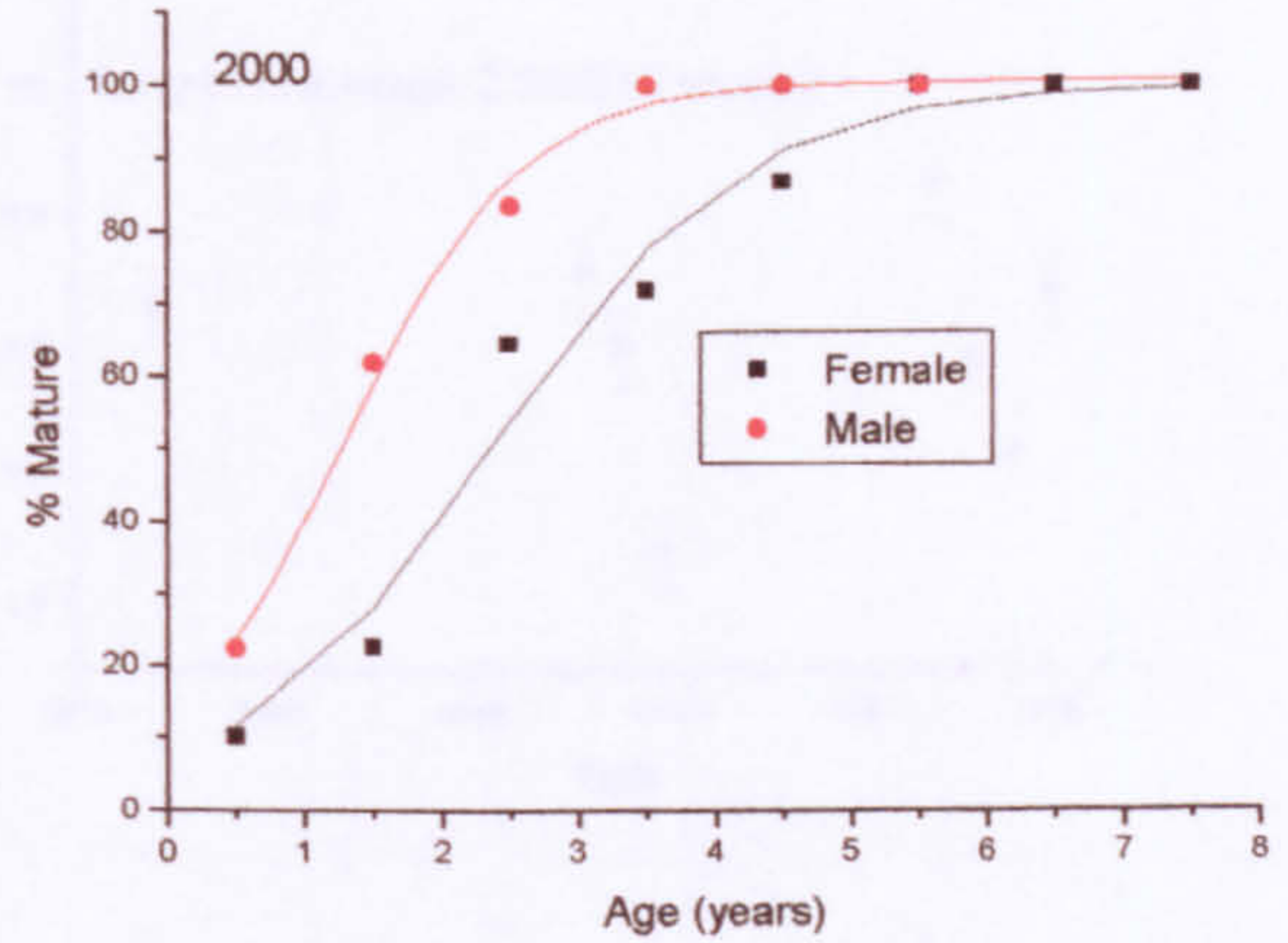
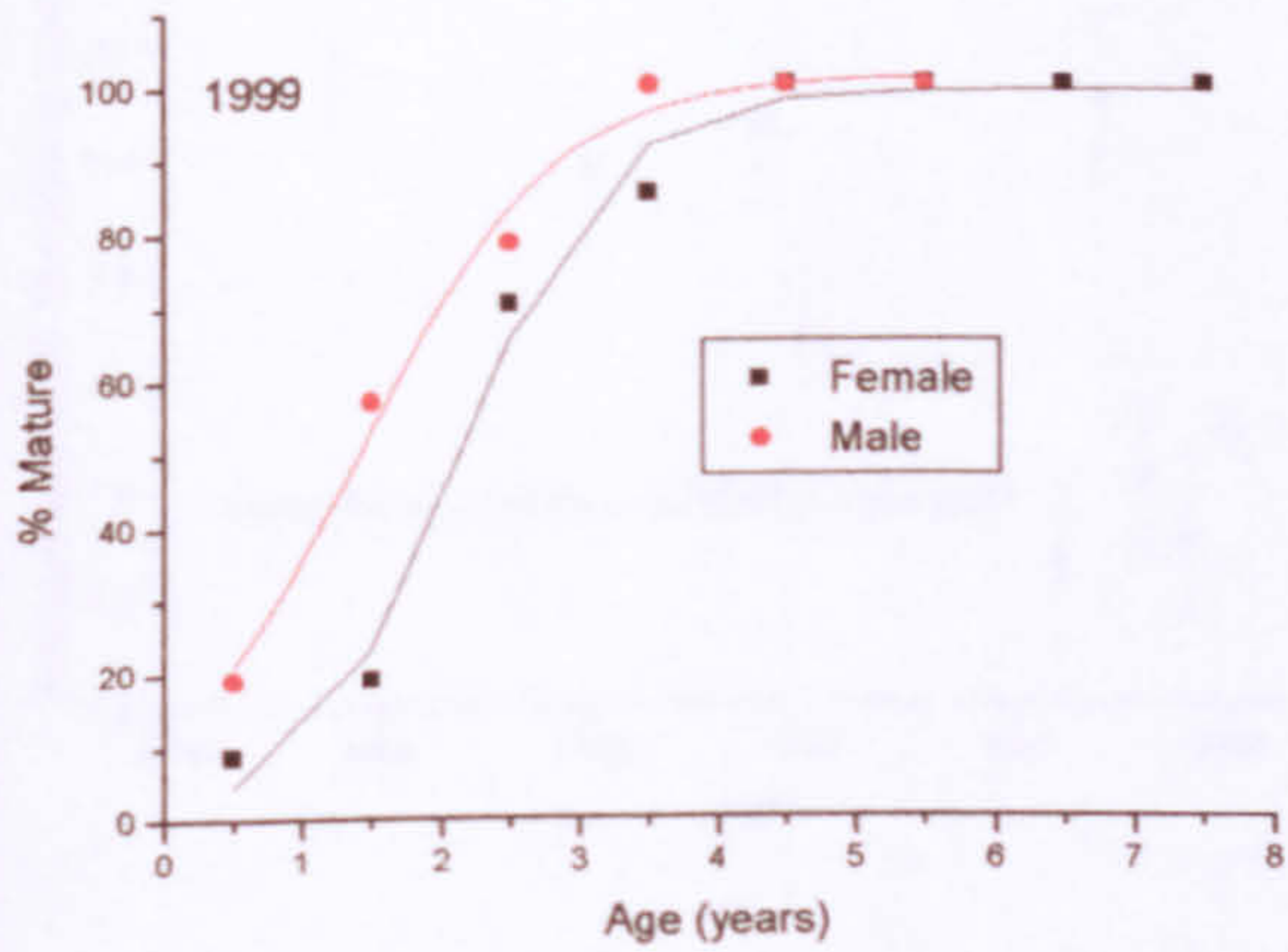


Figure 4.7. Long-term variation in average length at 50 % maturity (\pm SE) in male and female dab (maturity data from students' surveys were based on field scale only)

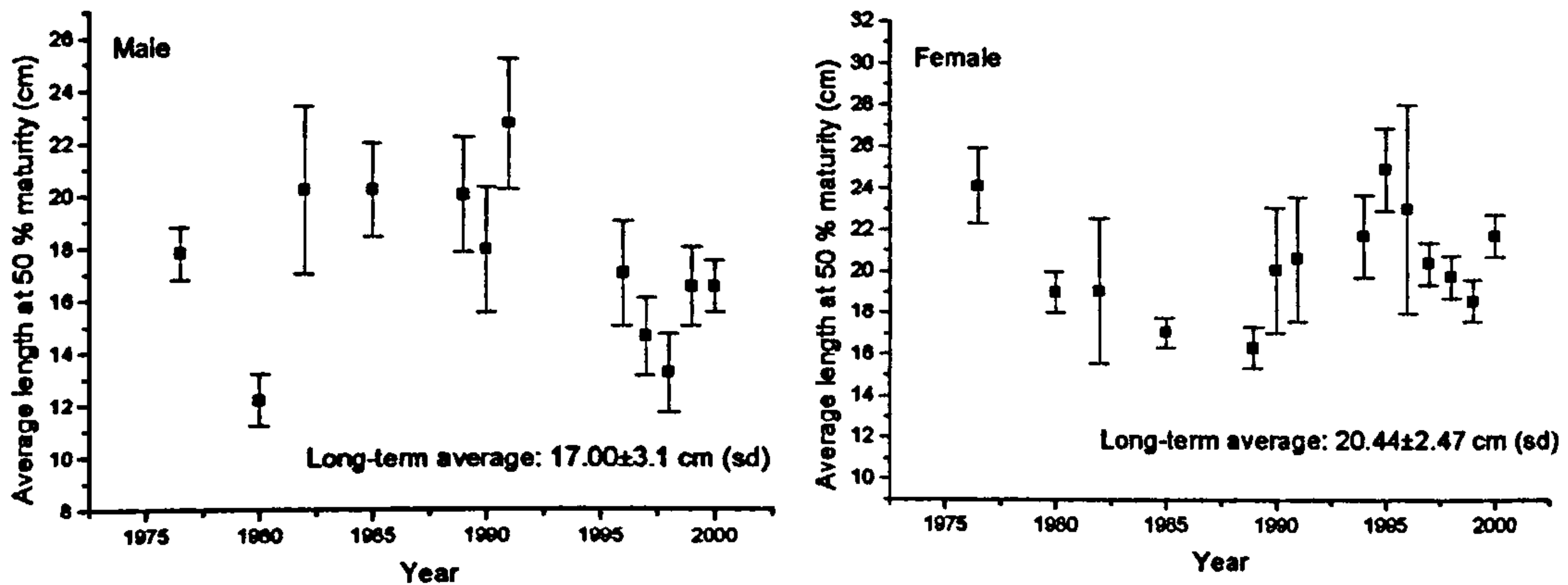
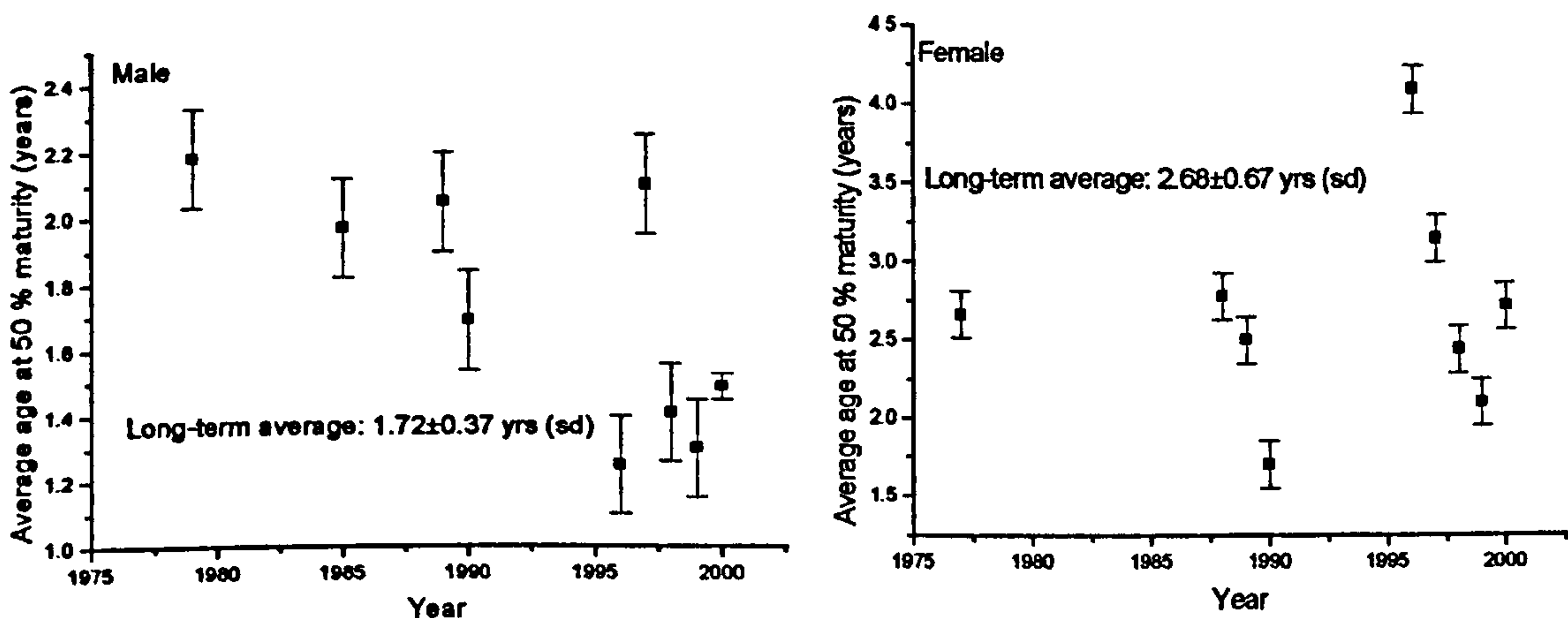


Figure 4.8. Long-term variation in average age at 50 % maturity (\pm SE) in male and female dab



The study of individual (potential) fecundity shows that it ranged between 5.12×10^4 and 9.63×10^5 eggs per spawning season in various sizes of dab (Appendix 4). Table 4.2 shows variation of fecundity with age. The estimated egg production per mature female is 3.51×10^5 whilst the total egg production in the study area is estimated as about 2.47×10^{11} (Table 4.3). The relationships between fecundity and length, somatic weight, ovary weight or age are given in Table 4.4. There is an increase in fecundity from age 3 and peaked at age 6, followed by a decline in ages 7 and 8 years (Figure 4.9). There is a significant negative correlation ($P < 0.05$) between relative fecundity and age (Figure 4.10). The relative fecundity is highest between ages 1 to 3, but declined to very low levels at ages 7 and 8. The variation

of absolute fecundity with length is given in Figure 4.11. Figures 4.12 and 4.13 showed significant positive correlation between the logarithm of fecundity and length ($r=0.791$; $d.f=73$; $F=120.38$, $P<0.05$), and logarithm of fecundity and somatic weight ($r=0.783$ $d.f=73$; $F=114.24$, $P<0.05$) respectively. The correlation between logarithm of fecundity and ovary weight was also significant ($r=0.322$; $d.f=73$; $F=8.35$, $P<0.05$), (Figure 4.14). Best fit for the relationship between potential fecundity and fish total length was given by a power equation (curvilinear relationship) with exponent close to three, Table 4.4. Though the best fit for the relationship between somatic weight and potential fecundity was given by a power relationship, it can be considered as linear, because the exponent is close to one. The correlation coefficients indicate both length and somatic weight provide adequate prediction of fecundity. Approximately, 80 % of the variation in fecundity was associated with changes in length or somatic weight. On the contrary, ovary weight was a poor predictor, explaining only about 30 % of the variation in fecundity.

Table 4.2. Summary table of fecundity and relative fecundity with age, somatic weight and gonad weight in dab on the North Wales Coast.

Age years	Somatic weight (g) (\pm SE)	Ovary weight (g) (\pm SE)	Average fecundity (\pm SE)	Relative fecundity No. egg/wt (\pm SE)	Sample size
1	39.55 \pm 6.56	4.95 \pm 1.06	120400 \pm 19362	3045 \pm 267	6
2	62.95 \pm 5.67	11.76 \pm 2.09	190000 \pm 47567	3018 \pm 515	7
3	119.58 \pm 5.54	15.45 \pm 2.12	359799 \pm 29545	3009 \pm 261	17
4	143.51 \pm 5.57	12.20 \pm 2.32	361973 \pm 32064	2526 \pm 199	21
5	173.28 \pm 6.95	9.79 \pm 1.25	458650 \pm 36636	2647 \pm 224	8
6	208.70 \pm 8.59	19.86 \pm 4.89	597915 \pm 67946	2865 \pm 336	12
7	260.44 \pm 14.93	6.02 \pm 1.16	569867 \pm 20176	2188 \pm 48	2
8	274.91	11.09	526933	1917	1

Table 4.3. Total egg production in a mature female dab population on the North Wales Coast

Age years	Potential fecundity F_i	Estimated Population Female N_i	(%) Mature Female	Estimated Mature Female P_i	Total egg production E
≥ 1	120400 \pm 19362	37259	8.65	3216	387168196
2	190000 \pm 47567	499483	19.05	95140	18076527619
3	359799 \pm 29545	583454	70.31	410241	147604209268
4	361973 \pm 32064	151406	85.37	129249	46784700189
5	458650 \pm 36636	31766	100	31766	14569475900
6	597915 \pm 67946	21550	100	21550	12885064259
7	569867 \pm 20176	9885	100	9885	5633132000
8	526933	1650	100	1650	8694400000
Total				702696	2.47×10^{11}

Average egg production per mature female $E_i = 351232$

Table 4.4. Fecundity-total length and fecundity–somatic weight , fecundity-ovary weight and fecundity-age relationships in dab on the North Wales Coast

Variables	Relationship	r	P	N
Fecundity-Total length (cm)	$F=41.55 TL^{2.86}$	0.791	0.0001	74
Fecundity-Somatic weight (g)	$F=4804.32 SW^{0.88}$	0.783	0.0001	74
Fecundity-Gonad weight (g)	$F=172818.99 OV^{0.28}$	0.322	0.0051	74
Relative Fecundity-Age (yrs)	$F=3317.54-144.95*A$	-0.811	0.0146	8

Figure 4.9. Variation of average fecundity with age in dab

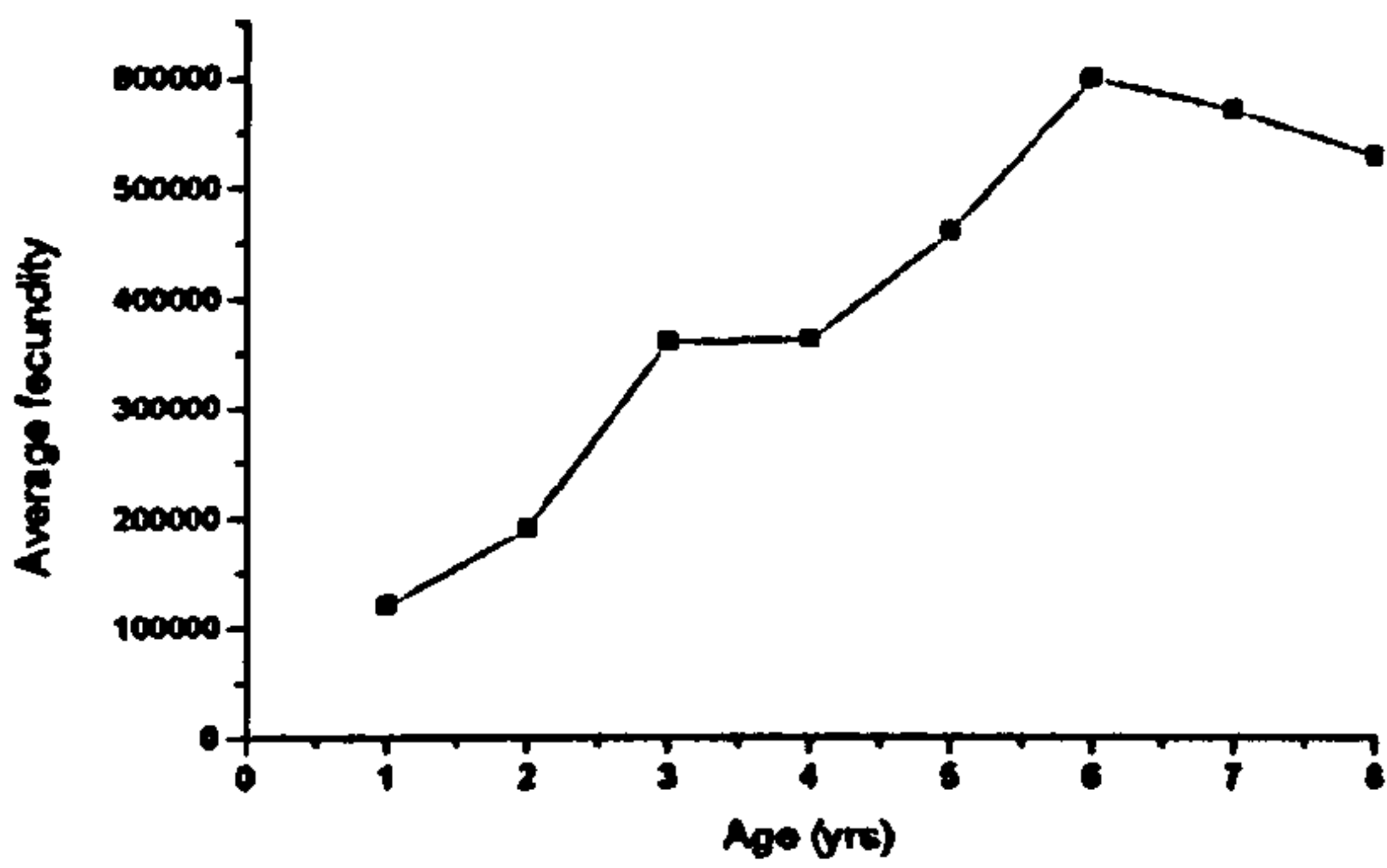


Figure 4.11. Scatter plot of Fecundity and Total length relationship in dab

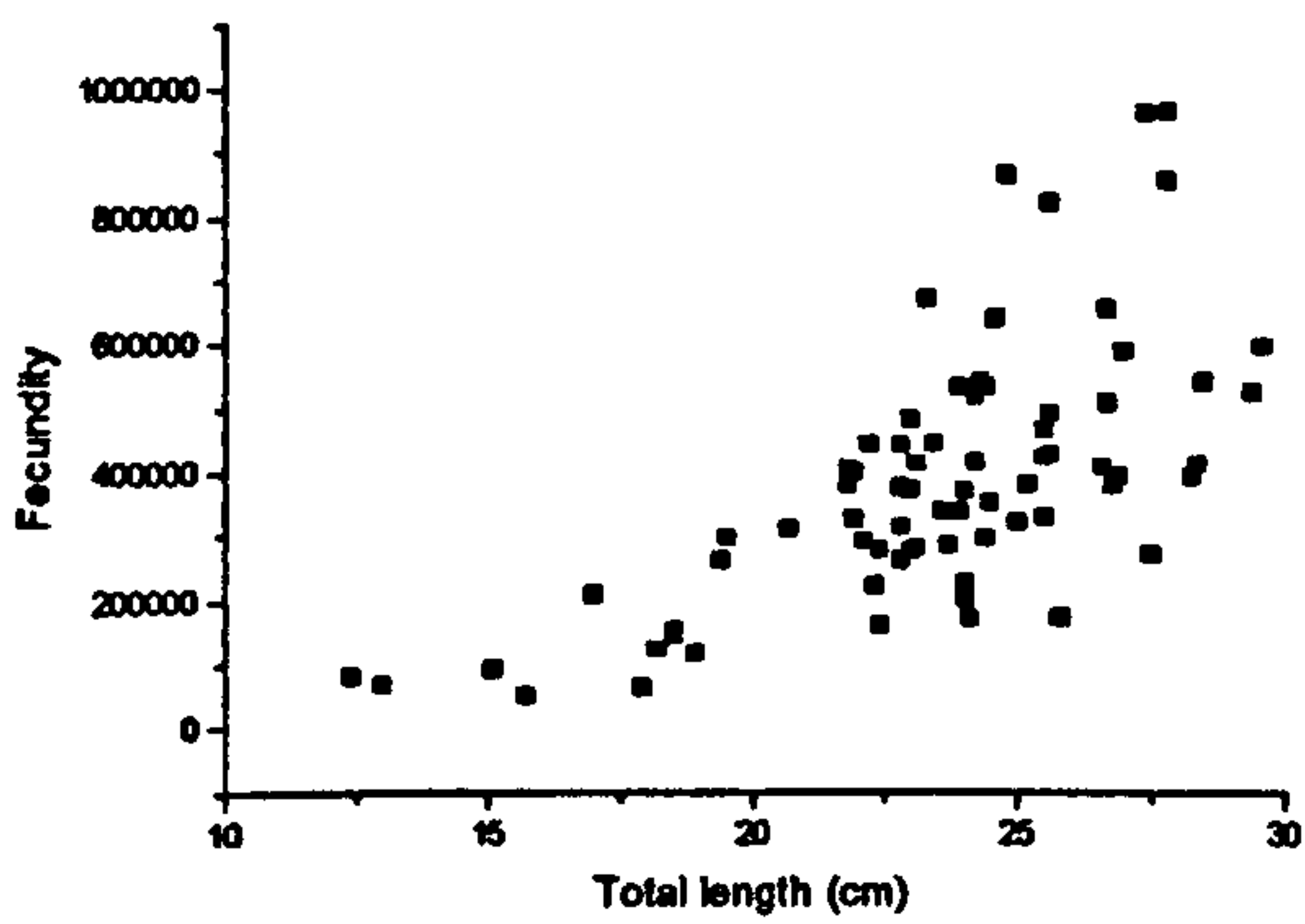


Figure 4.13. Logarithmic relationship between fecundity and somatic weight

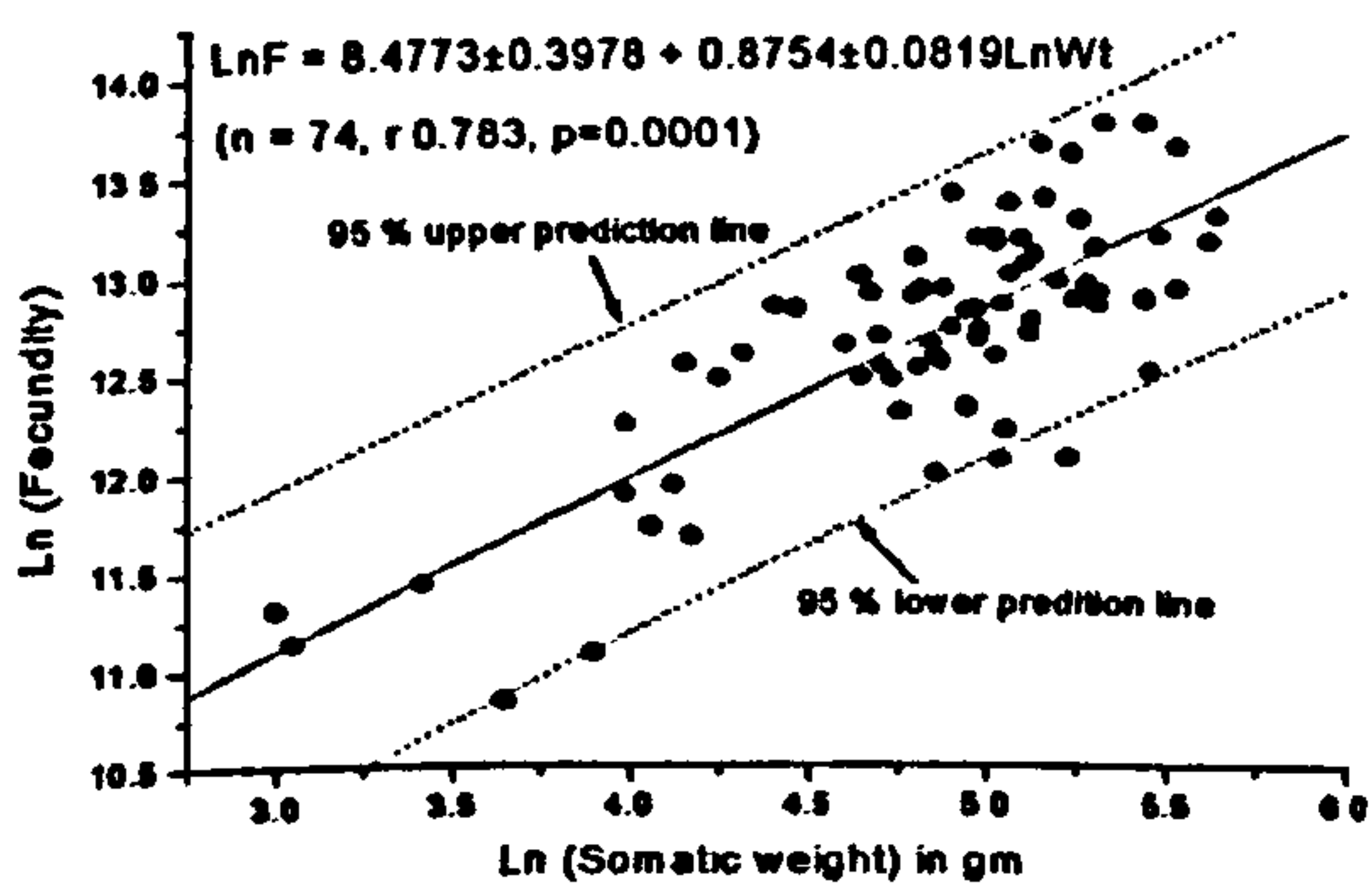


Figure 4.10. Linear regression of relative fecundity and age

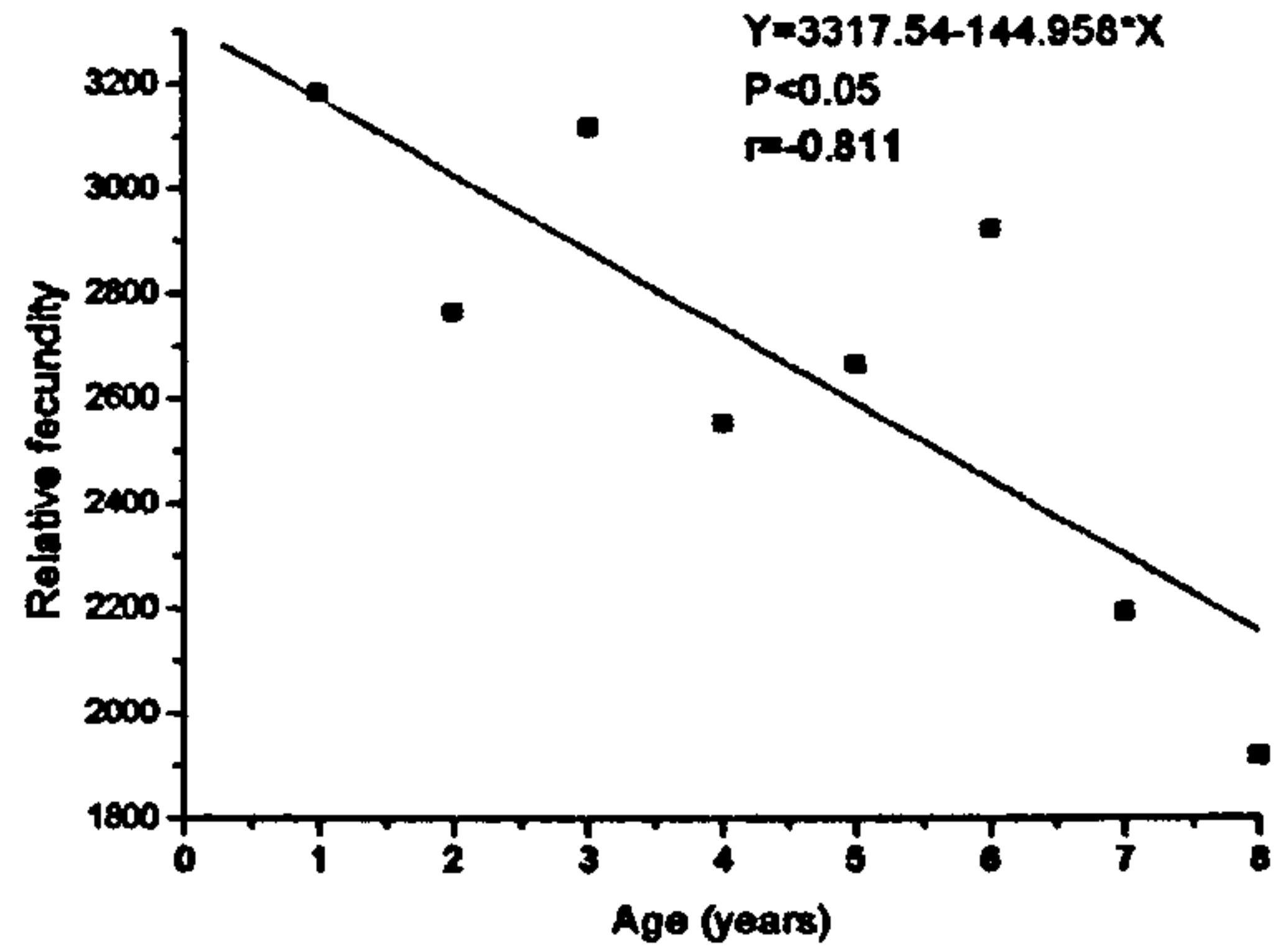


Figure 4.12. Logarithmic relationship between fecundity and length

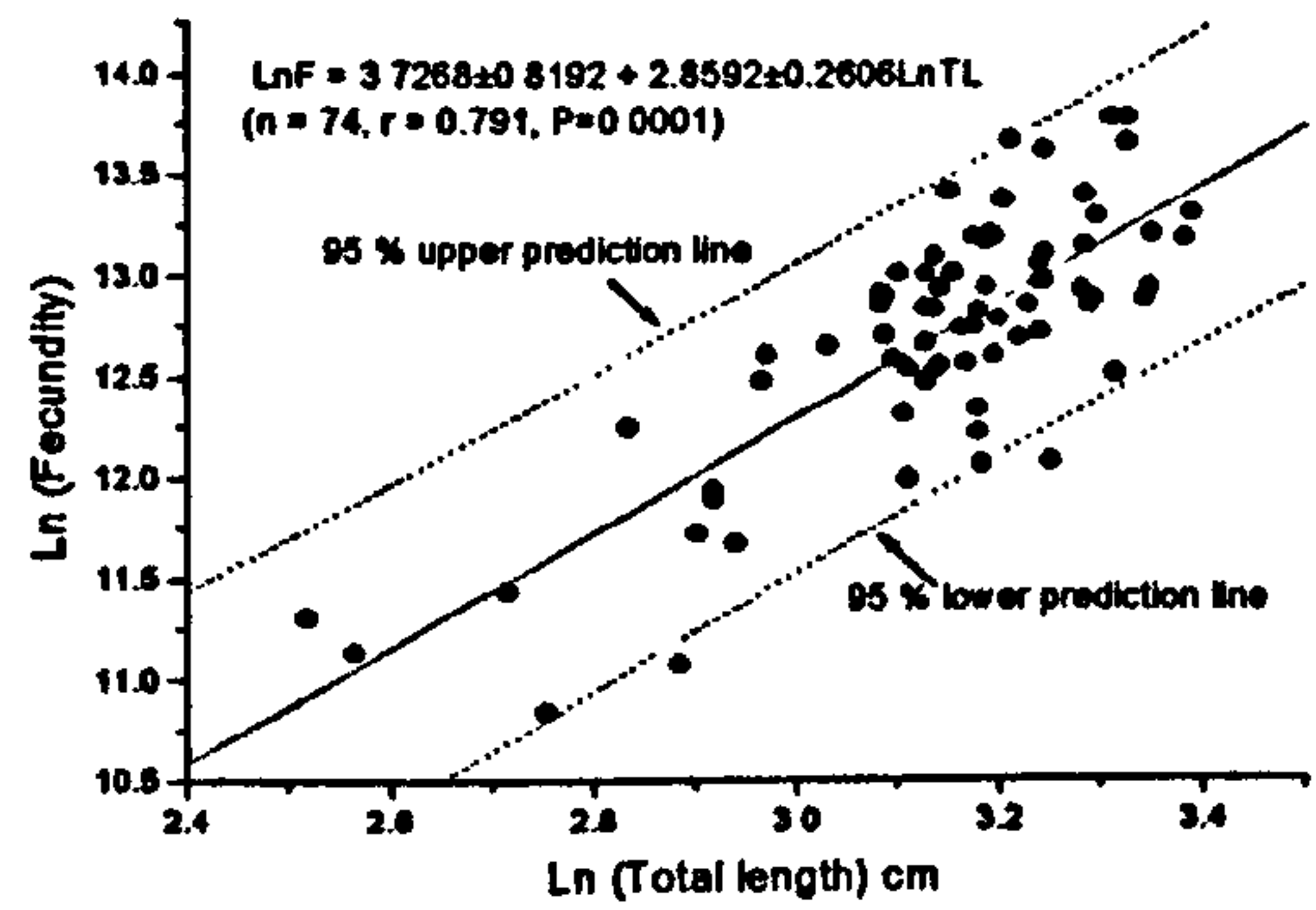
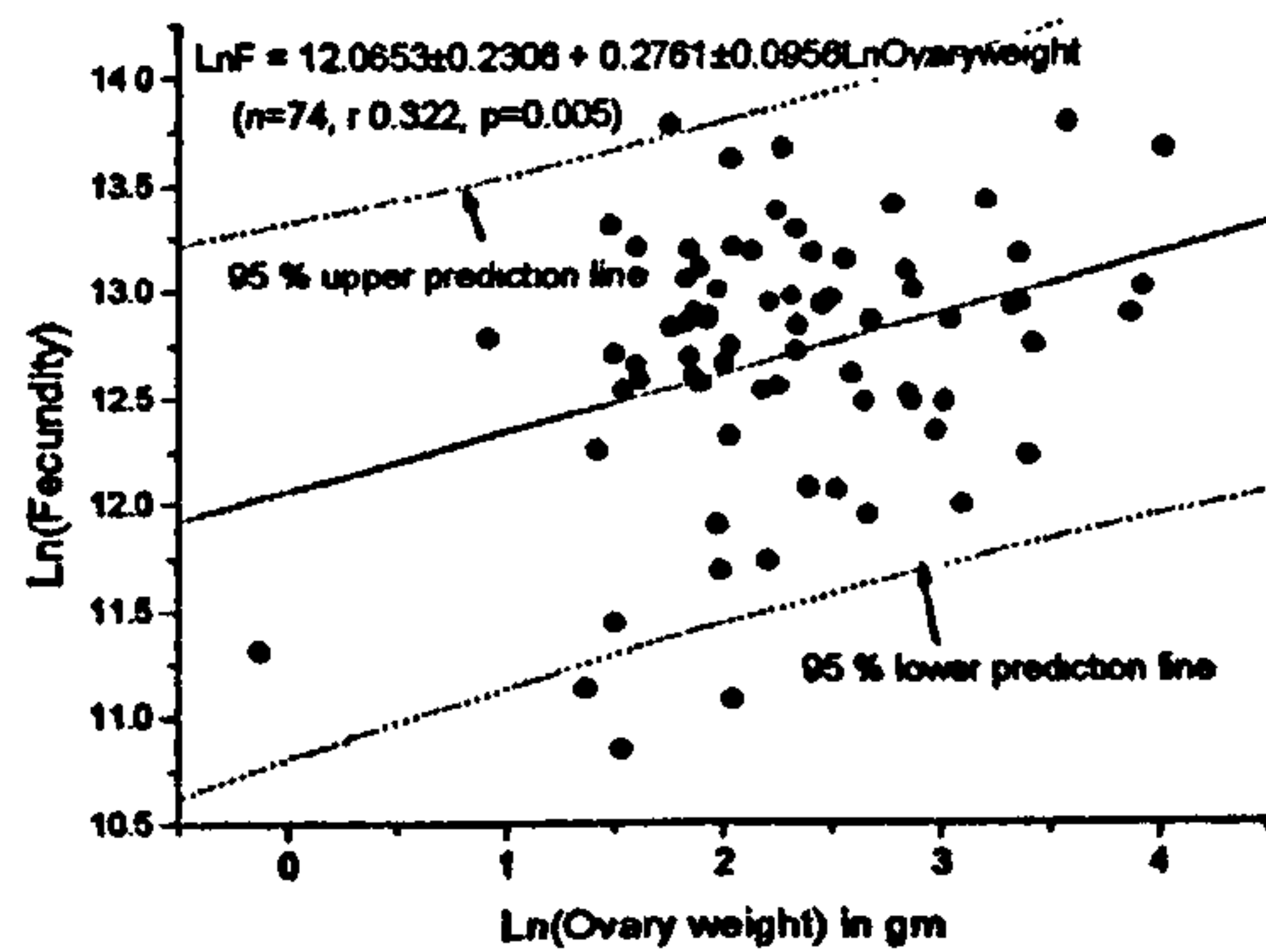


Figure 4.14. Logarithmic relationship between fecundity and ovary weight



There is minimum fluctuation in the mean egg diameter of the ovary of a matured 20 cm fish between May and October, (Table 4.5, Figure 4.15) in the spent and resting period. There is an increase in the egg size at the beginning of the spawning in November (0.40 mm) which peaked (0.58 mm) between December and March at the height of spawning. But in January 2001 samples, the average egg diameter of a ripe ovary was as high as 0.67 mm, more than the observed peak observed in 1999. The average egg size gradually declines in the running fish in April (0.24 mm). The average size is highest in the ripe and full fish (Stages V and VI), Table 4.6. The Kruskal-Wallis test indicates that at least one of the maturation stages has an egg size which is significantly different ($\chi_{830.39}$; d.f=4; P=0.001). The Scheffe Multiple Comparison Test (for unequal sample sizes), shows that the average size of resting stage III is similar (P=0.829) to spent stage 8 eggs. The egg sizes of the pre-spawning and spawning, IV-VII, stages are significantly different from each other and from the inactive stages (III and VIII), (P=0.001).

Table 4.5. Monthly variation in egg sizes (mm±SE) of a 20 cm mature fish ovary

Month	Stage III	Stage IV	Stage V/VI	Stage VII	Stage VIII	Average	N
Feb99			0.56±0.01	0.37±0.03		0.47	138
Mar99			0.58±0.06	0.40±0.02		0.49	100
Apr99				0.32±0.03	0.16±0.01	0.24	80
May99					0.10±0.01	0.10	20
Jun99	0.13±0.01					0.13	20
Jul99	0.13±0.00					0.13	20
Aug99	0.15±0.00					0.15	120
Sep99	0.17±0.01					0.17	80
Oct99	0.22±0.01					0.22	80
Nov99		0.40±0.01				0.40	161
Dec99		0.58±0.01				0.58	161
Jan01		0.54±0.04	0.67±0.04			0.61	40

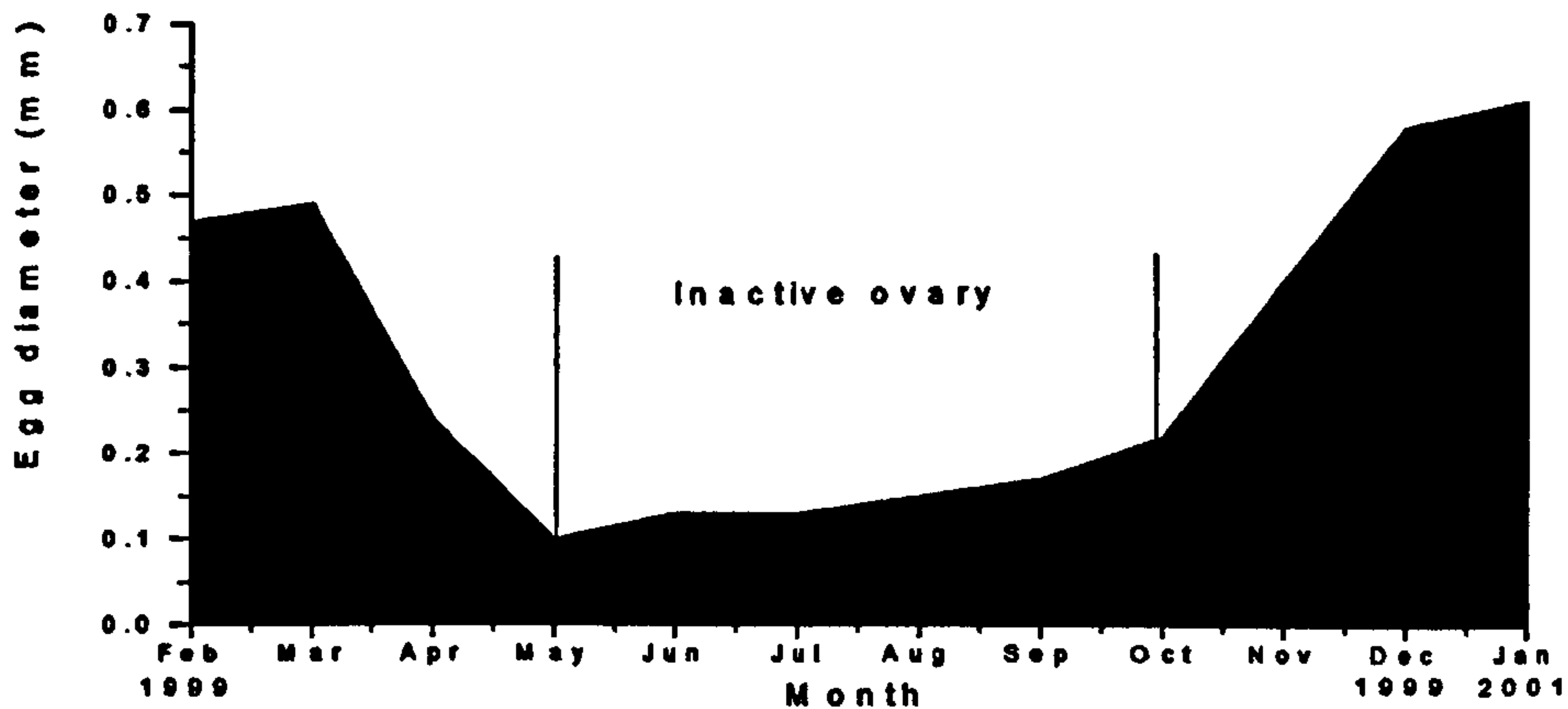
Table 4.6. Descriptive statistics for egg sizes of various maturity stages in dab

Maturation	Stage	N	Mean	SE	Median	Range
Resting	III	420	0.16	0.01	0.15	0.06-0.31
Ripening	IV	280	0.49	0.09	0.50	0.14-0.83
Ripe and full	V/VI	181	0.57	0.01	0.53	0.23-1.02
Running	VII	175	0.36	0.01	0.36	0.09-0.59
Spent	VIII	100	0.15	0.01	0.13	0.06-0.60

Kruskal-Wallis Test: χ (chi-square)=830.39, d.f=4, P=0.001**

** There is a significant difference (P<0.05) in the egg diameter (median value) between the maturation stages. Scheffe Multiple Comparison test showed that there is no significant difference (P=0.829) between the stage III (resting) and stage VIII (spent).

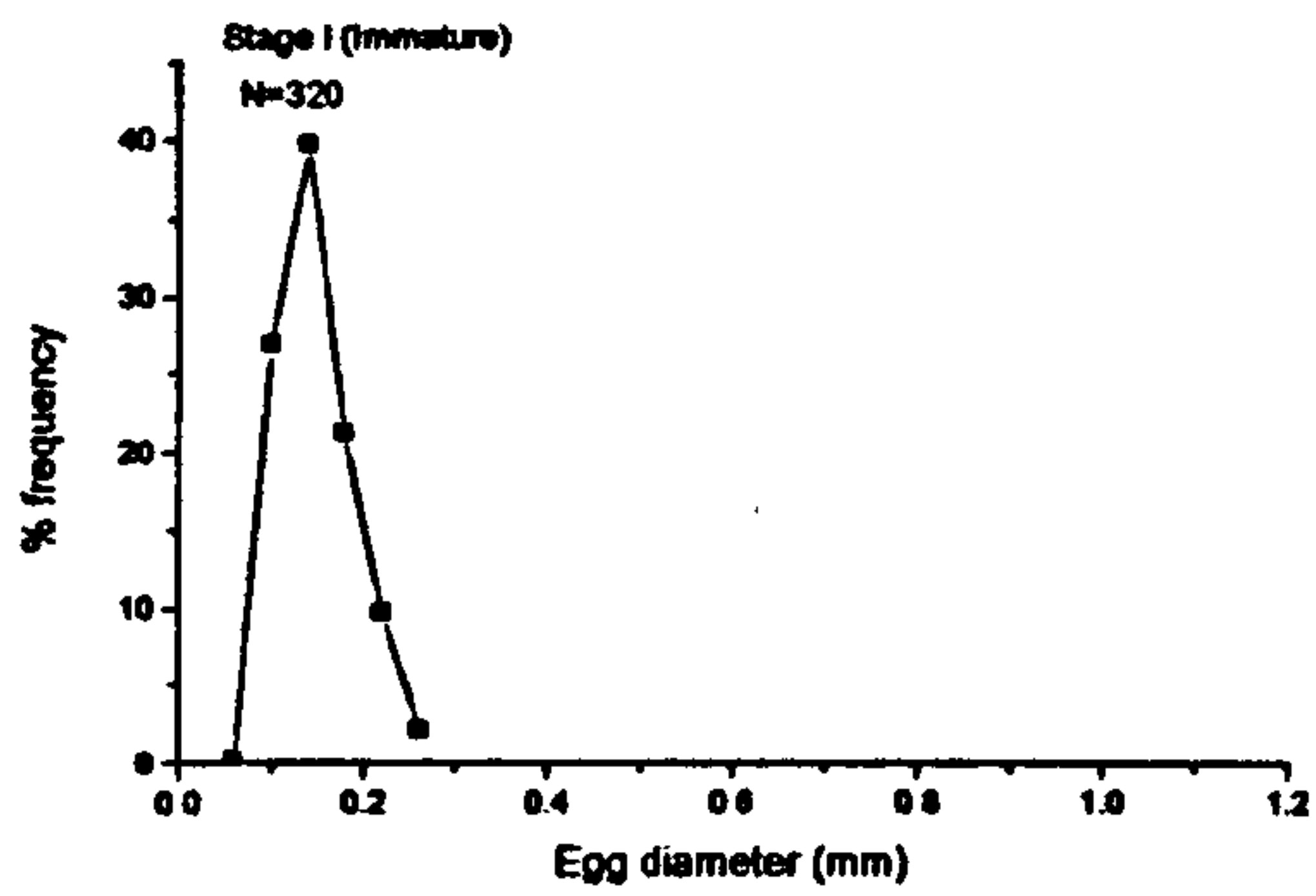
Figure 4.15. Monthly fluctuation in average egg size in a mature 20 cm fish in 1999 and 2001



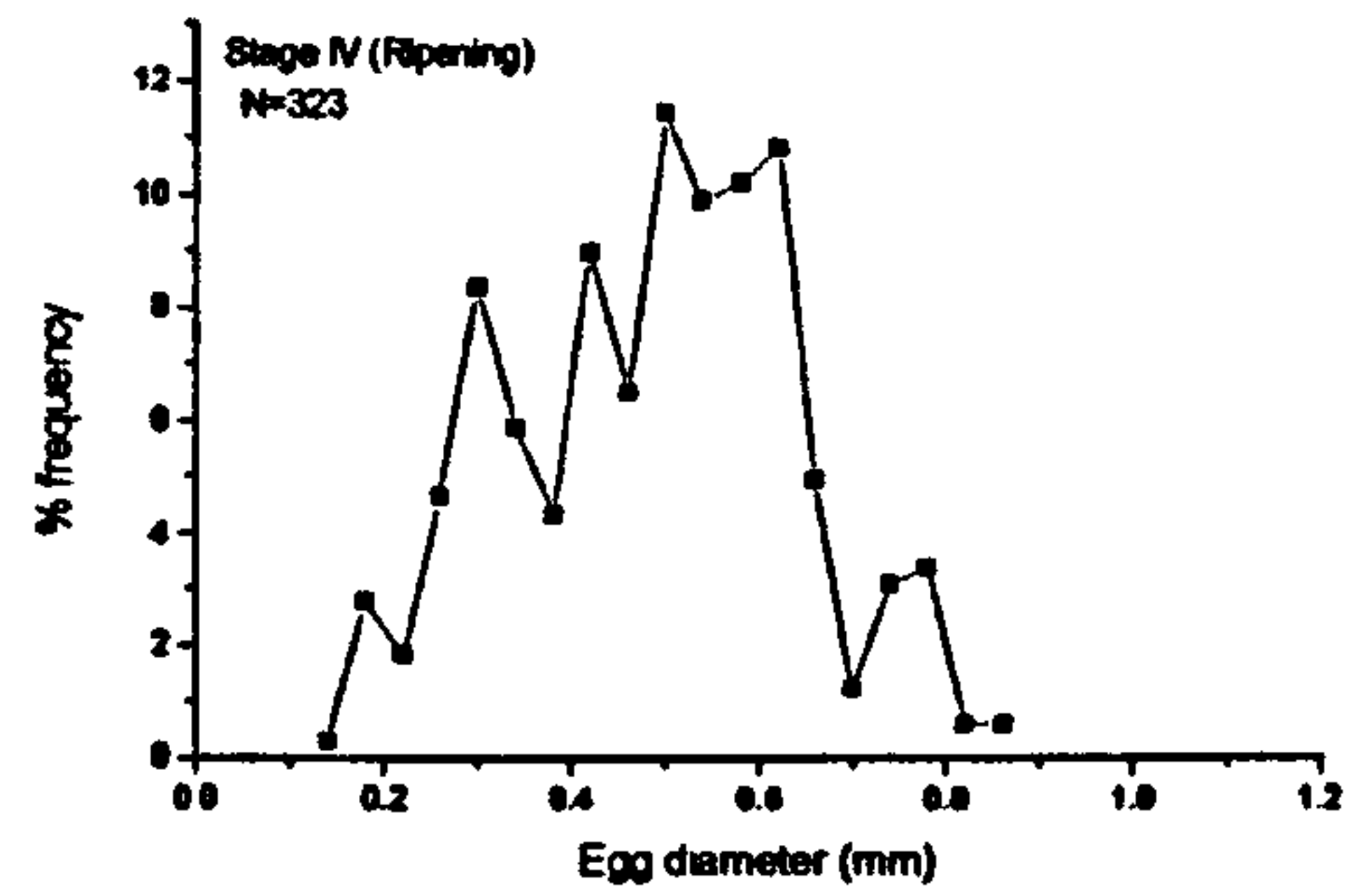
There is a shift in the mode of the size frequency distribution of the oocytes as the ovary develops (Figure 4.16). The mode shifts from about 0.10 mm in an immature fish to 0.50 mm in a ripe fish, and declines to 0.40 mm and then 0.10 mm in a running and spent fish respectively. There is a unimodal size frequency distribution of egg sizes in immature fish and resting fish (stages I, II, III). However, there is a polymodal distribution of egg sizes in the ripening and ripe fish (stages IV and VI). The progressive maturation to the spawning condition (Stages IV-VI) was evident from the increasing egg diameter of the most advanced mode at each stage. An increasing percentage of eggs matured during stages IV-VI and the maximum egg diameter advanced to 1.02 mm in the fully ripe stage. At this stage the most advanced mode contained hyaline eggs with oil globules. Figure 4.16G represents the spent stage, where a few residual eggs at 0.30 mm (1%), 0.58 mm (1%) and 0.62 mm (1%) remaining in the ovary, indicating some resorption.

Figure 4.16. Size frequency distribution of egg sizes in various maturity stages in dab on the North Wales Coast.

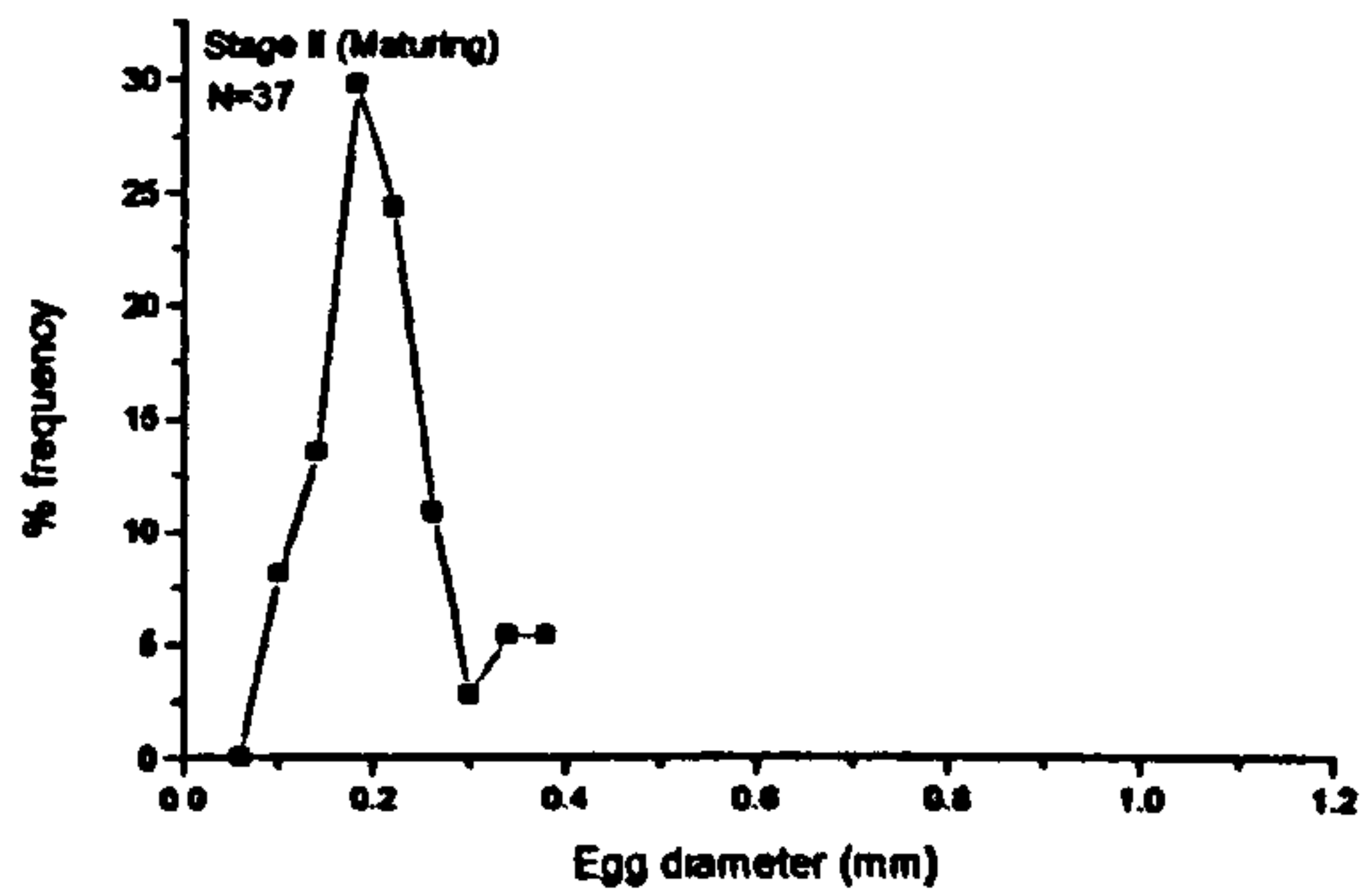
A-Stage I (Immature)



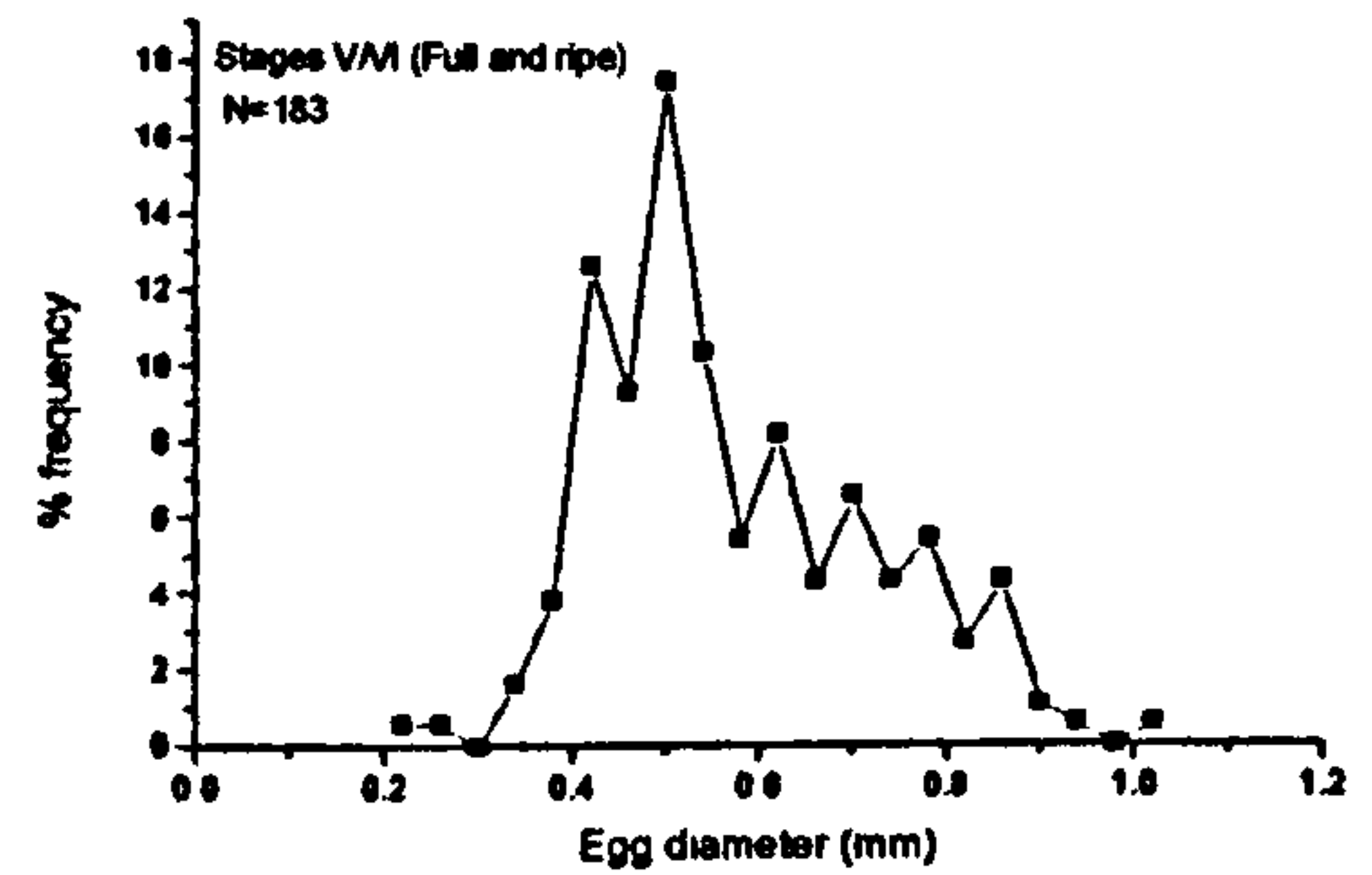
D-Stage IV (Ripening)



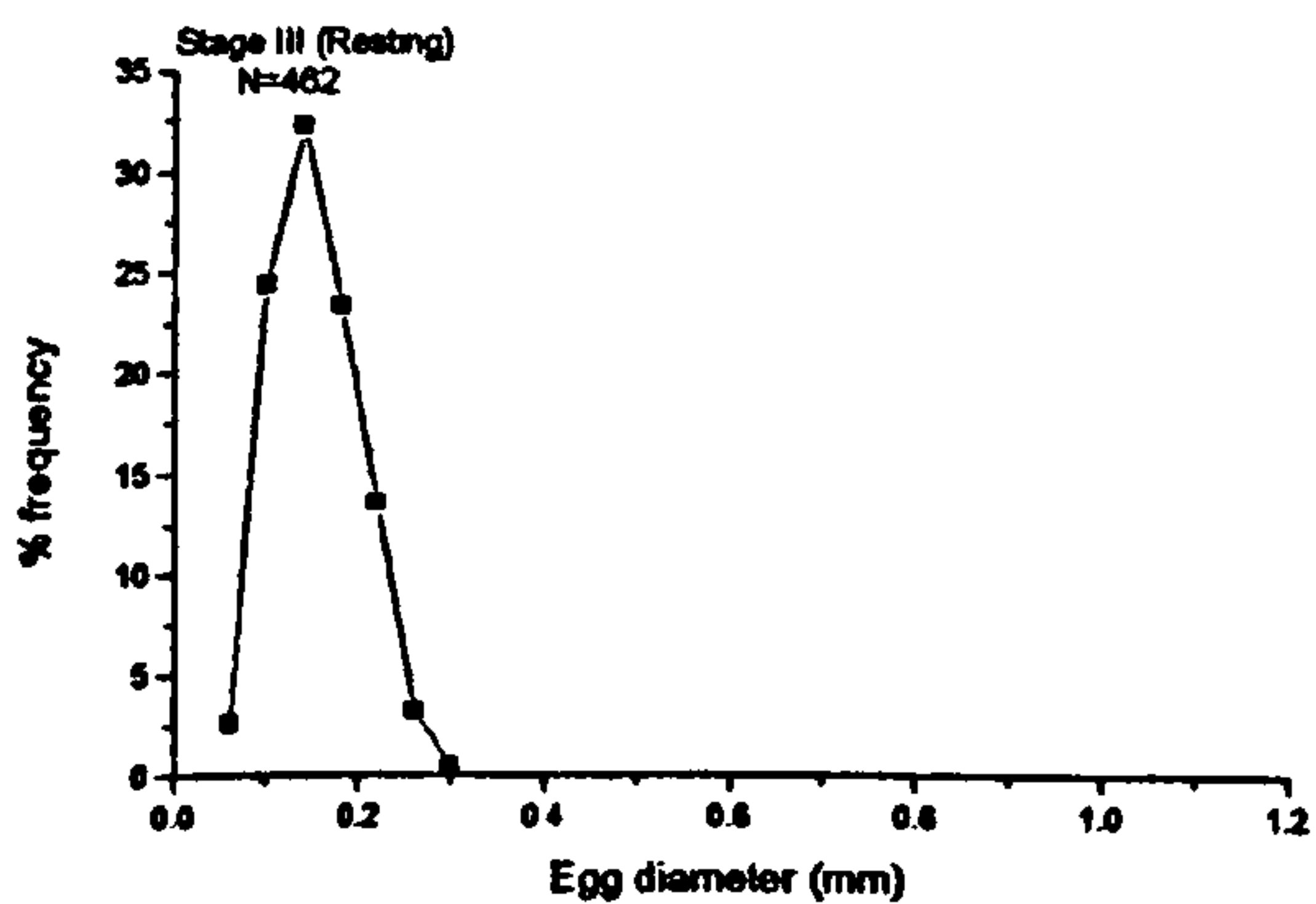
B-Stage II (Maturing)



E-Stages V / VI (Ripe and Full)



C-Stage III (Resting)



F-Stage VII (Running)

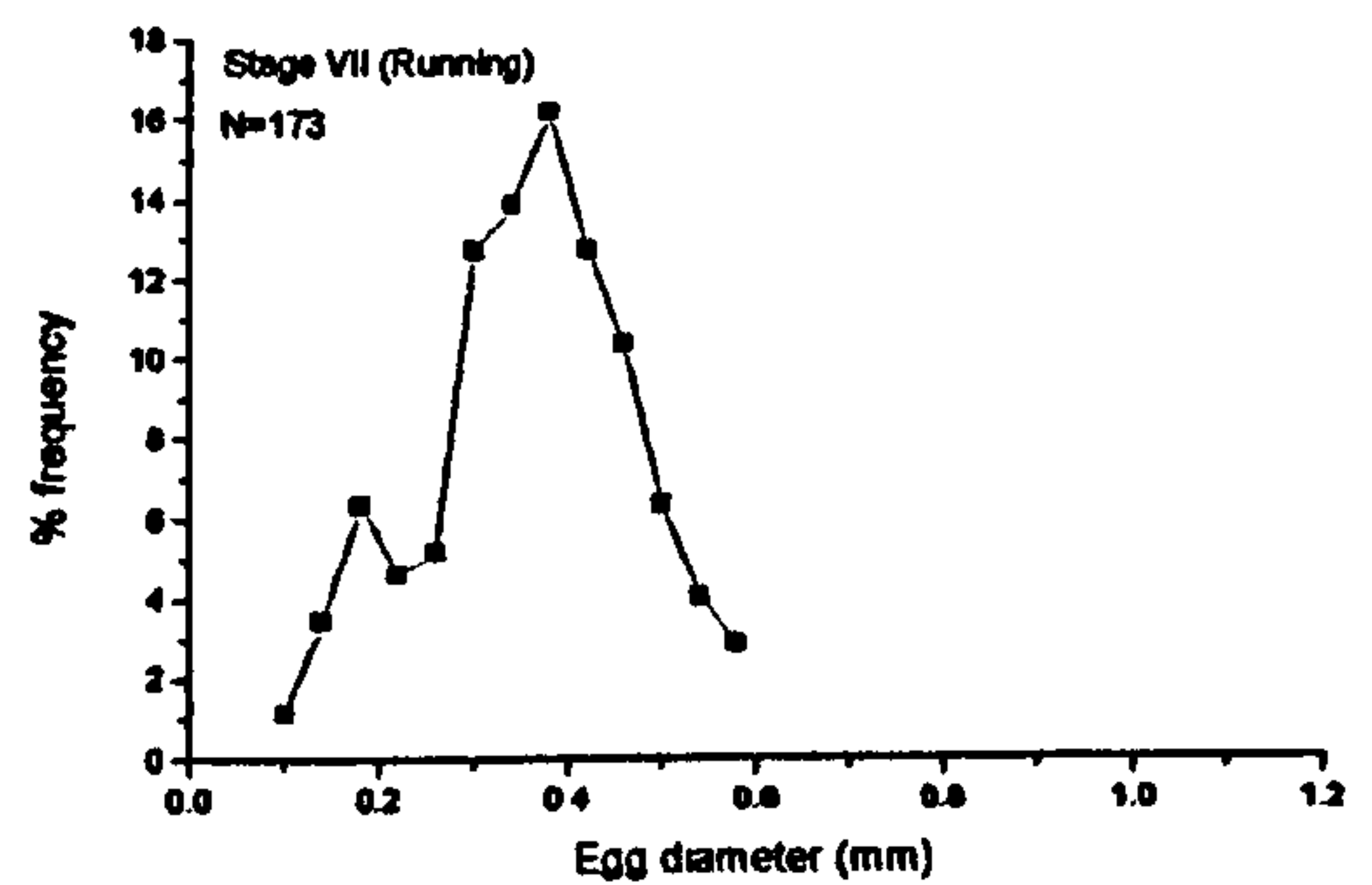
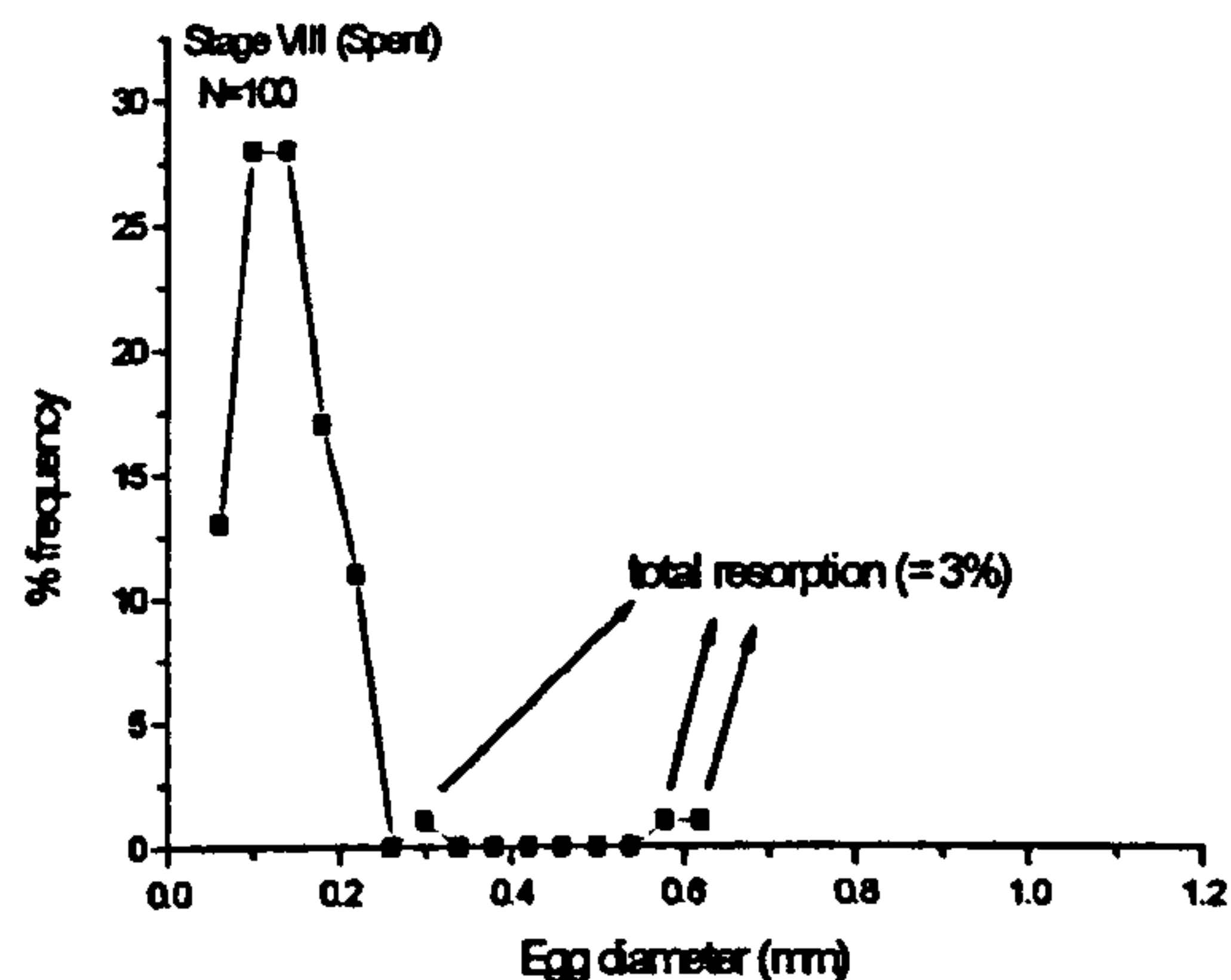


Figure 4.16 continued.

G-Stage VIII (Spent)



Monthly fluctuations in ovary, liver, carcass weights and the condition factor of various length groups in female and male dab are shown in Tables 4.7 and 4.8 respectively. As an example, for 21-25 cm females in the spawning season, there is a steady increase in average ovary weight from November 1999 (3.27 g) at the beginning of oogenesis to a peak in February 2000 (17.47 g), at the height of the spawning season. This pattern is similar in other female size groups. During this time, the ovary contributes substantially to the total weight of the individual fish. (In the field, sample was obtained with 36.7 cm and 23.4 cm female fish with ovary weight contributing 30.38 % and 36.99 % to the total carcass weight in February 1999 and February 2000 respectively). After attaining the maximum weight in February, the average ovary weight of a 21-25 cm fish sharply declines in March (1.46 g) and April (1.25 g), in the postspawning period. The inactive ovary shrinks further to its lowest size between May-October and remains relatively stable until the beginning of oogenesis again in November 2000. In the 21-25 cm female, the maximum weight of the liver is obtained in January-February (3.73-3.78 g) during the spawning season. There is a decline in the liver weight after spawning in March and April 2000 (1.39 g and 1.34 g respectively). Other size groups follow the same pattern with increased size of liver between summer-winter and the minimum in spring (Table 4.7). A cyclical pattern is also observed in the carcass of the female dab. The carcass weight increases significantly from summer and attains peak value at the height of winter. The maximum carcass weight occurs in the winter in July (130.14 g) and remains relatively stable until after spawning in March and April. The minimum carcass weight was in April 2000 (78.85 g) in the 21-25 cm fish. The fish are emaciated afterwards

(late March-May), with resulting carcass weight dropping down from peaked to low levels; from average 73.0 to 43.0 g, 130 to 79 g, 223 to 141 g and 511 to 228.33 g in the 16-20, 21-25 cm, 26-30 and ≥ 31 cm length groups respectively.

In general terms, the pattern of cyclical change in the sizes of gonad, liver and carcass and the resulting condition factor in the female is similar to the male (Table 4.8). The testes start increasing in size in October, the beginning of spermatogenesis. In the 16-20 cm male, the maximum weight of the testes is at the height of the spawning season in January (1.01 g); in the female, the maximum ovary weight was in February. The weight of the testes declines gradually after spawning, beginning in February 2000 (0.42 g) to the lowest weight in July 2000 (0.11 g). In the 1998/1999 season, the minimum testes weight occurred after spawning in March and April 1999 (0.07- 0.09 g). The size of the liver is generally stable between June and November but sharply declines in size during the peak spawning period between December and January. The minimum liver weight (0.54- 0.68 g) also occurred in March and April 2000. The maximum liver weight (1.39- 1.94 g) for the 16-20 cm male dab occurred between June and August in the summer of 1999. The carcass weight remains high between the summer and winter but declined to its lowest level, in March-April (as low as 34 gm in the 16-20 cm class), after spawning.

Tables 4.7 and 4.8. Cyclical changes in the gonad, liver, carcass weight and condition factor of female and male dab on the North Wales Coast, 1999-2001.

Table 4.7. Monthly variation in ovary weight, liver weight, carcass weight and condition factor (\pm S.E) of mature female dab of various size groups**Length group: 11-15 cm**

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	4.71 \pm 1.50	0.18 \pm 0.14	28.25 \pm 2.43	16.69 \pm 4.82	2.87 \pm 0.05	0.86 \pm 0.01
Mar	1999	4.37 \pm 1.38	0.85 \pm 0.27	25.33 \pm 2.40	17.38 \pm 3.85	3.34 \pm 0.98	0.85 \pm 0.03
Feb	2000	3.33 \pm 0.40	0.67 \pm 0.07	24.42 \pm 1.19	13.64 \pm 1.37	2.72 \pm 0.19	0.87 \pm 0.01
Mar	2000	2.62 \pm 0.51	0.63 \pm 0.10	24.67 \pm 1.56	10.64 \pm 1.76	2.54 \pm 0.31	0.81 \pm 0.03
May	2000	0.35 \pm 0.04	0.47 \pm 0.05	29.25 \pm 2.16	1.20 \pm 0.05	1.62 \pm 0.14	0.89 \pm 0.04
Jul	2000	0.27 \pm 0.04	1.01 \pm 0.15	33.00 \pm 3.00	0.82 \pm 0.04	3.07 \pm 0.75	1.01 \pm 0.04

Length group: 16-20 cm

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	9.64 \pm 2.15	1.96 \pm 0.20	51.00 \pm 5.00	18.90 \pm 6.12	3.84 \pm 0.77	0.91 \pm 0.04
Mar	1999	8.40 \pm 1.44	1.39 \pm 0.22	42.57 \pm 3.11	19.72 \pm 3.49	3.26 \pm 0.35	0.85 \pm 0.01
Jul	1999	0.56 \pm 0.31	1.16 \pm 0.78	64.00 \pm 19.00	0.88 \pm 0.25	1.81 \pm 0.74	0.95 \pm 0.08
Aug	1999	0.62 \pm 0.07	1.69 \pm 0.29	73.83 \pm 5.13	0.84 \pm 0.04	2.28 \pm 0.28	0.97 \pm 0.04
Sep	1999	0.62 \pm 0.03	1.46 \pm 0.29	60.35 \pm 3.14	1.02 \pm 0.04	2.42 \pm 0.19	0.90 \pm 0.03
Oct	1999	0.74 \pm 0.03	1.71 \pm 0.13	64.70 \pm 2.21	1.14 \pm 0.04	2.65 \pm 0.17	0.93 \pm 0.02
Nov	1999	1.90 \pm 0.10	1.88 \pm 0.10	62.21 \pm 1.68	3.05 \pm 0.13	3.02 \pm 0.12	0.95 \pm 0.01
Dec	1999	2.84 \pm 0.20	1.55 \pm 0.17	76.50 \pm 3.42	3.71 \pm 0.28	2.03 \pm 0.18	0.95 \pm 0.03
Feb	2000	9.77 \pm 0.49	1.95 \pm 0.07	57.03 \pm 1.44	17.14 \pm 1.68	3.42 \pm 0.07	0.91 \pm 0.01
Mar	2000	4.04 \pm 0.56	1.22 \pm 0.10	50.41 \pm 1.74	8.02 \pm 1.01	2.42 \pm 0.18	0.77 \pm 0.02
Apr	2000	1.02 \pm 0.18	0.80 \pm 0.08	46.57 \pm 3.40	2.20 \pm 0.63	1.72 \pm 0.18	0.72 \pm 0.02
May	2000	0.73 \pm 0.04	1.22 \pm 0.09	63.52 \pm 2.10	1.14 \pm 0.03	1.92 \pm 0.10	0.93 \pm 0.02
Jul	2000	0.68 \pm 0.04	1.73 \pm 0.11	72.89 \pm 2.00	0.94 \pm 0.03	2.37 \pm 0.10	1.02 \pm 0.02
Oct	2000	0.70 \pm 0.05	1.91 \pm 0.27	70.44 \pm 4.71	0.99 \pm 0.05	2.72 \pm 0.26	0.98 \pm 0.04
Jan	2001	7.18 \pm 0.81	2.23 \pm 0.28	74.67 \pm 4.98	9.62 \pm 1.65	2.99 \pm 0.42	0.94 \pm 0.04

Table 4.7 continued.

Length group: 21-25 cm

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	16.78 ± 2.87	3.30 ± 0.38	104.45 ± 7.58	16.07 ± 2.17	3.16 ± 0.32	0.88 ± 0.02
Mar	1999	13.37 ± 4.15	3.59 ± 0.57	82.00 ± 7.00	16.30 ± 2.60	4.37 ± 0.22	0.75 ± 0.01
Apr	1999	4.44 ± 0.78	1.59 ± 0.17	98.13 ± 2.92	4.53 ± 0.74	1.61 ± 0.15	0.73 ± 0.01
May	1999	1.07 ± 0.02	1.95 ± 0.22	118.00 ± 24.00	0.91 ± 0.18	1.65 ± 0.15	0.88 ± 0.11
Jun	1999	1.18 ± 0.14	3.04 ± 0.30	119.88 ± 9.64	0.98 ± 0.07	2.58 ± 0.18	0.98 ± 0.02
Jul	1999	1.02 ± 0.04	2.34 ± 0.14	110.37 ± 3.03	0.92 ± 0.03	2.10 ± 0.09	0.90 ± 0.01
Aug	1999	1.04 ± 0.04	2.49 ± 0.16	108.58 ± 2.72	0.96 ± 0.03	2.29 ± 0.11	0.92 ± 0.01
Sep	1999	1.04 ± 0.04	2.91 ± 0.22	107.42 ± 4.02	0.97 ± 0.03	2.71 ± 0.18	0.94 ± 0.02
Oct	1999	1.27 ± 0.05	2.82 ± 0.23	111.29 ± 3.46	1.14 ± 0.03	2.54 ± 0.02	0.91 ± 0.03
Nov	1999	3.23 ± 0.16	3.16 ± 0.13	121.24 ± 2.98	2.66 ± 0.11	2.60 ± 0.08	0.97 ± 0.01
Dec	1999	5.02 ± 0.24	2.41 ± 0.10	112.46 ± 2.34	4.46 ± 0.19	2.14 ± 0.08	0.94 ± 0.01
Feb	2000	17.47 ± 1.11	3.73 ± 0.17	102.38 ± 3.05	17.06 ± 0.83	3.65 ± 0.09	0.92 ± 0.01
Mar	2000	3.14 ± 0.51	1.39 ± 0.12	88.65 ± 2.96	3.54 ± 0.54	1.57 ± 0.12	0.75 ± 0.01
Apr	2000	1.46 ± 0.16	1.34 ± 0.10	78.85 ± 3.27	1.86 ± 0.22	1.70 ± 0.10	0.69 ± 0.01
May	2000	1.25 ± 0.04	2.14 ± 0.12	111.95 ± 3.15	1.11 ± 0.03	1.89 ± 0.07	0.90 ± 0.02
Jul	2000	1.23 ± 0.04	3.22 ± 0.15	130.14 ± 3.25	0.95 ± 0.02	2.47 ± 0.09	1.00 ± 0.01
Oct	2000	1.30 ± 0.08	2.54 ± 0.20	125.30 ± 5.42	1.13 ± 0.03	2.20 ± 0.13	0.96 ± 0.02
Jan	2001	7.97 ± 0.81	3.78 ± 0.23	129.71 ± 4.71	6.15 ± 0.48	2.53 ± 0.14	0.97 ± 0.02

Length group: 26-30 cm

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	36.55 ± 12.85	4.40 ± 1.09	164.67 ± 20.30	22.20 ± 4.66	2.67 ± 0.95	0.90 ± 0.03
Apr	1999	7.15 ± 0.94	3.05 ± 0.26	153.74 ± 5.50	4.65 ± 0.52	1.99 ± 0.15	0.74 ± 0.01
May	1999	2.27 ± 0.21	3.60 ± 0.50	187.75 ± 6.02	1.20 ± 0.08	1.91 ± 0.24	0.89 ± 0.02
Jun	1999	1.62	3.07	155.00	1.04	1.98	0.93
Jul	1999	1.76 ± 0.17	5.28 ± 0.42	179.42 ± 8.03	0.98 ± 0.07	2.94 ± 0.24	0.96 ± 0.02
Aug	1999	1.71 ± 0.07	4.07 ± 0.30	184.59 ± 7.40	0.93 ± 0.04	2.20 ± 0.11	0.96 ± 0.03
Sep	1999	2.13 ± 0.25	6.97 ± 1.57	214.00 ± 19.82	0.99 ± 0.08	3.26 ± 0.37	1.04 ± 0.05
Oct	1999	3.18 ± 0.56	6.49 ± 0.94	203.90 ± 19.95	1.56 ± 0.02	3.18 ± 0.34	0.97 ± 0.05
Nov	1999	4.81 ± 0.43	4.41 ± 0.31	182.87 ± 5.58	2.63 ± 0.21	2.41 ± 0.15	0.95 ± 0.02
Dec	1999	8.81 ± 0.79	4.40 ± 0.32	178.11 ± 5.57	4.95 ± 0.38	2.47 ± 0.16	0.97 ± 0.01
Feb	2000	31.76 ± 7.53	6.10 ± 0.45	195.33 ± 12.27	16.26 ± 3.36	3.12 ± 0.16	0.93 ± 0.04
Mar	2000	2.51 ± 0.36	2.03 ± 0.31	153.00 ± 13.03	1.64 ± 0.12	1.32 ± 0.10	0.74 ± 0.01

Table 4.7 continued.
Length group: 26-30 cm

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Apr	2000	2.85 ± 0.41	2.16 ± 0.16	140.88 ± 9.66	2.02 ± 0.36	1.54 ± 0.13	0.67 ± 0.01
May	2000	2.26 ± 0.09	4.02 ± 0.22	183.47 ± 4.80	1.23 ± 0.06	2.19 ± 0.08	0.91 ± 0.02
Jul	2000	2.19 ± 0.07	6.88 ± 0.36	222.91 ± 5.78	0.98 ± 0.02	3.08 ± 0.10	1.04 ± 0.02
Oct	2000	2.46 ± 0.21	4.70 ± 0.30	201.08 ± 9.14	1.22 ± 0.10	2.34 ± 0.12	1.02 ± 0.03
Jan	2001	13.90 ± 1.29	5.12 ± 0.41	185.00 ± 8.28	7.51 ± 0.60	2.77 ± 0.23	0.91 ± 0.03

Length group: ≥31 cm

Month	Year	Ovary wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	109	30.30	511.00	21.33	5.95	1.03
Apr	1999	8.78 ± 5.71	4.11 ± 1.47	228.33 ± 16.17	3.85 ± 2.28	1.80 ± 0.55	0.75 ± 0.05
July	1999	3.22	5.86	279.00	1.15	2.10	0.97
Aug	1999	2.70	4.44	280.00	0.97	1.59	0.93
Mar	2000	33.69	6.49	251	13.42	3.59	0.76
Apr	2000	3.55	2.58	240	1.48	1.08	0.70
May	2000	3.61 ± 0.33	6.84 ± 0.56	298.20 ± 18.94	1.21 ± 0.12	2.29 ± 0.26	0.97 ± 0.05
Jul	2000	3.45 ± 0.25	12.33 ± 0.70	345.00 ± 13.11	1.00 ± 0.05	3.57 ± 0.23	1.07 ± 0.03
Oct	2000	3.78 ± 0.63	5.57 ± 1.27	277.50 ± 4.50	1.36 ± 0.25	2.01 ± 0.49	0.95 ± 0.00
Jan	2001	21.71	6.32	255	8.52	2.48	0.90

B. Male

Table 4.8. Monthly variation in gonad weight, liver weight, carcass weight and the condition factor (\pm S.E) of mature male dab of various size groups

Length group: 11-15 cm

Month	Year	Testes wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	0.07 \pm 0.01	0.30 \pm 0.11	17.50 \pm 2.50	0.41 \pm 0.03	0.84 \pm 0.04	0.82 \pm 0.04
Mar	1999	0.14 \pm 0.07	0.29 \pm 0.13	26.67 \pm 2.35	0.51 \pm 0.22	1.07 \pm 0.42	0.84 \pm 0.05
Sep	1999	0.06 \pm 0.01	0.54 \pm 0.10	27.86 \pm 1.59	0.22 \pm 0.02	1.95 \pm 0.28	0.92 \pm 0.03
Oct	1999	0.22 \pm 0.05	0.87 \pm 0.13	32.00 \pm 3.00	0.68 \pm 0.09	2.72 \pm 0.14	0.91 \pm 0.05
Nov	1999	0.23 \pm 0.02	0.48 \pm 0.04	26.68 \pm 1.16	0.86 \pm 0.07	1.78 \pm 0.11	0.95 \pm 0.02
Dec	1999	0.33 \pm 0.06	0.21 \pm 0.02	24.50 \pm 3.50	1.35 \pm 0.06	0.84 \pm 0.06	0.82 \pm 0.02
Feb	2000	0.11 \pm 0.02	0.21 \pm 0.02	19.0 \pm 1.31	0.56 \pm 0.12	1.12 \pm 0.07	0.83 \pm 0.02
Mar	2000	0.05 \pm 0.01	0.33 \pm 0.02	24.70 \pm 1.05	0.22 \pm 0.02	1.33 \pm 0.10	0.86 \pm 0.02
Apr	2000	0.07	0.34	28	0.25	1.20	0.83
May	2000	0.04 \pm 0.01	0.50 \pm 0.06	29.73 \pm 1.39	0.14 \pm 0.01	1.68 \pm 0.14	0.95 \pm 0.03
Jul	2000	0.03 \pm 0.00	0.39 \pm 0.04	25.56 \pm 1.07	0.10 \pm 0.01	1.51 \pm 0.14	0.92 \pm 0.02
Oct	2000	0.19 \pm 0.01	0.72 \pm 0.07	29.75 \pm 1.42	0.62 \pm 0.04	2.42 \pm 0.18	0.97 \pm 0.02

Length group: 16-20 cm

Month	Year	Testes wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	0.39 \pm 0.05	0.85 \pm 0.08	49.31 \pm 3.53	0.80 \pm 0.07	1.73 \pm 0.16	0.84 \pm 0.03
Mar	1999	0.07 \pm 0.04	0.59 \pm 0.05	33.67 \pm 3.28	0.20 \pm 0.14	1.76 \pm 0.23	0.79 \pm 0.06
Apr	1999	0.09	0.34	49.00	0.18	0.67	0.75
Jun	1999	0.11 \pm 0.02	1.39 \pm 0.39	62.00 \pm 12.00	0.18 \pm 0.03	2.24 \pm 0.26	0.92 \pm 0.14
Jul	1999	0.22 \pm 0.11	1.19 \pm 0.17	73.00 \pm 1.00	0.31 \pm 0.15	1.63 \pm 0.25	0.89 \pm 0.03
Aug	1999	0.14 \pm 0.03	1.94 \pm 0.29	67.40 \pm 5.35	0.20 \pm 0.03	2.88 \pm 0.42	0.97 \pm 0.05
Sep	1999	0.12 \pm 0.01	1.11 \pm 0.09	53.28 \pm 2.00	0.22 \pm 0.03	2.08 \pm 0.21	0.88 \pm 0.03
Oct	1999	0.33 \pm 0.02	1.08 \pm 0.07	50.10 \pm 1.43	0.66 \pm 0.03	2.15 \pm 0.12	0.86 \pm 0.01
Nov	1999	0.73 \pm 0.05	1.04 \pm 0.06	56.03 \pm 2.00	1.30 \pm 0.06	1.86 \pm 0.07	0.93 \pm 0.01
Dec	1999	0.92	0.70	66	1.40	1.06	0.80
Feb	2000	0.42 \pm 0.03	0.78 \pm 0.11	51.25 \pm 4.06	0.82 \pm 0.05	1.53 \pm 0.14	0.81 \pm 0.05
Mar	2000	0.18 \pm 0.04	0.54 \pm 0.05	38.58 \pm 2.75	0.46 \pm 0.07	1.40 \pm 0.12	0.73 \pm 0.03
Apr	2000	0.13 \pm 0.03	0.68 \pm 0.05	41.67 \pm 5.24	0.32 \pm 0.08	1.63 \pm 0.10	0.67 \pm 0.03

Length group: 16-20 cm continued (Table 4.8)

Month	Year	0.14 ± 0.01	0.91 ± 0.05	51.59 ± 1.78	0.28 ± 0.02	1.77 ± 0.10	0.87 ± 0.02
May	2000	0.14 ± 0.01	0.91 ± 0.05	51.59 ± 1.78	0.28 ± 0.02	1.77 ± 0.10	0.87 ± 0.02
Jul	2000	0.11 ± 0.01	1.15 ± 0.09	54.90 ± 2.21	0.20 ± 0.04	2.10 ± 0.12	0.94 ± 0.02
Oct	2000	0.41 ± 0.04	1.05 ± 0.07	56.65 ± 3.16	0.71 ± 0.05	1.82 ± 0.13	0.96 ± 0.02
Jan	2001	1.01 ± 0.24	0.78 ± 0.09	57.50 ± 6.36	1.76 ± 0.26	1.36 ± 0.01	0.87 ± 0.02

Length group: 21-25

Month	Year	Testes wt. (g)	Liver wt. (g)	Carcass wt. (g)	GCR (%)	HCR (%)	K C-Factor
Feb	1999	1.34	1.33	86.00	1.56	1.55	0.96
Apr	1999	0.44 ± 0.07	0.78 ± 0.08	70.67 ± 3.21	0.62 ± 0.11	1.11 ± 0.11	0.78 ± 0.05
Jun	1999	0.34	2.03	91.00	0.37	2.23	0.87
July	1999	0.37	2.16	99.00	0.37	2.18	1.01
Aug	1999	0.15 ± 0.02	1.35 ± 0.19	87.25 ± 10.30	0.17 ± 0.01	1.55 ± 0.18	0.85 ± 0.05
Sep	1999	0.27 ± 0.05	2.22 ± 0.31	99.00 ± 4.81	0.28 ± 0.05	2.24 ± 0.31	0.90 ± 0.03
Oct	1999	0.92 ± 0.17	1.68 ± 0.50	81.33 ± 7.69	1.13 ± 0.10	2.06 ± 0.43	0.88 ± 0.04
Nov	1999	1.54 ± 0.24	1.56 ± 0.13	82.80 ± 4.47	1.86 ± 0.26	1.89 ± 0.13	0.89 ± 0.04
Dec	1999	1.45 ± 0.21	1.03 ± 0.07	87.70 ± 3.69	1.65 ± 0.21	1.17 ± 0.05	0.87 ± 0.03
Feb	2000	1.19 ± 0.36	1.66 ± 0.37	80.40 ± 9.54	1.48 ± 0.32	2.07 ± 0.32	0.82 ± 0.08
Apr	2000	0.16 ± 0.03	0.73 ± 0.20	59.00 ± 6.00	0.28 ± 0.07	1.24 ± 0.22	0.62 ± 0.02
May	2000	0.30 ± 0.05	1.57 ± 0.17	80.00 ± 3.63	0.37 ± 0.07	1.96 ± 0.18	0.81 ± 0.03
Jul	2000	0.21 ± 0.05	1.90 ± 0.25	88.78 ± 4.24	0.23 ± 0.04	2.14 ± 0.21	0.89 ± 0.04
Oct	2000	0.61 ± 0.06	1.42 ± 0.16	88.17 ± 3.21	0.70 ± 0.06	1.61 ± 0.18	0.90 ± 0.04

The contribution of the gonad and liver to the total monthly carcass weight is illustrated in Figures 4.17 and 4.18 for the female 21-25 cm length group. There is comparatively slight variation in GCR between June-October. The GCR in this size group rises gradually from November (2.66 %) to a peak in February 2000 (17.06 %). In the partially spent condition in March 2000 and April 2000, it declines sharply and reaches its lowest level (0.95 %) during the gonad resting period in summer (June 2000). This cyclical trend is similar in the 16-20 cm and 26-30 cm size groups of the female dab. The 11-15 cm and ≥ 31 cm size groups were poorly sampled and the data is insufficient for cyclical trend analysis. The HCR is also comparatively stable between June-December, ranging from 2.10 % in July 1999 to 2.71% in September 1999 (Figure 4.18). The HCR attained maximum value (3.16 %) in February 2000, before dropping to (1.57 %) in March 2000, in the postspawning period. It would seem there was however a delay in the cyclical pattern in the liver condition in the 1998/1999 spawning season for the 21-25 cm female fish. The peak HCR was achieved in March 1999 (4.37 %) and the minimum was in April 1999 (1.61 %). There is a seasonal variation in condition factor of the 21-25 cm female; it remains relatively high and stable between June 1999 and February 2000, ranging from 0.90 to 0.98, (Figure 4.19). There is a sharp decline in the condition factor in March, reaching lowest levels in April (0.69). The pattern of fluctuation in the condition factor is similar in the 16-20 cm, 26-20 cm and ≥ 31 cm female dab. Summary of the observed changes in K for the female is given below.

Length groups	Min	Month	Max	Month
16-20 cm	0.72	April	1.02	July
21-25 cm	0.69	April	1.00	July
26-30 cm	0.67	April	1.04	July/September
≥ 31 cm	0.70	April	1.07	July

The cyclical changes in the gonad, liver in relation to carcass weight (GCR, HCR and respectively), with also the condition factor, in the 16-20 cm male dab are illustrated graphically in Figures 4.17, 4.18 and 4.19. The peaked value of the GCR occurs in January but starts declining in February (0.82 %) to its lowest level in July (0.20 %). It remains relatively stable between March 1999-September 1999. The GCR in male starts increasing in October, a month earlier than the female. The highest levels of HCR in male are found between June 1999-October 1999 with the maximum in August 1999 (2.88 %), but gradually declines from November 2000 to further lower levels in winter-early spring (December 1999-March 2000), 1.06 % in December. The minimum HCR in 1999 was in April (0.67 %). Similarly, the condition factor remains relatively high and stable between June-November (0.86 – 0.92) in the 16-20 cm male dab. The condition factor gradually declines in December

and reaches minimum levels between March-April (0.67–0.73). The maximum condition in August (0.97). Summary of the observed changes in K for the male of various size groups is given below.

Length groups	Min	Month	Max	Month
16-20 cm	0.67	April	0.97	August
21-25 cm	0.62	April	1.01	July

Figure 4.17. An illustration of monthly variation in Gonado-Carcass Ratio (GCR) in a 21-25 cm female dab and 16-20 cm male dab, 1999-2001 (Error bars indicate S.E).

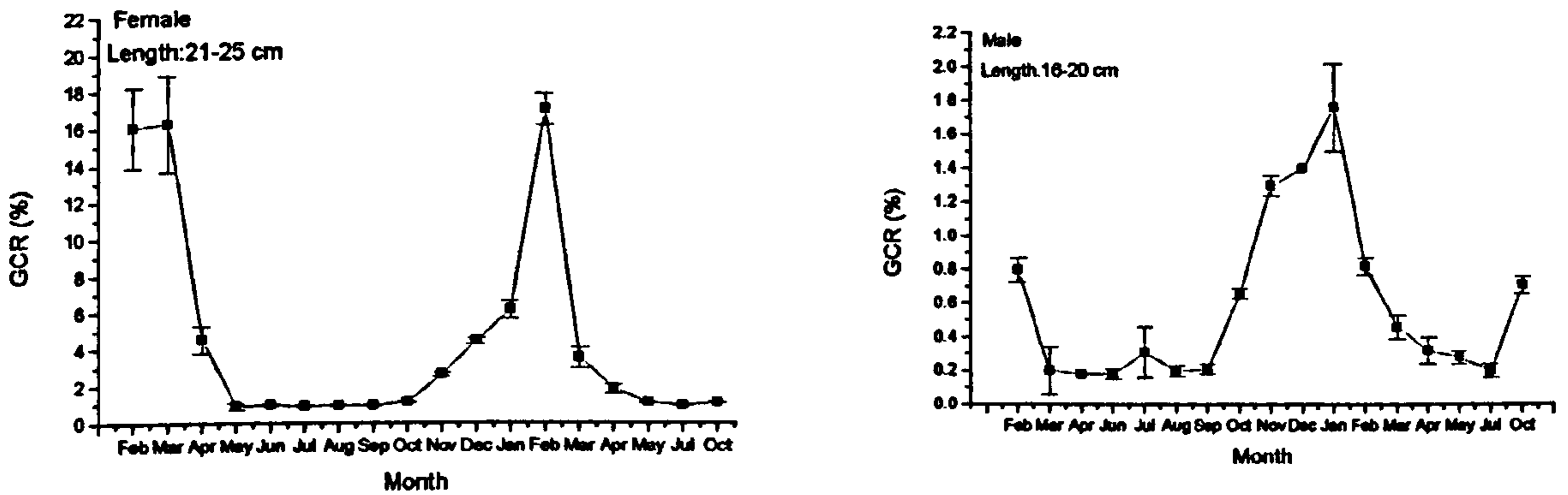


Figure 4.18. An illustration of monthly variation in Hepato-Carcass Ratio (HCR) in a 21-25 cm female dab and 16-20 cm male dab, 1999-2001

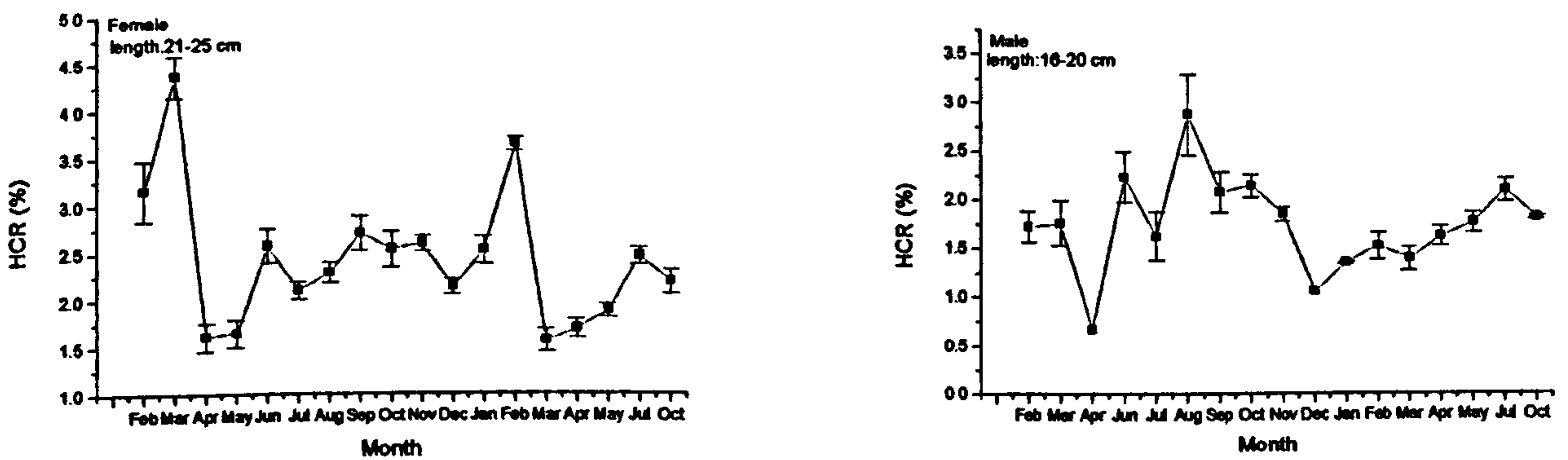
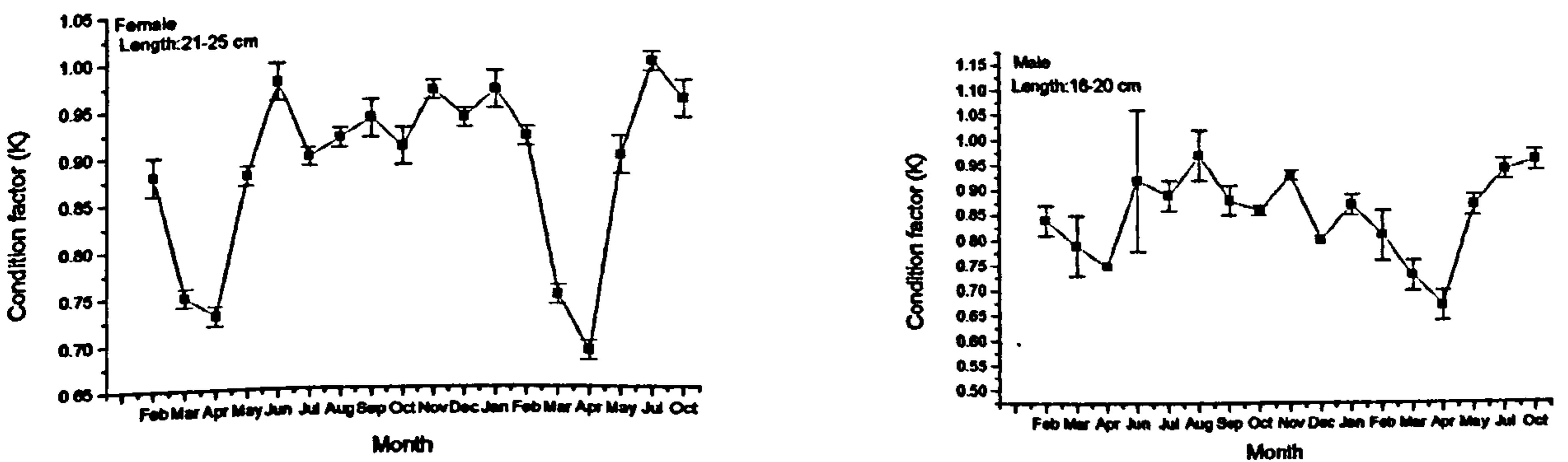


Figure 4.19. An illustration of monthly variation in the Condition Factor, i.e. of carcass, in a 21-25 cm female dab and 16-20 cm male dab, 1999-2001



The monthly variation in ovary weight in relation to fish length is described by a power curve (Table 4.9). There are significant differences ($P < 0.05$) in the fitted constants between months. It is revealed that water content in the ovary in a 20 cm fish decreases at the beginning and during the spawning season (November–February) but increases after the spawning season.

Table 4.9. Fish length and ovary weight relationships for mature dab, 1999-2001

<i>Ovary (g) = a (Fish length (cm))^b</i>							
Month	Year	a	b	r	n	% GCR 20 cm fish	Ovary (%) Water content
Feb	1999	1.3×10^{-4}	3.794	0.908	21	13.35	71.39
Mar	1999	1.04×10^{-2}	2.339	0.700	12	19.38	68.76
Apr	1999	2.2×10^{-3}	2.110	0.745	24	4.41	87.81
May	1999	10^{-5}	3.668	0.754	9	1.35	82.97
Jun	1999	4.0×10^{-5}	3.303	0.738	10	1.07	87.78
July	1999	4.6×10^{-6}	3.920	0.805	63	0.98	86.75
Aug	1999	6.0×10^{-5}	3.116	0.880	77	0.84	84.30
Sep	1999	2.0×10^{-5}	3.526	0.895	65	0.99	83.92
Oct	1999	6.4×10^{-7}	4.640	0.853	78	1.13	83.96
Nov	1999	7.1×10^{-4}	2.680	0.618	149	3.21	78.85
Dec	1999	10^{-4}	3.745	0.667	98	4.12	76.00
Feb	2000	10^{-3}	3.150	0.750	166	20.15	67.90
Mar	2000	1.3×10^{-4}	2.966	0.895	48	6.04	83.53
Apr	2000	3.1×10^{-4}	2.692	0.778	44	1.48	83.84
May	2000	10^{-5}	3.316	0.906	161	1.21	84.21
July	2000	3×10^{-5}	3.384	0.942	201	0.91	82.20
Oct	2000	2×10^{-5}	3.567	0.878	54	1.08	81.62
Jan	2001	7×10^{-5}	3.668	0.735	55	9.81	67.24

Covariance analysis

Common fitted constants:

Term	Exponents
a	0.0006
b	2.7476

Common equation $W = 0.0006 * L^{2.7476}$

There are significant differences in the ($F_a=153.55$; $F_b=81.59$, $P < 0.05$) fitted constants (a and b) between months. The large increase in ovary weight during the spawning period (late autumn and winter) may be mainly responsible for the observed differences from the resting seasons (late spring and summer).

4.4 DISCUSSION

The annual maturity cycle was analysed on a monthly basis for the period 1999-2001 from the relative frequencies of maturity stages in the samples. The onset of spermatogenesis in males is in October whilst oogenesis in females begins in November. Thus there is a month difference in the onset of spawning activity between the male and female. The peak of the reproductive activity is in January for males and in February in females. The active reproductive season (from the onset of gametogenesis to spawning (running stage)) for the males is from October to February whilst in the females it runs from November to March. It was however found that some females can remain in running condition up to April and the males up to July. Rijnsdorp (1989) observed that the male plaice in the North Sea were in spawning condition in December (and continued a longer time until March) whilst the female was ready from January until in March. In the present study very few female fish are seen in running condition in February but the proportion increased significantly by March. Beginning in March also, there is an increasing proportion of spent female fish which peaked in April and May. The present finding of maturity cycle is similar to the findings by Bakhsh (1982). Similarly, Van der Land (1991) found that the spawning of dab in the southern and southeastern North Sea starts in January and reaches a peak in March and April. This was confirmed by Rijnsdorp *et al.* (1992) who studied the spatial distribution of dab during the peak spawning periods. They found out that the peak abundance coincided with the area of high egg density. Htun-Han (1978b) concluded that gonad development in the female dab culminates annually, in February and March, in a short and precise spawning season and oogenesis starts in October. In the males, Htun-Han observed that spermatogenesis starts in September and the actual spawning was between December and March. It thus suggests that the dab in the North Sea have an extended spawning period by one month in comparison with the Anglesey dab populations. In Icelandic waters, the spawning reaches its peak in May, Jonsson (1966).

This study found that the male dab matures at a smaller length and age than the female. This trend is similar to other studies on flatfish (Rijnsdorp, 1989; Deniel, 1990; Lozan, 1992; Rijnsdorp *et al.*, 1992). In the historical data, it is however significant to note the relative stability in the age (2.7 years) and length (20.00 cm) at 50 % maturity in the female dabs over the 25 years in the study area and the gradual decline in age at 50 % maturity (from about 2 years to 1.5 years) in the male dab. This observation for the females underscored the relative stability of the dab population on the North Wales Coast over a quarter of a century. However, there are regional variations in the age and length at 50 % maturity. The

dab population in the coast of Brittany (Deniel, 1990) mature at a later age (3 years) and length (27 cm) than the Anglesey dab, see Chapter 1. In the North Sea (German Bight), the male dab matures also at a later age (1.7 years) but at a much reduced length (Lozan, 1992). Annual differences in the $L_{50\%}$ and $A_{50\%}$ have been related to annual differences in growth rate. Rijnsdorp (1989) revealed that slower-growing plaice reached sexual maturity at a smaller length but higher age than faster-growing plaice. Fishing intensity could also result in reduced $L_{50\%}$ and $A_{50\%}$ as a life-history compensatory mechanism. It should also be noted that sampling procedures may bias the results of size at maturity estimation. In estimating the length and age at maturity, it is important to spread the sampling over a wide area and extended period. Also changes in spatial distribution of the species during spawning period should be considered, as there is migration between offshore and inshore coastal waters (Harding *et al.*, 1978). Morgan and Colbourne (1999) studied variation in maturity at age and size in the American plaice (*Hippoglossoides platessoides*). They concluded that maturation was closely related to total population abundance over the life of a cohort, with cohorts maturing at an earlier age and smaller size when population size was low. Cohorts which experienced higher temperatures appeared to mature earlier and smaller as did cohorts which experienced increased juvenile growth and increased adult mortality. The variability in maturation has also been attributed to genetic differences and variation induced by the environment to which the individuals are exposed (Morgan and Colbourne, 1999). A variety of species have been shown to exhibit inter-population differences in maturation, e.g. American plaice, *Hippoglossoides platessoides*, (Walsh, 1994); brown trout, *Salvelinus fontinalis*, (Hutchings, 1993). In addition, intra-population changes in maturation over time have been demonstrated for Atlantic cod in the northeast Arctic (Jorgensen, 1990) and North Sea plaice (Rijnsdorp, 1989). Changes in maturation have also been associated with changes in abundance. At low population size, growth rate has been found to increase in response to increased food resources, and is thought to result in maturation at a younger age (Rijnsdorp, 1993). Increased temperature has also been shown to lead to earlier maturity through increased growth (Sandstrom *et al.*, 1995). Changes in mortality have also been identified as a cause of variation in maturity in fishes. Increased mortality can either cause fish maturity at a smaller size or younger age (Kaperski and Kozlowski, 1993 and Fox, 1994 respectively). Increased mortality is thought to favour a decrease in age and size at maturity as this increases the probability of reproducing before death. The level of adult mortality relative to juvenile mortality is also thought to affect age and size at maturity (Hutchings, 1993). Though there are differences in age and length at maturity between the same populations or different populations of the same species, it is often recognized that the onset of sexual maturity is usually more of a function of size than age (Fossen *et al.*, 1999)

The gonad weight in dab increases with body size and this is in agreement with earlier works by Bakhsh (1982) and Ortega-Salas (1980), and for plaice (Basimi, 1978). It is therefore important that samples of dab are grouped into smaller size classes when studying seasonal changes in gonad, liver or condition factor. The variation in the gonadocarcass ratio (GCR) showed a distinct seasonal periodicity with the highest value in winter (February) at the height of the spawning season and the lowest value in the resting period in summer. As the spawning season progresses, the egg sizes increase resulting in increased ovary weight in the winter period. This period also coincides with low feeding rate (as will be shown in the next chapter). When the eggs are released in the spring, the ovary shrinks and the fish becomes emaciated. With resumption of active feeding again, the condition factor rises to the maximum in July-August whilst the GCR declined to its yearly minimum. Tveiten *et al.* (1998) reported that the reproductive cycle of male and female arctic charr involved temporal changes in growth rate and condition factor. They observed that during winter and early spring, growth rates were low, and both male and female arctic charr also had low condition factors. Seasonal changes in condition and gonadocarcass indices in female dab were reported by Ortega-Salas (1980) from the coast of Isle of Man, Htun-Han (1978a) from the British North Sea coast and Knust (1996) in the German and Dogger Bank. They found similar annual periodicity of these parameters, with a low condition factor and high gonadocarcass in late winter and early spring during the spawning season and a maximum condition in summer, when the GCR was low. The testes remain relatively small when developed and do not contribute significantly to the total body weight (< 2.0 %). In contrast, the weight of ovaries can reach 15-25 % of the wet carcass weight and thus contributes a significant part of the body mass. The peaked value of the GCR in male is 1 month earlier than the females, and occurs between December-January. However the lowest condition is also in the spring (March-April) but some males can remain in spawning condition until June. This is a reproductive strategy which ensures the continuous fertilisation of any remaining eggs. Similar conclusions have been made by Bohl (1957), Simpson (1959b), Jonsson (1966) and Saborowski and Buchholz (1997) for dab.

The condition factors were almost identical in both sexes during the gonad resting periods (when no growth in gonad occurred). But the condition factor of the males declines gradually from late autumn (December) and reaches low values in the spring. The females however appear to maintain a relatively stable condition (between late autumn and winter) until spring, when a significant drop in condition can be observed (Figure 4.19). Saborowski and Buchholz (1997) made similar observations for dab in the southern North Sea. They attributed this sexual difference in condition factor to the growth of the gonad in the females.

The energy for gonad growth is obtained from food, which must be available during the period of female gonadal development in the autumn.

There is a progressive increase in liver weight, from the beginning of summer, up to the winter period in the female dab. The female continues to feed right through the autumn (October-November). This might explain the continuous rise in the liver weight in this period, which peaks between January- February at the height of the spawning season. It is hypothesised that the nutrient reserves in the liver are utilised during peak spawning activity in the winter when feeding rate is low in dab. It has been determined that the food consumption in dab during this period (winter) is relatively low. Thus the liver shrinks after spawning in March and April and hence the condition of fish reaches all time low during this period (early spring). Saborowski and Buchholz (1996) noted that with a rich food supply, the nutrients are stored in the liver. They observed that, in the female, liver weight increases until the winter due to continuous feeding. The declining HCR in the peak spawning season in the female in the German Bight, North Sea, was attributed to the following:

- 1) The decreasing food availability in the environment cannot meet the energy demand; thus the storage products in the liver have been used to fuel metabolic processes.
- 2) The maturing gonads need additional energy, which cannot be supplied by feeding and must be obtained from the liver. This observation by Saborowski and Buchholz (1996) will be tested in chapter 6.
- 3) At the beginning of the spawning season, females feed less due to sexual activity. This was indicated by the high number of empty stomach in the females during the spawning season in the study by Saborowski and Buchholz (1996). This situation is observed in the present study (next chapter) where there is a significant drop in the SGI (Stomach-Gut-Index) in October and the elevated number of empty stomachs in this month. It will be shown in the next chapter that the fish feeds continuously during the spawning period but at a lower rate.

Larson (1974), in a study of the brook trout, *Salvelinus fontinalis*, suggested that the decrease in liver weights in the prespawning season might be due to the passage of materials from the liver to the gonads and concluded that the weight changes of the liver play an important role in gonad maturation. This confirms the generally held view that there is an inverse relationship between liver weight and ovary weight, that the liver weight decreases as the ovary weight increased during vitellogenesis. Yoneda *et al.* (1998) found that the seasonal cycle of GCR was inversely related to the HCR for anglerfish (*Lophiomus*

setigerus) in the East China Sea. They found a significant inverse correlation between the development of the ovary and the reduction in the weight of the fish liver. They supported an earlier observation by Nagahama (1987) who suggested that the rapid accumulation of yolk as oogenesis progresses may be one of the reasons for the decrease in the fish liver weight. It is however observed in this study that noticeable decline in the liver weight is only obvious in March-April. In fact such a relationship is not found in the female dab, indicating that the food reserves in the liver may not be fully mobilized for gonad maturation. Also, there was a positive significant correlation (Pearson) between GCR and HCR ($r=0.600$, $N=66$, $P<0.05$) in the female. Food intake and the muscle (carcass) tissue might be the main sources of energy for gonad development as would be shown in Chapter 6. Lee (1972) and Htun-Han (1978b) also observed that dab continues to feed during the period of gonad maturation in the Isle of Man and the North Sea. This might explain the observation why the HCR and the K remain in females relatively high at the peak spawning in February. It is reported that wild turbot feed actively and build reserves during oocytes recruitment, in anticipation of vitellogenesis; they also continue feeding during vitellogenesis (Bromley, 1980; Bromley *et al.*, 2000).

Current study shows there is a decline in the water content of the ovary as oogenesis progress (November-February) when the ovary enlarges. Basimi and Grove (1985a) made similar observations and attributed these to the deposition of yolk. The water content however rises again during the post-spawning period. The dramatic increase in the size of the gonads as the spawning season progresses mainly accounts for the significant difference ($P<0.05$) in the fitted constants (Gauld and Hutcheon, 1990).

The monthly changes in the weight of the liver in relation to the body size, Hepatocarcass ratio (HCR) also follow a cyclical trend. The HCR begins to rise during the resting period, which is the period of active feeding by the fish and storage of food in the liver. In the females, the HCR peaked in the winter (February) and reach its lowest value in spring (March-April), which is the post-spawning period. This is similar to the results of Saborowski and Buchholz (1996), who also found that the maximum values of HCR appeared in early winter and the minimal value in early summer (May-July). Saborowski and Buchholz (1996) found that the February HCR values were significantly higher than the summer and autumn values in the North Sea dab. The situation is however different in the males. The peak value of HCR in the male is mainly reached in the summer months (July -August) but also reaches it lowest value in the spring, which is identical to that found in the North Sea by Saborowski and Buchholz (1996). In females, there is a negative correlation between GCR and K (condition factor); $r=-0.165$, $N=66$, $P=0.184$. In the males, there is a positive correlation

between GCR and K; ($r=0.035$, $N=41$, $P=0.829$). This is likely because there is no marked difference in the weight of the testes between spawning season and resting period as in the females. In females, there is a positive correlation between HCR and the K; ($r=0.369$, $N=66$, $P=0.002$). Also in males, there is a positive correlation between HCR and K ($r=0.572$, $N=41$, $P=0.001$).

Saborowski and Buchholz (1996) found maximum values (1.05-1.10) of the condition factor for female dab in the autumn (October/November) and the minimum of 0.90-0.95 in the spring (April/May) for the North Sea dab. This period of maximum condition is 2 months later than the findings made in this study for the female dab, which is between July-September. They also found that, in male dab, maximal values of 1.05 were found in late summer (August/September) whilst minimal values were found in late winter (February/March). However, this study found that maximal condition factor values between July-August for male dab. In both sexes, the minimum condition factors occur in April. Saborowski and Buchholz (1996) concluded that seasonal fluctuations in condition factor in the North Sea dab is more distinct in males than females. In the North Sea, as in the present study, both species increase in weight in summer, but the males experience a sharp decline in weight in autumn.

The estimated average egg size in a fully ripe female dab is about 0.60 mm, which is about 33 % higher than in the North Sea, 0.45 mm (Htun-Han 1978b). Jones (1974) reported an average egg diameter of 0.75 mm in the North Sea dab populations. In terms of diameter, a 0.45 mm egg has 41 % less diameter than a 0.75 mm. On the other hand, a 0.45 mm egg has a volume of 0.0477 mm³, compared with 0.2209 mm³ for a 0.75 mm egg (Prof. J. Davenport, pers. comm.). This implies a remarkable 78.4 % decrease in egg volume. This tremendous decline in egg volume might imply far smaller embryos and/or shorter incubation in the current North Sea dab populations. Also, the decline might occur as a result of compensatory mechanisms to fishing pressure and dwindling food resources in the North Sea, allowing the oocytes to be fully ripe at a reduced size. Size frequency distributions of egg sizes (oocytes) in dab ovaries of various maturity stages showed that each ovary has a group of large and small group of oocytes. This pattern of oocyte distribution is related to the duration of the spawning season. Oocyte size frequency distribution of various maturation stages have been used as a criterion to determine if a fish has determinate fecundity (Nichol and Acuna, 2001). Oocyte size has also been used to explain the seasonal ovarian development in *Solea solea* L. (Ramsay and Witthames, 1996). Jones (1974) observed that the recruitment of vitellogenic oocytes in turbot is determinate, with a finite number of pre-vitellogenic oocytes being selected for vitellogenesis (egg deposition) each year. Hickling and Rutenberg (1936) have shown that fish with a short spawning season, such as Haddock

and Herring, display the same pattern of oocyte size-frequency distribution. According to Jones (1974), the large developing oocytes are shed at the oncoming spawning season, and form a distinct group separate from the smaller resting oocytes, which do not develop until the current spawning period has passed. Significantly, however, ripening and ripe maturity stages (IV and V) exhibited a polymodal egg size distribution. This egg development sequence in the egg diameter frequency distribution appears to support the theory that dab is a serial batch spawner. The oocytes are shed in a series of egg batches during the spawning season (Mcvoy, 1984). Morse (1981) observed that multiplicity of modes in egg diameter frequency distribution indicates that eggs are continuously matured and shed during protracted spawning season. The observation in this study supports the findings by Htun-Han (1978b) who observed that, as in most fishes, spawning in the North Sea dab is intermittent during the season, with only a proportion of ripe eggs taking in water and being discharged at a time. Htun-Han noted that this was in view of the limited space in the ovary, which prevents all the eggs ripening at the same time. Rombards *et al.* (1999) found a unimodal distribution of egg diameter in the sand lance (*Ammodytes sp.*) and concluded that the species might be single-batch spawner. Rijnsdorp (1989) suggested that the maturing oocytes increase in size several-fold as they become ripe until they are shed. He also noted that during the final phase of maturation in plaice, the oocytes hydrate and greatly increase in size. Htun-Han (1978b) also pointed out that the rapid increase in the size of the Stage IV oocytes is due to the rapid absorption of fluid, which decreases their specific gravity and allows them to float when shed.

Egg size has been used to explain the intraspecific differences in fecundity between individuals of the same length (Scott, 1962). It has also been used to explain the variability in relative fecundity between flatfish species in the North Sea. For example, in dab in the North Sea, it varies between 4193 eggs g⁻¹ in dab to 156 eggs g⁻¹ in plaice (Jones, 1974). This difference in relative fecundity between plaice and dab has been attributed to the differences in the average egg size between these species. In the North Sea, the estimated average egg size is 0.75 and 1.93 mm in dab and plaice respectively (Jones 1974). In the present study, relative fecundity varies from 1719 eggs g⁻¹ in the oldest fish (8 years) to 3045 eggs g⁻¹ in the youngest fish (1-year). The estimated average relative fecundity is 2652 eggs g⁻¹ and this is lower by 38 and 58 % than the North Sea estimates for dab by Lee (1972) and Jones (1974) respectively. Bakhsh's estimates in 1982 ranged from 1594 to 4734 eggs g⁻¹ between 13 and 24 cm fish. In the summer flounder, relative fecundity ranged from 1077 eggs g⁻¹ to 1269 eggs g⁻¹ (Morse, 1981). Thus fecundity in dab is relatively high. High egg production relative to body weight is believed to be maintained by serial (batch) spawners (Morse, 1981). Fecundity correlated significantly with body length. The estimates of individual fecundity in

this study indicate that the reproductive potential in the Irish Sea dab is largely dependent on fish aged 3 years and older. With very old fish (7 and 8 years) there is however a decline in the relative fecundity. The contribution of the very old females to the continuity of the population may therefore be minimal. In heavily exploited fisheries, the loss of older established spawners leads to increased dependence on first time spawners for the provision of eggs. Very young fish (ages 1 and 2) also generally produce fewer number of eggs, which are shed over a shorter spawning season than is the case of established spawners (Ramsay and Witthames, 1996; Bromley *et al.*, 2000). But Nichol and Acuna (2001) found that, in the yellowfin sole, total fecundity was substantially lower in fish that have spawned at least once. The increase in fecundity with body size has been related to the observation that the amount of energy available for egg production and the body cavity accommodating the eggs increase with fish size (Jonsson and Jonsson, 1997). Beacham and Murray (1993) had argued that differences in fecundity between pacific salmon populations could be explained in terms of differential mortality and age at maturity. They argued that the increased fecundity of northern populations could be a compensation for higher mortality and higher age at maturity. The interactions between feeding and fecundity have been investigated in a number of fish species (Horwood and Walker, 1990; Thorpe *et al.*, 1990). It has been argued that the level of resources invested in reproduction depends on the food supply. The available food regime may confound the effects of feeding and body size on fecundity (Bromley *et al.*, 2000). The results of fecundity studies on Sole (*Solea solea* L.) in the North Sea and English Channel in 1987 and 1988 showed that fecundities at length can differ significantly across years and areas (Millner *et al.*, 1991). The probable reasons for this were attributed to changes in food abundance. Rijnsdorp *et al.* (1991) showed a positive correlation between fecundity and growth of plaice.

Bromley *et al.* (2000) observed that the level of atretic eggs in turbot vitellogenic oocytes were less than 5 % and suggested that the development of vitellogenic oocytes in turbot followed a similar pattern to that seen in other flatfish. In this study, a few residual eggs from previously spawned batches are evident in the egg size frequency distribution in the spent stages, probably indicating that a total of 3 % resorption may occur. It is therefore likely that this observation by Bromley *et al.* may be applicable to dab. The potential fecundity estimates in this study may not therefore be seriously affected by atresia.

Morse (1981) observed that reproductive strategy shown by summer flounder tends to maximise reproductive potential and avoid catastrophe. The strategy was a combination of a) extended spawning season with variable duration b) early maturation (2 or 3 years), c) high

fecundity d) serial spawning and e) extensive migration offshore during spawning. Some, if not all, of these characteristics are exhibited by dab.

The next chapter will seek to examine the diet and feeding habits of dab in the study area.

CHAPTER FIVE

Feeding Ecology of *Limanda limanda* L.

5.1 INTRODUCTION

The study of diel patterns in feeding is relevant for multispecies assessment models that incorporate trophic interactions, since patterns affect predation estimation (Adlerstein and Welleman, 2000). Series of 24-hour fishing surveys were undertaken in several months with the specific aim of studying diel feeding periodicity, sex-specific estimation of gastric evacuation rate and daily ration of dab in different seasons. The approach is to use formulae for gastric emptying rate (in terms of mass reduction with time) together with sequential observations of the mass of stomach contents to calculate the rate of food intake of the natural populations (Daan, 1973; Elliot and Persson, 1978; Basimi and Grove, 1985b; Seyhan and Grove, 1998). To assess the effect of the dab population on the ecosystem (prey populations) in the study area, the size-specific total consumption by dab of the major taxonomic groups has been derived on seasonal bases.

In recent years the attention of marine scientists has been increasingly directed to species interaction. This interest is not only of purely scientific origin, but may also be related to the obvious need of modern fisheries management to quantify the predator-prey relationships which affect commercially important fish stocks. Thus, efforts to investigate the food of commercial fish stocks have been initiated in several countries of the North Atlantic (Anon., 1980; Palsson, 1983), in order to establish the biological basis for species interaction models of fish stocks.

5.2 STOMACH CONTENT DATA ANALYSIS

Diet may be analysed by numeric, volumetric and gravimetric methods. These analyses may include the frequency of occurrence and relative quantity (abundance, volume or weight) of a prey in the diet (Windell and Bowen, 1978; Hislop, 1980; Costello, 1990).

The diet of a fish can be studied with a view to assessing the species' nutritional standing in the context of the fish community. Such a study may consider seasonal variation in the diet and /or

dietary comparison either between different subgroups of the same species or different species living in the same or comparable habitats. The aim of such studies will be to discern competition for food but also to monitor the feeding intensity of a population throughout the day to discern diel rhythm or feeding periodicity.

5.2.1 Occurrence method

Percentage occurrence is defined as the number of predators in which a prey taxon occurs as percentage of the total number of predators whose stomachs were analysed. The method is quick and requires the minimum of apparatus. It however gives little indication of the relative amount or bulk of each food category present in the stomach.

The method has been used to indicate interspecific competition by assuming that where the occurrence of a food item exceeds 25 % in two or more predators, competition was likely (Johnson, 1977). The method can also be used to illustrate seasonal changes in diet composition (Frost, 1977).

5.2.2 Numeric method

The number of individuals in each food category is recorded for all stomachs and the total is expressed as a percentage of the total individuals in all food categories in the stomachs (Crisp *et al.*, 1978; Hislop, 1980). The mean number of individuals per stomach in each food category may be calculated (Bulkely *et al.*, 1976).

This method is faster but its accuracy depends on the accurate identification of the prey items. The method has been criticized on the grounds that it over-emphasizes the importance of small prey items taken in large numbers. Another drawback is that the method is less reliable when the bulk of the prey item is already masticated in the stomach. In this regard percentage occurrence may be more suitable as an indicator of the diet components. Both methods do not also take into consideration prey size which could be a useful index of the feeding strategy of the different size categories of predator (Gwyther, 1978).

5.2.3 Gravimetric method

In this method, the weight of food may be determined 'wet' or 'dry'. The wet weight is more convenient where large amounts of stomach materials are to be analysed. Dry weight method is widely deemed as more acceptable where accurate estimation is sought, for example, in the case of caloric food intake. It is however time consuming for routine work.

In wet weight determination, surface water is most often removed by blotting them on tissue paper (Parker, 1963). Dry weight is on the other obtained by evaporating water until constant weight is achieved (Man and Hodgkiss, 1977).

Total weight of food category can be expressed as a percentage of the overall weight of the stomach contents. Gravimetric measurement of stomach contents is usually considered to overemphasize the contribution of single heavy items to the diet (George and Hadley, 1979). The method in any case gives reasonable estimates and is easy to apply.

Variation in mean weight of stomach content has also been employed to monitor diel rhythm of feeding behaviour and also to indicate differences in feeding intensity (Staples, 1975).

5.3 MATERIALS AND METHODS

In order to cover size specific changes in the feeding habits of the predator (dab), their length range has been divided into length groups. The smallest length groups (≤ 15 cm) have not been adequately sampled since the juvenile fish are not always accessible to the commercial bottom trawl, or not available in the fishing area. The largest length (≥ 31 cm) groups are often poorly sampled because of the scarcity of the oldest group. The medium length groups (16-20 cm, 21-25 cm and 26-30 cm), on the other hand, have been adequately sampled. Generally, however, the sampling covers the life span of the predator in the sampled area, from 0-group to the oldest groups. A total of 2842 stomachs were analysed.

5.3.1 Stomach-Gut Index (SGI)

The gut (stomach and intestine) of each dab was removed, weighed to the nearest mg. To monitor the occurrence of diel feeding pattern and seasonal feeding intensity, the position of food in specific regions of the alimentary tract was recorded according to the following system (Basimi and Grove, 1985b):

- i. SO: Food only in the stomach
- ii. SI: Food in stomach and intestine
- iii. IO: Food in the intestine only
- iv. E: No food

An index for food ingestion, the weight of the gut, (stomach and intestine), (W_s) was calculated in relation to the carcass weight (W_c) which represents the total weight minus the weight of the gonad, liver, stomach and intestines and expressed as stomach-gut index, Saborowski and Buchholz (1996). The SGI represents a value for total ingested food.

$$SGI = \frac{W_s}{W_c} \times 100 \text{ -----(5.1)}$$

The stomachs were then removed and stored in a freezer (for samples which may not be analysed for 24 hours). The stomach contents were dissected out and identified as far as possible by separating the prey organisms according to systematic groups. Species identification was facilitated by means of recognizable body parts e.g. rostrum and appendages of decapods, thorax of crabs, siphons and foot of mollusc, arms and discs of ophiuroids, debris of shells. The identification was undertaken with reference to Barrett and Yonge (1958), Campbell (1982) and Hayward *et al.* (1996). Each food organism or particle was dried on a blotting paper to remove surface water. Wet weight of each taxon was estimated to within 1 mg of accuracy. The total number of each prey for each monthly sample was noted.

5.3.2 Diet composition

a) Percentage importance of prey by wet weight

The importance of prey item, in relation to the total diet, in a monthly sample was estimated from:

$$\frac{W_i}{W_t} \times 100 \text{ -----(5.2)}$$

Where W_i is the weight (g) of prey i ,

W_t is the total weight (g) of all prey items found in all the stomachs analysed.

b). Percentage abundance by number of each prey

$$\frac{N_i}{N_t} \times 100 \text{ -----(5.3)}$$

Where N_i is the number of prey i ,

N_t is the total number of all prey items found in all the stomachs analysed.

c). Percentage frequency of occurrence of each prey

$$\frac{F_i}{F_t} \times 100 \text{ -----(5.4)}$$

Where F_i is the number of fish with at least one item of prey i ,

F_t is the total number of fish samples, whose stomachs (including empty stomachs) were analysed.

d) An Index of Relative Importance for each Food (IRIF) prey item was calculated according to (Knust, 1996):

$$\text{IRIF} = \frac{1}{3} \left(\frac{F_i}{F_t} \times 100 + \frac{N_i}{N_t} \times 100 + \frac{W_i}{W_t} \times 100 \right) \text{ -----(5.5)}$$

5.3.3 Diet overlap index

For all predator size groups, with sufficient data, the degree of intra-specific diet overlap was determined based on percentage weight of the stomach contents. The similarity in diet composition between various size groups of dab was estimated by using a food overlap index, C , (Horn, 1966; MacArthur and Levins, 1967; Carter *et al.*, 1991):

$$C = \frac{2 \sum_{i=1}^S P_{x_i} \cdot P_{y_i}}{\sum_{i=1}^S P_{x_i}^2 + \sum_{i=1}^S P_{y_i}^2} \text{-----}(5.6)$$

Where P_{x_i} = proportion of total diet of predator x taken from food i
 P_{y_i} = proportion of total diet of predator y taken from food i
 S = total number of food categories

The overlap index varies from 0.0, when the two diets have no shared items, to 1.0 when all food categories are used in the same proportions by both species (Carter, 1987; Horppila *et al.*, 2000). Following the convention adopted by Langton (1982) and Hoines and Bergstad (1999), diet overlap was categorised as low ($C=0.00-0.29$), moderate ($C=0.30-0.59$), or high ($C \geq 0.60$). Labropoulou and Eleftheriou (1997) and Xie *et al.* (2000) also noted that Diet overlap is generally considered to be biologically significant when the value exceeds 0.60.

5.3.4 Seasonal comparison of total diet composition

Comparison of total diet composition in dab between months was undertaken by the non-parametric statistical method, the Spearman Rank Correlation Coefficient (Fritz, 1974). This method is applied to percentage data by weight of prey items. The food items are ranked serially according to their percentage wet weight, in descending order. The method uses the ranks of measurements to determine a measure of correlation. The procedure adopted has been slightly modified in accordance with Siegel and Castellan (1988). After food items have been ranked, the correlation coefficients were calculated using:

a) When there are no ties:

$$r = 1 - \frac{6 \sum d^2}{N^3 - N} \text{-----(5.7)}$$

Where, r = Spearman rank correlation coefficient (uncorrected for ties)
 N = number of ranks
 d = difference between ranks

And

b) When there are tied observations:

$$r_s = \frac{(N^3 - N) - 6 \sum d^2 - (T_x + T_y)/2}{\sqrt{(N^3 - N)^2 - (T_x + T_y)(N^3 - N) + T_x T_y}} \text{-----(5.8)}$$

Where T_x and T_y are correction factors for ties in samples x and y ;

$$T_x = \sum_{i=1}^g (t_i^3 - t_i) \text{-----(5.9)}$$

r_s = Spearman rank correlation coefficient (corrected for ties)
 g = is the number of groupings of different tied ranks
 t_i = is the number of tied ranks in the i th grouping

Since the number of ranks in all samples were less than 50, the significance of r or r_s was determined by referring to the critical values of r in the statistical table (Siegel and Castellan, 1988).

5.3.5 Diet diversity, breadth and evenness

Diet diversity is a function of the number of prey items (species richness or species abundance) and the evenness with which the individuals are distributed among these species (species evenness or species equitability). Species evenness in prey items usually has been defined as the ratio of observed diversity to maximum diversity (Hurlbert, 1971). Diet diversity of dab for each month was measured with the complement of Simpson's index (D) (Garcia-Berthou, 1999):

$$D = 1 - \sum_i \frac{n_i(n_i - 1)}{N(N - 1)} \text{-----(5.10)}$$

Where n_i is the number of individuals of prey type i , and N is the total number of prey (Hurlbert, 1971; Garcia-Berthou, 1999). All dependent variables (total number of prey, number of food categories) were log transformed (Log (D+1)) for Simpson's index of diversity (D).

The Shannon-Weiner information statistics (H'), also an index of diet diversity, was calculated from (Carter, 1987):

$$H' = - \sum_{i=1}^s P_i \text{Log}_2 P_i \text{-----(5.11)}$$

P_i is the proportion of total number of individuals of prey species i and s is the number of prey species. The diet evenness (J) was calculated from (Carter, 1987):

$$J = \frac{H'}{H'_{\max}} \text{-----(5.12)}$$

The diet breadth was calculated from (Levins, 1968):

$$B = \left(\sum p_i^2 \right)^{-1} \text{-----(5.13)}$$

P_i is the proportion by number of each individual prey items in the diet (Hulbert, 1978; Krebs, 1989). Levins (1968) suggested that B increases from 1 as the breadth becomes broader. Low values indicate diets dominated by few prey items and high values indicate generalist diets (Gibson and Ezzi, 1987; Krebs, 1989).

5.3.6 Gastric evacuation rate, GER

The rate of gastric evacuation was determined from the quantity of food in the stomach remaining over the diurnal periods by sex and size groups on seasonal bases. A 4-hourly survey was undertaken within a 24-hour period (10:00, 14:00, 18:00, 22:00, 02:00 and 06:00 hr). The quantity of food remaining in the stomach after every 4-hour is weighed and this is plotted against the time interval. The assumption is that after the peak amount of food in the stomach is

attained, there is a successive decline in the stomach contents in the hours following and that no further food intake takes place during the ensuing decline in the stomach contents. Thus the observed decline in stomach contents should be a close representation of the gastric evacuation rate in the wild. Since the rate of evacuation is proportional to the amount of food in the stomach, thus for any given quantity of food W_0 in the stomach at a time t_0 , the value remaining W_t at a subsequent t is given by (Elliott, 1972; Thorpe, 1977; Jobling, 1981):

$$W_t = W_0 e^{-b(t-t_0)} \text{ ----- (5.14)}$$

Or by log transformation to obtain the linear equation:

$$\text{Log}_e W_t = \text{Log}_e W_0 - b(t-t_0) \text{ ----- (5.15)}$$

Thus a plot of $\text{Log}_e W_t$ versus $(t-t_0)$ should result in a straight line with a descending slope ($= -b$), (rate of gastric evacuation).

5.3.7 Daily ration and total food consumption

The daily ration was calculated from the exponential method of Elliott and Persson (1978), Chapter 1. This method is based on the estimation of food consumption from the quantity of food present in the stomach and knowledge of the rate of evacuation of stomach contents. Daily consumption was estimated for short time intervals, 4-hourly, (relative to 24-hour feeding cycle), and total food consumption during the feeding cycle was obtained by summation of all non-negative consumption estimates (Gwyther, 1978; Jobling, 1981 for reviews; Sainsbury, 1986). The results of the food consumption estimates were compared with the power model of Basimi and Grove (1985b), using the same data.

The total food consumption (by weight) by the dab population in the study area was based on the method by Santos *et al.* (1999) as follows:

The monthly consumption of prey i , is given by:

$$C_i = N \times P_i \times W \times D \times F \text{-----} (5.16)$$

Where

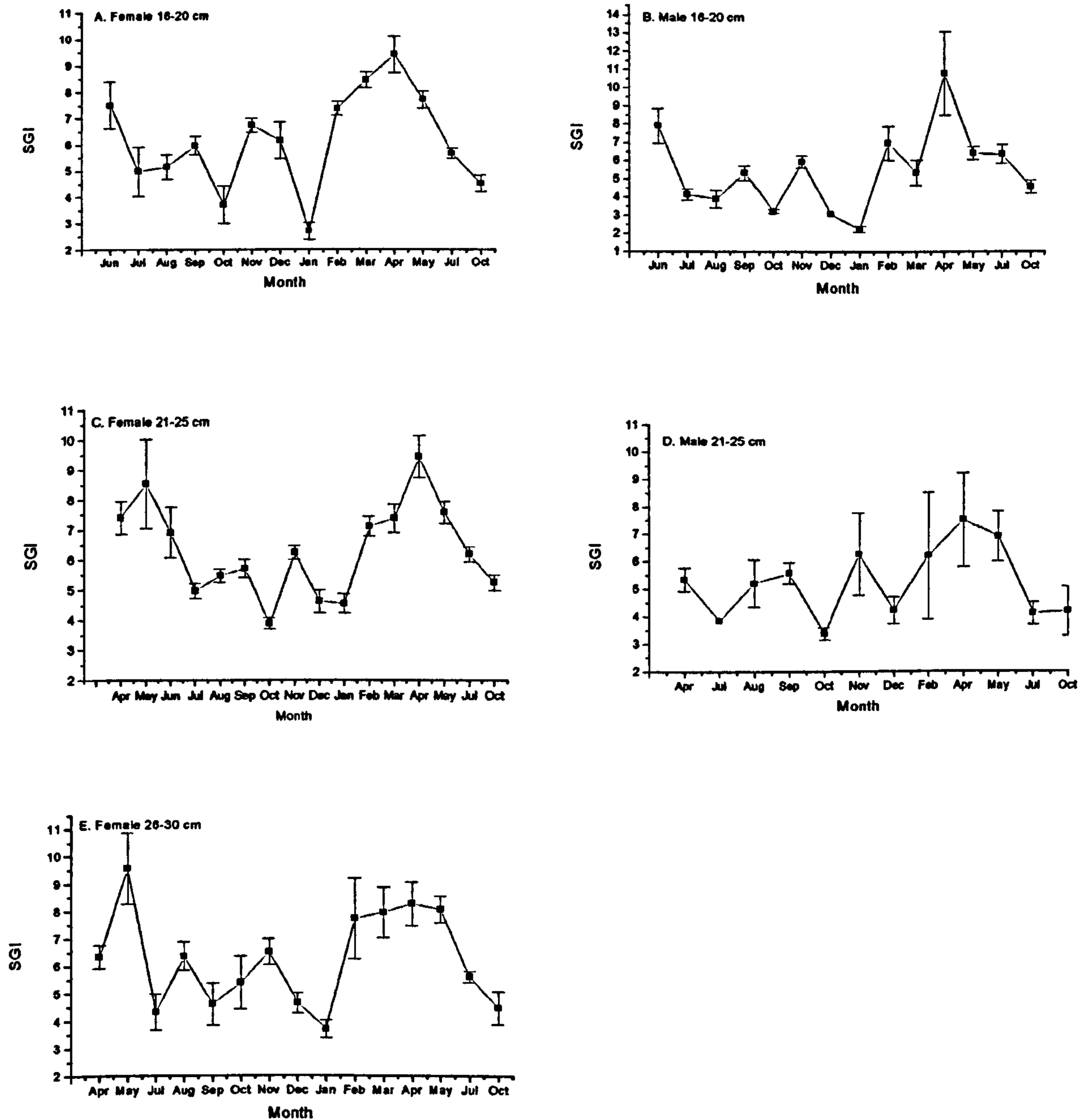
- i = Identifies prey categories
- N = The estimated population size (number) of dab in the study area
- P_i = Average proportion by weight of prey category i in the diet
- W = Average weight of daily food intake
- D = Number of days in a month
- F = Feeding frequency in a day in the wild (=1, Gwyther, 1978)

5.4 RESULTS

5.4.1 Stomach-Gut Index, seasonal occurrence of empty stomach and mean stomach content

There was a seasonal pattern in the Stomach Gut Index value (Figure 5.1) in different length groups for both male and female dab. Generally, peak values were observed in late spring, May, for the larger females. In the females, the peak values varied between 8.3-9.5 in April-May for the various length groups. In the males, the highest values were between 7.5-10.8 also in April. The lowest values were generally in the cold seasons of autumn and winter (October- January).

Figure 5.1. Monthly variation in Stomach-Gut Index (SGI) of different size groups of dab, 1999-2001. Error bars are S.E of the mean.



The percentage of totally empty stomachs reflected a seasonal pattern (Figure 5.2). Most individuals with empty stomachs were found in the cold season (October-February), whilst with the approach of the warm season in spring and summer, most stomachs were at least partially

filled. In October 1999 and January 2001, 81.4 % and 77.3 % of the dab sampled had no food in their stomachs. In April 2000 and May 2000, only 8.6 % and 59.6 % of the total samples had no food in their stomach. This study also indicates some diel periodicity in the occurrence of empty stomach (Figure 5.3). The number of totally empty stomachs appears to be generally higher during the day-time (10:00-18:00 hr) than at night time. On average, between 28.4 to 43.5 % of dabs had empty stomachs between 10:00 and 18:00 hr (Day-time) but 14.73 to 16.2 % had no food in stomachs between 22:00 and 02:00 hr (Night time) during the 24-hour fishing surveys between November-July (Appendix 5).

Figure 5.2. Seasonal variation in occurrence of empty stomachs in dab between 10:00 and 14:00 hr.

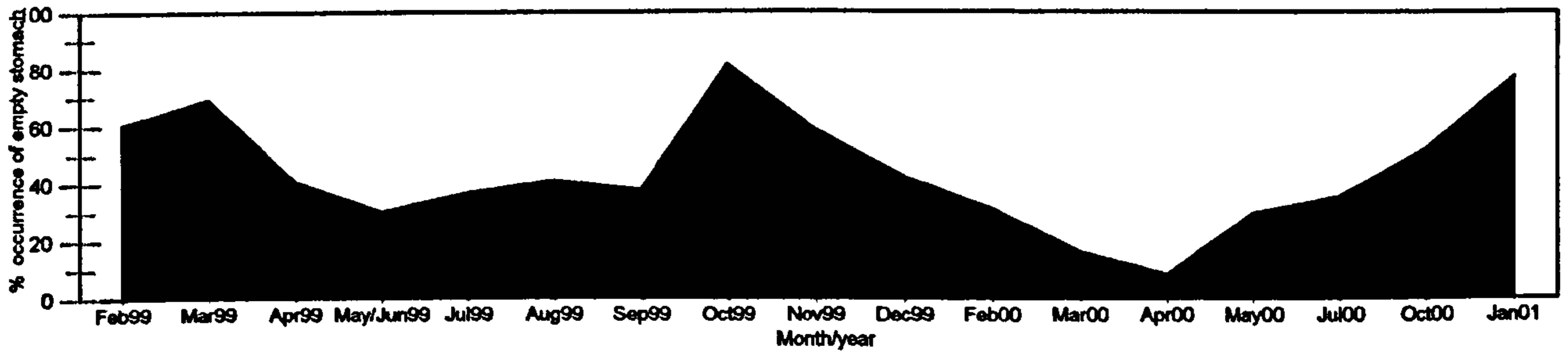
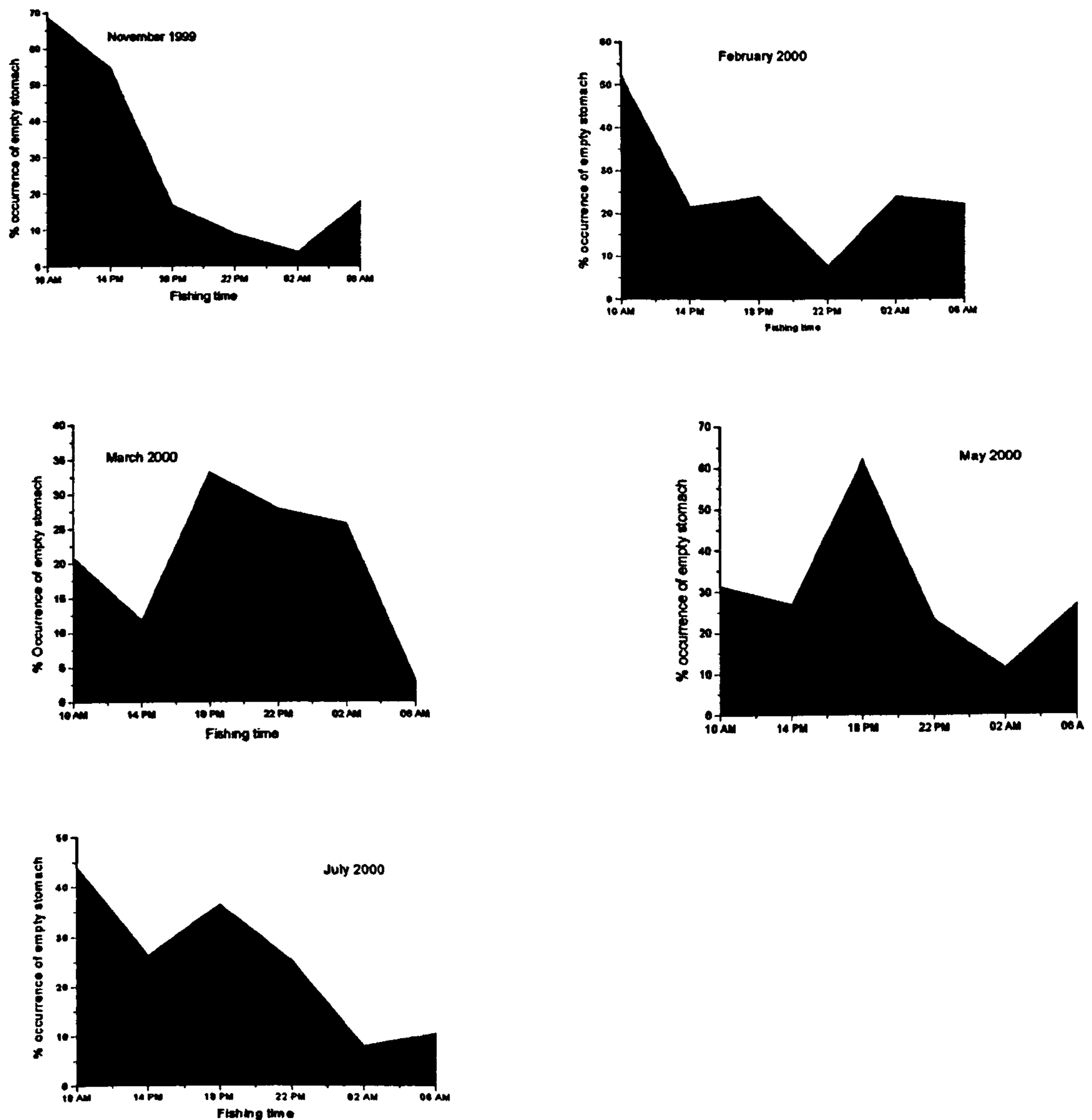


Figure 5.3. Diel periodicity in occurrence of empty stomach (IO and E) in a 24-hour feeding period (10:00–06:00 hr)



Appendix 6 shows the mean stomach content of dab per time of day, sex and length. The results show that, by and large, there are generally no significant differences ($P>0.05$) in the mean stomach contents between male and female dab of length classes 11-15 cm, 16-20 and 21-25 cm and 26-30 cm. But they are usually higher in the females than males. In February, for example, the mean stomach contents for the females of length classes 11-15 cm, 16-20 cm and 21-25 cm were 0.138 g, 0.403 g and 0.600 g respectively. In males of the same length groups in February, the mean stomach contents were 0.054 g, 0.151 g and 0.427 g respectively. In May also the mean stomach contents for the females of length classes 11-15 cm, 16-20 cm and 21-25 cm were 0.155 g, 0.685 g and 1.091g respectively. In males of the same length groups in May, the mean stomach contents are 0.144 g, 0.269 g and 0.906 g respectively.

Similarly the mean stomach contents by length groups and months are shown in Appendix 7. The results indicate that though the mean stomach contents are generally higher in late spring and summer (May and July) than autumn or winter, especially in fish belonging to the size groups of 16-20 and 26-30 cm, these differences are in most cases not significant ($P>0.05$). In the 16-20cm females, the mean stomach contents in November and February were 0.390g and 0.382 g respectively whilst in May and July, the mean stomach contents were 0.576 g and 0.610 g respectively. Also, in the 21-25 cm females, the mean stomach contents were 0.560 g and 0.600 g in November and February respectively whilst in May and July, the mean stomach contents were 1.091 g and 1.233 g respectively.

5.4.2 Diet composition

The results of this study show that the dab diet is largely dominated by the following main taxonomic groups; Echinodermata, Mollusca, Crustacea, Polychaeta and Hydrozoa (Appendix 8) throughout the year. The ophiuroids (brittlestars) were the main food organisms. The main species are *Amphiura (=Acrocnida) brachiata* and *Ophiura texturata*. For example, in November 1999 and April 2000 the IRIF values for the ophiuroids were 68 and 64 respectively. The species *Amphiura brachiata* contributed 38% by weight (45.6 % number) and 70 % by weight (48.7 % by number) to the total diet in November 1999 and April 2000 respectively. The dominant decapod crustaceans were the swimming crabs, *Liocarcinus (=Macropipus) depurator*, the hermit crab *Pagurus bernhardus*, masked crab *Corystes cassivelaunus* and the burrowing shrimp (*Upogebia deltaura*). The main amphipod was *Ampelisca brevicornis*.

Table 5.1 shows the seasonal variation in the importance (IRIF) of the main taxonomic prey groups in the diet. The average IRIF, in descending order is estimated as follows; the ophiuroids (34.5), the bivalves (22.6), the crustaceans (18.6), the polychaetes (15.1) and the hydroids (5.23). The results indicate some seasonal course in composition of crustaceans and ophiuroids in the diet. The IRIF values for the crustaceans were generally high in summer (51.7 in July 1999 and 52.6 in August 1999). During this period the swimming crab *Liocarcinus depurator* respectively formed 17% and 14 % by weight (33 % and 26 % by number) of the total diet. The IRIF values were generally lower in autumn and winter (4.0 in November 1999, 3.1 in February 2000, 6.2 in March 2000 and 3.6 April 2000) for this prey category. There are large variations in the IRIF values for the ophiuroids in the diet. However, these prey taxon appear to be important in the cold season with IRIF value of 68.4 in November 1999 and 79.4 in February. In July 1999 and August 1999, the IRIF values were substantially lower, with 8.36 and 15.30 respectively. The molluscs were dominated by the bivalves (the lamellibranch) *Ensis sp.*, *Angulus (=Tellina) sp.*, *Abra alba*, and *Donax sp.* There is large variability in the occurrence of the gastropod in the diet, especially the species *Philine aperta* (Appendix 8). The IRIF value for this gastropod was 21.9 in August 1999 but declined to 1.0 in December 1999. The dominant polychaetes are the tubeworm *Lagis koreni*, *Nereis sp.*, *Nephtys sp.* and the paddle worm *Phyllodoce sp.* The highest IRIF values for the polychaetes were 34 and 55 in July 2000 and December 1999; the species *Lagis koreni* formed 21% and 47% by weight (35 % and 45 % by number) of the total diet during this period. The species *Obelia geniculata* and *Gonothyraea loveni* dominated the hydroid in the diet. There is an indication of size-specific food preference for the main taxonomic prey groups as will be shown in the next section.

Table 5.1. Summary of monthly Index of Relative Importance (IRIF) of major taxonomic groups as food for dab, 1999-2000

Month	Crustacea	Ophiuroid	Echinoid	Bivalve	Gastropod	Polychaete	Hydroid
Feb	26.10	10.25	0.00	25.58	0.00	0.00	23.37
Mar	18.03	2.70	3.00	11.48	4.80	30.94	5.41
Apr	27.85	21.45	0.00	35.50	9.85	4.85	9.32
M-J	28.05	55.66	10.57	12.91	0.00	1.78	0.00
Jul	51.71	16.78	0.00	29.32	2.37	2.48	0.00
Aug	52.59	8.36	0.00	18.50	24.74	6.98	2.08
Sep	12.26	32.42	3.39	35.35	0.20	7.18	5.94
Oct	12.17	15.30	0.51	32.19	1.20	9.01	8.98
Nov	3.98	68.38	0.21	8.85	0.61	7.15	5.91
Dec	12.63	1.76	1.83	20.75	1.55	54.97	2.81
Feb	3.12	79.60	0.35	10.82	0.00	8.30	5.21
Mar	6.20	56.36	0.79	26.95	0.20	16.65	4.79
Apr	3.63	64.05	0.00	26.61	0.45	18.07	0.92
May	16.30	43.89	0.18	25.41	0.16	14.90	2.56
Jul	14.35	24.00	1.12	30.17	0.00	33.58	1.53
Oct	8.22	50.56	2.30	11.61	3.01	24.76	4.85
Ave	18.57	34.47	1.52	22.63	3.07	15.10	5.23

5.4.3 Size-specific diet preference and intraspecific diet overlap

There is generally a similarity in diet composition between the size groups (Table 5.2). The ophiuroids are the dominant diet component in the size groups 11-15 cm, 16-20cm, 21-25 and 26-30 cm size groups. This prey category contributes by weight 33.1 %, 39.9 %, 34.5 % and 38.15% respectively to the total diet compositions in these size groups. The polychaetes are the next major important component in the smallest dab (11-15cm), contributing about 22.9 % of the total diet by weight. However, the proportion of the polychaetes gradually declines with increasing size of dab, 16-20 cm (13.1 %), 21-25 cm (11.6 %) and 26-30 cm (5.7 %). The bivalves formed major components in the diet of the larger fish and their contribution to total diet (by weight) increases with increasing size of dab, 11-15 cm (11.2 %), 16-20 cm (10.9 %), 21-25 cm (23.0 %), 26-30 cm (27.8 %) and ≥ 31 cm (31.4 %). The razor shell, *Ensis sp.*, formed the major part of the bivalves in the diet of the large fish (21-25 cm and 26-30 cm). However, the contribution of *Ensis sp.* to the total diet of the larger size dab becomes greatly reduced when percentage numbers are computed. The thin-shelled bivalve, *Angulus sp.*, and also *Abra alba* form a large part of the total bivalve diet (by weight) in the small and medium size groups. The gastropods were detected in the diet of the size groups (16-20 cm, 21-25 cm and 26-30 cm) but relatively their largest contribution was in the 21-25 cm class with 3.8 % by weight, which largely

composed of *Patella sp.* and *Philine aperta*. The crustaceans were also an important diet component in all the size groups of dab, ranging from 11.6 % in the 21-25 cm group to 24.4 % in the ≥ 31 cm. Numerically, the hydroids were also an important diet component in the small dab (about 15 % of the total diet).

Table 5.2. Summary of diet composition (% Weight and %Number) of different size groups of dab, 1999-2000.

Size groups Taxon	11-15cm		16-20 cm		21-25 cm		26-30 cm		≥31 cm	
	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%
Hydrozoa										
<i>Obelia sp.</i>	0.18	9.91	1.10	4.35	0.58	4.17	0.44	3.40	0.07	6.60
<i>Gonothyræa sp.</i>	0.28	3.74	1.03	0.43	0.09	1.33	0.22	2.88	0.00	0.00
<i>Sertularia sp.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.65	0.00	0.00
Others	0.11	1.10	0.08	0.22	0.58	0.28	0.37	0.33	0.00	0.00
Total	0.57	14.75	2.20	5.00	1.25	5.78	1.08	7.25	0.07	6.60
Crustacean										
Decapoda										
<i>Liocarcinus sp.</i>	14.86	13.86	3.87	6.43	4.30	7.28	3.44	6.70	11.20	11.76
<i>Pagurus sp.</i>	0.00	0.00	1.31	0.84	1.88	1.57	1.51	2.59	0.00	0.00
<i>Corystes sp.</i>	0.00	0.00	0.00	0.00	1.28	0.78	3.40	1.19	0.00	0.00
<i>Upogebia sp.</i>	0.00	0.00	0.64	0.95	0.84	0.38	2.40	2.57	0.00	0.00
<i>Carcinus maenas</i>	0.00	0.00	6.09	2.36	0.60	0.31	0.00	0.00	0.00	0.00
<i>Cancer pagurus</i>	0.00	0.00	0.00	0.00	0.45	0.59	0.57	1.27	13.17	10.00
<i>Pirimela sp.</i>	0.00	0.00	0.22	1.25	0.42	0.29	0.24	0.33	0.00	0.00
<i>Macropodia deflexia</i>	0.00	0.00	0.00	0.00	0.03	0.06	0.01	0.06	0.00	0.00
<i>Galathea dispersa</i>	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.00	0.00
<i>Maia squinado</i>	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00
<i>Crangon crangon</i>	0.00	0.00	0.00	0.00	0.36	0.31	0.05	0.95	0.00	0.00
<i>Achelia sp.</i>	0.01	0.06	0.06	0.10	0.01	0.05	0.03	0.24	0.00	0.00
Others	0.81	1.92	2.34	1.43	1.36	1.21	2.09	2.23	0.00	0.00
Total	15.68	15.84	14.53	13.36	11.55	12.89	13.74	18.13	24.37	21.76
Amphipoda										
<i>Ampelisca sp.</i>	0.04	1.10	0.59	4.14	0.05	3.15	0.00	0.00	0.00	0.00
<i>Caprella linearis</i>	0.00	0.00	0.42	0.95	0.00	0.34	0.00	0.00	0.00	0.00
Others	0.00	0.00	0.17	0.38	0.00	0.06	0.00	0.00	0.00	0.00
Total	0.04	1.19	1.18	5.47	0.05	3.55	0.00	0.00	0.00	0.00
Isopoda										
<i>Idotea sp.</i>	0.00	0.00	0.00	0.00	0.03	0.20	0.00	0.00	0.00	0.00
Cirripedia										
<i>Elminius modestus</i>	0.00	0.00	0.00	0.00	0.04	0.33	0.10	0.22	0.00	0.00
<i>Balanus balanus</i>	0.00	0.00	0.00	0.00	0.00	0.02	0.26	0.19	0.00	0.00
Total	0.00	0.00	0.00	0.00	0.04	0.35	0.36	0.41	0.00	0.00
Grand total	15.72	16.94	15.71	18.83	11.67	16.99	14.10	18.54	24.37	21.76
Echinodermata										
Ophiuroidea										
<i>Ophiura texturata</i>	9.55	6.29	8.69	10.61	3.38	6.29	9.85	8.82	0.01	0.91
<i>Amphiura brachiata</i>	23.54	16.55	30.61	26.00	27.89	28.96	27.07	26.33	28.54	17.12
<i>Amphipholis sp.</i>	0.00	0.00	0.49	0.42	1.88	1.05	0.00	0.00	0.00	0.00
<i>Ophiothrix fragilis</i>	0.00	0.00	0.00	0.00	0.05	0.04	0.11	0.05	6.26	4.83
Others	0.09	0.06	0.13	0.09	1.33	0.96	1.12	0.64	0.00	0.00
Total	33.09	22.90	39.92	37.12	34.53	37.30	38.15	35.84	34.81	22.86
Echinoidea										
<i>Echinocardium sp.</i>	1.09	1.79	4.69	2.22	0.69	0.59	1.75	2.09	0.00	0.00
<i>Echinus esculentus</i>	0.00	0.00	0.13	0.06	0.05	0.05	0.71	0.21	0.00	0.00
Grand total	34.18	24.69	47.74	39.40	35.27	37.94	40.61	38.14	34.81	22.86

Table 5.2 continued.

Size groups Taxon	11-15cm		16-20 cm		21-25 cm		26-30 cm		≥31 cm	
	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%
Polychaeta										
<i>Nereis sp.</i>	0.49	0.48	3.38	4.91	1.22	1.91	0.41	1.77	5.60	4.00
<i>Lagis koreni</i>	15.09	19.15	8.83	13.05	5.10	8.83	4.00	6.45	6.81	11.22
<i>Nephtys sp.</i>	0.52	0.45	0.18	0.13	0.42	0.18	0.42	0.31	0.00	0.00
<i>Phyllodoce sp.</i>	0.13	0.00	0.05	0.06	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sternaspis scutata</i>	0.00	0.00	0.00	0.00	4.21	1.56	0.00	0.00	0.00	0.00
<i>Aphrodite sp.</i>	0.00	0.00	0.54	0.07	0.13	0.08	0.84	0.56	0.00	0.00
<i>Nirine cirratulus</i>	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00	0.00	0.00
<i>Arenicola</i>	0.00	0.00	0.03	0.06	0.09	0.26	0.00	0.00	0.00	0.00
Others	6.66	3.08	0.05	0.27	0.35	0.19	0.06	0.19	0.00	0.00
Total	22.88	23.16	13.06	18.55	11.62	13.11	5.74	9.28	12.41	15.22
Nemertine	0.03	0.49	0.06	0.18	0.15	0.35	0.71	2.38	0.01	0.91
Mollusca										
Bivalvia										
<i>Ensis sp.</i>	0.00	0.00	4.04	2.41	14.59	4.22	23.75	9.66	3.51	2.29
<i>Abra alba</i>	2.22	1.00	0.68	1.30	0.89	1.22	0.19	0.21	0.00	0.00
<i>Gari depressa</i>	0.00	0.00	0.00	0.00	0.12	0.20	0.00	0.00	0.00	0.00
<i>Angulus sp.</i>	5.12	10.58	2.42	7.34	1.10	3.13	0.82	1.91	5.62	3.64
<i>Donax sp.</i>	0.49	2.38	0.44	1.17	0.18	1.08	0.47	2.26	0.49	4.00
<i>Pholas dactylus</i>	0.02	0.06	0.00	0.00	0.02	0.06	0.00	0.00	0.00	0.00
<i>Venus sp.</i>	0.00	0.00	0.04	0.02	0.08	0.10	0.00	0.00	0.00	0.00
<i>Scrobicularia sp.</i>	0.12	0.11	0.08	0.07	0.10	0.14	0.00	0.00	0.00	0.00
<i>Solecurtid</i>	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00
<i>Pecten maximus</i>	0.01	0.06	0.06	0.18	0.05	0.21	0.65	0.43	0.00	0.00
<i>Mytilus edulis</i>	0.02	0.06	0.20	0.09	0.18	0.21	0.43	0.95	20.00	20.00
<i>Mya sp.</i>	0.00	0.00	0.03	0.03	0.17	0.09	0.00	0.00	0.00	0.00
<i>Acanthocardium sp.</i>	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00
<i>Macra sp.</i>	0.00	0.00	0.07	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Others	3.18	4.75	2.84	3.40	5.47	5.78	1.44	4.41	1.82	2.73
Total	11.17	18.99	10.90	16.07	22.99	16.52	27.76	19.83	31.44	32.65
Gastropoda										
<i>Patella sp.</i>	0.00	0.00	0.00	0.00	1.59	1.66	0.00	0.00	0.00	0.00
<i>Philine aperta</i>	0.00	0.00	0.24	0.50	1.51	2.82	0.54	1.88	0.00	0.00
<i>Natica alderi</i>	0.00	0.00	0.00	0.00	0.05	0.10	0.07	0.16	0.00	0.00
<i>Monodonta sp.</i>	0.01	0.06	0.00	0.02	0.24	0.23	0.08	0.11	0.00	0.00
<i>Patina sp.</i>	0.00	0.00	0.00	0.00	0.30	0.51	0.00	0.00	0.00	0.00
<i>Alvania cancellata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.16	0.00	0.00
<i>Gibbula adonsoni</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.23	0.00	0.00
<i>Nassarius reticulatus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
<i>Tritonalia sp.</i>	0.00	0.00	0.00	0.00	0.01	0.06	0.00	0.00	0.00	0.00
<i>Urasalpinx sp.</i>	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00	0.00	0.00
<i>Nucella sp.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.10	0.00	0.00
<i>Lithorina sp.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.06	0.00	0.00
Others	0.00	0.00	0.00	0.00	0.08	0.40	0.00	0.00	0.00	0.00
Total	0.01	0.06	0.24	0.52	3.81	5.80	0.89	2.70	0.00	0.00
Grand total	11.18	19.05	11.14	16.57	26.80	22.32	28.65	22.53	31.44	38.82
Algae										
Phaeophyceae	0.00	0.00	0.10	0.81	0.80	2.63	1.56	1.56	0.00	0.00
Fish										
<i>Sprattus sprattus</i>	0.56	0.43	0.06	0.08	0.01	0.15	0.06	0.06	0.00	0.00
Sipuncula										
<i>Golfingia elongata</i>	0.00	0.00	0.00	0.00	0.99	0.40	0.00	0.00	0.00	0.00
Stone	0.01	0.11	0.00	0.00	0.25	0.32	0.05	0.30	0.00	0.00
Unidentified food										
Partly digested	14.80		12.78		11.15		7.45		0.22	

For all the predator (dab) size groups with sufficient data the degree of intraspecific diet overlap in all the months, was determined based on percentage weight of the stomach contents (Table 5.3). The high average intraspecific overlap index, mostly $C \geq 0.60$, indicates strong similarity in diet between all size categories. Spatial comparison of diet overlap between Caernarfon Bay dab populations and Red Wharf Bay dab populations (Table 5.4) shows generally small overlap, ($C=0.0-0.29$), among the small dab (11-15 cm), to moderate overlap ($C=0.3-0.59$), among the medium to large dab (16-20 cm, 21-25 and 26-30 cm).

The results of a seasonal comparison of total diet composition (by weight) by Spearman Rank Correlation Analysis (Table 5.5) indicate seasonal trend in diet composition. In general significant correlations ($P < 0.05$) were observed between months within the same season. For instance, the results show significant correlation in the total diet composition between September 1999 and October 1999 ($r=0.644$); September 1999 and November 1999 ($r = 0.842$), and May 2000 and July 2000 ($r=0.933$). The correlation became insignificant for diet composition between February 1999 and September 1999 ($r=0.105$); March 1999 and August 1999 ($r=0.132$) and, December 1999 and July 2000 ($r=0.120$).

Table 5.3. Food overlap index between various size groups of dab

11-15 cm																	
	Feb	Mar	Apr	M-J	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jul	Oct	Ave
L(cm)	99	99	99	99	99	99	99	99	99	99	00	00	00	00	00	00	
16-20	0.590	0.449					0.831	0.516	0.993	0.800	0.990	0.935	0.674	0.730	0.733	0.917	0.763
21-25	0.015	0.884					0.773	0.369	0.999	0.820	0.987	0.902	0.683	0.660	0.479	0.945	0.710
26-30	0.066						0.674	0.023	0.994	0.818	0.946	0.889	0.896	0.650	0.532	0.839	0.666
≥31	0.996													0.501	0.540	0.977	0.754

16-20 cm																	
	Feb	Mar	Apr	M-J	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	July	Oct	Ave
L(cm)	99	99	99	99	99	99	99	99	99	99	00	00	00	00	00	00	
11-15	0.590	0.449					0.831	0.516	0.993	0.800	0.990	0.935	0.674	0.730	0.733	0.917	0.763
21-25	0.008	0.793	0.147	0.907	0.153	0.807	0.988	0.725	0.992	0.892	0.999	0.986	0.975	0.959	0.897	0.986	0.763
26-30	0.395		0.338	0.017	0.305	0.872	0.616	0.593	0.995	0.860	0.805	0.430	0.750	0.997	0.869	0.983	0.655
≥31	0.996		0.793		0.000	0.712								0.891	0.796	0.956	0.735

21-25 cm																	
	Feb	Mar	Apr	M-J	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	July	Oct	Ave
L(cm)	99	99	99	99	99	99	99	99	99	99	00	00	00	00	00	00	
11-15	0.590	0.449					0.831	0.516	0.993	0.800	0.990	0.935	0.683	0.660	0.479	0.945	0.710
16-20	0.008	0.793	0.147	0.907	0.153	0.807	0.988	0.725	0.992	0.892	0.999	0.986	0.975	0.959	0.897	0.986	0.763
26-30	0.126		0.873	0.268	0.599	0.958	0.577	0.568	0.993	0.963	0.960	0.748	0.914	0.999	0.855	0.952	0.757
≥31	0.006		0.512		0.407	0.366								0.450	0.367	0.466	0.368

26-30 cm																	
	Feb	Mar	Apr	M-J	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jul	Oct	Ave
L(cm)	99	99	99	99	99	99	99	99	99	99	00	00	00	00	00	00	
11-15	0.066						0.674	0.023	0.994	0.818	0.946	0.889	0.896	0.650	0.532	0.839	0.666
16-20	0.395		0.338	0.017	0.305	0.872	0.616	0.593	0.995	0.860	0.805	0.430	0.750	0.997	0.869	0.983	0.655
21-25	0.126		0.873	0.268	0.599	0.958	0.577	0.568	0.993	0.963	0.960	0.748	0.914	0.999	0.855	0.952	0.757
≥31			0.729		0.856									0.974	0.657	0.897	0.823

≥31 cm																	
	Feb	Mar	Apr	M-J	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jul	Oct	Ave
L(cm)	99	99	99	99	99	99	99	99	99	99	00	00	00	00	00	00	
11-15	0.996													0.501	0.540	0.977	0.754
16-20	0.996		0.793		0.000	0.712								0.891	0.796	0.956	0.735
21-25	0.006		0.512		0.407	0.366								0.450	0.367	0.466	0.368
26-30			0.729		0.856									0.974	0.657	0.897	0.823

Table 5.4. Diet overlap between Caernarfon and Red Wharf Bay dab populations

Size (cm)	Feb99- Apr99	Aug99- Sep99	Nov99- Dec99	Apr99- Apr00	May99- May00	Jul99- Jul00	Average
11-15		0.1839	0.1422				0.1631
16-20	0.3492	0.6374	0.1960	0.2288	0.7455	0.4230	0.4300
21-25	0.1052	0.2791	0.1026	0.3207	0.9189	0.6112	0.3896
26-30	0.0948	0.3818	0.2022	0.4771	0.2170	0.9027	0.3793
≥31	0.000						0.0000

Table 5.5. Correlation coefficients (r) from seasonal comparison of total diet composition in dab (% weight) by Spearman Rank Correlation method on the North Wales Coast

Mtn/Yr	Mar99	Apr99	M-J99	Jul99	Aug99	Sep99	Oct99	Nov99	Dec99	Feb00	Mar00	April00	May00
Feb99	0.327**	0.192				0.105	0.188	0.091	0.083				
Mar99		0.111			0.132								
Apr99			0.151	0.290*	0.519**								
M-J99				0.379**	0.191								
Jul99					0.541**								
Sep99					0.100		0.662**	0.842**					
Oct99								0.719**					
Nov99									0.132	0.555**			
Dec99					0.567**					0.257			
Feb00											0.372**	0.431**	
Mar00												0.594**	
May00										0.750**	0.433**	0.634**	
Jul00								0.303	0.120	0.664**	0.500**	0.742**	0.935**

- ** Correlation not significantly different at P=0.05 level
- Correlation not significantly different at P=0.10 level

5.4.4 Diet diversity, breadth and evenness

The results show that diet diversity and diet breadth have an inverse relationship to diet evenness (Figure 5.4). The diet diversity and breadth increase with increasing fish length to an optimum level and then decline in the very large fish, whilst diet evenness is higher in the smallest and largest fish but lower in the medium and larger sized fish. There is no significant difference ($P>0.05$) in the median values of Simpson's Diversity Index between the size groups (Table 5.6). In general, however, the average value of Simpson's Diversity rises with increasing size of dab from $D=0.97$ in the small fish (11-15 cm) to a peak $D=1.23$ in the medium size fish (21-25 cm) but declines to its lowest level, $D=0.96$, in the largest fish, ≥ 31 cm. Another index of diversity, Shannon-Weiner Diversity Index, showed no significant difference ($P<0.05$) in the average value between the size groups (Table 5.7). The average value is used here because data was normal and homogenous, in contrast to the Simpson's Index. There is an inverse relationship between average Diet Evenness and average Simpson Diet diversity Index ($r=-0.291$; $df=4$), Figure 5.4. There was a significant difference ($P<0.05$) in the Diet Evenness (Table 5.8) between the size groups. The highest value was in the smallest (11-15 cm) and largest (≥ 31 cm) size groups, which had comparatively low diet diversity. The difference could be attributed to the largest size group ≥ 31 cm, which has a more even diet, with a median value $J=0.85$. The diet of the medium and larger fish (16-20 cm, 21-25 cm and 26-30 cm) were less even; these groups had a more diverse diet. There was no significant difference ($P>0.05$) in the median value of the Diet Breadth (Table 5.9) between the size groups. However, the average diet breadth gets broader gradually from the small fish, 11-15 cm, ($B=3.86$) to the maximum ($B=5.27$) in the medium, 21-25cm. It slowly narrows down from the larger 26-30 cm ($B=4.84$) to $B=3.99$ in the largest fish, ≥ 31 cm.

Figure 5.4. Variations in Diet Diversity, Breadth and Evenness among different size groups of dab on the North Wales Coast, 1999-2000

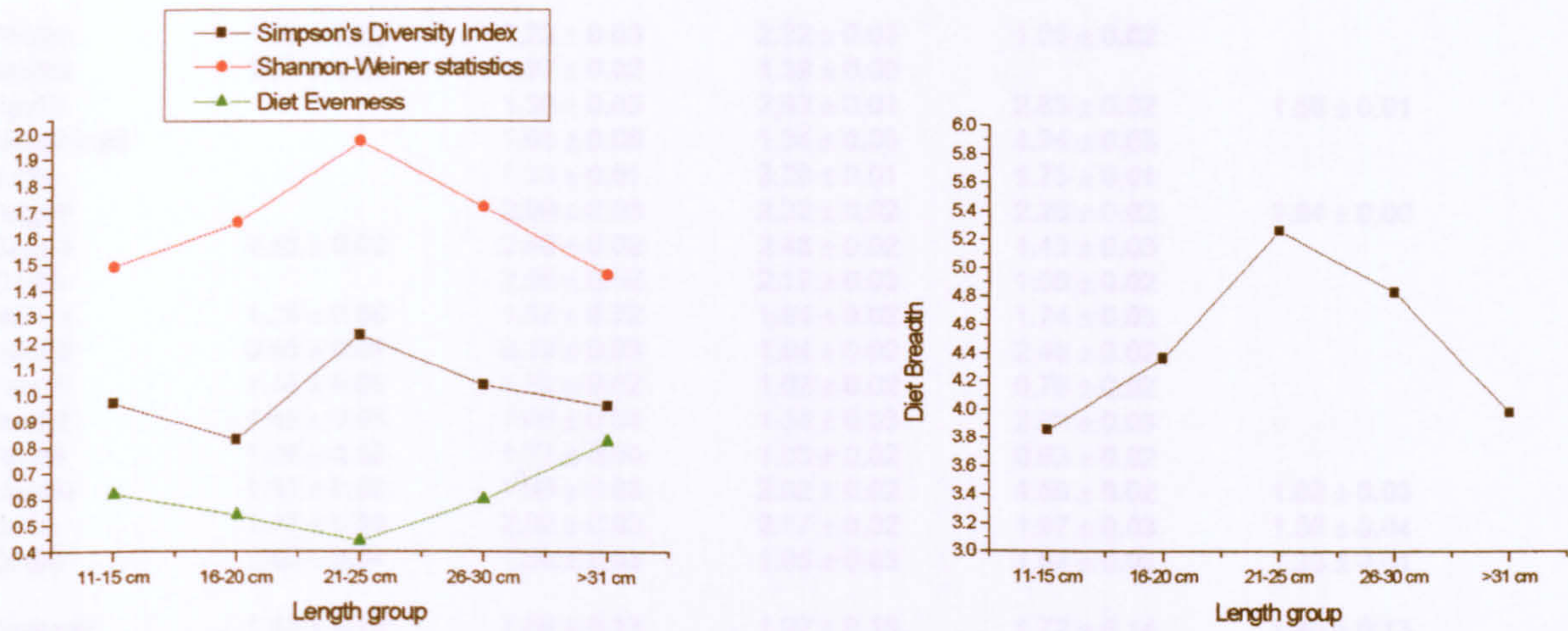


Table 5.6. Monthly variation in Simpson's Diet Diversity (D) in different size groups of dab

Length class (cm)	11-15	16-20	21-25	26-30	≥31
Feb99	0.68 ± 0.45	0.91 ± 0.37	1.17 ± 0.30	0.53 ± 0.57	
Mar99	0.62 ± 0.50	0.92 ± 0.35	0.64 ± 0.50		
Apr99		0.61 ± 0.67	2.47 ± 0.20	1.81 ± 0.23	0.69 ± 0.45
May/Jun99		1.18 ± 0.39	0.95 ± 0.35	1.00 ± 0.33	
Jul99		0.62 ± 0.50	2.95 ± 0.16	0.86 ± 0.41	
Aug99		1.08 ± 0.32	0.70 ± 0.16	1.30 ± 0.21	0.71 ± 0.57
Sep99	1.25 ± 0.01	0.36 ± 0.19	1.26 ± 0.19	0.87 ± 0.37	
Oct99		1.63 ± 0.22	1.26 ± 0.27	0.68 ± 0.45	
Nov99	1.07 ± 0.38	1.04 ± 0.20	0.90 ± 0.19	0.93 ± 0.25	
Dec99	0.56 ± 0.57	0.70 ± 0.56	1.29 ± 0.22	1.63 ± 0.25	
Feb00	1.07 ± 0.34	0.68 ± 0.23	0.82 ± 0.25	0.94 ± 0.38	
Mar00	1.52 ± 0.91	0.59 ± 0.26	0.95 ± 0.27	1.08 ± 0.32	
Apr00	0.92 ± 0.37	0.82 ± 0.27	1.02 ± 0.29	0.88 ± 0.39	
May00	1.05 ± 0.30	0.51 ± 0.20	0.93 ± 0.24	1.18 ± 0.24	0.92 ± 0.35
Jul00	0.98 ± 0.31	0.40 ± 0.20	1.09 ± 0.21	0.97 ± 0.24	0.84 ± 0.40
Oct00	0.95 ± 0.35	1.20 ± 0.23	1.22 ± 0.22	0.94 ± 0.25	1.66 ± 0.49
Average±SE	0.97± 0.08	0.83 ± 0.09	1.23 ± 0.15	1.04 ± 0.09	0.96 ± 0.18
Median	0.98	0.76	1.06	0.94	0.84

Data not normal ($P < 0.05$) but (Levene's test) variance homogenous, $P > 0.05$, (thus non-parametric test).

Kruskal-Wallis Test: $\chi^2 = 7.32$; $df = 4$; $P = 0.12$. There is no significant difference ($P > 0.05$) in the median values of Simpson's diversity index between the size groups.

Table 5.7. Monthly variation in Shannon-Weiner's Information Statistics (H') in different size groups of dab

Length class (cm)	11-15	16-20	21-25	26-30	≥31
Feb99	1.55 ± 0.02	1.23 ± 0.03	2.22 ± 0.03	1.06 ± 0.02	
Mar99	1.33 ± 0.01	1.97 ± 0.02	1.39 ± 0.00		
Apr99		1.36 ± 0.05	2.93 ± 0.01	2.63 ± 0.02	1.56 ± 0.01
May/Jun99		1.01 ± 0.06	1.34 ± 0.03	1.94 ± 0.03	
Jul99		1.33 ± 0.01	3.20 ± 0.01	1.75 ± 0.01	
Aug99		2.00 ± 0.03	2.22 ± 0.02	2.26 ± 0.02	1.04 ± 0.00
Sep99	2.53 ± 0.02	2.46 ± 0.02	2.48 ± 0.02	1.43 ± 0.03	
Oct99		2.55 ± 0.02	2.17 ± 0.03	1.55 ± 0.02	
Nov99	1.25 ± 0.06	1.57 ± 0.02	1.84 ± 0.02	1.74 ± 0.03	
Dec99	0.95 ± 0.01	0.72 ± 0.03	1.94 ± 0.02	2.46 ± 0.02	
Feb00	1.44 ± 0.05	1.12 ± 0.02	1.02 ± 0.02	0.76 ± 0.02	
Mar00	1.48 ± 0.06	1.66 ± 0.04	1.54 ± 0.03	2.08 ± 0.03	
Apr00	1.06 ± 0.02	1.71 ± 0.04	1.03 ± 0.02	0.93 ± 0.02	
May00	1.87 ± 0.03	1.99 ± 0.03	2.02 ± 0.02	1.59 ± 0.02	1.82 ± 0.03
Jul00	1.47 ± 0.03	2.02 ± 0.03	2.17 ± 0.02	1.97 ± 0.03	1.56 ± 0.04
Oct00	1.46 ± 0.04	1.90 ± 0.03	1.95 ± 0.03	1.57 ± 0.03	1.33 ± 0.01
Average	1.49 ± 0.13	1.66 ± 0.13	1.97 ± 0.15	1.72 ± 0.14	1.46 ± 0.13

Data normal ($P > 0.05$) and variance homogenous ($P > 0.05$). Thus one-way anova test; One-Way Anova Test: ($F=1.77$; $df=4$; $P=0.15$). There is no significant difference ($P > 0.05$) in the average Shannon-Weiner diversity index between the size groups.

Table 5.8. Monthly variation in Diet Evenness (J) in different size groups of dab

Length class (cm)	11-15	16-20	21-25	26-30	≥31
Feb99	0.68 ± 0.22	0.62 ± 0.11	0.60 ± 0.08	0.96 ± 0.04	
Mar99	0.84 ± 0.04	0.70 ± 0.05	1.00 ± 0.00		
Apr99		1.18 ± 0.18	0.48 ± 0.05	0.52 ± 0.06	0.85 ± 0.04
May/Jun99		0.62 ± 0.19	0.55 ± 0.10	0.59 ± 0.07	
Jul99		0.88 ± 0.03	0.31 ± 0.03	0.81 ± 0.04	
Aug99		0.55 ± 0.07	0.22 ± 0.05	0.42 ± 0.08	1.00 ± 0.00
Sep99	0.39 ± 0.07	0.31 ± 0.07	0.26 ± 0.05	0.62 ± 0.09	
Oct99		0.42 ± 0.07	0.89 ± 0.08	0.87 ± 0.06	
Nov99	0.62 ± 0.15	0.25 ± 0.07	0.25 ± 0.06	0.34 ± 0.09	
Dec99	1.03 ± 0.02	1.12 ± 0.05	0.31 ± 0.06	0.43 ± 0.05	
Feb00	0.51 ± 0.13	0.35 ± 0.08	0.40 ± 0.08	0.75 ± 0.11	
Mar00	0.63 ± 0.18	0.38 ± 0.10	0.40 ± 0.09	0.63 ± 0.08	
Apr00	0.65 ± 0.09	0.39 ± 0.10	0.45 ± 0.09	0.74 ± 0.08	
May00	0.47 ± 0.09	0.30 ± 0.07	0.37 ± 0.06	0.35 ± 0.07	0.62 ± 0.09
Jul00	0.47 ± 0.09	0.31 ± 0.07	0.31 ± 0.07	0.36 ± 0.08	0.71 ± 0.11
Oct00	0.51 ± 0.11	0.32 ± 0.07	0.31 ± 0.07	0.58 ± 0.08	0.91 ± 0.03
Average	0.62 ± 0.06	0.54 ± 0.07	0.44 ± 0.06	0.60 ± 0.05	0.82 ± 0.07
Median	0.62	0.41	0.39**	0.59	0.85**

Data not normal ($P < 0.05$) and but variance homogenous, $P > 0.05$, (thus non-parametric test). Kruskal-Wallis Test: $\chi=13.75$; $df=4$; $P=0.01$. There is significant difference ($P < 0.05$) in the median values of Diet Evenness index between the size groups. ** (Scheffe multiple comparison test denotes significance difference ($P < 0.05$) for sizes 21-25 cm and ≥31 cm.

Table 5.9. Monthly variation in Diet Breadth in different size groups of dab

Length class (cm)	11-15	16-20	21-25	26-30	≥31
Feb99	4.46	2.28	7.81	2.78	
Mar99	3.57	6.37	4.00		
Apr99		1.80	15.28	11.28	4.50
May/Jun99		2.33	2.48	5.41	
Jul99		3.57	6.45	5.44	
Aug99		5.65	5.04	6.74	2.67
Sep99	9.71	8.81	7.93	2.84	
Oct99		10.09	7.01	4.45	
Nov99	2.76	2.77	3.90	4.00	
Dec99	2.27	1.67	3.68	8.31	
Feb00	3.19	1.92	1.64	1.50	
Mar00	3.95	3.85	2.81	6.72	
Apr00	1.86	4.17	1.70	1.70	
May00	4.82	5.19	4.37	2.60	5.15
Jul00	2.68	5.16	5.84	5.66	4.06
Oct00	3.15	4.36	4.30	3.15	3.57
Average	3.86 ±0.64	4.37 ±0.62	5.27 ±0.83	4.84 ±0.69	3.99 ±0.42
Median	3.19	4.01	4.34	4.45	4.06

Data not normal ($P < 0.05$) but variance homogenous, $P > 0.05$, (thus non-parametric test).

Kruskal-Wallis Test: $\chi^2 = 2.24$; $df = 4$; $P = 0.69$. There is no significant difference ($P > 0.05$) in the median values of Diet Breadth between the size groups.

5.4.5 Gastric evacuation rate, daily ration and total food consumption

The estimated GER (ghr^{-1}), the daily ration (g) and the daily ration (as % body weight) are shown in Table 5.10. Figure 5.5 shows the monthly variation in daily food intake between the length groups in male and female dab from the Elliott and Persson method. The daily ration increases with increasing size of the female dab between 11 cm and 30 cm but declines sharply in fish larger than 30 cm. In males also, the daily ration increases between 11 cm and 20 cm but declined in fish larger than 20 cm. The results indicate that the amount of food eaten in May and July was higher than in February and March in all the size categories (Figure 5.5). In females, for example, the daily ration for the 11-15 cm fish in February was 0.118 g compared to 0.356 g in May. The daily ration as percentage of body weight for this size of fish was 0.46 % and 1.45 % in February and May respectively. There is also an increase in the rate of gastric evacuation from 0.081 ghr^{-1} to 0.143 ghr^{-1} within this period for this size of fish respectively. This pattern was similar in the males. This observation is repeated in the larger fish also. For example, in the 21-25 cm female, there is a rise in the daily ration from 0.520 g in February to 1.969 g in July, reflecting an increase of over 270 %. For males in the 16-20 cm size class, the daily ration varied from 0.187 g in March to 1.377 g in July, giving an increase of over 600 %. The estimates of gastric evacuation rate and daily food intake by Gwyther (1978) on dab in the same area are

shown in Tables 5.11 and 5.12 respectively. The difference in daily food intake between the female and male dab may be illustrated in the size groups 16-20 and 21-25 cm. The daily food intake in these size groups was higher in November, February and July in the females than males. In November, for example, the food intake in the 16-20 cm and 21-25 cm females were 0.827 g and 1.085 g respectively, whilst the comparative values for similar-sized males were 0.758 g and 0.601 g. In the German Bight, Temming and Hammer (1994) estimated daily food consumption as 0.78 g d^{-1} (1.7 % bw) and 0.86 g d^{-1} (1.9 %) for males and females of 16 cm respectively in winter (Table 5.13). The corresponding estimates for the 19 cm dab were 1.17 g d^{-1} (1.5 % bw) and 1.25 g d^{-1} (1.6 % bw). Thus in the German Bight, the food consumption by the 16 cm and 19 cm females is estimated to be 10 % and 7 % higher than the 16 cm and 19 cm males respectively. Lozan (1992) observed that food intake in the female dab was significantly higher than the male dab, based on laboratory experiments and comparison of gut length. The power model of Basimi and Grove (1985b) gave estimates of daily food intake that were slightly higher than the estimates by the exponential model of Elliott and Persson (1978). But the Basimi and Grove model gave zero estimates of food intake in some size groups for certain months. Hence to exercise caution and prudence, the conservative estimates of Elliott and Persson (1978) will be used in further analyses, for example, in the estimation of total food consumption in the study area in the next section and the energy allocation study in Chapter 6.

Figure 5.5. Seasonal daily food intake (g) per sex and size group in dab (from the Elliott and Persson method)

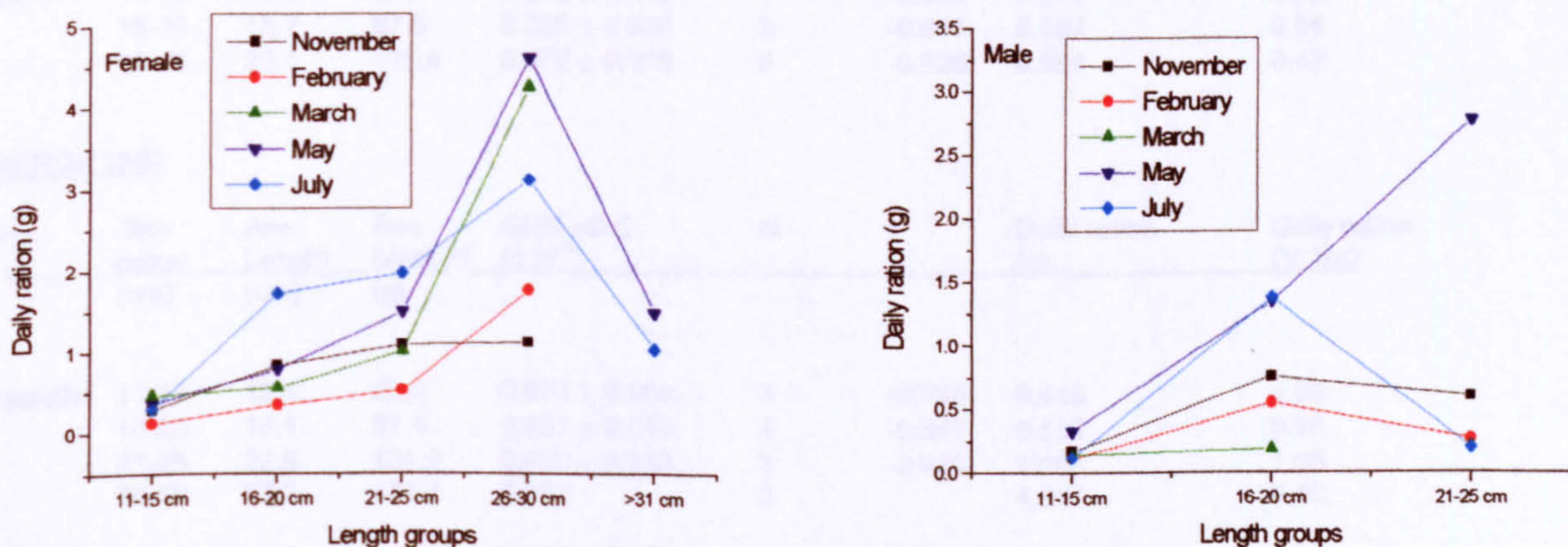


Table 5.10. Estimated daily gastric evacuation rate (GER) and food consumption in dab on the North Wales Coast

A. Elliott and Persson Method (1978)

NOVEMBER, 1999

Sex	Size Range (cm)	Ave. Length (cm)	Ave. (Weight (g)	GER \pm S.E (g hr ⁻¹)	N*	r	Daily ration (g)	Daily ration (% bw)
Female	11-15	14.3	30.4	0.154 \pm 0.049	4	-0.913	0.281	0.93
	16-20	18.2	68.8	0.177 \pm 0.049	6	-0.875	0.827	1.20
	21-25	23.1	135.9	0.092 \pm 0.025	6	-0.908	1.085	0.80
	26-30	26.7	203.0	0.078 \pm 0.022	5	-0.903	1.212	0.60
Male	11-15	14.1	29.1	0.042 \pm 0.011	5	-0.913	0.169	0.58
	16-20	18.1	62.0	0.093 \pm 0.015	5	-0.964	0.758	1.22
	21-25	21.0	92.6	0.081 \pm 0.043	3	-0.883	0.601	0.65
All	11-15	14.2	29.7	0.061 \pm 0.035	5	-0.711	0.188	0.63
	16-20	18.2	64.3	0.122 \pm 0.041	6	-0.829	0.671	1.05
	21-25	23.0	133.0	0.088 \pm 0.022	6	-0.919	0.909	0.68

N* = Number of points used in regression to estimate Gastric evacuation rate (GER)

FEBRUARY 2000

Sex	Size Range (cm)	Ave. Length (cm)	Ave. (Weight (g)	GER \pm S.E (g hr ⁻¹)	N	r	Daily ration (g)	Daily ration (% bw)
Female	11-15	13.5	25.8	0.081 \pm 0.008	5	-0.986	0.118	0.46
	16-20	19.6	68.6	0.022 \pm 0.014	3	-0.932	0.341	0.50
	21-25	22.2	128.2	0.072 \pm 0.014	6	-0.936	0.520	0.41
	26-30	27.6	251.2	0.049	2		1.760	0.70
Male	11-15	12.3	18.5	0.198 \pm 0.047	4	-0.948	0.113	0.61
	16-20	18.3	54.7	0.228	2		0.549	1.00
	21-25	21.3	90.4	0.223 \pm 0.092	4	-0.870	0.267	0.30
All	11-15	13.2	24.1	0.092 \pm 0.018	6	-0.932	0.078	0.32
	16-20	18.2	67.6	0.025 \pm 0.009	3	-0.941	0.367	0.54
	21-25	22.1	125.4	0.077 \pm 0.016	6	-0.926	0.584	0.47

MARCH 2000

Sex	Size range (cm)	Ave. Length (cm)	Ave. (Weight (g)	GER \pm S.E (g hr ⁻¹)	N	r	Daily ration (g)	Daily ration (% bw)
Female	11-15	13.1	22.5	0.079 \pm 0.008	3	-0.995	0.448	1.99
	16-20	18.1	57.4	0.031 \pm 0.014	4	-0.847	0.553	0.96
	21-25	22.6	101.0	0.098 \pm 0.033	3	-0.949	1.008	1.00
	26-30	27.3	171.2	0.032	2		4.257	2.49
Male	11-15	12.7	21.1	0.078 \pm 0.021	4	-0.937	0.140	0.67
	16-20	17.3	42.7	0.069 \pm 0.007	4	-0.991	0.189	0.44
All	11-15	12.9	21.9	0.083 \pm 0.017	4	-0.960	0.386	1.76
	16-20	18.0	55.6	0.030 \pm 0.008	3	-0.876	0.283	0.51

MAY 2000

Sex	Size range (cm)	Ave. Length (cm)	Ave. (Weight (g)	GER \pm S.E (g hr ⁻¹)	N	r	Daily ration (g)	Daily ration (% bw)
Female	11-15	13.2	24.6	0.143 \pm 0.017	4	-0.980	0.356	1.45
	16-20	18.6	70.2	0.100 \pm 0.022	6	-0.917	0.783	1.12
	21-25	23.1	126.2	0.100 \pm 0.037	6	-0.853	1.492	1.18
	26-30	27.2	206.4	0.083 \pm 0.019	4	-0.949	4.612	2.23
	\geq 31	31.4	337.0	0.187 \pm 0.051	3	-0.965	1.485	0.44
Male	11-15	13.2	24.8	0.142 \pm 0.038	3	-0.966	0.330	1.57
	16-20	18.0	56.5	0.391 \pm 0.106	4	-0.933	1.354	2.40
	21-25	21.5	88.5	0.265 \pm 0.009	3	-0.999	2.773	3.13
All	11-15	13.2	24.7	0.128 \pm 0.024	5	-0.950	0.391	1.58
	16-20	18.4	64.8	0.111 \pm 0.025	6	-0.912	0.571	0.88
	21-25	22.8	119.4	0.113 \pm 0.030	6	-0.887	1.633	1.37

July 2000

Sex	Size range (cm)	Ave. Length (cm)	Ave. (Weight (g)	GER \pm S.E (g hr ⁻¹)	N	r	Daily ration (g)	Daily ration (% bw)
Female	11-15	13.4	25.8	0.265 \pm 0.047	3	-0.985	0.293	1.14
	16-20	18.9	75.9	0.145 \pm 0.009	3	-0.998	1.712	2.26
	21-25	23.1	139.6	0.100 \pm 0.008	5	-0.990	1.969	1.41
	26-30	27.6	247.1	0.217 \pm 0.027	4	-0.986	3.119	1.26
	\geq 31	31.8	383.8	0.094 \pm 0.046	3	-0.898	1.030	0.27
Male	11-15	13.3	24.2	0.028 \pm 0.003	3	-0.993	0.122	0.50
	16-20	17.9	60.8	0.088 \pm 0.022	3	-0.969	1.377	2.27
	21-25	21.5	96.9	0.283 \pm 0.054	3	-0.982	0.202	0.21
All	11-15	13.3	24.9	0.041 \pm 0.008	3	-0.982	0.121	0.47
	16-20	18.6	71.2	0.070 \pm 0.004	3	-0.998	1.211	1.70
	21-25	22.9	135.3	0.101 \pm 0.009	5	-0.987	2.020	1.49

B. Basimi and Grove Method (1985b)

Month: November

Year: 1999

Size group	Female		Male		Combined	
	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)
11-15	0.154	0.51	0.292	1.00	0.430	1.45
16-20	1.317	1.92	1.159	1.87	1.290	2.01
21-25	1.959	1.44	0.415	0.45	1.902	1.43
26-30	1.818	0.90				
\geq 31						

Month: February

Year: 2000

Length group (cm)	Female		Male		Combined	
	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)
11-15	0.415	1.61	-	-	0.417	1.73
16-20	0.644	0.94	-	-	0.697	1.03
21-25	1.650	1.29	0.520	0.58	1.738	1.39
26-30	1.598	0.64				
≥31						

Month: March

Year: 2000

Length group (cm)	Female		Male		Combined	
	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)
11-15	0.741	3.29	0.487	2.30	0.732	3.34
16-20	0.852	1.44	0.307	0.72	0.636	1.14
21-25	1.672	1.66				
26-30						
≥31						

Month: May

Year: 2000

Length group (cm)	Female		Male		Combined	
	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)
11-15	0.188	0.76	0.054	0.22	0.335	1.36
16-20	1.829	2.61	-	-	1.691	2.61
21-25	3.345	2.65	0.653	0.74	3.598	3.01
26-30	1.771	0.86				
≥31	0.199	0.06				

Month: July

Year: 2000

Length group (cm)	Female		Male		Combined	
	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)	Daily ration (g)	Daily ration (% bw)
11-15	-	-	0.229	0.95	0.322	1.29
16-20	1.636	2.16	2.243	3.69	1.793	2.52
21-25	3.827	2.74	-	-	3.709	2.74
26-30	1.571	0.64				
≥31	0.637	0.17				

Table 5.11. Gastric evacuation rate of dab in Anglesey waters (Gwyther, 1978)

Size groups	Average Wt. (g)	GER g hr ⁻¹	
		Summer	Winter
Small (16-20 cm)	50.2 ±2.8	0.253	0.298
Medium (20-25 cm)	107.8 ±4.7	0.153	0.308
Large (26-30 cm)	210.4 ±9.4	0.345	0.253

Table 5.12. Estimated daily food ration (g) of dab in Anglesey waters (Gwyther, 1978)

Month	Small		Medium		Large	
	Wet wt.	% bw.	Wet wt.	% bw.	Wet wt.	% bw.
Jan	0.31	0.62	0.92	0.85	1.59	0.76
Mar	2.15	4.28	8.73	8.10	3.21	1.53
May	3.71	7.39	7.18	6.66	10.2	4.85
Aug	3.31	6.59	6.41	5.95	7.42	3.53
Sep	1.07	2.13	3.13	2.90	2.57	1.22
Nov	2.07	4.12	3.89	3.61	7.13	3.34

Table 5.13. Gastric evacuation rate, daily food consumption of food by dab in the German Bight, Temming and Hammer (1994)

A. Gastric evacuation rate (These estimates were obtained by re-analysing the stomach content data from Temming and Hammer, 1994)

Season	Size	Male		Female	
		GER (g hr ⁻¹)	N	GER (g hr ⁻¹)	N
Winter	16 cm	0.062±0.010	5	0.099±0.008	5
	19 cm	0.221±0.033	7	0.057±0.006	6

B. Daily ration

Season	Size	Male		Female	
		Daily ration (g)	% bw	Daily ration (g)	% bw
Winter	16 cm	0.78	1.70	0.86	1.90
	19 cm	1.17	1.50	1.25	1.60

The estimated average monthly estimated food consumption by the resident population of dab in the study area was about 5.3×10^4 kg (Table 5.14). It is estimated that the medium size dab (16-20 cm) population takes a monthly average of 47.6 % (25111 kg) of the total food consumed by the entire dab population. The dab population of the largest size group ≥ 31 consumes the least

amount of food (127.2 kg), which is about 0.24 % of the monthly average. The ophiuroids were the main diet in all the months for all size categories (forming 38 % - 56 % of the monthly average). There is seasonal variation in the estimated total food consumption. The average food consumption by the total dab population was about 6662 kg in February, which is 12.6 % of the total food consumed in the five months. On the other hand, 22138 kg (41.9 %) of food was consumed in July alone. Analysis by size category also shows that monthly food consumption by the 16-20 cm and 21-25 peaked in the warm season July, but declined drastically in the cold season, February and March.

Table 5.14. Estimated monthly total food consumption (kg) by dab of various size groups

Size: 11-15 cm

Major taxon	Nov99	Feb00	Mar00	May00	Jul00	Average
Hydrozoa	0.05	3.12	1.37	0.00	0.00	0.90
Crustacean	0.15	0.00	49.36	1953.24	177.56	436.06
Polychaete	29.47	45.47	901.51	1088.56	1076.58	628.32
Ophiuroidea	1336.18	767.58	2960.10	778.71	230.97	1214.71
Echinoidea	0.00	0.00	0.00	0.00	54.64	10.93
Bivalve	21.86	46.48	1327.89	1435.59	128.20	592.00
Gastropod	0.00	0.00	0.00	0.00	0.00	0.00
Fish	0.00	0.00	0.00	50.37	0.00	10.07
Algae	0.00	0.00	0.00	0.00	0.00	0.00
Stone	0.00	0.00	0.00	5.24	0.00	1.05
Partly digested	1155.00	157.14	154.46	52.86	23.14	308.52
TOTAL	2542.71	1019.79	5394.69	5364.57	1691.09	3202.56

Size: 16-20 cm

Major taxon	Nov99	Feb00	Mar00	May00	Jul00	Average
Hydrozoa	36.45	88.99	143.68	45.05	100.39	82.91
Crustacean	20.80	159.97	275.82	4136.04	3678.33	1654.19
Polychaete	166.19	304.57	739.64	3389.67	15082.15	3936.44
Ophiuroidea	15233.87	12113.55	8296.96	10696.34	12566.05	11781.35
Echinoidea	66.16	6.56	134.60	69.15	132.28	81.75
Bivalve	510.29	686.63	1536.50	4636.86	16956.41	4865.34
Gastropod	0.00	0.00	0.00	0.00	0.00	0.00
Fish	0.00	0.00	0.00	15.04	461.20	95.25
Algae	10.47	0.00	0.00	0.00	0.00	2.09
Stone	0.00	0.00	0.00	0.00	0.00	0.00
Partly digested	10618.43	736.65	492.85	457.24	747.14	2610.46
TOTAL	26662.66	14096.92	11620.05	23445.39	49723.95	25109.78

Size: 21-25 cm

Major taxon	Nov99	Feb00	Mar00	May00	Jul00	Average
Hydrozoa	53.13	10.98	235.28	111.16	569.82	196.07
Crustacean	283.28	218.73	1971.54	2671.18	4254.58	1879.86
Polychaete	161.60	345.05	460.78	1417.81	3525.14	1182.08
Ophiuroidea	6336.48	7004.68	11267.55	12461.67	12064.39	9826.95
Echinoidea	0.00	2.03	0.00	0.00	350.82	70.57
Bivalve	228.25	359.14	1229.43	8277.86	10112.97	4041.53
Gastropod	7.30	0.00	39.34	6.93	0.00	10.71
Fish	0.00	0.00	0.00	0.00	25.79	5.16
Algae	16.63	0.00	0.00	0.00	0.00	3.33
Stone	0.00	0.00	0.00	0.00	0.00	0.00
Partly digested	6443.45	462.24	199.89	170.16	307.20	1516.59
TOTAL	13530.12	8402.85	15403.81	25116.77	31210.71	18732.85

Size: 26-30 cm

Major taxon	Nov99	Feb00	Mar00	May00	Jul00	Average
Hydrozoa	2.94	0.00	335.80	34.44	20.23	78.68
Crustacean	11.41	463.97	1299.67	861.43	1003.66	728.03
Polychaete	3.25	0.00	807.65	333.78	1143.20	457.58
Ophiuroidea	1119.39	2181.83	2572.48	4438.08	937.29	2249.81
Echinoidea	0.00	0.00	329.07	0.00	7.89	67.39
Bivalve	56.17	480.23	2744.29	2969.12	2798.83	1809.73
Gastropod	16.46	0.00	0.00	0.00	0.00	3.29
Fish	0.00	0.00	0.00	83.26	0.00	16.65
Algae	1.09	0.00	0.00	0.00	0.00	0.22
Stone	0.00	0.00	0.00	0.00	0.00	0.00
Partly digested	1018.00	2.49	0.00	43.39	15.48	215.87
TOTAL	2228.71	3128.52	8088.96	8763.50	5926.58	5627.25

Size: ≥31 cm

Major taxon	May00	Jul00	Average
Hydrozoa	0.06	0.06	0.06
Crustacean	0.00	15.57	7.79
Polychaete	2.84	16.24	9.54
Ophiuroidea	88.65	54.72	71.69
Echinoidea	0.00	0.00	0.00
Bivalve	56.95	17.55	37.25
Gastropod	0.00	0.00	0.00
Fish	0.00	0.00	0.00
Algae	0.00	0.00	0.00
Stone	0.00	0.00	0.00
Partly digested	1.63	0.00	0.82
TOTAL	150.13	104.14	127.15

5.4.6 Benthos composition

The benthic population is dominated by the polychaetes, bivalves and ophiuroids (Table 5.15). The tubeworm, *Lagis koreni*, is a major component of the polychaete populations, forming about 38 % and 33 % of the population in Red Wharf Bay and Conwy Bay respectively in 1999. The

Nephtys sp. dominated the polychaete populations in both sites in 2000, contributing 61.5 % and 32.8 % in Red Wharf Bay and Conwy Bay respectively. The ophiuroid population is dominated by *Amphiura* sp., which formed about 84 % and 68 % of the ophiuroids in Red Wharf Bay and Conwy Bay respectively in 1999. Among the bivalve species, the dominant species included *Abra alba* (18 %), *Angulus* sp. (14 %), *Nucula* sp. (30 %), *Mysella bidentata* (28 %) and *Spisula subtruncata* (9 %) in 1999. *Nucula* sp. and *Mysella bidentata* were abundant in the survey area also in 2000. Crustaceans were not abundant in the grab samples. The few numbers found were dominated by the swimming crab, *Liocarcinus* sp., the hermit crab *Pagurus bernhardus*, the masked crab *Corystes cassivelaunus* and the amphipods (*Ampelisca brevicornis* and *Caprella linearis*). Nemertines and hydroids were also present in the survey area.

Table 5.15. The abundance (NM⁻²) of some commonly occurring benthic species in the study area from grab samples in Red Wharf Bay (RWB) and Conwy Bay (CWB), 1999 and 2000. Courtesy of student autumn (October) surveys.

Major taxon	1999		2000	
	RWB	CWB	RWB	CWB
Polychaete				
<i>Lagis koreni</i>	412.50	786.25	6.25	3.75
<i>Nephtys sp.</i>	75.00	113.75	38.75	23.75
<i>Lanice sp.</i>	52.50	56.25		
<i>Aphrodite sp.</i>	16.25	37.50	10.00	10.00
<i>Cirratuloidea</i>	143.75	802.50		
<i>Other polychaetes</i>	161.25	850.00	8.04	45.00
Total	861.25	2646.25	63.04	72.50
Echinoderm				
Ophiuroidea				
<i>Amphiura sp.</i>	185.00	261.25	3.75	11.25
<i>Ophiura sp.</i>	36.25	122.50	16.25	20.00
Echinoidea				
<i>Echinocardium cordatum</i>	6.25	5.00		
Total	448.75	772.50	40.00	31.25
Bivalve				
<i>Abra alba</i>	207.50	33.75		
<i>Angulus sp.</i>	80.00	260.00	0.00	3.75
<i>Donax sp.</i>	1.25	2.50		
<i>Gari fervensis</i>	28.75	135.00		
<i>Nucula sp.</i>	570.00	152.50	245.00	122.5
<i>Spisula subtruncata</i>	82.50	135.00		
<i>Mysella bidentata</i>	261.25	423.75	8.75	192.5
<i>Other bivalves</i>	63.75	48.75	0.0	7.5
Total	1295.00	1057.5	253.75	326.25
Gastropod	5.00	8.75	4.29	16.25
Crustacea				
Decapod	3.75	2.50	1.43	3.75
Amphipod	32.5	40.00	0.00	15.00
Total	36.25	42.50	1.43	18.75
Nemertine	15.00	30.00		
Hydroid	1.25	0.00	18.75	10.00

5.5 DISCUSSION

The analysis of stomach content data is the most readily available tool with which to infer fish feeding behaviour, and several approaches have been made with such data to study temporal patterns of feeding (Daan, 1973; Adlerstein and Welleman, 2000). Approaches have ranged from qualitative inference from relationships between stomach content characteristics and time of day or light level at sunrise or sunset (Daan, 1973), to models combining the analysis of stomach content weight and digestion rates (Basimi and Grove, 1985b; Seyhan and Grove, 1998). The stomach contents of both sexes show an indication of a seasonal cycle, with SGI reaching peaked values in late spring and lowest values between autumn-winter. The occurrence of empty stomachs also follows a seasonal pattern with significantly high number of stomachs being without food in the autumn-winter period (October-February). It is significant to recognise that this period (autumn-winter) falls within the spawning season of the dab. Thus feeding rate in dab is higher in late spring and summer. This food is probably stored as reserves in the liver, which results in the rise of the lipid content (and energy) in the liver in the summer and early autumn. Saborowski and Bucholz (1996) also found that SGI values peaked in the summer for the North Sea dab. This observed seasonal course of the SGI with its maximum in the mid-summer suggests that dabs feed continuously, Saborowski and Bucholz (1997). This study suggests that dabs do not stop feeding entirely in autumn or winter. However their feeding rates become significantly reduced. The sharp rise in the SGI in late spring in the bigger females (21-25 cm and 26-30 cm) could also suggest feeding for 'catch-up growth' on emerging from spawning in emaciated conditions (Jobling and Johansen, 1999). As found in Chapter 4, the liver and carcass are severely depleted after spawning; the fish would therefore need to build up these organs. Once these organs are built up, the fish feeds normally in the summer, hence the relatively stable SGI in the summer. Seasonal periodicity in feeding behaviour of dab has also been reported from other regions: Knust (1996) found a maximum food intake in German Bight dab in summer and low feeding activity in spring during spawning. Ortega-Sales (1980) found that the wet weight of ingested food by dab from the Isle of Man was lowest in winter and highest in summer. Thus it may be correct to conclude that dab, especially, the females feed vigorously in the postspawning period in spring and early summer to build up energy that has been utilised in spawning. The feeding rate however declined in the autumn once gametogenesis commences and this decline continues until the end of winter, the peak spawning season. Arntz, 1971 also reported similar seasonal changes in food uptake and food consumption in dab from the Baltic Sea. The occurrence of significant numbers of fish with

empty stomachs in March 1999, as compared to March 2000, could probably be accounted for by different sampling times between the two periods, as it has been illustrated in this study that the stomach fullness varies between time of day.

The current study shows diel periodicity in feeding cycles. The number of fish with empty stomachs was higher in daytime than night-time; also a tendency of higher mean stomach contents at night (Appendix 6). This observation contradicts the theory by Bregnballe (1961) and de Groot (1971), who noted that dab is an exclusive daytime feeder. Gwyther and Grove (1981) also suggested from demand–feeding experiments that day-time feeding is preferred by dab. However, the occurrence of empty stomach may be related to how long the fish feeds between meals (and also how long the fish takes to fill the stomach) in summer and winter. In summer, the feeding rate of fish is higher due to the increased temperature whilst the feeding rate is lower in winter due to low temperature. Thus the probability of encountering fish with an empty stomach would be higher in the autumn and winter. Gwyther (1978) however cautioned that feeding of the dab population cannot be described as occurring regularly at the same time. Carter *et al.* (1991) found that the levels of food intake in dab and plaice vary between time of day depending on the substrate (mud and sand). In general however, their study showed that the lowest levels of food intake were in the early afternoon on the mud substrate but later in the day on the sand and that there was crepuscular and nocturnal feeding by both species. In a survey of the occurrence of empty stomachs in flatfish, Wimpenny (1953) found that a large percentage were empty in October due to the cessation or lull in feeding at the end of the summer month, which is consistent with the present study. Jobling (1974) suggested that the occurrence of the empty stomachs indicated a seasonal variation in food intake, perhaps due to water temperature effects upon digestion and metabolism. He proposed that the bigger the animal size, the longer is the time to clear the stomach. Carter (1987) on the hand suggested the prevalence of empty stomachs in dab may imply that food is either scarce, or abundant but difficult for the fish to locate.

This study shows that the rate of gastric evacuation and the daily food intake were higher in late spring/summer than winter. This observed pattern in the seasonal food intake in dab is in agreement with findings by Gwyther (1982) and for plaice by Basimi and Grove (1985b) in the coastal waters off Anglesey. Basimi and Grove found that in the spring/summer months, the proportion of feeding fish (plaice) was higher, the average stomach contents were also higher

than in winter/spring. They reported that feeding conditions were ideal in summer and gradually deteriorated towards the autumn, winter and early spring.

The present analysis shows that there is a great variety in the food composition of dab. The many studies on the diet of dab show that they are able to utilize a considerable range of prey species (Macer, 1967; Braber and de Groot, 1973; Wyche and Shackley, 1986; Ortega-Sales, 1988c; Carter *et al.*, 1991; Temming and Hammer, 1994; Saborowski and Buccholz, 1996; Knust, 1996; Beyst *et al.*, 1999). This study shows that the ophiuroids were the dominant prey, followed by the molluscs, crustaceans and polychaetes and these diet components were similar to that found by Gwyther (1978). In the North Sea, Saborowski and Buccholz (1996) also found that the ophiuroids represented about 50 % by weight of the stomach content. Other prey items which formed the diet in the North Sea were the polychaetes, molluscs, crustaceans. Occasionally, like in the present study, echinoids were also found. Temming and Hammer (1994) found that the German Bight dab feeds significantly on ophiuroids. The next most important item was molluscs, with fish, crustaceans and polychaetes forming minor components. Rosenberg and Selander (2000) reported that flatfishes, such as dab, commonly prey on the arms of the ophiuroid, *Amphiura filiformis*.

The analysis by the Spearman rank correlation method indicates seasonal variation in the diet components. Wyche and Shackley (1986) also observed seasonal changes in the diet composition of dab in Carmarthen Bay in South Wales. They observed that *Philine aperta* occurred in the diet in July-October but noted that crustaceans only occurred occasionally in the diet of plaice and dab in October. They also noted that the ophiuroids, *Amphiura brachiata* predominated and the *Ophiura texturata* occurred occasionally. Knust (1987) illustrated distinct seasonal periodicity in the diet composition of dab in the German Bight. Knust found that in July and August, the crustaceans (mainly juvenile decapods, amphipods and cumaceans) constitute the main part of the diet. The echinoderms were preferred in the autumn and spring, whilst the polychaetes were mainly preferred in spring. Knust (1996) found that in the Dogger Bank, the food composition of dab changed during the year. In spring and autumn, the main part of the food comprised of ophiuroids whilst in summer, mainly on crustaceans. In July, juvenile decapods, mainly *Liocarcinus holsatus* and *Pagurus bernhardus*, were the most important. Lande (1976) investigated the food of dab from the coastal water of Norway and found a great variation of different food taxa throughout the year. Lande recorded that the polychaetes were

dominant in the diet of dab in late autumn and winter. The molluscs attained their peak in March in the coastal waters of Norway.

Many authors (Hall *et al.*, 1990; Greenstreet, 1996; Frid and Hall, 1999) have described the consumption of benthic macrofaunal species by the dab. Frid and Hall noted that trends in fish stomach samples over time might reflect food availability and allow inferences to be made about changes in the composition of the benthic community. The stomach contents of dab have been correlated with benthic infaunal population densities (Knust, 1986; Knust 1990; Kroncke and Knust, 1992). Knust (1990) found correlations between abundance in the benthos and the Index of Relative Importance of Food (IRIF) in dab. Some of the observed variation in the diet of dab has been attributed to the opportunistic feeding behaviour of this species (Kaiser and Ramsay, 1997; Carter *et al.*, 1991). The periodicity in food composition has been related to comparable seasonal changes in the macrobenthos (Knust, 1996). Knust (1996) concluded that the structure of the macrobenthic fauna, which are available as food resource, strongly influence the diet composition of dab. Knust (1987) noted that the occurrence of decapods and amphipods in the food of dab in the German Bight coincided with the abundance of these taxa in the benthos. Kaiser and Ramsay (1997) observed that fishing activity increases feeding opportunity for dabs. Beyst *et al.* (1999) reported an opportunistic utilisation by flatfish of the available food resources in the Belgian surf zone ecosystem. They found that dietary overlap occurs between 0- and 1- groups of plaice, sole, brill, turbot and dab only when it involved prey species that were dominant in the Belgian surf zone, such as shrimps and mysids. Saborowski and Buccholz (1996) noted that stomach contents of dab reflect the typical benthic epi-fauna in the locality. Jobling (1974) noted that stomach contents may indicate the relative abundance of prey species, and to some extent, the vulnerability of each prey species to predation. It has been shown that the benthos composition in the study area is dominated by the following major groups: the polychaetes, ophiuroids and bivalves. This compares favourably with the diet composition in this study.

Though there is a shift in the preference for polychaetes and bivalves by juvenile and adult dabs, there is considerable overlap in diet composition between the various size groups in this study. The intra-specific overlap was moderate to high in most of the months. It has been shown that intraspecific diet overlap values are considerably higher than interspecific ones (Palsson, 1983; Bergstad, 1991; Carter *et al.*, 1991; Horpilla *et al.*, 2000). The moderate to high diet overlap values can be attributed largely to the dominant contribution to the total diet by the ophiuroids (*Amphiura* sp.), crustaceans (*Liocarcinus depurator*) and polychaetes (*Lagis* sp.) in all size

groups. Braber and de Groot (1973) reported a shift in the relative importance of prey in the diet of dab in the North Sea as the size of the fish increases. This was consistent with the observation made in this study for polychaetes and molluscs. Carter *et al.* (1991) also observed that the dietary composition of plaice was found to vary with fish size. As found in this study, Carter *et al.* (1991) observed increase in diet breadth with increasing size of the fish (11-15 cm to 26-30 cm). But in the largest fish (≥ 31 cm), whose distribution is generally in offshore areas, the dominance of large bivalves in their diet results in the narrowing down of the diet breadth. This gives rise to high diet evenness among this size group of fish. Munk (1997) observed that the relative size of prey is one of the major determinants of a predator's preference.

Hoinés and Bergstad (1999) noted that when prey items are very abundant, the extensive diet overlap might not reflect strong competitive interaction. In terms of inter-specific food overlap, it is generally believed that species occupy the same area because resources are unlimited (Ross, 1986; Gerking, 1994). Workers like Goulding, (1980) and Prejs and Prejs (1987) have, however, related increased diet similarity with diminishing resources and others have shown that food partitioning increases during periods of low resource base (Zaret and Rand, 1971). Jepson *et al.* (1997) showed that sympatric *Cichlia sp.* use food and space in a manner that would reduce interspecific competition in the event that resource demands exceed supply. Hoinés and Bergstad (1999) however believed that the superabundant prey would have an effect on the diet composition and in turn influence the level of intra- and inter-specific diet overlap. They observed that the gadoids are adapted to minimise the overlap of food resources, and also to take advantage of very abundant prey. This present study supports observations by Hoinés and Bergstad (1999). The ophiuroid, *Amphiura brachiata*, the polychaete, *Lagis koreni*, and the bivalves, *Abra alba* and *Angulus sp.*, by virtue of their abundance in the study area, certainly have an effect on the highly biological significant intra-specific diet overlap values observed between the different size groups in this study. It was also observed in the present study that, though, there was strong diet overlap between the various size groups, the size of prey items like the crustaceans, were however different, increasing with increasing size of the predator. This is particularly true with the burrowing shrimp *Upogebia sp.* and the masked crab, *Coenostes sp.* This observation is also true in the case of the razor shells, *Ensis sp.* and mussels (*Mytilus edulis*). Huge proportions of juveniles of the swimming crab, *Liocarcinus depurator*, were present in the diet of the various sizes in July-August 1999, in varying proportions, indicating that this food resource is shared when abundant and a small size. But as this prey becomes larger, it was hardly seen in the diet of the smallest size groups. Instead, groups of eggs masses alone were

found in the smallest predator whilst berried specimens were found in the larger dabs. This observation could probably be explained on the activity of the large dab, which might attack the egg-carrying crabs, and in the process causing the eggs to fall off and become available to the juvenile dabs. Also, the gastropod, *Philine aperta*, formed a major component of the diet in the various size groups in July-August 1999. It is likely that this period coincides with the spatfall of the swimming crab and the gastropod, *Philine aperta*. The presence of *patella* sp., an intertidal species, in the diet of dab probably came about as a result of stormy weather, which dislodges the prey species and thereby making them available on the feeding grounds of the dab.

Diet overlap is often assumed to be related inversely to competition intensity, since high competition tends to result in niche segregation between competing groups (Zaret and Rand, 1971; Keast, 1977), but positive relationships between competition and overlap have also been reported (Sandheinrich and Hubert, 1984). Other workers have suggested that overlap indexes are not appropriate measures of competition (Colwell and Futuyma, 1971; Hulbert, 1978). The calculated values of such indexes depend on how the food categories are defined and must therefore be used with caution (Horpilla *et al.*, 2000).

Seasonal effects on diet breadth and diet overlap have been reported in fish species (Gray *et al.*, 1997; Xie *et al.*, 2000). The general conclusion is that low dietary niche breadth might reflect heavy feeding on a one prey, which reaches a peak of abundance in a particular season. Thus, seasonal variation in diet overlap has frequently been interpreted in relation to the fluctuation of the resource base. Difference in seasonal patterns of feeding intensity has been found to be an important strategy of interspecific resource partitioning in some fish communities (Keast, 1978; Jepsen *et al.* 1997). Frid and Hall (1999) also found that Levin's diet breadth varied significantly in dab between time periods and suggested that this might reflect differences in the percentage frequency of occurrence of prey items and the dominance of few prey species in sampled stomachs.

Knust (1996) found seasonal periodicity in diet diversity between the dab populations in German Bight and the Dogger Bank. In the German Bight, the mean diversity of food was 1.84 in August and this was significantly higher than in spring and autumn. On the Dogger Bank, however, no significant differences in mean number of prey species and in diversity of food were found during the year. The mean diversity index ranged from 0.45 to 1.80 in the Dogger Bank, without any

significant peak (Knust, 1996). In contrast to the German Bight, the mean number of prey species on Dogger Bank was higher in spring and significantly lower in summer.

In the next chapter, the seasonal cycle in lipid composition and energy mobilization in dab is investigated.

CHAPTER SIX

Annual Cycle of Lipid Composition and Energy Allocation in *Limanda limanda* L.

6.1 INTRODUCTION

The significance of fish liver and muscle tissue as storage organs for lipids in plaice and dab have been investigated by Dawson and Grimm (1980) and Saborowski and Buchholz (1996) respectively. Dawson and Grimm showed that lipid supplies 75 % of energy for metabolism and so forms the major energy reserve. They found that the lipid content in the liver of a 35 cm female plaice declined from a peak in the summer in June (62.9%) to a minimum after spawning in April (13.6 %). The decline in lipid concentration between December and March (spawning period) was attributed to the metabolism of lipid as the source of energy during starvation in the female plaice. In the case of the North Sea dab, Saborowski and Buchholz (1996) found that the total lipid content of the liver showed a distinct seasonal cycle with 400 mg g⁻¹ FW in summer and a minimum of 50-100 mg g⁻¹ FW in spring. They found that the lipid content of the muscle ranged from 5 to 6 mg g⁻¹ FW and did not vary significantly between seasons.

Henderson *et al.* (2000) noted that relative liver weights in fish may provide a useful indicator of the mobilization of energy for somatic and gonadal growth. Ortega-Salas (1980) and Lozan (1992) have studied seasonal variation in the liver weight for dab in the Isle of Man and the North Sea respectively. They found that the female livers were proportionally heavier than the males in winter, with the HSI (hepatosomatic index) much higher for females than males of the same age. Lozan suggested that the energy gained during the peak feeding season in summer is probably consumed for somatic growth. He showed that after the gonads have developed by the end of the year, dab stores the additional surplus energy in the liver to use for metabolism during winter. Larson (1974) reported that the increase in the gonadosomatic index during the period of gonad maturation is mainly due to deposition of large amounts of nutrients (glycogen, lipid and proteins in the developing eggs and spermatozoa). Part of this utilisable material is also believed to come from ingested food. Larson also observed that, for brown trout, the major proportion of energy comes from reserves of food deposited during the active feeding season in organs such as the liver and muscles.

In order to cover the energy demand for the winter, individual dabs have to store energy and nutrients during the productive summer season. Lipids, preferably accumulated in the liver and the muscle tissue, are particularly important for energy storage and energy production due to their high calorific value (Saborowski and Buchholz, 1996). Information is thus required on the lipid storage and mobilization, and hence the energy available for different activities during the course of the year.

The aim of this chapter is therefore to investigate the seasonal lipid, energy and ash compositions of the gonad, liver and carcass of both the male and female dabs. The energy composition of selected prey species will also be determined. Finally, an attempt will be made to demonstrate how the demands of routine metabolism and gamete production are met from food intake and the utilization of body reserves.

6.2 MATERIALS AND METHODS

6.2.1 Energy determination

The determinations were carried out separately for an average 20 cm fish of each sex, since the modal length is about around 20 cm in the length frequency distribution and this size dominates the length composition in the study area.

The samples (gonad, carcass and liver) were dried at 60°C for 36 hours in an oven until no change in mass could be observed. Since these organs can show variability in biochemical parameters in different areas (Koprivnajak *et al.*, 1996), the organs were homogenised by pestle and mortar (and where necessary using a ball mill grinder) to obtain a powdered sample. The liver gives a paste-like appearance when oven dried (in summer and autumn) and was also therefore, as a check, freeze-dried at -40°C for four days. Incidentally, it was still pasty and there was no significant difference in water content between the oven dried and freeze dried liver samples. Thus finely ground silica was added in a ratio of 3:1 (Silica: Liver) and the mixture ground to a fine, dry powder.

6.2.1.1. Bomb calorimetry

The dried weights of the products were determined and weighed aliquots of the homogenous powder (≥ 200 mg) of the gonad, carcass and liver were ignited in a Gallenkamp Ballistic

Bomb Calorimeter (Model Number: CBB-330-010L) for energy determination. Weighed dried samples are burnt in an oxygen atmosphere pressurised in excess of 20 atmospheres. The heating of the bomb casing is then detected by a thermocouple attached to a recorder.

The machine was first calibrated by burning 5 samples of granulated sugar that ranged from 200 mg to 1000 mg. Three 200 mg samples of each organ were then burnt and the temperature changes were then converted into caloric value using the equation:

$$E = \frac{\left(\frac{B-a}{b}\right) \times 17 \text{ KJ}}{W} \text{ -----(6.1)}$$

Where:

1 g sugar = 17 kJ energy

E = Energy content (kJ) for 1 gram of sample

B = Adjusted bomb reading

a, b = Intercept and slope from the sugar calibration regression line

W = Sample weight

Kilojoules were converted to Kilocalorie from: 1 kcal g⁻¹ = 4.1843 kJ g⁻¹

This bomb calorimetric method was also used in the caloric energy determination in the prey species of the dab. However, in the case of the brittlestar (*Amphiura brachiata*), the wet oxidation method was also used (See below). Crisp (1971) observed that calcium salts burn endo-thermically. Thus when the sample contains large quantities of inorganic material (high carbonate content, for example), and the ash weight constitutes a considerable fraction of the dry weight of the sample, not all the heat is released on ignition in the bomb calorimeter. The caloric value would therefore be underestimated due to endothermic reactions. This is true in the case of echinoderms and barnacles. It is estimated from the present study that echinoderms contain about 67 % ash. Crisp (1971) thus proposed that caloric content of such organisms can be measured more reliably by a chemical method. In the present study, the bomb calorimeter method gave 0.97 kcal g⁻¹ for the brittlestar whilst the wet oxidation method gave 1.64 kcal g⁻¹. This shows that the bomb calorimeter method underestimated the caloric content in the brittlestar by 69 %. The result of the wet oxidation for the brittlestar was therefore used in the energy allocation model in the present study.

6.2.1.2 Wet oxidation method

For smaller samples (<200 mg), energy contents were measured by the wet oxidation method using chromic acid (Forster and Gabbott, 1971). In principle, the wet oxidation method relies on the spectrophotometric determination of the amount of unreduced dichromate remaining after an oxidation reaction between the sample and a wet oxidation mixture containing a known amount of potassium dichromate. The digestion mixture is prepared by precisely weighing 2.5 g of potassium dichromate, initially mixed with 10 ml of distilled water and gradually made up to 500 ml with concentrated sulphuric acid. Three replicates of each sample (1-2 mg depending on expected energy content) were precisely weighed using an analytical balance (*Ohaus Analytical Plus*) and added to 12 ml digestion tubes and 2 ml of digestion mixture added. 2 ml of digestion mixture was added to three empty tubes to serve as controls. The sample and control tubes were then placed in a hot block at 100 °C for 1 hour. After cooling, the samples were diluted to 50 ml of distilled water and the absorbency was read at 347 nm wavelengths, using a CE303 grating spectrophotometer (Cecil Instruments), in 5 mm path length quartz glass cuvettes. Blank readings were procured by preparing sulphuric acid solution (2 ml of concentrated acid made up to 50 ml with distilled water). Standard solutions (without heating in the hot block) contain 2 ml of digestion mixture made up to 50 ml with distilled water.

Calculation of energy content in wet oxidation:

There is 10 mg of potassium dichromate present in the 2 ml of the digestion mixture; the amount reduced by the sample is therefore calculated as follows:

The standard solution of diluted digestion mixture usually gives an absorption reading of 0.75, relative to the blank. Initially assume that the heated control tubes give the same reading. If the sample gave a reading of $E = 0.4$, then the fraction of dichromate that has disappeared is;

$$\text{Reduced } K_2Cr_2O_7 = (0.75 - 0.4)/0.75 * 10 = 4.67 \text{ mg}$$

3 mg of dichromate is the equivalent of 0.489 mg of oxygen, thus 4.67 mg is equivalent to 0.761 mg of oxygen consumed. An oxycalorific coefficient (for protein/fat/carbohydrate mixtures in animal prey) is 3.38 cal $mg^{-1} O_2$. Then 1 mg of dichromate is equivalent to 0.163 mg oxygen and which is equivalent to 0.551 cal.

Thus, 10 mg of the dichromate is equivalent to 5.51 cal, which is the maximum energy capacity of 2 ml of the digestion mixture. In general:

$$\text{Energy (cal) in sample} = (0.75-E)/0.75 \times 5.51$$

In normal circumstances, the control tubes in the hot block will lose a little colour due the present of impurities; let assume this absorbance reading is 0.7. Thus, the maximum energy capacity '5.51' cal in the equation can no longer be used and should be replaced by;

$$(0.7 / 0.75) * 5.51 = 5.14 \text{ cal.}$$

This is the energy capacity that should be used to calculate energy in the sample. Ruohonen and Grove (Unpublished) found that on average wet oxidation only detects 71 % of the energy in typical mixtures of nutrients. Thus the results of the wet oxidation method were divided by 0.71 to correct for the insufficient oxidation.

6.2.2 Lipid determination

The total lipid content of known quantities of dried samples of liver and carcass for each sex was determined by the gravimetric method of Hopkins *et al.* (1984). A sample is homogenised in chloro-methanol solution, containing BHT (Butylated HydroxyToluene) as anti-oxidant, centrifuged, purified by addition of 0.9 % aqueous sodium chloride, centrifuged, and the upper aqueous layer aspirated and discarded.

The detailed analytical steps involved are as outlined below:

1. 20 mg of powdered liver (or 50 mg of carcass) is placed in separate centrifuge tubes (each organ in triplicates).
2. 3 ml of chloroform-methanol (2:1) solution is added to the product in the tubes. The chloroform-methanol extracts the lipid. The resulting solution is left for 30 minutes at room temperature.
3. The solution is centrifuged for 10 minutes at 4000 rpm.
4. The supernatant is pipetted to a weighed, graduated centrifuge tube.
5. Steps 2, 3 and 4 are repeated twice again so that the total supernatant in the weighed graduated centrifuge tube is 9 ml. The reason is to ensure complete extraction of the lipid.
6. 1 ml of chloroform-methanol (2:1) solution is added to the supernatant to make it up to 10 ml.
7. 2 ml of 0.9 % aqueous sodium chloride (NaCl) is added to make a total volume of 12 ml solution. The NaCl solution removes impurities.
8. The solution is centrifuged at 4000 rpm for 20 minutes
9. The upper phase NaCl layer, containing the impurities, is aspirated and discarded.

10. The lower, lipid-containing layer is evaporated to dryness in a water bath at 70 °C for 20 minutes, and then dried on a hot block at 50°C for 10 minutes. The dried lipid and the centrifuge tube are weighed and the weight of the lipid determined from the weight of the empty centrifuge tube.

Other methods involving the use of chloro-methanol for lipid extraction from aquatic animals have been reported by Henderson *et al.* (1996, 2000), Saborowski and Buchholz (1996) and Parish *et al.* (1999).

6.2.3 Ash determination

Total inorganic concentration (ash) of all the organs were obtained by ashing samples at 500 °C for 4 hour (Pomory and Lawrence, 1999) in a muffle furnace. A 20 mg sample of powdered gonad, liver and carcass (each in triplicate) was used. The powdered dried samples were precisely weighed on pre-weighed aluminium foil.

6.2.4 Energy allocation

Studies of ecological energetics and the construction of energy budgets are one particular field of marine ecology which has advanced greatly in recently years (Hopkins *et al.*, 1984). In this study, the model of partial energy level changes in dab is that based on the method by Edwards *et al.* (1969), Dawson and Grimm (1980) and Bakhsh (1982). Suffice to note that there are other models for energy allocation during reproductive season in fish (Roff, 1983; Henderson *et al.*, 1996).

The oxygen uptake of 0-group dab at 10°C, under resting conditions, has been shown to obey the following relationship (Edwards *et al.*, 1969). That is the change in the rate of respiration is a function of weight and temperature:

$$Q_{O_2} = 0.449 W^{0.666} \text{ (6.2)}$$

Where Q_{O_2} = Oxygen consumption as ml hr⁻¹ at 10 °C

W = Total weight of the fish (g)

This formula was used to estimate the gross metabolic energy required by 20 cm fish in the spawning season. The formula was however corrected to ambient temperature in the Anglesey waters. The average ambient water temperature in the study area between November and February is about 8°C.

The corrected formula is given as, after Hoar (1966):

$$\text{Log}Q_{10} = \frac{10x(\text{Log}R_1 - \text{Log}R_2)}{10 - T_2} \text{-----(6.3)}$$

Where Q_{10} = 2.63 (Backiel, 1971)
 R_1 = Oxygen consumption at 10°C
 R_2 = Oxygen consumption at ambient temperature T_2

The oxygen consumption in ml_{O2} was converted to calories, using the relationship (Brett and Groves, 1979):

$$1 \text{ ml O}_2 = 4.63 \text{ Cal-----(6.4)}$$

However since dab expend energy in searching for food, for example, a routine metabolic rate has to be used. But simple doubling of the standard metabolic rate originally proposed by Winberg (1956) does not seem appropriate, especially in view of recent measurements of activity levels of fish in the wild. Soofiani and Hawkins (1985), Minton and McLean (1982) and Adams *et al.* (1982) have concluded that routine metabolic rates are only a little above the standard rate. In line with this argument and from consideration of the fact that dab is a demersal species and not very active, it should suffice to increase the standard metabolic rate by 25 % to obtain routine metabolic rate.

6.3 RESULTS

Changes in dry weight proximate compositions of body organs in male and female dab are given in Tables 6.1-6.6. Figure 6.1 shows that in the female dab, after spawning, there is a drastic decline in the gonad weight in April and the minimum values (dry weight) were between June and October, with a range of 0.10 - 0.20 g. The maximum values occur at the height of the spawning season in February (5.06 g dry weight). There is a reduction in water content in the ovary beginning in November (pre-spawning period), with the minimum between January-February (about 67 %), and a maximum value was over 80 % between April-October (resting period). The dry gonad weight in the male is at its lowest level between April-September (range 0.02-0.03 g) and water contributes about 90 % to its weight between March-April. The maximum dry testes weight is in January (0.19 g), in the peak spawning season. The dry weight of the liver varies between 0.10 g in April to 0.94 g in July-October in the female (Figure 6.2). Similarly for the male, it varies from 0.08 gm in April to 0.66 g in July.

The water composition in the liver varies from 57 % in October to 88 % in April in the female, and in the male from 66 % in July to 88 % also in April.

The dry carcass weight is relatively stable between May-February for females and June-December for males (Figure 6.3). The water content in the carcass remains relatively stable at an average level of about 80 % for much of the year in both sexes. There is a sharp drop in dry carcass weight from 17.09 g in October to 9.83 g in April in the female. In the male, the decline is from 14.60 g in September to 7.76 g in April also.

A. Female

Table 6.1. The composition of the ovaries of female dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g)	Dry weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	11.41 \pm 0.86	3.26 \pm 0.15	0.163 \pm 0.015	19.46 \pm 0.65
Mar	1999	14.15 \pm 1.76	4.42 \pm 0.90	0.202 \pm 0.020	25.91 \pm 0.27
Apr	1999	2.82 \pm 1.45	0.35 \pm 0.19	0.029 \pm 0.000	1.92 \pm 0.02
May	1999	1.06 \pm 0.21	0.18 \pm 0.03	0.011 \pm 0.001	0.86 \pm 0.01
Jun	1999	0.90 \pm 0.15	0.11 \pm 0.02	0.009 \pm 0.000	0.50 \pm 0.01
Jul	1999	0.83 \pm 0.06	0.11 \pm 0.01	0.008 \pm 0.000	0.57 \pm 0.01
Aug	1999	0.67 \pm 0.04	0.10 \pm 0.01	0.008 \pm 0.000	0.52 \pm 0.01
Sep	1999	0.75 \pm 0.03	0.12 \pm 0.01	0.011 \pm 0.000	0.65 \pm 0.01
Oct	1999	0.88 \pm 0.03	0.10 \pm 0.01	0.012 \pm 0.001	0.81 \pm 0.02
Nov	1999	2.53 \pm 0.23	0.40 \pm 0.06	0.044 \pm 0.001	3.22 \pm 0.06
Dec	1999	3.22 \pm 0.29	0.79 \pm 0.10	0.057 \pm 0.002	4.74 \pm 0.06
Feb	2000	15.68 \pm 1.19	5.06 \pm 0.43	0.272 \pm 0.016	27.17 \pm 0.41
Mar	2000	3.64 \pm 0.93	0.69 \pm 0.21	0.041 \pm 0.004	3.97 \pm 0.04
Apr	2000	0.87 \pm 0.06	0.14 \pm 0.01	0.011 \pm 0.001	0.76 \pm 0.02
May	2000	0.93 \pm 0.26	0.14 \pm 0.01	0.012 \pm 0.001	0.78 \pm 0.00
July	2000	0.76 \pm 0.06	0.13 \pm 0.01	0.011 \pm 0.000	0.71 \pm 0.00
Oct	2000	0.91 \pm 0.06	0.17 \pm 0.01	0.015 \pm 0.000	0.86 \pm 0.01
Jan	2001	7.52 \pm 1.03	2.48 \pm 0.04	0.158 \pm 0.004	14.99 \pm 0.65

Table 6.2. The composition of the liver of female dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g)	Dry weight (g)	Lipid weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	2.98 \pm 0.50	0.77 \pm 0.22	0.26 \pm 0.02	0.036 \pm 0.000	4.98 \pm 0.07
Mar	1999	2.79 \pm 0.24	0.62 \pm 0.04	0.15 \pm 0.01	0.056 \pm 0.003	3.64 \pm 0.05
Apr	1999	1.16 \pm 0.42	0.10 \pm 0.08	0.03 \pm 0.01	0.006 \pm 0.000	0.59 \pm 0.01
May	1999	1.73	0.32	0.12 \pm 0.01	0.013 \pm 0.000	2.04 \pm 0.07
Jun	1999	1.22 \pm 0.50	0.28 \pm 0.17	0.13 \pm 0.01	0.007 \pm 0.000	2.32 \pm 0.05
Jul	1999	1.89 \pm 0.23	0.46 \pm 0.09	0.23 \pm 0.02	0.016 \pm 0.001	3.58 \pm 0.01
Aug	1999	1.80 \pm 0.20	0.53 \pm 0.08	0.29 \pm 0.01	0.014 \pm 0.001	4.11 \pm 0.05
Sep	1999	2.01 \pm 0.19	0.71 \pm 0.10	0.49 \pm 0.02	0.018 \pm 0.001	5.85 \pm 0.09
Oct	1999	2.19 \pm 0.30	0.89 \pm 0.22	0.53 \pm 0.01	0.022 \pm 0.001	7.65 \pm 0.14
Nov	1999	2.12 \pm 0.15	0.61 \pm 0.08	0.33 \pm 0.01	0.024 \pm 0.000	4.72 \pm 0.05
Dec	1999	1.69 \pm 0.13	0.54 \pm 0.06	0.22 \pm 0.02	0.015 \pm 0.000	4.22 \pm 0.01
Feb	2000	2.69 \pm 0.10	0.69 \pm 0.07	0.26 \pm 0.03	0.058 \pm 0.003	4.54 \pm 0.02
Mar	2000	1.35 \pm 0.19	0.26 \pm 0.04	0.08 \pm 0.00	0.021 \pm 0.001	1.56 \pm 0.01
Apr	2000	0.95 \pm 0.12	0.19 \pm 0.03	0.06 \pm 0.01	0.016 \pm 0.000	1.16 \pm 0.01
May	2000	1.62 \pm 0.24	0.51 \pm 0.12	0.29 \pm 0.01	0.021 \pm 0.003	3.85 \pm 0.03
July	2000	2.36 \pm 0.29	0.94 \pm 0.14	0.60 \pm 0.07	0.016 \pm 0.000	7.24 \pm 0.02
Oct	2000	2.19 \pm 0.16	0.94 \pm 0.08	0.56 \pm 0.06	0.040 \pm 0.004	7.59 \pm 0.01
Jan	2001	2.23 \pm 0.48	0.91 \pm 0.13	0.47 \pm 0.06	0.039 \pm 0.001	6.59 \pm 0.02

Table 6.3. The composition of the carcass of female dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g) Carcass	Dry weight (g) Carcass	Lipid weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	85.50 \pm 2.50	18.51 \pm 0.06	2.21 \pm 0.20	1.27 \pm 0.02	107.18 \pm 2.81
Mar	1999	73.00 \pm 16.00	14.64 \pm 1.95	1.38 \pm 0.15	1.00 \pm 0.02	84.76 \pm 2.22
Apr	1999	64.00 \pm 5.78	12.64 \pm 0.68	0.87 \pm 0.18	0.66 \pm 0.02	76.59 \pm 5.91
May	1999	78.57 \pm 12.21	14.28 \pm 2.38	1.28 \pm 0.11	0.97 \pm 0.05	71.83 \pm 1.52
Jun	1999	84.50 \pm 10.50	17.38 \pm 2.70	2.07 \pm 0.15	1.09 \pm 0.05	96.07 \pm 0.80
Jul	1999	84.38 \pm 2.49	16.53 \pm 0.67	1.56 \pm 0.47	0.77 \pm 0.01	93.72 \pm 1.82
Aug	1999	79.71 \pm 2.66	16.17 \pm 0.79	2.65 \pm 0.30	0.89 \pm 0.05	88.59 \pm 0.89
Sep	1999	76.13 \pm 2.81	16.09 \pm 0.77	1.30 \pm 0.04	0.83 \pm 0.03	93.86 \pm 1.39
Oct	1999	78.00 \pm 2.15	17.09 \pm 0.64	1.47 \pm 0.32	1.11 \pm 0.10	99.13 \pm 1.10
Nov	1999	78.92 \pm 2.23	15.99 \pm 0.59	0.97 \pm 0.09	0.98 \pm 0.03	91.68 \pm 0.90
Dec	1999	78.09 \pm 2.70	16.31 \pm 0.72	1.40 \pm 0.19	1.06 \pm 0.03	94.82 \pm 3.17
Feb	2000	77.80 \pm 2.10	16.39 \pm 0.59	0.96 \pm 0.19	1.13 \pm 0.04	97.71 \pm 3.17
Mar	2000	60.33 \pm 2.27	9.96 \pm 0.61	0.63 \pm 0.06	0.77 \pm 0.03	55.86 \pm 1.41
Apr	2000	59.00 \pm 2.04	9.83 \pm 0.51	0.90 \pm 0.01	0.76 \pm 0.04	54.08 \pm 0.98
May	2000	76.70 \pm 4.01	15.25 \pm 1.09	1.31 \pm 0.17	1.03 \pm 0.03	84.54 \pm 0.62
July	2000	83.40 \pm 2.21	18.26 \pm 0.58	1.75 \pm 0.26	0.96 \pm 0.02	100.10 \pm 2.35
Oct	2000	84.30 \pm 2.35	18.24 \pm 0.52	1.26 \pm 0.15	0.97 \pm 0.02	102.19 \pm 0.01
Jan	2001	76.67 \pm 4.98	16.54 \pm 1.30	1.43 \pm 0.04	1.11 \pm 0.05	89.76 \pm 1.10

B. Male

Table 6.4. The composition of the testes of male dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g)	Dry weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	0.85 \pm 0.24	0.10 \pm 0.03	0.010 \pm 0.000	0.58 \pm 0.03
Apr	1999	0.30 \pm 0.10	0.02 \pm 0.00	0.003 \pm 0.000	0.11
Jun	1999	0.15	0.02 \pm 0.00	0.002 \pm 0.001	0.10 \pm 0.01
Jul	1999	0.22 \pm 0.11	0.03 \pm 0.02	0.004 \pm 0.001	0.20 \pm 0.02
Aug	1999	0.15 \pm 0.02	0.02 \pm 0.00	0.001 \pm 0.000	0.13 \pm 0.03
Sept	1999	0.20 \pm 0.02	0.03 \pm 0.00	0.002 \pm 0.000	0.14 \pm 0.01
Oct	1999	0.54 \pm 0.07	0.07 \pm 0.01	0.007 \pm 0.000	0.43 \pm 0.01
Nov	1999	1.12 \pm 0.06	0.13 \pm 0.01	0.013 \pm 0.000	0.81 \pm 0.02
Dec	1999	1.05 \pm 0.13	0.12 \pm 0.02	0.012 \pm 0.001	0.72 \pm 0.03
Feb	2000	0.51 \pm 0.04	0.06 \pm 0.00	0.007 \pm 0.000	0.32 \pm 0.01
Mar	2000	0.39 \pm 0.03	0.04 \pm 0.01	0.004 \pm 0.000	0.23
Apr	2000	0.16 \pm 0.03	0.02 \pm 0.01	0.003 \pm 0.000	0.12 \pm 0.00
May	2000	0.18 \pm 0.00	0.02 \pm 0.00	0.002 \pm 0.000	0.12 \pm 0.00
July	2000	0.14 \pm 0.02	0.02 \pm 0.00	0.002 \pm 0.000	0.11 \pm 0.01
Oct	2000	0.47 \pm 0.04	0.07 \pm 0.01	0.007 \pm 0.000	0.36 \pm 0.00
Jan	2001	1.40 \pm 0.13	0.19 \pm 0.00	0.020 \pm 0.001	1.04 \pm 0.03

Table 6.5. The composition of the liver of male dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g)	Dry weight (g)	Lipid weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	1.12 \pm 0.26	0.29 \pm 0.03	0.16 \pm 0.01	0.004 \pm 0.000	2.47 \pm 0.11
Apr	1999	0.67 \pm 0.13	0.08 \pm 0.02	0.02 \pm 0.00	0.004 \pm 0.000	0.53 \pm 0.01
Jun	1999	1.70	0.59	0.32 \pm 0.05	0.019 \pm 0.001	4.57 \pm 0.22
Jul	1999	1.51 \pm 0.34	0.48 \pm 0.23	0.20 \pm 0.01	0.014 \pm 0.001	3.74 \pm 0.08
Aug	1999	1.60 \pm 0.29	0.45 \pm 0.12	0.24 \pm 0.01	0.012 \pm 0.001	3.57 \pm 0.08
Sep	1999	1.73 \pm 0.30	0.55 \pm 0.16	0.34 \pm 0.01	0.018 \pm 0.001	4.62 \pm 0.12
Oct	1999	1.34 \pm 0.08	0.39 \pm 0.05	0.18 \pm 0.01	0.009 \pm 0.000	3.28 \pm 0.02
Nov	1999	1.36 \pm 0.09	0.37 \pm 0.06	0.18 \pm 0.01	0.014 \pm 0.000	2.83 \pm 0.04
Dec	1999	0.79 \pm 0.09	0.18 \pm 0.06	0.08 \pm 0.01	0.008 \pm 0.000	1.27 \pm 0.03
Feb	2000	0.80 \pm 0.23	0.22 \pm 0.15	0.10 \pm 0.01	0.010 \pm 0.002	1.83 \pm 0.02
Mar	2000	0.67 \pm 0.14	0.10 \pm 0.02	0.03 \pm 0.01	0.007 \pm 0.000	0.69 \pm 0.01
Apr	2000	0.65 \pm 0.12	0.10 \pm 0.03	0.03 \pm 0.00	0.008 \pm 0.000	0.61 \pm 0.02
May	2000	1.12 \pm 0.08	0.21 \pm 0.03	0.07 \pm 0.01	0.013 \pm 0.001	1.43 \pm 0.02
July	2000	1.82 \pm 0.16	0.66 \pm 0.00	0.34 \pm 0.03	0.029 \pm 0.000	4.92 \pm 0.02
Oct	2000	1.16 \pm 0.14	0.35 \pm 0.07	0.20 \pm 0.01	0.015 \pm 0.000	2.70 \pm 0.02
Jan	2001	0.91 \pm 0.09	0.20 \pm 0.07	0.10 \pm 0.02	0.008 \pm 0.000	1.48 \pm 0.01

Table 6.6. The composition of the carcass of male dab (20 cm length). Estimates given are averages \pm S.E

Month	Year	Wet weight (g)	Dry weight (g)	Lipid weight (g)	Ash weight (g)	Gross energy content (kcal)
Feb	1999	62.33 \pm 4.53	15.63 \pm 1.12	1.78 \pm 0.06	1.46 \pm 0.03	93.09 \pm 1.40
Apr	1999	65.00 \pm 3.71	12.50 \pm 0.82	1.24 \pm 0.19	0.95 \pm 0.06	74.50 \pm 0.97
Jun	1999	74.00 \pm 0.00	14.83 \pm 0.41	1.25 \pm 0.15	0.80 \pm 0.02	79.15 \pm 2.12
Jul	1999	77.50 \pm 1.00	14.69 \pm 0.43	1.18 \pm 0.20	0.89 \pm 0.02	79.37 \pm 1.91
Aug	1999	76.50 \pm 4.92	15.11 \pm 1.10	1.47 \pm 0.07	0.86 \pm 0.05	83.72 \pm 1.58
Sep	1999	71.14 \pm 2.92	14.60 \pm 0.95	1.27 \pm 0.08	0.73 \pm 0.04	86.53 \pm 2.55
Oct	1999	68.86 \pm 2.03	14.52 \pm 0.39	0.90 \pm 0.03	0.76 \pm 0.05	89.56 \pm 0.92
Nov	1999	71.10 \pm 1.20	13.95 \pm 0.54	0.96 \pm 0.04	0.93 \pm 0.02	81.59 \pm 1.85
Dec	1999	74.50 \pm 8.50	14.58 \pm 2.38	0.90 \pm 0.05	0.96 \pm 0.03	82.64 \pm 1.26
Feb	2000	61.00 \pm 4.36	11.05 \pm 1.88	0.75 \pm 0.10	0.98 \pm 0.03	59.44 \pm 0.18
Mar	2000	58.00 \pm 1.00	8.50 \pm 1.53	0.71 \pm 0.12	0.65 \pm 0.00	46.66 \pm 0.42
Apr	2000	52.50 \pm 0.50	7.76 \pm 0.71	0.36 \pm 0.10	0.64 \pm 0.01	43.15 \pm 1.07
May	2000	67.08 \pm 2.33	11.81 \pm 0.62	0.97 \pm 0.18	0.98 \pm 0.06	64.89 \pm 1.47
July	2000	76.64 \pm 1.92	16.33 \pm 0.59	1.40 \pm 0.09	1.00 \pm 0.07	87.96 \pm 2.12
Oct	2000	73.33 \pm 2.21	14.92 \pm 0.76	1.22 \pm 0.25	1.22 \pm 0.06	82.20 \pm 0.24
Jan	2001	67.50 \pm 6.50	13.28 \pm 1.06	1.01 \pm 0.13	1.01 \pm 0.02	72.61 \pm 0.56

Figure 6.1. Monthly variation in the dry weight (\pm S.E) of gonad of a 20-cm dab 1999-2001

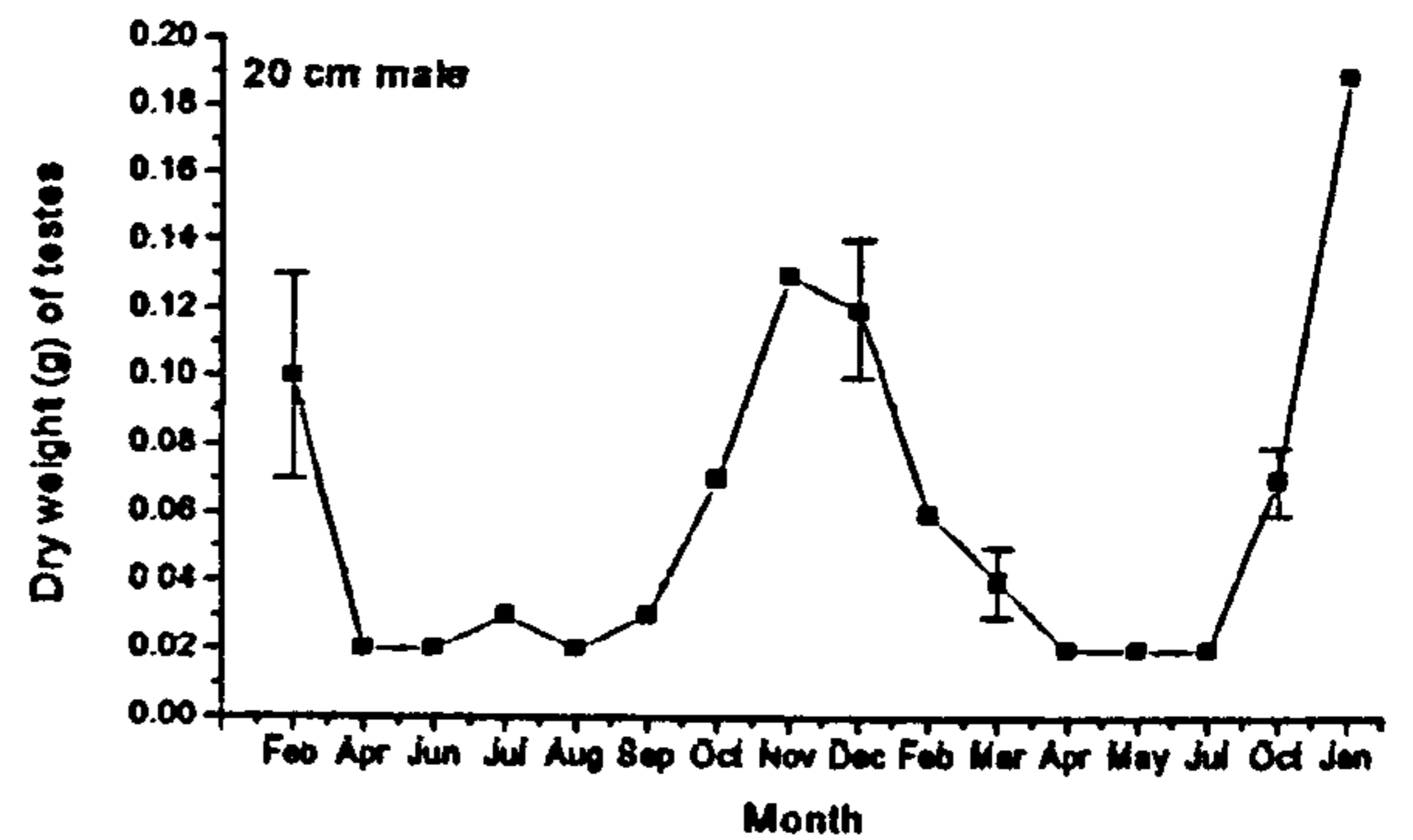
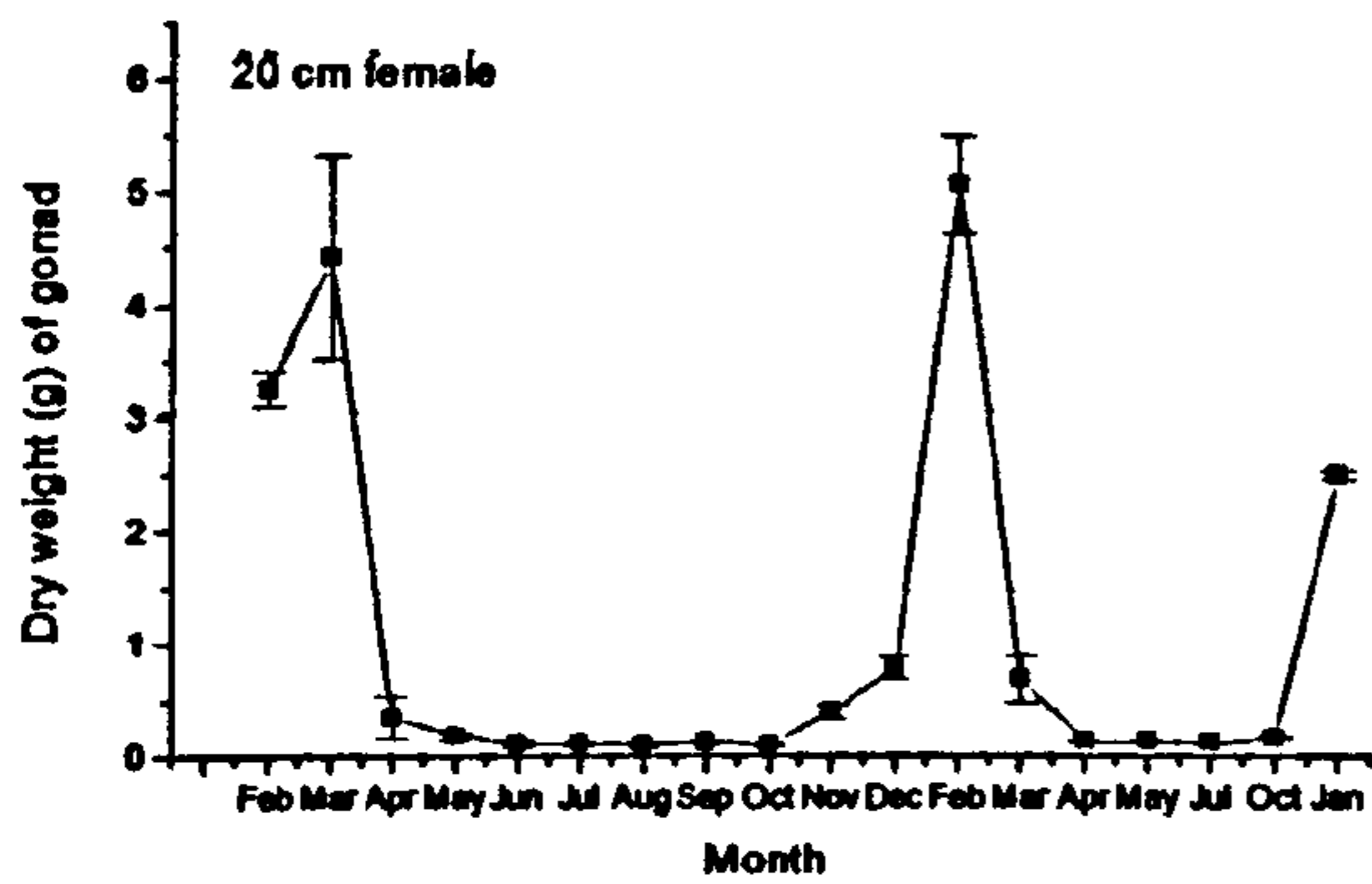


Figure 6.2. Monthly variation in dry weight (g) of liver of a 20-cm dab, 1999-2001

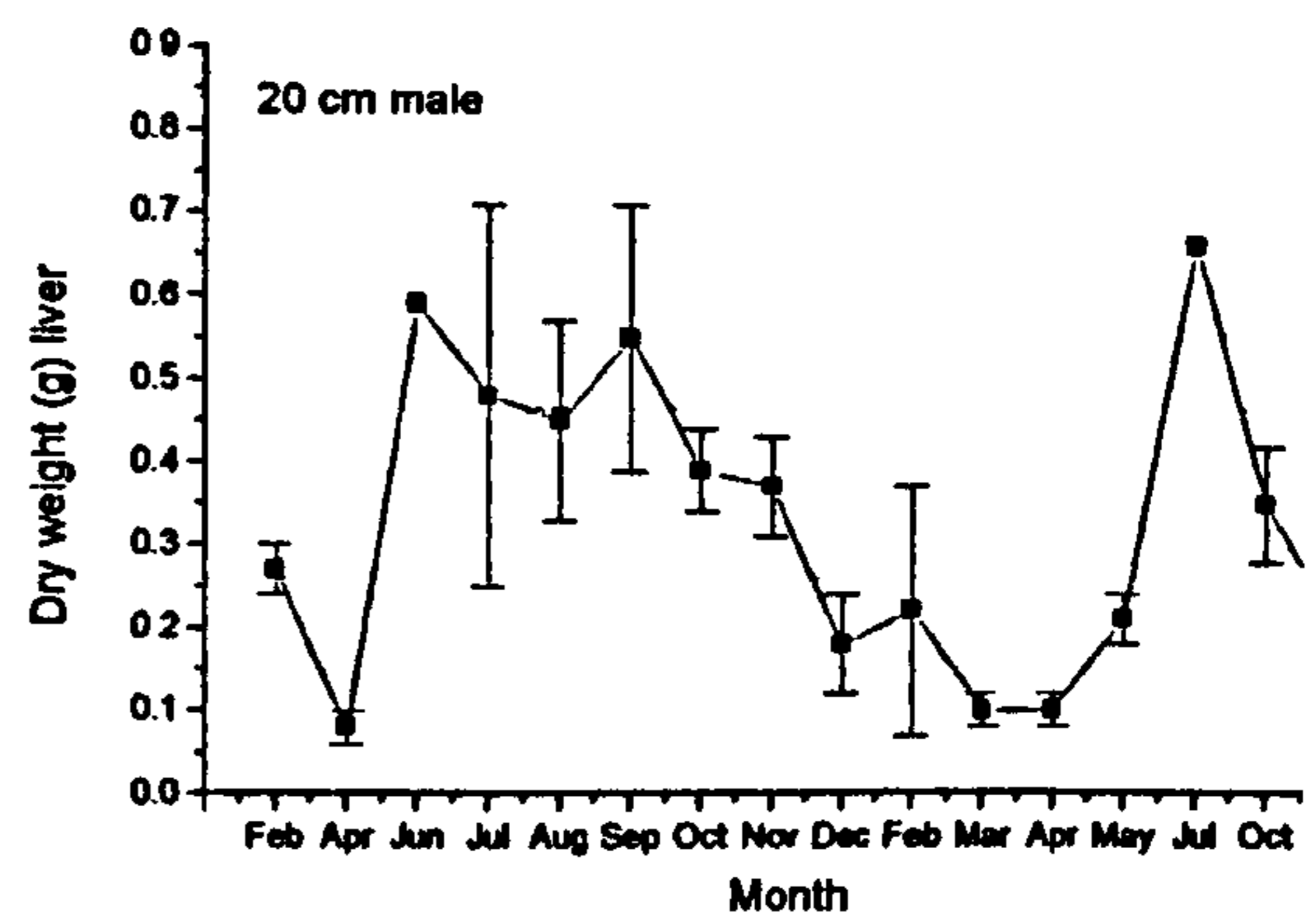
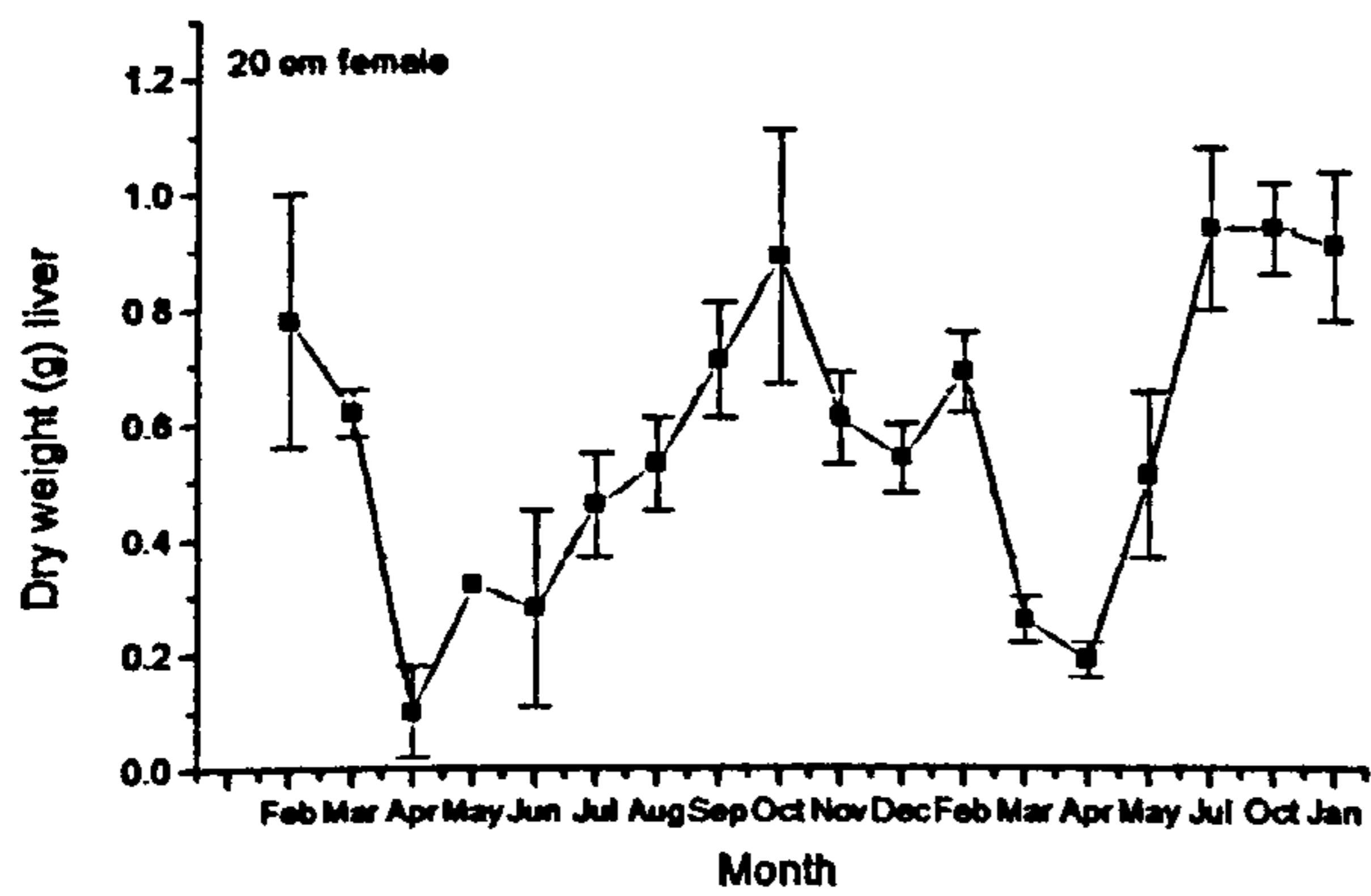
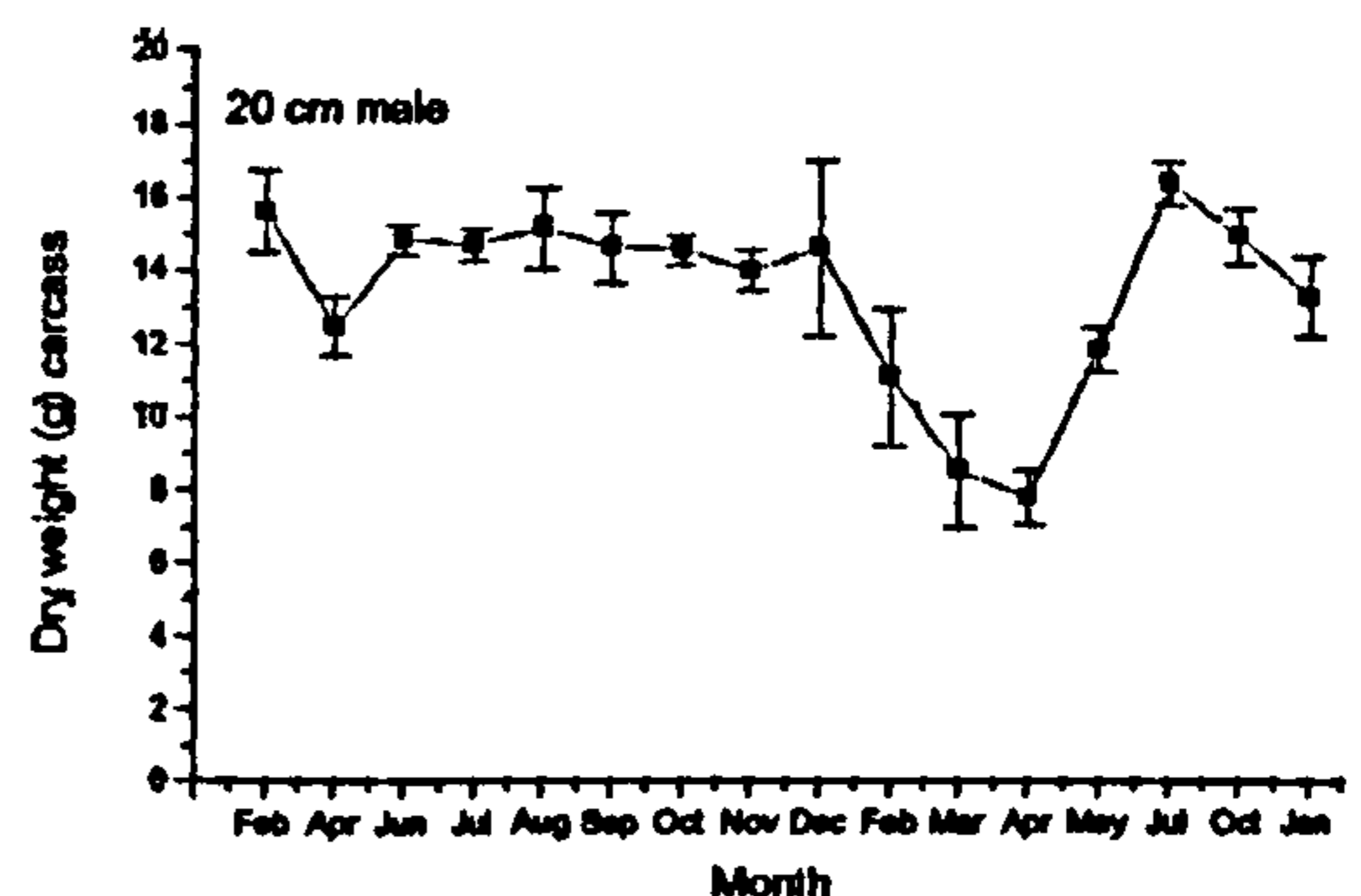
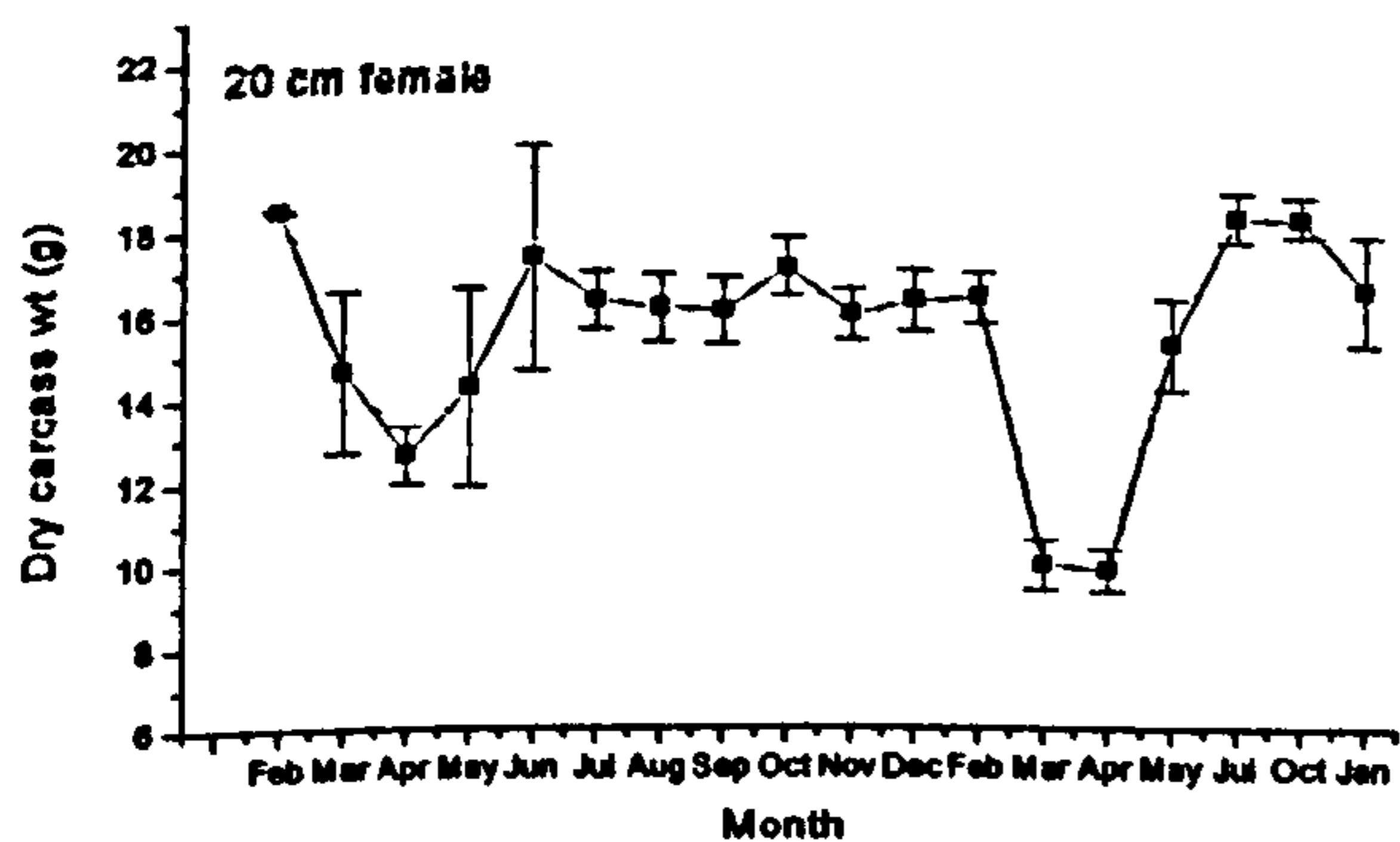


Figure 6.3. Monthly variation in dry weight of carcass (g) of a 20-cm dab, 1999-2001



The pattern of annual cyclical change in gross energy content in various body organs is illustrated in Figures 6.4-6.6. In the ovary, there is marked seasonal fluctuation in the gross energy content, which ranged from 0.50 kcal in June 1999 to 27.17 kcal in February 2000. Outside the spawning season between May and October, the gross energy content is low and varies between 0.50 - 0.86 kcal in the female. But with the onset of oogenesis in November, there is a steady increase in the energy content in the ovary from 3.22 kcal to the maximum at the height of the spawning season in February, Figure 6.4. The energy per unit mass (g) of the ovary varies from 4.40 kcal in June 1999 to 6.03 kcal in January 2001. In the male testes, there is also fluctuation in the gross energy content, with minimum values occurring in the summer. A sharp rise is observed in October 1999 (0.43 kcal), which is the onset of spermatogenesis, until it peaked in January (1.04 kcal). There are also annual cyclical changes in gross energy content in the liver of both sexes (Figure 6.5). In the females, it is at a maximum in the summer and autumn, with values of 7.24 kcal and 7.59 kcal in July and October 2000 respectively, but declined to low levels in March and April 2000 (1.56-1.16 kcal). In the male liver, the gross energy content remains at peak levels in summer and the beginning of autumn (June- September), with a range of 3.57-4.57 kcal. It then declined steadily in October (3.28 kcal), the onset of spermatogenesis, until it reaches minimum levels in March and April (0.69 - 0.61 kcal). The energy per unit dry weight of female liver (g) ranged from 5.86 kcal g⁻¹ in March 1999 to 8.61 kcal g⁻¹ in October 1999. In comparison with the gonad and liver, the bulk of the gross energy reserve is found in the carcass (due to its larger size) (Figure 6.6). It ranged from 54 kcal in April to 107 kcal in February in the female carcass and from 43 kcal in April to 93 kcal in February 1999 in the male carcass. However the energy per unit dry weight in the liver is higher than in the gonad and carcass.

Figure 6.4. Monthly variation in gross energy content (kcal) in gonad of a 20-cm dab, 1999-2001

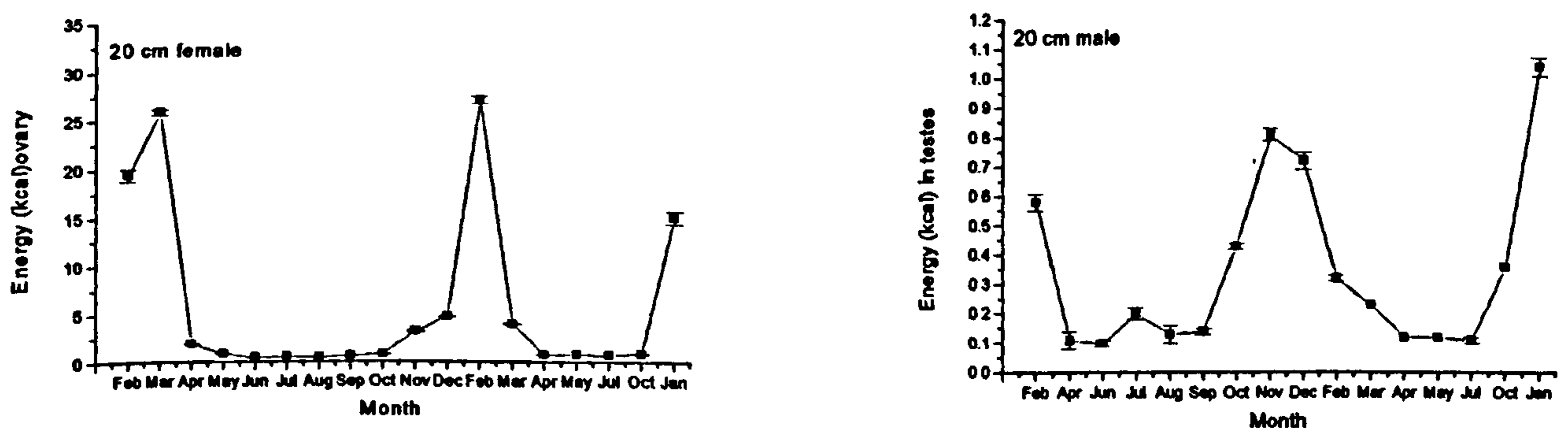


Figure 6.5. Monthly variation in gross energy content (kcal) in liver of a 20-cm dab, 1999-2001

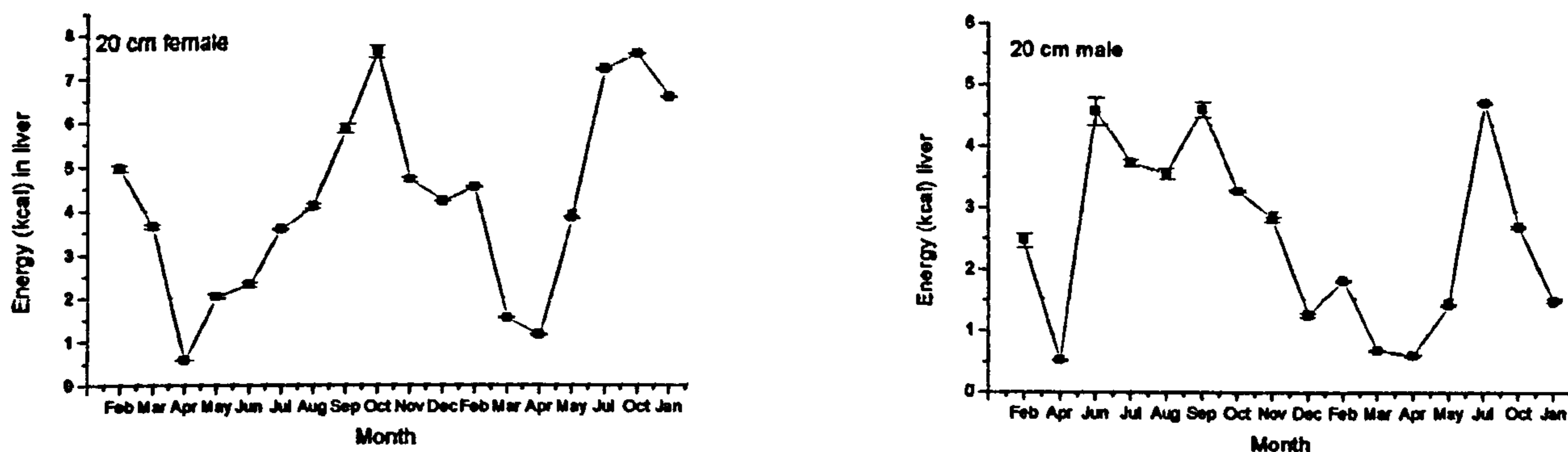
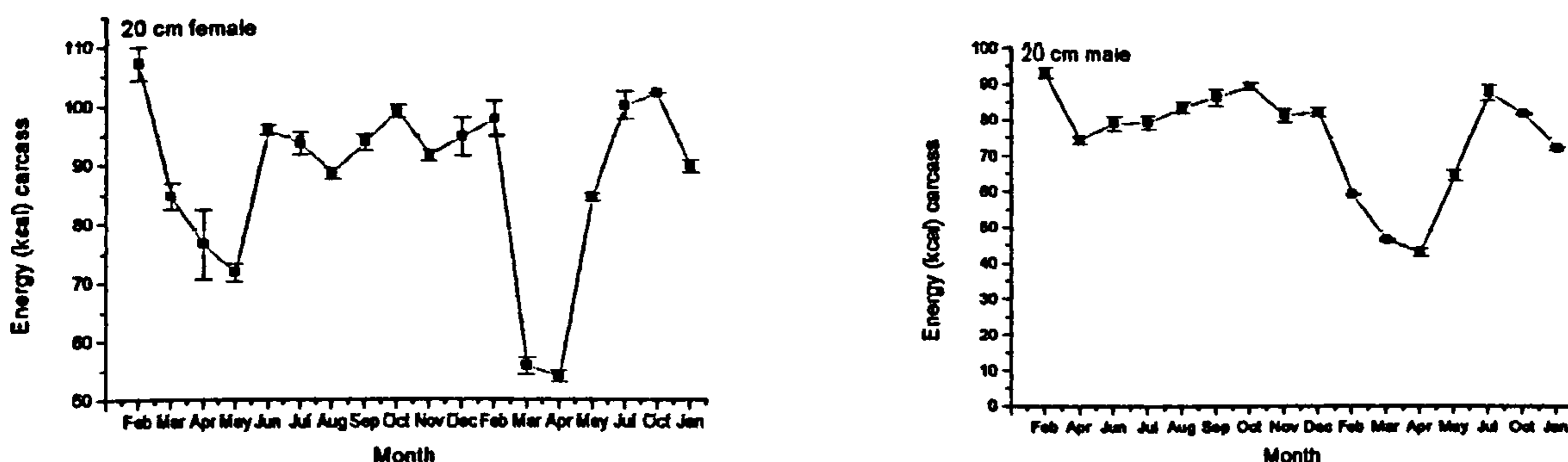


Figure 6.6. Monthly variation in gross energy content (kcal) in carcass of a 20-cm dab, 1999-2001



Both the male and female dab show large seasonal variation in total lipid contents in the liver (Figure 6.7). The period of low lipid concentration in the female liver is between March-April (24-32 %) in the post-spawning period. During this period the total lipid weight varies between 0.03-0.08 g. In summer and autumn (July-October), the total lipid concentration reached peak value; the total lipid weights were 0.60 g (63 %) and 0.56 g (60 %) in July 2000 and October 2000 respectively. In the male liver, the peak total lipid weight was observed in the summer and early autumn (as was the gross energy content), July (0.34 g) and September (0.34 g). These represent 52 % and 62 % of total lipid composition by weight respectively in the male liver. There is however a rapid decline in lipid concentration from October (at the start of spermatogenesis) to the minimum lipid weight in March/April (0.02-0.03 g) as was observed in the female liver. In comparison with the liver, there is less

variability in the monthly values of the total lipid content in the carcass in both sexes (Figure 6.8). Whilst the lipid concentration can range from about 24 to 69 % in the liver, it varies between 5 to 16 % and from 5 to 11 % in the female and male carcass respectively. Also, the lowest concentration of total lipid in the carcass occurs in April for the female (0.63 g) and the male (0.36 g).

Figure 6.7. Monthly variation in total lipid weight (g) in liver of a 20-cm dab, 1999-2001

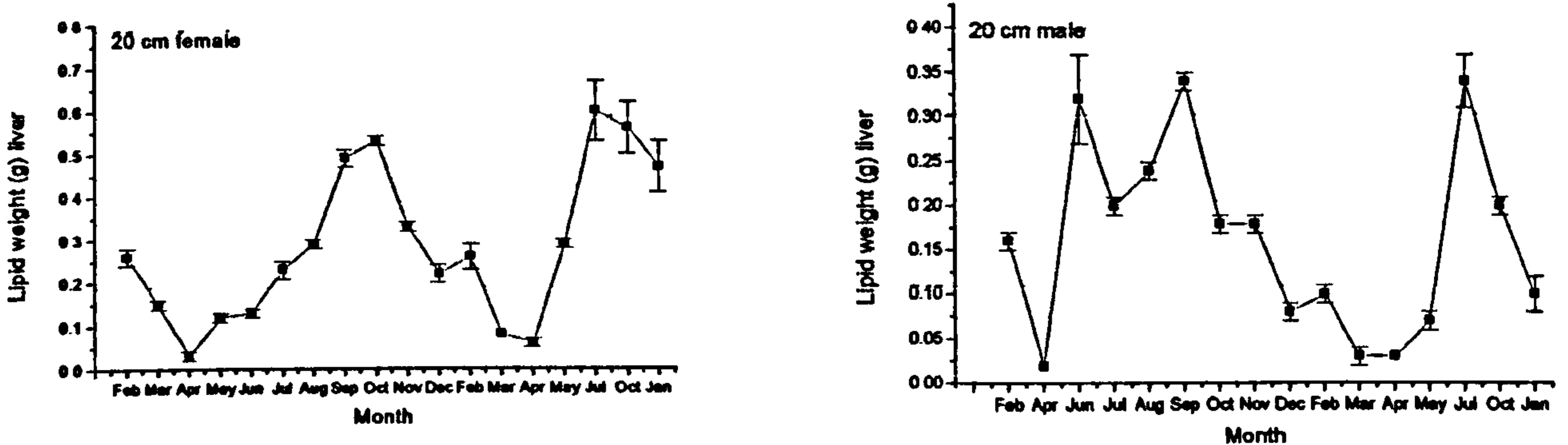
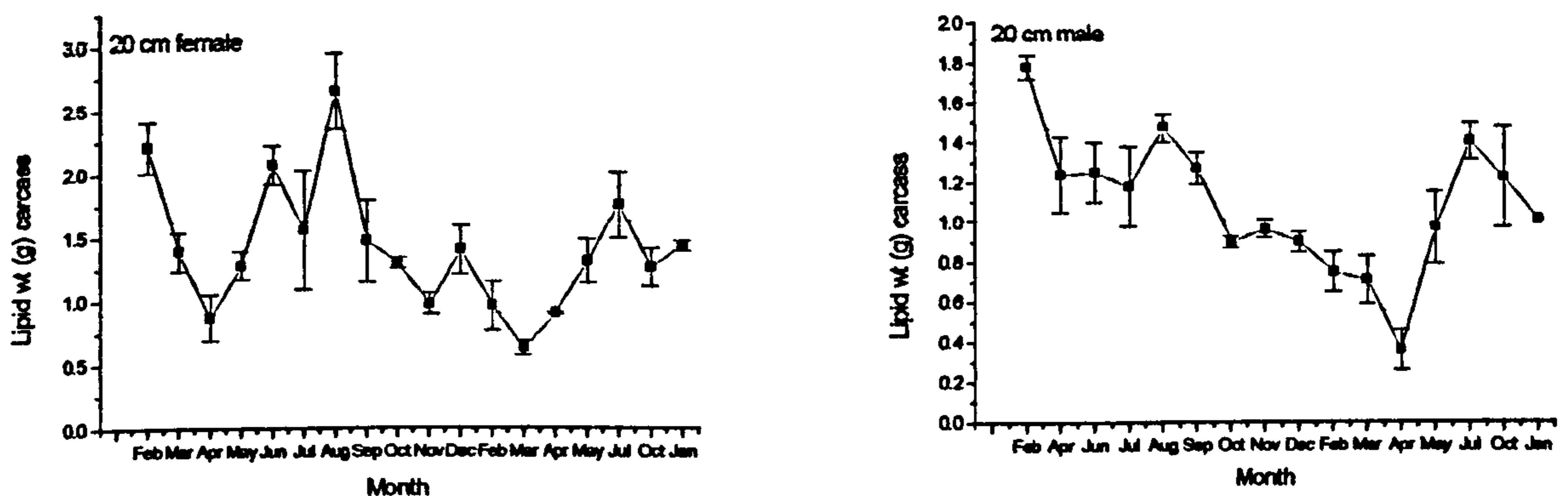


Figure 6.8. Monthly variation in lipid weight (g) in carcass of a 20-cm dab, 1999-2001



There is a significant decline ($P < 0.05$) in water content with increasing lipid concentration (and hence caloric energy) in the liver in both male and female dab (Figures 6.9 and 6.10).

Figure 6.9. Plot of monthly % water content against % lipid (by weight) in liver of male and female dab, 1999-2001

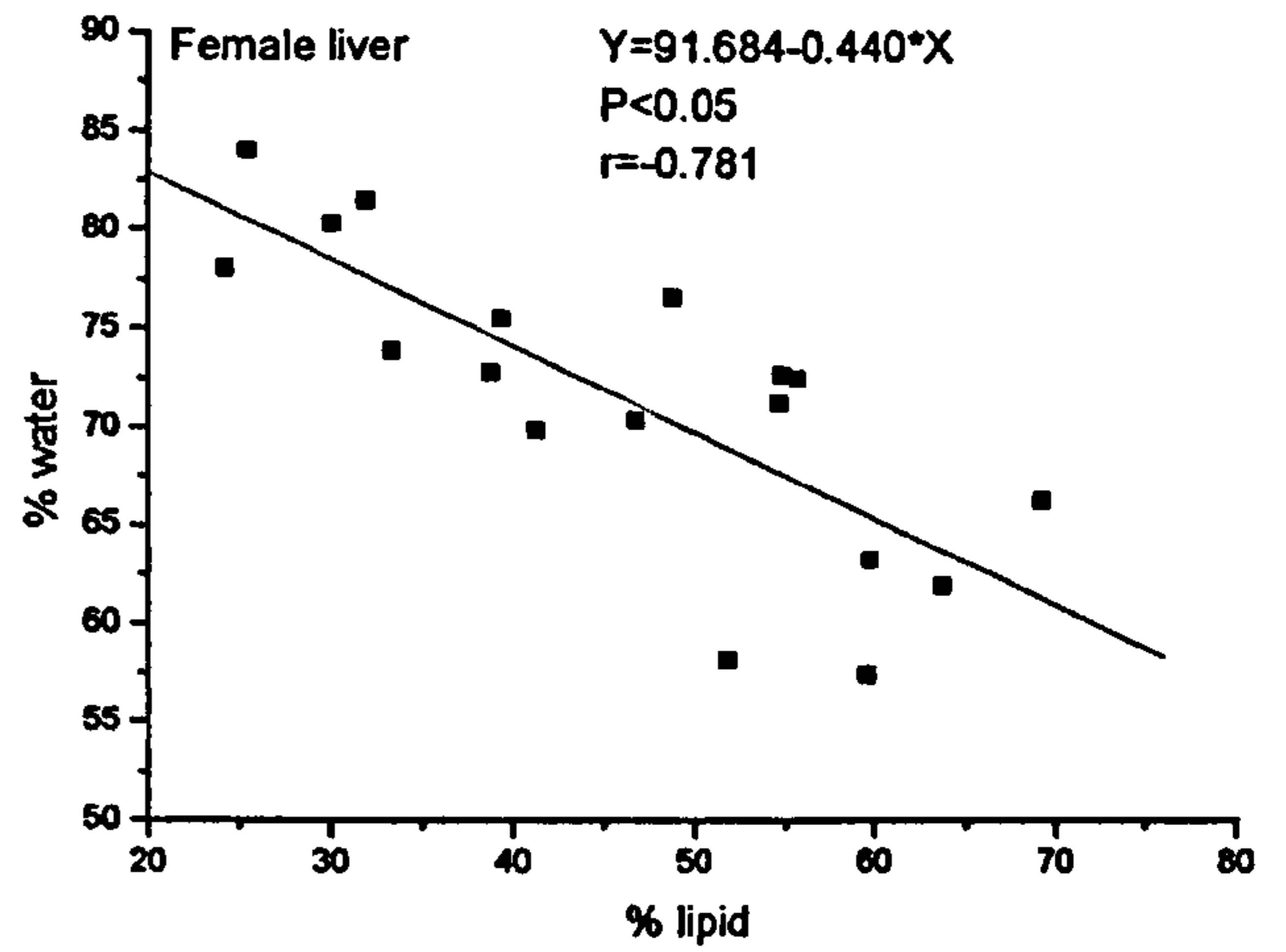
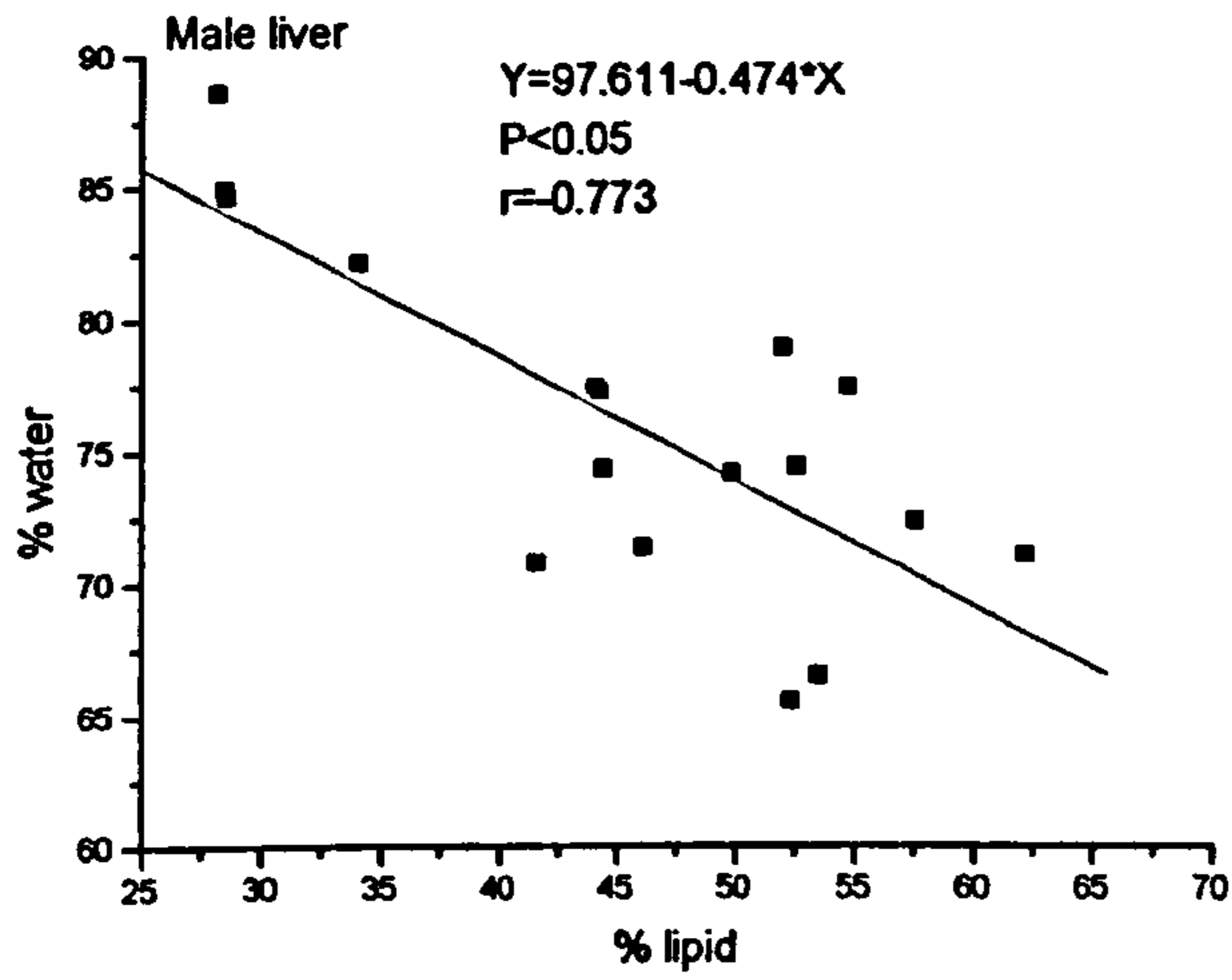
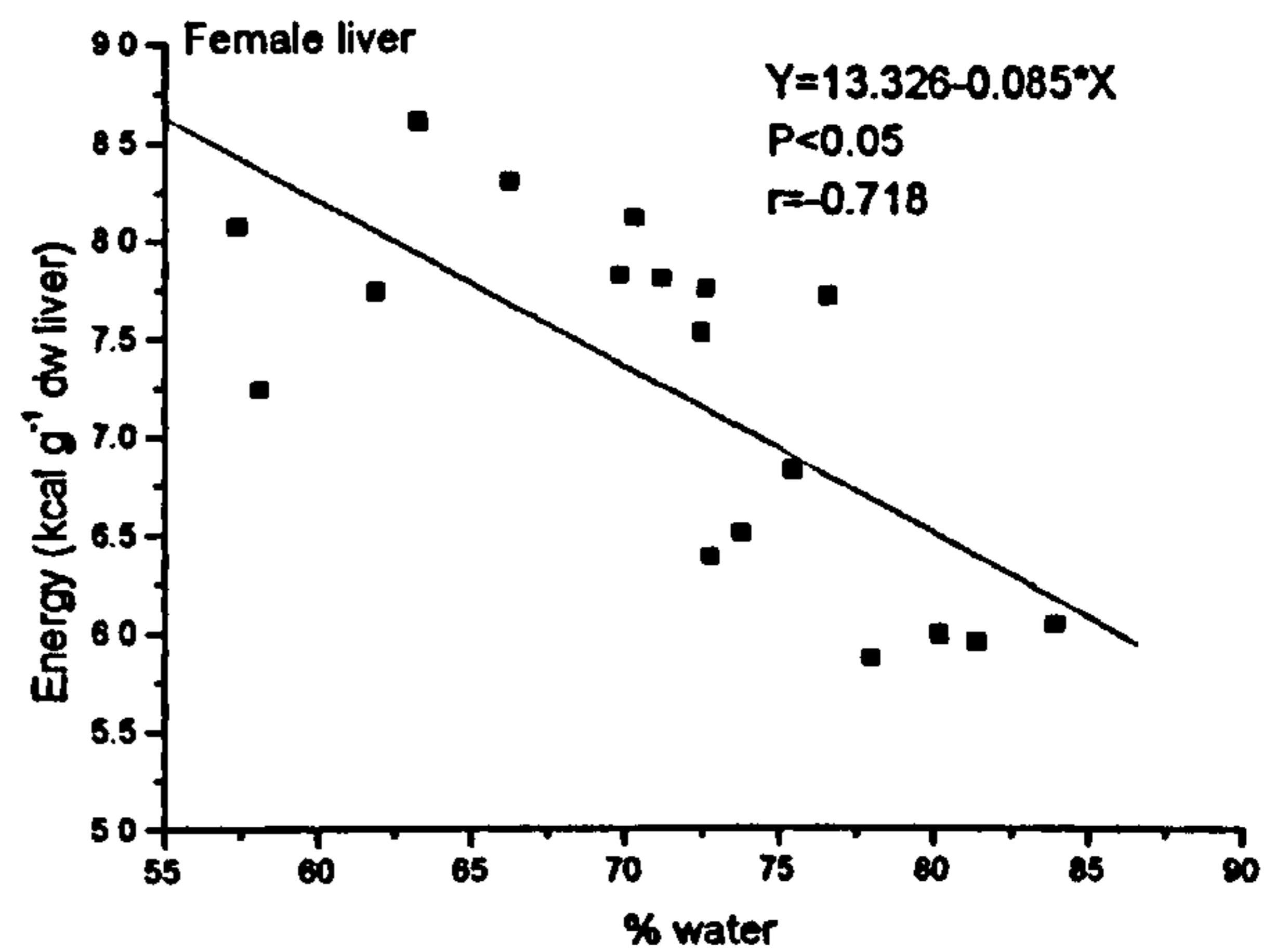
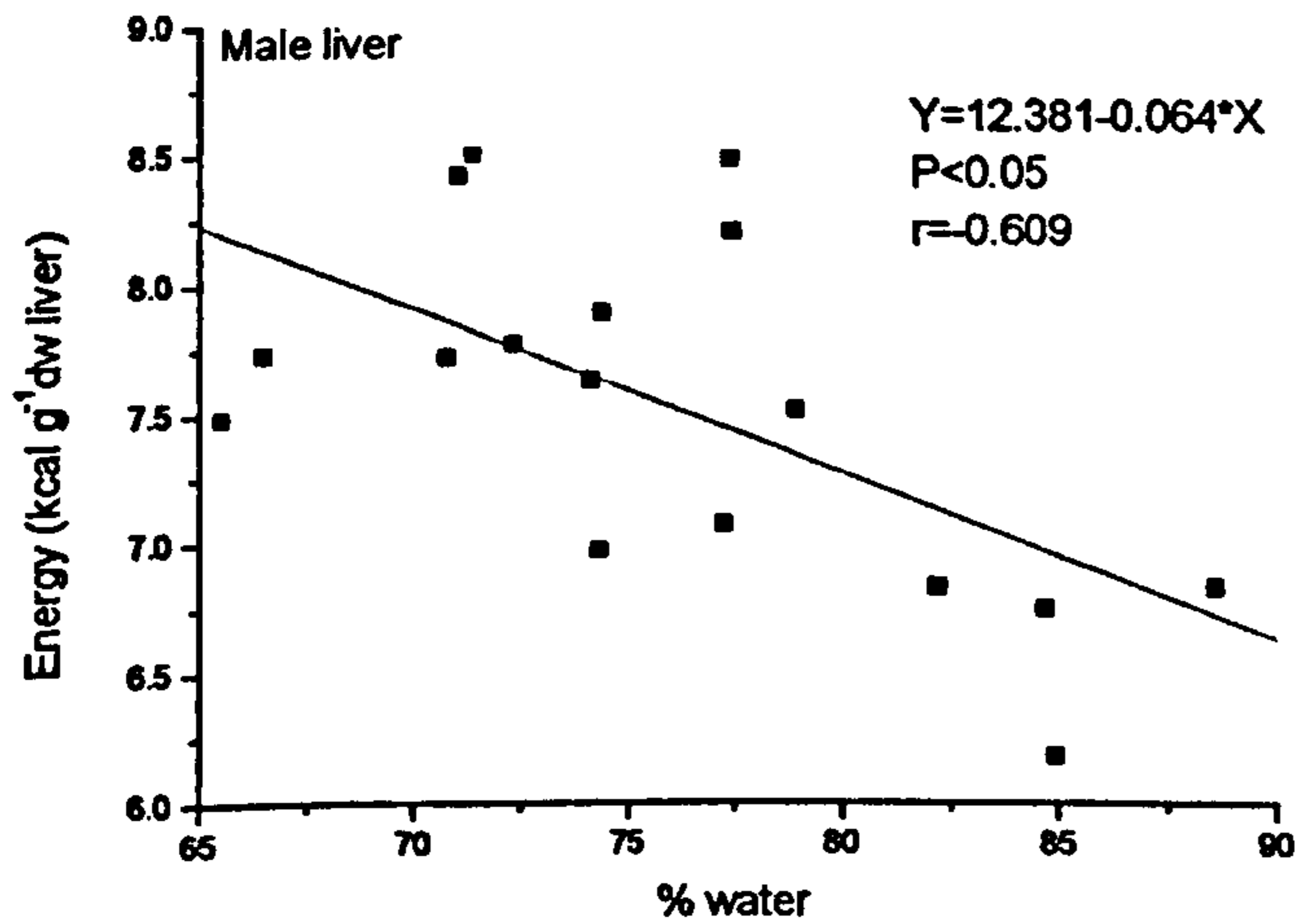


Figure 6.10. Plot of monthly calorific content against % water in liver of male and female dab, 1999-2001



There is also a significant ($P < 0.05$) negative correlation between ash content and lipid composition (and hence energy content) in the liver of male and female dab (Figures 6.11 and 6.12). The percentage ash contents in the female liver vary from 1.68 % in the summer (July), the gonad resting period, to 8.92 % in the spring (March), the postspawning period. The total ash content declined significantly (and remained relatively stable) between May-October in the ovary, but rises to a peak in February (0.27 g), Table 6.1. The total ash weights are very low in the male gonad (0.01-0.02 g) and liver (0.01–0.03 g), Table 6.4. There is considerable perturbation in ash level in the carcass of male and female dab (Figure 6.13). The minimum ash weight in the carcass of both sexes in April (0.64-0.66 g) and the maximum in February (1.27-1.46 g).

Figure 6.11. Plot of % lipid content against % ash weight in male and female liver

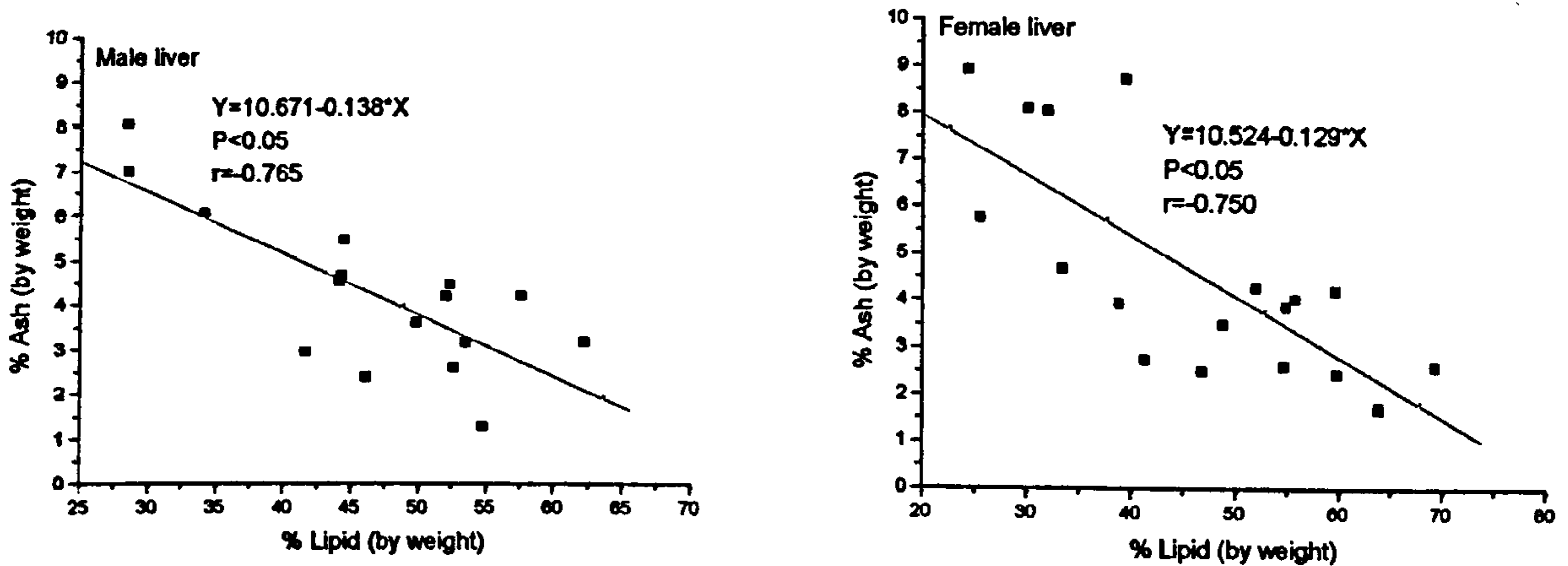


Figure 6.12. Plot of % ash content against calorific energy in male and female liver

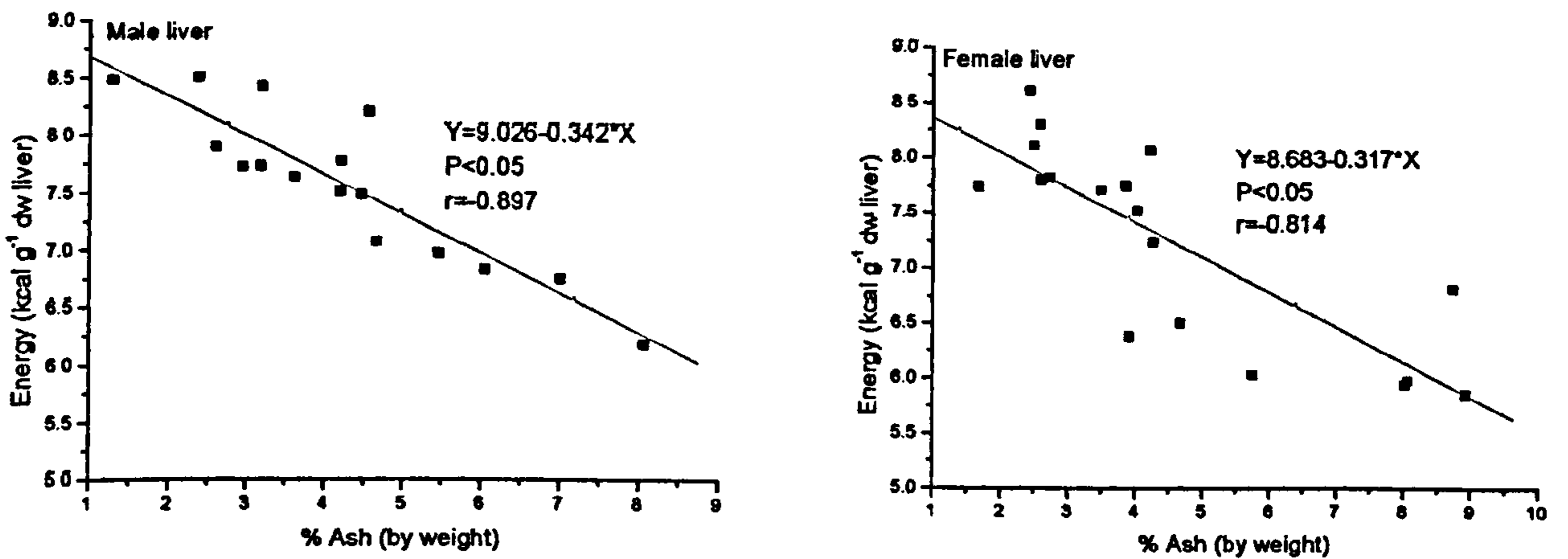


Figure 6.13. Monthly variation in ash weight in carcass (g) of a 20-cm dab

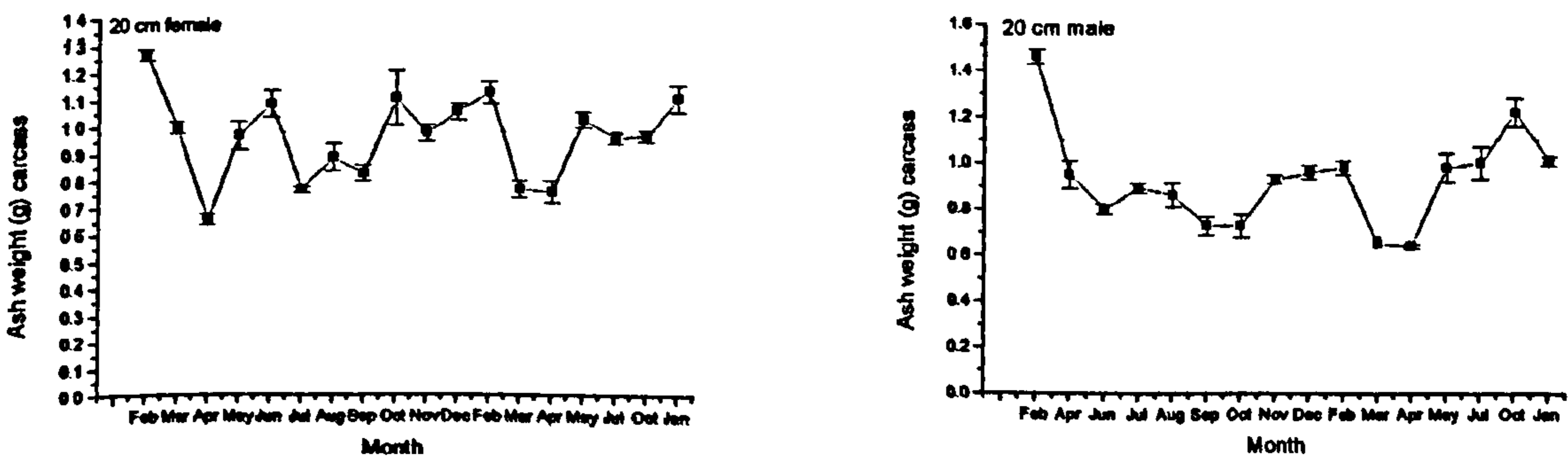
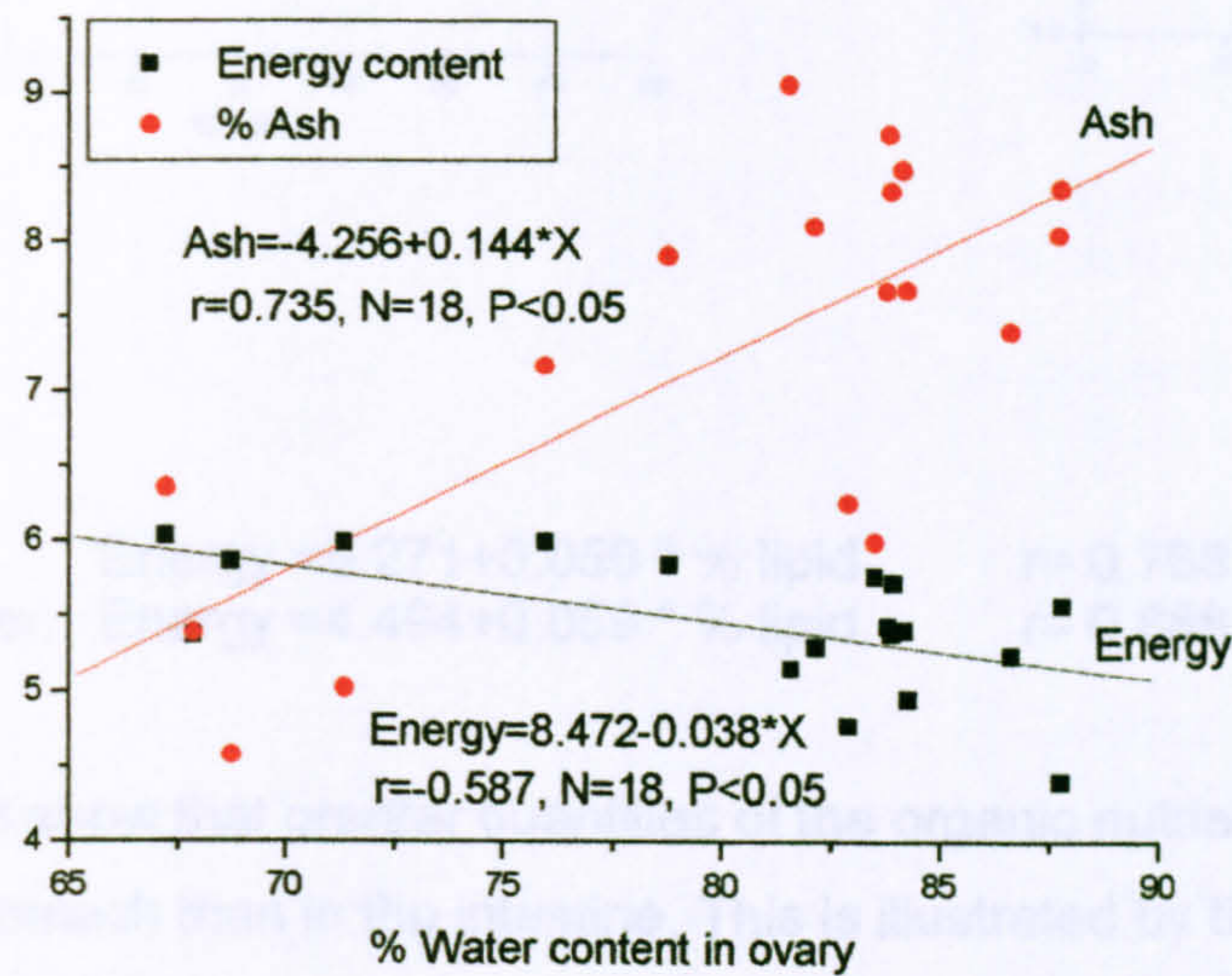


Figure 6.14 showed significant positive correlation ($P < 0.05$) between ash content and water content in the female gonad. The figure also showed significant negative correlation ($P < 0.05$) between energy content and water content in the ovary. The plot of % lipid composition against energy content in the male and female liver shows a significant positive correlation (Figure 6.15)

Figure 6.14. Plot of seasonal relationship % water content against % ash content and energy content ($\text{kcal g}^{-1}\text{dw}$) of ovary.

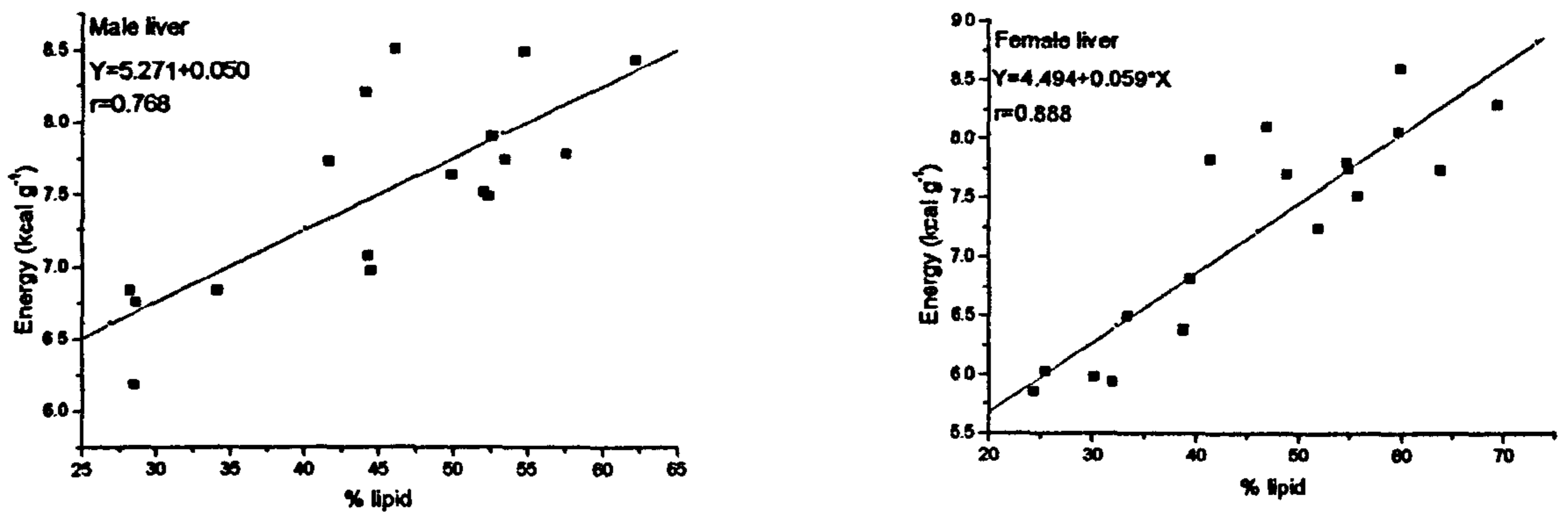


Summary:

$$\% \text{ Ash} = -4.56 + 0.144 * \% \text{ water}, \quad r = 0.735, N = 18, P < 0.05$$

$$\text{Energy} = 8.472 - 0.038 * \% \text{ water}, \quad r = -0.587, N = 18, P < 0.05$$

Figure 6.15. Plot of % lipid composition against energy content in the male and female liver



Summary:

Male liver: Energy = $5.271+0.050 * \% \text{ lipid}$ $r= 0.768, n=17, P<0.05$
 Female liver: Energy = $4.494+0.059 * \% \text{ lipid}$ $r= 0.888, n=18, P<0.05$

Tables 6.7 and 6.8 show that greater quantities of the organic nutrients in the food are absorbed in the stomach than in the intestine. This is illustrated by the higher ash content (inorganic content) in the intestine as compared to the stomach.

Table 6.7. Ash content of diet from the stomach and intestinal regions of the alimentary canal of a 20 cm dab

Gut Area	Wet weight (g)	Dry weight (g)	Ash weight (g)	Main diet components
Stomach	4.77	0.90	0.22	Crab
Intestine	4.07	0.70	0.12	Crab, Bivalve Siphon
Stomach	1.09	0.13	0.08	Ophiuroid
Intestine	0.48	0.19	0.15	Ophiuroid
Stomach	0.39	0.15	0.11	Ophiuroid
Intestine	0.74	0.31	0.24	Ophiuroid, Mollusc
Stomach	0.89	0.19	0.12	Ophiuroid
Intestine	1.94	0.47	0.19	Ophiuroid, Crustacean
Stomach	1.15	0.26	0.10	Ophiuroid, Hydroid
Intestine	2.54	0.16	0.14	Ophiuroid, Bivalve
Stomach	1.07	0.21	0.08	Ophiuroid, Polychaete
Intestine	0.99	0.36	0.29	Mollusc
Stomach	0.65	0.14	0.08	Ophiuroid, Polychaete
Intestine	0.90	0.26	0.15	Mollusc, Polychaete
Stomach	2.03	0.33	0.04	Crustacean
Intestine	0.84	0.18	0.09	Crustacean
Stomach	5.14	0.85	0.03	Bivalve foot
Intestine	2.38	0.64	0.44	Ophiuroid, Crustacean

Table 6.8. Summary of ash content of diet from the stomach and intestinal regions of the alimentary canal of a 20 cm dab from present survey

Gut Area	Sample Size (n)	Total Fresh weight (g)	Total Dry weight (g)	Total Ash weight (g)	Ash % dw ⁻¹
Stomach	9	17.17 ± 0.59	3.16 ± 0.01	0.86 ± 0.02	27.22
Intestine	9	14.88 ± 0.39	3.28 ± 0.06	1.81 ± 0.03	55.18

The bivalves contained the highest energy per g tissue whilst the echinoderms contained the least amount of energy per g among the selected food items of dab (Table 6.9) investigated for energy content studies.

Table 6.9. Energy content (\pm SE) in some natural diet components (selected prey taxons) from the survey area

Prey items	Fresh weight (g)	Dry weight (g)	Dry weight (%)	Energy kcal g ⁻¹ dw
<i>Amphiura brachiata</i>	5.30	2.56	48.43	1.64 \pm 0.02
<i>Liocarcinus depurator</i>	7.27	2.36	32.46	2.65 \pm 0.08
<i>Ensis ensis</i>	4.12	0.99	27.03	4.83 \pm 0.04
<i>Nereis sp.</i>	1.99	0.44	22.11	3.73 \pm 0.07
<i>Hydroid</i>	1.26	0.50	39.68	3.33
<i>Brown algae</i>	3.11	1.04	33.44	3.55 \pm 0.26
Average \pm SE	3.84 \pm 0.83	1.32 \pm 0.34	33.86 \pm 3.47	3.29 \pm 0.36

It has been shown in Chapters 2 and 4 that mature dab lose weight after spawning in comparison with the previous autumn. Appropriate calculations are now possible to estimate how the demands of metabolism, activity and gamete production are met from feeding and by utilization of body reserves during this period.

In Tables 6.10-6.12 (females) and 6.13-6.15 (males) such calculations are made based on a 20 cm fish since this is the most abundant length class in the samples. In each case, the energy lost as gametes and from depletion of carcass and liver reserves is added to the energy required for routine metabolism. Some energy will be gained from the digestible fraction of the food ingested in this period.

In both cases, estimated food intake and depletion of reserves is adequate for routine metabolism and spawning products.

There appears to be a relatively larger excess energy availability for males. This could be explained on the basis of the observation that the males have extended spawning season and thus the testes may be a "dynamic pool" with constant release and replacement of sperm, a phenomenon common in multiple spawners.

Tables 6.10-6.15. Changes in energy level in a standard 20 cm dab

A. Female

Table 6.10. Changes in energy level in a standard 20 cm female

a) The energy lost as eggs between February and June:

Ovary energy content in February 1999:	19.46 kcal
Ovary energy content in June 1999:	<u>0.50 kcal</u>
Energy lost:	<u>18.96 kcal</u>

b) The energy lost from the liver between October and April :

Liver energy content in October 1999:	7.65 kcal
Liver energy content in April 2000:	<u>1.16 kcal</u>
Energy lost:	<u>6.49 kcal</u>

c) The energy lost from the carcass between October and April:

Carcass energy content in October 1999:	99.13 kcal
Carcass energy content in April 2000:	<u>54.08 kcal</u>
Energy lost:	<u>45.05 kcal</u>

Table 6.11. Summary of the calculation for the energy requirement during spawning season for the female dab:

Month/Year	Total weight (g)	Resting O ₂ consumption ml hr ⁻¹ at 10°C	O ₂ consumption at 8°C	Cal hr ⁻¹	Total Metabolism kcal/mth
November 1999	86.90	8.78	7.24	33.51	24.13
December 1999	84.89	8.65	7.13	33.00	23.76
February 2000	97.00	9.45	7.79	36.06	25.96
Total					73.85

Routine metabolism: 1.25 x 73.85 kcal = 92.31 kcal

SUMMARY FOR FEMALE:

A.

The metabolic energy utilised in winter =	92.31 kcal
Total energy required in spawning =	<u>18.96 kcal</u>
Total	<u>111.27 kcal</u>

B.

The usable energy reserves (the difference between high and low condition) in carcass and liver (45.05+6.49 kcal in Table 6.10): 51.54 kcal

Thus the total energy requirement for the cold season is much higher than that stored in the carcass and liver. The extra energy required must therefore be obtained from food intake during the winter period.

Energy level from food intake in 20 cm female dab in winter:

The estimated daily food intake from the present study (Chapter 5) for female dab is = 0.817 g (wet weight). The equivalent dry weight conversion is 33.86 % (Table 6.9), which is = 0.280 g dry weight.

Since natural dry foods of dab contain an average 3.29 kcal g⁻¹ (Table 6.9), it can thus be estimated that a 20 cm female dab consumes 82.91 kcal during the winter period. Only 80 % of this is however assimilated (Gwyther, 1978), which gives 66.34 kcal.

Thus for the female dab, the partial energy budget is constructed as follows:

Table 6.12. Summary of energy budget for a 20 cm female dab

<u>Energy source:</u>		<u>Energy requirement:</u>	
Food intake	66.34 kcal	Routine Metabolism	92.31 kcal
Usable body reserves (Carcass and Liver)	51.54 kcal	Gonad development	18.96 kcal
Total:	117.88 kcal	Total:	<u>111.27 kcal</u>

Thus there is an excess energy of (117.88 -111.27) kcal = 6.61 kcal in winter which could be used to support other activities.

B. Male

Table 6.13. Changes in energy level in a standard 20 cm male dab:

a. The energy lost from testes between November and July:

Testes energy content in November 1999:	0.81 kcal
Testes energy content in July 2000:	<u>0.11 kcal</u>
Energy lost:	<u>0.70 kcal</u>

b. The energy lost from the liver between September and April:

Liver energy content in September 1999:	4.62 kcal
Liver energy content in April 2000:	<u>0.61 kcal</u>
Energy lost:	<u>4.01 kcal</u>

c. The energy lost from the carcass between October and April:

Carcass energy content in October 1999:	89.56 kcal
Carcass energy content in April 2000:	<u>43.15 kcal</u>
Energy lost:	<u>46.41 kcal</u>

Table 6.14. Energy requirement for basal metabolism in a 20 cm male fish:

Month/Year	Total weight (g)	Resting O ₂ consumption ml hr ⁻¹ at 10°C	O ₂ consumption at 8°C	Cal hr ⁻¹	Total Metabolism Kcal/mth
November 1999	77.64	8.15	6.72	31.09	22.39
December 1999	79.50	8.28	6.82	31.59	22.74
February 2000	70.86	7.67	6.32	29.25	21.06
Total					66.19

Routine metabolism: 1.25 x 66.19 kcal = 82.74 kcal

SUMMARY FOR MALE:

A.

The metabolic energy utilised in winter = 82.74 kcal
 Total energy required in spawning = 0.70 kcal

Total 83.44 kcal

B.

The usable energy reserves (the difference between high and low condition) in carcass and liver (46.41+4.01 kcal in Table 6.13): 50.42 kcal

Thus the energy requirement for the cold season is higher than that in the carcass and liver. The extra energy required must therefore be obtained from food intake during the winter period.

Energy level from food intake in a 20 cm male dab in winter:

The estimated daily food intake from the present study male dab is = 0.758 g (wet weight). The equivalent dry weight value is 33.86 %, which is = 0.257 g dry weight.

Since natural dry foods contain 3.29 kcal g⁻¹, it can thus be estimated that a 20 cm male dab consume 76.10 kcal during the winter period. Only 80 % of this are however assimilated, which gives 60.88 kcal.

Thus for the male dab, the partial energy budget is constructed as follows:

Table 6.15. Summary of energy budget for a 20 cm male dab

Energy source:		Energy requirement:	
Food intake	60.88 kcal	Routine Metabolism	82.74 kcal
Usable body reserves (Carcass and Liver)	50.42 kcal	Gonad development	0.70 kcal
Total:	111.30 kcal	Total:	<u>83.44 kcal</u>

Thus there is an excess energy of (111.30 -83.44) kcal = 27.86 kcal in winter which could be used to support other activities.

6.4 DISCUSSION

The biochemical composition and energy content of a fish is governed by the quality and quantity of ingested food as well as necessary energy expenditure, typically measured indirectly by oxygen consumption (Flowerdew and Grove, 1980). It is now a known fact that lipid energy reserves are important for adult fish. Fat is an easily mobilised energy reserve which can be used for activity during spawning when the energy uptake is extremely low (Jonsson and Gravem, 1985; Jonsson and Jonsson, 1998). The liver is generally regarded as the primary site of stored lipid reserves in fish (Kjesbu *et al.*, 1991; Hemre *et al.*, 1993). In cod, only about 1 % of the wet weight of the muscle tissue consists of lipid (Lie *et al.*, 1988), compared to more than 50 % in the liver. Lipid reserves are utilised during periods of food limitation and during the annual period cycle of gonad maturation (Yaragina and Marshall, 2000). Henderson *et al.* (1996) observed that visceral fat may constitute the bulk of surplus energy that is allocated for reproductive activity in the Walleye (*Stizostedion vitreum*). This interpretation was based on the fact that ovarian lipid levels increased as visceral fat levels declined. The decline in visceral fat levels was associated with most of the increase in ovarian size and ovarian energy density. Henderson *et al.* (1996) reported that the variation in liver size was due to the allocation of lipids to the ovary, which suggests the liver is the conduit for the transfer of lipids from the visceral deposits to the ovary. Tveiten *et al.* (1998) pointed out that lipid stores are important for maintenance of the maturation process in fish and that rates of deposition of energy reserves are crucial to the timing of reproduction. A similar observation was made by Simpson (1992) for *Salmo salar L.* In salmonids, for example, energy stores and rates of energy acquisition during spring are important determinants whether or not an individual will mature in the following autumn (Dutil, 1986).

However, flatfish do not have visceral deposits as lipids like those found in the salmonids. In dab, fat is primarily stored in the liver. The significance of lipids as storage products is obvious from this study on dab in the seasonal cycle of lipid concentrations in the female liver, ranging from about 25-30 % in the spring (March-April, 1999) to about 69 % towards the end of summer in September. This suggests that the lipid levels are built up as food reserves in the liver during the summer months, which coincides with the period of intensive feeding. These reserves appear to be utilised during the peak spawning season (December-February), resulting in a significant decline in the lipid concentration in the liver during the post-spawning months (March-April). With increasing food intake towards the end of spring in May, the lipid concentration rises sharply to a peak in September. With a decline in feeding rate in autumn (October) and with the onset of gametogenesis, the lipid concentration in the female liver declines gradually, from 59.8 % to 30.2 % between October 1999 and April,

2000. This sequence of events supports the observation that the lipid reserves in the liver are utilised during reproductive activity. Saborowski and Buchholz (1996) showed a distinct seasonal cycle in the lipid content of the dab liver with the maximum in summer and the minimum in spring. Maximal values in males were similar to those of females and appeared at similar times. The lipid content in the muscle did not vary significantly between seasons. Saborowski and Buchholz also attributed the rise in lipid concentration after winter to increased feeding activity in late spring with the availability of sufficient food supply. They however added that the elevation of food conversion rate in mature dab in late spring, due to temperature rise, could contribute significantly to the progressive accumulation of lipids. The sharp rise in Stomach-Gut Index and the increase in daily food ration in May in the medium to large size groups of dab in this study support this observation of active feeding in late spring and early summer. The lipid concentrations in the liver (per dry weight) in the spawning season (December-February) were observed to be lower in the female dab than the male dab in both 1999 (Male; 44.5 %; Female 37.4 %) and 2000 (Male: 44.2 %; Female: 40.4 %). Saborowski and Buchholz (1996) made similar observations and they suggested that this could reflect the elevated nutrient requirements for ovary maturation compared to the maturation of the testes. This observation might also explain the reason for the relatively higher excess energy remaining after spawning in the males, as compared to the females, as derived in the energy allocation model.

Purchase and Brown (2001) noted much of the energy stored in cod is lipid in the liver. They concluded therefore that fish with higher hepatosomatic indices have more lipid reserves. They found that the water content of the liver can be used as an inverse measure of lipid storage; as lipids are metabolised they are replaced by water. Lambert and Dutil (1997) found that muscle energy content in cod ranged from 5 kJ g⁻¹ for muscle of 78 % water, to 1.5 kJ g⁻¹ for muscle of 90 % water. Jonsson and Jonsson (1998) also observed that the percentage water content in fish is a good indicator of the relative amount of energy, proteins and lipids. The lower the water content, the greater the lipid concentration and higher the energy density. Flowerdew and Grove (1980) also found a negative correlation between water content and lipid content. Poor feeding or starvation in winter tends to cause a lower lipid level and a higher water content. This study also found an inverse correlation between lipid composition and water content in the female ($r=-0.781$, $P<0.05$, $N=18$) and male livers ($r=-0.773$, $P<0.05$, $N=16$). For instance, in the female liver, there is a gradual decline in the water content from late spring in May 2000 (72.5 %) to autumn in October 2000 (57.4 %). This coincides with a relative rise in lipid weight per unit mass within this period (from 556 mg g⁻¹ to 638 mg g⁻¹). This increase in lipid levels also result in the rise in the energy density within this period, ranging from 7.52 to 8.07 kcal g⁻¹ dw of liver tissue. This observation is

also true for the female gonad. As the water content reduces during oogenesis to its lowest in February (67.9 %), the energy content per unit mass of the ovary also rises to its highest level (6.82 kcal g⁻¹).

In contrast to the liver, there are no marked seasonal changes in percentage lipid concentration (per dry weight) in the carcass between winter and summer. There is high variability in the lipid composition of the male and female carcass, which tends to blur any seasonal pattern. The seasonal percentage concentration in the carcass ranges from 5.1 to 16.4 % in females and from 4.6 to 11.4 % in males. Saborowski and Buchholz (1996) also found that the lipid content in the carcass did not vary significantly between winter and summer in the North Sea. This may suggest that there may not be any distinct transfer of carcass lipids into other organs. But the carcass forms a much larger organ than the liver and in terms of gross lipid concentration, it may play a significant role as a source of food (and energy) reserve, as has been illustrated in the energy budget allocation for dab in this chapter. Dawson and Grimm (1980) estimated the maximum lipid concentration (per dry weight) in the liver and carcass of plaice during summer as 62.9 % and 18.0 % respectively. But in view of the relatively smaller size of the liver, they noted that the contribution of the liver to the total energy reserves is almost insignificant. They therefore concluded that the principal energy reserve is fat in the carcass and not in the liver. The significance of this observation is supported in this study by the relatively low usable energy reserve in the female liver during the reproductive season (6.49 kcal), compared to 45.05 kcal in the female carcass. This study has estimated that the female dab derives 66.34 kcal energy from food intake, to complement its total energy requirement for reproduction, swimming, searching for food and other activities.

It emerges from this study that the energy requirements for oogenesis (18.96 kcal) and spermatogenesis (0.70 kcal) are comparatively small and that the bulk of the energy is being utilised for routine metabolism, 92.31 kcal and 82.74 kcal for female and male respectively. Bakhsh (1982) made similar observations. Female dabs allocate substantially more into liver and gonad weight than males during the peak breeding season. For a 20-cm female, peak gonad weight was 11.2 times larger than a male of similar size, reflecting a substantial 18.4 % more investment when expressed as GCR. Female peak liver weight was 1.6 times larger than the male liver, with 3.8 % more investment as indicated by the HCR. The largest carcass weight of the female was about 10 % larger than male carcass weight. Huber and Bengston (1999) studied the energy allocation in *Menidia menidia* and *Menidia beryllina* and also concluded that the females invest more into liver and gonad growth than the males. Roff (1984) reported that the cessation of growth during the reproductive season may occur when

the energy demand for reproduction exceeds the available energy supply. In dab there is a significant reduction in carcass weight during the post-spawning period in spring and a rapid increase in early summer. In autumn the dab accumulates reserves in the liver and carcass. Stored reserves are utilised through the winter and reach a minimum in March-April, when the liver and carcass are depleted resulting in the poor condition of the fish.

The ash content has an inverse relationship with the lipid and energy levels in the liver and gonad. The higher the lipid and energy contents in the summer and autumn, the lower the ash content in the female liver. Saborowski and Buchholz (1996) pointed out that the storage of nutrients is not related only to the amount of ingested food but should also be reflected in the proximate composition of the prey. Thus in terms of energy contents, the bivalves provide large amounts of energy per g in the food of dab, though it frequently contains ophiuroids (which provide very low energy per g in food of dab). The low calorific value of ophiuroids was also highlighted by Temming and Hammer (1994). The study showed that in spite of being the dominant prey species by all size groups, the ophiuroid, *Amphiura brachiata* is a low energy diet component (1.64 kcal g⁻¹). This observation could probably be explained on the basis of the studies by Grove *et al.* (1978) and Ruohonen and Grove (1996), which postulated that fish increase feeding frequency and food intake as diet energy content decreases. This observation could more possibly be explained on the optimum foraging theory (J. Davenport, pers. comm.); that is the relatively high abundance of this species in the study area could be a cause for its preponderance in the diet.

Growth and reproduction are important components of fitness and are therefore worthy of discussion in relation to energy mobilization. In fish growth is of particular significance as fecundity is generally an increasing function of body size (Wootton, 1979). Energy channelled into gonads detracts from somatic growth and future fecundity (Ware, 1982). Thus there is a trade-off between growth and reproduction. Energy in excess of maintenance requirements may be channelled into somatic or reproductive tissues (Roff, 1983). This surplus energy can therefore be measured as the increase in weight of the somatic and gonadal tissues (Ware, 1980).

The next chapter contains summary and conclusions of the present study, including suggestions for future research.

CHAPTER SEVEN

SUMMARY AND CONCLUSIONS

7.1 INTRODUCTION

The primary objective of this study was to carry out population studies on dab on the North Wales Coast over a 3-year academic period, 1998-2001. Towards the realisation of this objective, a two-pronged sampling programme was instituted: 1) Sampling surveys onboard the University Research Vessel *Prince Madog* and 2) Sampling from commercial fishing trawlers. Samples from the survey programme were used to derive estimates of population size and parameters (stock number, growth, mortality, length and age at maturity). Samples from 24-hour fishing survey were also used to determine gastric evacuation rates and food consumption estimates. Samples from the commercial fisheries were used to complement survey data in the study of seasonal variation in GCR, HCR, K, lipid, energy, ash composition, diet studies and length and weight relationships.

The history of exploitation of the dab stocks in the study area has been followed from the analyses of 34-year historical survey data, 1966-2000.

The aim of this chapter is to summarise the outcome of the present investigation and make suggestions for future research.

7.2 Population Size and Stock Identity

The total estimated population number of dab in the present study area was about 2.34×10^6 . When the 0- and 1-year old groups are omitted from this estimate due to mesh selection problems, the estimate becomes 1.36×10^6 . An earlier estimate in the survey area made from samples collected 20 years ago, which omitted the 0- and 1-groups, was 1.20×10^6 . Thus the population does not appear to have changed significantly over this period. The 2-year old fish have been the dominant year class between 1966-2000. The present study also demonstrated seasonal and diurnal variations in catch rates. The catch rate in autumn-summer was higher than in early spring-winter. For example, in February 2000 (42 hr^{-1}) and July 2000 (141 hr^{-1}). It is also shown that catch rates were significantly higher at night-time than daylight. The average catch rates in November and July ranged $17\text{-}167 \text{ hr}^{-1}$ and $77\text{-}210 \text{ hr}^{-1}$ respectively in daylight (22:00-14:00 hr). In contrast, the catch rate at

night (22:00-02:00 hr) ranged 575-1549 hr⁻¹ and 577-997 hr⁻¹ in November and July respectively. There is a decline in the catch rates of dab with increasing depths and they were virtually absent from the trawl catches at depths of ≥40 m. There was seasonal variation in sex ratio, with females being more dominant in autumn. The long-term sex ratio (F: M) in autumn and spring was 1.83: 1 and 1.15:1 respectively.

There was no significant difference in anal fin, dorsal fin, caudal fin and vertebral counts between male and female dab in the study area nor with a previous survey, Bakhsh (1982). The studies of body proportions in male and female dab suggest significant difference in the multiplicative factors for predicting either head length or body depth from total length of the fish.

Head length versus total length (TL) in cm:

$$\text{Male:} \quad \text{Head length} = 0.214 \times \text{TL}$$

$$\text{Female:} \quad \text{Head length} = 0.210 \times \text{TL}$$

Body depth versus total length in cm:

$$\text{Male:} \quad \text{Body depth} = 0.366 \times \text{TL}$$

$$\text{Female:} \quad \text{Body depth} = 0.378 \times \text{TL}$$

The annual growth in weight (W) in relation to length was nearly isometric ($b \approx 3.0$) for both male and female dab:

$$\text{Male:} \quad W = 0.012 \times \text{TL}^{2.913}$$

$$\text{Female:} \quad W = 0.009 \times \text{TL}^{3.036}$$

There were however seasonal variations in the length and weight relationships. After spawning, the growth in weight in relationship to length becomes negatively allometric ($b \ll 3.0$) in March and April due to the poor emaciated condition of the fish as result of spawning and low feeding rate in the spawning season. After resumption of active feeding in late spring and summer, the growth in weight in relation to length becomes either isometric ($b \approx 3.0$) or positively allometric ($b \gg 3.0$) between July and September. There were significant differences in the coefficients of length and weight relationships between males and females

in October, November and February, principally attributed to differential rates of gametogenesis between the two sexes.

7.3 Growth and Mortality Rates

The 1st April was determined as 'birthday' of the dab from the study of seasonal deposition of opaque zone on the edge of the otolith. The study also shows that the greatest deposition of the growth zone (opaque) was in late spring-summer and this event coincided with a large increase in the length of dab. The observed mean length at age in February-March tends to be smaller possibly due to spawning migration and the arrivals of new recruits into the fishery.

There has been relative stability in the mean lengths of the younger stages of both the male and female dab (1,2 and 3 years old) between 1966-2000. There were however fluctuations in the mean length of the older fish (≥ 4 years), but these were based on smaller samples.

There were seasonal differences in the parameters of the Von Bertalanffy growth functions. The autumn values are shown below.

Von Bertalanffy growth equations for male and female dab

Male:

$$L_t = 26.2 \left[1 - e^{-0.36(t+0.66)} \right] \text{----- 1999}$$

$$L_t = 25.7 \left[1 - e^{-0.30(t+1.53)} \right] \text{----- 2000}$$

Female:

$$L_t = 33.2 \left[1 - e^{-0.29(t+0.77)} \right] \text{----- 1999}$$

$$L_t = 33.4 \left[1 - e^{-0.25(t+1.55)} \right] \text{----- 2000}$$

The estimated long-term average total mortality rate was significantly higher in the male (1.95 yr^{-1}) than the female dab (1.16 yr^{-1}). The range of the estimated natural mortality rate (M) was ($0.47\text{-}0.53 \text{ yr}^{-1}$) and ($0.39\text{-}0.53 \text{ yr}^{-1}$) in males and females respectively. Thus, based on the estimated average long-term total mortality rates (Z), the fishing mortality rates (F) can be suggested as $1.42\text{-}1.48 \text{ yr}^{-1}$ and $0.63\text{-}0.77 \text{ yr}^{-1}$ for the male and female dab respectively.

This suggests that the fishing mortality rate had been significantly higher on the male population than the females.

7.4 Reproductive Biology

There were cyclical cycles in the gonad weight, liver weight and condition factors, with distinct reproductive seasons for both sexes. The onset of gametogenesis begins a month earlier in the male than female dab. The peak spawning activity (maximum testes weight) in the males occurs in January whilst it occurred in February (maximum ovary weight) in the females. The maximum testes weight for the 16-20 cm male was 1.01 g (GCR = 1.8 %) in January. In the 16-20 cm female, the maximum ovary weight was 9.77 g (GCR = 17.1 %) in February. Based on the present study, the reproductive season for dab on the North Wales Coast was classified as follows:

Period	Stages	Female	Male
Pre-spawning*	Ripening	November-December	October-November
Spawning	Ripe	January-March	December-January
Post-spawning	Spent	April-May	February-June
Resting	Inactive	June-October	July-September

*Onset of gametogenesis

The condition factors were nearly identical for both sexes during the non-reproductive season. The maximum condition was observed in the summer (July-September) and was 1.01 and 1.07 for the males and females respectively. The minimum condition factor was observed in April and was 0.67 and 0.72 for the 16-20 cm male and female dab respectively.

In the 16-20 cm female dab, the maximum weight of the liver was in January (2.23 g; HCR=3.0 %). The minimum liver weight was in April (0.80 g; HCR=1.7 %). In the 16-20 cm male dab, however, the maximum liver weight was in August (1.94 g; HCR= 2.9 %) and the minimum also in April (0.34 g; HCR=0.7 %).

The maximum average egg diameter (0.56-0.67 mm) was observed in a fully ripe ovary of a 20 cm fish between January-February. After spawning in March, the average egg diameter declined to a minimum (0.10-0.22 mm). The total estimated egg production in the study area was 2.47×10^{11} eggs. The average egg production per mature female was estimated as

3.51 x 10⁵ eggs. There is a decline in relative fecundity from the youngest fish aged 1 year (3045 eggs g⁻¹) to the oldest fish aged 8 years (1917 eggs g⁻¹). The following relationships were established between fecundity and total length, somatic weight and gonad weight:

Variables	Relationship	P
Fecundity-Total length	F= 41.6 TL ^{2.86}	0.0001
Fecundity-Somatic weight	F= 4804.3 SW ^{0.88}	0.0001
Fecundity-Gonad weight	F= 172819 OV ^{0.28}	0.0051
Relative fecundity-Age	F= 3317.5-145*A	0.0146

The average length (20 cm) and age (2.7 years) at 50 % maturity in the female dab have remained relatively stable between 1976-2000. Although the length at 50 % maturity for the male was about 17 cm, the age at 50 % maturity has declined gradually from about 2 years to about 1.5 years over this period.

Estimated length and age at 50 % maturity in dab, autumn 1999-2000

Year	Male		Female	
	L _{50%} cm	A _{50%} yr.	L _{50%} cm	A _{50%} yr.
1999	14.43 ±0.54	1.42 ±0.11	18.33± 0.93	2.14± 0.09
2000	13.28 ±0.14	1.27 ±0.08	18.03± 0.14	2.36± 0.19

Long-term average length and age at 50 % maturity, 1976-2000

1976-2000	17.00 ±3.10	1.72 ±0.37	20.44 ±2.47	2.68 ±0.67
-----------	-------------	------------	-------------	------------

As oogenesis progresses in a 20 cm fish, the water content in the ovary declined significantly in winter, probably as a result of yolk deposition and increase in lipid content (and energy). This relationship is illustrated in a regression analysis of % water content against % ash content, and % water against energy content (kcal g⁻¹ dw) in a mature 20 cm dab ovary.

Relationship between % water content against % ash content and energy content (kcal g⁻¹) per dry weight of ovary:

$$\% \text{ Ash} = -4.56 + 0.144 * \% \text{ water}, \quad r=0.735, N=18, P<0.05$$

$$\text{Energy} = 8.472 - 0.038 * \% \text{ water}, \quad r=-0.587, N=18, P<0.05$$

7.5 Feeding Ecology

Five major taxonomic groups dominated the diet of dab in the present study: the ophiuroids, bivalves, crustaceans, polychaetes and hydroids. The ophiuroid, *Amphiura brachiata*, was the dominant species in the diet of all size groups. However, the study suggests size-selective preference for some prey groups. The contribution of the polychaetes to the total diet declines with increasing size of the fish; 22.9 % by weight in the 11-15 cm length group to 5.7 % in the 26-30 cm length group. On the contrary, the bivalves increase in proportion in the diet with increasing size of the fish, from 11.2 % (by weight) in the 11-15 cm group to 31.4 % (by weight) in the ≥ 31 cm group. There is a significant ($C \geq 0.60$) diet overlap between the size groups of dabs. This has been related to the dominance of the ophiuroid (*Amphiura brachiata*), the polychaete (*Lagis koreni*), the bivalves (*Angulus sp.* and *Abra alba*) and the crustacean (*Liocarcinus depurator*) in the diet of all sizes. Diet diversity increased from 0.97 in the small size dab (11-15 cm) to a peak at 1.23 in the medium dab (21-25 cm); it however declined to lower levels (1.04 and 0.96) in the larger and largest size groups (26-30 cm and ≥ 31 cm length groups respectively). The diet breadth becomes broader from 3.86 in the small size group to a peak (5.27) in the medium size group (21-25 cm); it narrows down to 4.84 and 3.99 in the 26-30 cm and ≥ 31 cm groups respectively. There were significant differences in Diet Evenness between the size groups. The diet was more even in the smallest group 11-15 cm (0.62) and the largest group ≥ 31 (0.82) than the medium groups (16-20 cm, 0.54; 21-25 cm, 0.44) and larger group 26-30 cm (0.60). Thus there is an inverse relationship between diet evenness and diet diversity and also between diet evenness and diet breadth.

In general, the daily food intake in dab was higher in the warmer months, late spring and summer, than autumn-winter. For instance, in May 2000, it was estimated that female dab in length groups 21-25 cm and 26-30 cm consume 1.492 g and 4.612 g food per day respectively. In February, however, female dab of similar length groups consume 0.520 g and 1.760 g per food per day respectively. Though the average stomach contents were generally higher in the spring-summer period than autumn-winter, there were no significant differences in most cases. Similarly, though the average stomach contents were generally higher in the female than the male, there were usually no significant differences between them.

7.6 Lipid Composition and Energy Allocation

An investigation into the biochemical composition of the gonad, liver and carcass of an average 20 cm male and female fish was undertaken. There were distinct seasonal changes in the lipid and energy composition in the liver of both sexes. The lipid composition per gram dry weight of liver was significantly higher in the summer and autumn period. The maximum lipid content in the liver was 61.8 % and 69.3 % in the male and female livers in September respectively. In both sexes, the lipid content in the liver declined sharply as a result of spawning in the spring, reaching minimum levels in April (28.2 %) and March (24.3 %) in the male and female respectively.

The study found an inverse relation between lipid composition (%) and water content in the livers of both sexes:

$$\begin{array}{ll} \text{Male liver:} & \% \text{ water} = 97.611 - 0.474 * \% \text{ Lipid} \quad r = -0.773, n=17, P < 0.05 \\ \text{Female liver:} & \% \text{ water} = 91.684 - 0.440 * \% \text{ Lipid} \quad r = -0.781, n=18, P < 0.05 \end{array}$$

The cyclical changes in energy content per gram dry weight of the liver follows similar pattern as the lipid composition. The energy content per gram dry weight of the liver was at a peak in October (8.50 kcal g⁻¹ and 8.61 kcal g⁻¹) in male and female respectively. After spawning in the spring, the energy content in the liver declined to 6.18 kcal g⁻¹ (April) and 5.86 kcal g⁻¹ (March) in the male and female respectively. The relationship between energy (kcal g⁻¹) and water (%) in the liver is given below:

$$\begin{array}{ll} \text{Male liver:} & \text{Energy} = 12.381 - 0.064 * \% \text{ water} \quad r = -0.609, n=17, P < 0.05 \\ \text{Female liver:} & \text{Energy} = 13.326 - 0.085 * \% \text{ water} \quad r = -0.718, n=18, P < 0.05 \end{array}$$

The significance of lipid as a source of energy is illustrated by the significant correlation between lipid composition and energy content in both male and female livers given in the following relationships:

$$\begin{array}{ll} \text{Male liver:} & \text{Energy} = 5.271 + 0.050 * \% \text{ lipid} \quad r = 0.768, n=17, P < 0.05 \\ \text{Female liver:} & \text{Energy} = 4.494 + 0.059 * \% \text{ lipid} \quad r = 0.888, n=18, P < 0.05 \end{array}$$

The regression relationship between % ash and % lipid in the liver is given by the following equations:

$$\begin{array}{ll} \text{Male liver:} & \% \text{ Ash} = 10.671 - 0.138 * \% \text{ lipid} \quad r = -0.765, n=16, P < 0.05 \\ \text{Female liver:} & \% \text{ Ash} = 10.524 - 0.129 * \% \text{ lipid} \quad r = -0.750, n=18, P < 0.05 \end{array}$$

The regression relationship between % ash and energy (Kcal g⁻¹) in the liver is given by the following equations:

Male liver:	% Ash = 9.026 - 0.342 * Energy	r = -0.897, n = 16, P < 0.05
Female liver:	% Ash = 8.683 - 0.317 * Energy	r = -0.814, n = 18, P < 0.05

Seasonal variation in energy content per gram in the gonad and carcass is not as dramatic as in the liver. The relatively small size of the testis (1.4 g; 2.1 % GCR) and the huge size of the ovary (15.7 g; 20.2 % GCR) at the peak of spawning season showed that reproductive investment is much lower in the males than the females. However, in view of the larger mass of the carcass, it has been concluded in this study that the bulk of the energy required for reproductive effort is obtained from the carcass and food intake. It is estimated that female dab obtained 45.1 kcal and 66.3 kcal gross total energy from the carcass and food respectively and this is more than sufficient to meet the total requirement (111.3 kcal) for routine metabolism and gonad development. In comparison to the carcass and food intake, the total energy gained from the liver is estimated as 6.5 kcal. In the male also, the energy requirement (83.4 kcal) for routine metabolism and gonad development is also mainly obtained from the carcass (46.4 kcal) and food intake (60.9 kcal). The liver contributes only 4.0 kcal.

7.7. Constraints and Future Research

The present work is a result of research investigations conducted on the population ecology of dab on the North Wales Coast during a three-year period. The main constraint was the difficulty in having the University Research Vessel *Prince Madog* to conduct regular monthly sampling activity. Clearly, this was not possible in view of the demands by other departments of the University on the vessel's ship time. This necessitated parallel sampling from the commercial fisheries. The obvious disadvantage of having samples from the commercial sector is that the samples are likely to be biased, since the fishermen invariably target commercial sized fish that will fetch them decent income in the market. Also, regulation on minimum size limit requires them to land only bigger fish. Thus, the fish in the size category 11-15 cm were usually missing in samples from the commercial fisheries and could not be therefore adequately studied on a continuous seasonal basis.

A major extension of this work is to use the estimated parameters as input parameters in virtual population analysis (VPA), or cohort analysis, and the yield per recruitment analysis. A major requirement for these analyses will be the availability of accurate data of total landings

of dab in the study area. The VPA analysis will give fishing mortality (F-array) per age groups and thus give the fishing pattern (or strategy) on the stock. The yield per recruit analysis will estimate the total stock size (biomass) and also the optimum fishing effort requires for maximum sustainable yield. The VPA result is also useful in detecting whether there is selective fishing on the juveniles (immature) or the spawning stock, which might be useful for management intervention by way of mesh size regulation, sanctuary or close season for protecting the resources from either growth or recruitment overfishing. Finally, such VPA could estimate levels of recruitment over time and help establish whether the apparent stability of the dab population is supported.

Also, due to the constraints on the availability of the research vessel, the study on benthos composition and abundance is conducted only in the autumn (October). Ideally, to be able to relate the benthos abundance to the diet of the dab, it would be worthwhile to conduct a seasonal study on the composition of the benthos in the survey area. It is hoped that the study may explain the seasonal variability in the composition of the diet.

The seasonal composition of the liver and carcass has been conducted essentially predicated on the premise that the lipid is the main source of energy in fish. However, this study can be extended further to investigate the role of glycogen in energy mobilization mechanism in dab.

8.0 REFERENCES

- Adams, S. M. (Ed)(1990). Biological Indicators of Stress in Fish (*Am. Fish. Soc. Symp. 8*), American Fisheries Society, Bethesda, MD.
- Adams, S. M., R. B. McLean and J. A. Parrotta (1982). Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. *Trans. Am. Fish. Soc.* **111**(5): 549-558
- Adlerstein, S. A. and H. C. Welleman (2000). Diel variation of stomach contents of North Sea cod (*Gadus morhua*) during a 24-hour fishing survey: an analysis using generalized additive models. *Can. J. Fish. Aquat. Sci.* **57**: 2363-2367
- Al-Hossaini, M. and T. J. Pitcher (1988). The relation between daily rings, body growth and environmental factors in Plaice, *Pleuronectes platessa* L., juvenile otoliths. *J. Fish Biol.* **33**: 409-418
- Ali, M. and R. J. Wootton (1999). Coping with resource variation: effect of constant and variable intervals between feeding and reproductive performance at first spawning of female three-spined Sticklebacks. *J. Fish Biol.* **55**: 211-220
- Anderson, K. P. and W. Ursin (1977). A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorous circulation and primary production. *Medd. Dan. Fish. Havnunders. N.S.7*: 319-435
- Anon., (1980). Report of the Ad Hoc working group on Multispecies Assessment Model Testing. *ICES C. M. 1980/G: 2*, 18 pp. (*mimeo*).
- Arntz, W. E. (1971). Die Nahrung der Kliesche, *Limanda limanda* (L), in der kieler Bucht-Berichte der Deutschen Wissenschaftlichen Kommission fur Meeresforschung **22**: 129-183
- Backiel, T. (1971). Production and food consumption of the predatory fish in Vistula River. *J. Fish Biol.* **3**: 369-405
- Bagenal, T. B. (1957a). Annual variation in fish fecundity. *J. Mar. Biol. Ass. U.K.*, **36**: 377-382
- Bagenal, T. B. (1957b). The breeding and fecundity of the long rough dab, *Hippogloissoides platessoides* (Fabr.), and the associated cycle in condition. *J. Mar. Bio. Ass. U.K.*, **36**: 339-375
- Bagenal, T. B. (1963). Variation in plaice fecundity in the Clyde area. *J. Mar. Biol. Ass. U. K.*, **39**: 391-399
- Bagenal, T.B. (1966). The ecological and geographical aspects of fecundity of plaice. *J. Mar. Biol. Ass. U.K.* **46**: 161-186

- Bagenal, T. B. (1969). The relationship between food supply and fecundity in brown trout, *Salmo trutta* L. *J. Fish Biol.* **1**: 167-182
- Bagenal, T. B. (1973). Fish fecundity and its relationship with stock and recruitment. In: B.B Parrish (ed.), Fish Stocks and Recruitment. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer.* **164**: 186-198
- Bagenal, T. B. (1974). Ageing of fish. *Unwin Hyman*, London
- Bagenal, T. B. (1978). Aspects of fish fecundity. In: Ecology of freshwater fish production (Gerking, S. D., ed.). pp75-101. *Blackwell scientific publication*
- Bagenal, T. B. and F. W. Tesch (1978). Age and Growth. In: Methods for assessment of fish production in freshwaters (T.B. Bagenal, ed.). 3rd Edition, pp 101-137. IBP Handbook No. 3, *Bulletin Scientific Publications, Oxford*
- Bagge, O. and E. Nielsen (1989). Changes in abundance and growth of plaice and dab in subdivision 22 in 1962-1985. *Rapp-P.V. Com. Perm. Int. Explo. Mer.* **190**: 183-192
- Bailey, K. M. (1994). Predation on juvenile flatfish and recruitment variability. *Neth. J. Sea Res.* **32(2)**: 175-189.
- Bajkov, A. D. (1935). How to estimate the daily food consumption of fish under natural conditions. *Trans. Am. Fish. Soc.* **65**: 288-289
- Bakhsh, A. A. (1982). Population studies of the flatfish *Limanda limanda* (L.) in Anglesey waters. *Ph.D. thesis, University of Wales*, 125 pp
- Banda, M. C. (1992). Age and growth determination of Chambo species from opercular bones. *GOM/FAO/UNDP Chambo Fisheries Research Project. FI:DP/MLW/86/013 Field Document 17.*
- Bannister, R. C. A. (1977). North Sea Plaice. In: Gulland, J. A. (ed.). Fish population Dynamics. *Wiley, Lon.* pp. 243-282.
- Barange, M., I. Hampton and B. A. Roel (1999). Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from Acoustic surveys. *S. Afr. J. Mar. Sci.* **21**: 367-391
- Barrett, J. and C. M. Yonge (1958). Collins pocket guide to the sea shore. *Collins, St. James Place, London.* pp. 272
- Basimi, R. A. (1978). Feeding and growth in an inshore population of plaice, *Pleuronectes platessa* L. *Ph.D. Thesis, University of Wales*
- Basimi, R. A. and D. J. Grove (1985a). Studies on the feeding, growth and reproduction of a recruited inshore population of *Pleuronectes platessa* L. at Anglesey, North Wales. *J. Fish. Biol.*, **27**: 765-783

- Basimi, R. A. and D. J. Grove (1985b). Estimates of daily food intake by an inshore population of *Pleuronectes platessa* L. off eastern Anglesey, North Wales. *J. Fish. Biol.*, **27**: 505-520
- Baxter, I. G. (1959). Fecundity of winter-spring and summer-autumn herring spawners. *J. Cons. Per. Int. Explor. Mer.*, **25**: 73:80
- Beacham, T. D. and C. B. Murray (1993). Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *J. Fish Biol.* **42**: 485-508
- Beddington, J. R. and J. G. Cooke (1983). The potential yield of fish stocks. *FAO Fish. Tech. Pap.* **247**: 47 pp.
- Begg, A. B., W. J. Overholtz and N. J. Munroe (2001). The use of internal otolith morphometrics for identification of haddock (*Melanogrammus aeglefinus*) stocks in Georges Bank. *Fish. Bull.* **99** (1): 1-14
- Bels, V. L. and J. Davenport (1996). A comparison of food capture and ingestion in juveniles of two flatfish species, *Pleuronectes platessa* and *Limanda limanda* (Teleostei: Pleuronectiformes). *J. Fish Biol.* **49**: 303-321
- Bergstad, O. A. (1991). Distribution and trophic ecology of some gadoid fish of the Norwegian Deep. 2. Food-web linkages and the comparisons of diets and distributions. *Sarsia* **75**: 315-325
- Beverton, R. J. H. (1964). Differential catchability of male and female plaice in the North Sea and its effect on estimates of stock abundance. *Rapp. Cons. Explor. Mer.* **155**: 103-112
- Beverton, R. J. H and S. J. Holt (1956). A review of methods for estimating mortality rates in fish populations, with reference to sources of bias in catch sampling. *Rapp. P. V. Reun. Int. Explor. Mer.* **140**: 67-83
- Beverton, R. J. H. and S. J Holt (1957). On the dynamics of exploited fish population. *Fish. Invest. Lond. Ser. 2*, **19**: 1-533.
- Beverton, R. J. H. and S. J. Holt (1959). A review of the lifespan and mortality rates in fish in nature, and their relation to growth and other physiological characteristics. In: CIBA foundation, colloquia on ageing. Vol. 5. The lifespan of animals, edited by G.E.W. Wolstenholme and M. O. O'Connor. *London, Churchill, Vol. 5*: 142-80
- Beyst, B., A. Cattrijsse and J. Mees (1999). Feeding ecology of juveniles flatfishes of the surf zone of a sandy beach. *J. Fish Biol.* **55**: 1171-1186
- Bohl, H. (1957). Di biologie der kliesche (*Limanda limanda* L.) in der Nordsee. *Ber. dtsh. Wiss. Komm. Meer.* **XVI**: 1-57

- Bolle, L. J., R. Drapper, J. I. J. Witte and H. W. Van der Veer (1994). The nursery grounds of dab (*Limanda limanda* L.) in the Southern North Sea. *Neth. J. Sea Res.*, **32(3/4)**: 299-307
- Braber, L. and S. J. de Groot (1973). The food of five flatfishes (*Pleuronectiformes*) in the Southern North Sea. *Neth. J. Sea Res.* **6**: 163-172
- Bregnballe, F. (1961). Plaice and flounder as consumers of the microscopic bottom fauna. *Medd. Dawn. Fisk. -og. Havunders.* **3**: 133-182
- Brett, J. R. and T. D. D Groves (1979). Physiological energetics. In: Hoar, W.S., Randall, D. J. and Brett, J.R. (Eds.). *Fish physiology, vol. VIII, pp. 279-352. New York, Academic Press.*
- Brett, J. R. and D. A. Higgs (1970). Effects of temperature on the rate of gastric digestion on fingerling sockeye salmon, *Oncorhynchus nerka*. *J. Fish. Res. Bd. Can.* **27**: 1767-1779
- Bromley, P. J. (1980). Effect of dietary protein, lipid and energy content on the growth of turbot (*Scophthalmus maximus* L.). *Aquaculture* **19**: 359-369
- Bromley, P.J., C. Ravier and P. R. Witthames (2000). The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawners. *J. Fish Biol.* **56**: 264-278
- Bulkley, R. V., V. L. Spykermann and L. E. Inman (1976). Food of the pelagic young of walleye and five species in Clear Lake Iowa. *Trans. Am. Fish. Soc.* **105**: 77-83
- Burd, A. C. and D. H. Cushing (1962). I. Growth and recruitment in the herring of the Southern North Sea. II. Recruitment of the North Sea herring stocks. *Fish. Invest.* **2**, **23(5)**: 71 pp.
- Burd, A. C and G. J. Howlett (1974). Fecundity studies on North Sea herring. *J. Cons. Int. Explor. Mer*, **35(2)**: 107-120
- Campana, S. E. (1984). Interactive effects of age and environmental modifiers on the production of daily growth increments in otoliths of plainfin midshipman, *Porishthys notatus*. *Fisheries Bulletin US* **82**: 165-177
- Campana, S. E. and J. D. Neilson (1985). Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.*, **42**: 1014-1032
- Campbell, A. C (1982). The hamlyn guide to the seashore and shallow seas of Britain and Europe. *Hamlyn Publishing Group Ltd. London. New York. Sidney. Toronto.* 320 pp.
- Campos, W. L., M. Kloppmann and H. V. Westernhagen (1994). Inferences from the horizontal distribution of dab, *Limanda limanda* (L.) and flounder, *Platichthys flesus* (L.) Larvae in the south-eastern North Sea. *Neth. J. Sea Res.*, **32(3/4)**: 277-286

- Carter, C. G. (1987). Food utilisation by plaice, *Pleuronectes platessa* L. and dab, *Limanda limanda* L. off eastern Anglesey in summer. *Unpublished M. Sc. thesis, University of Wales*. 135 pp.
- Carter, C. G., D. J. Grove and D. M. Carter (1991). Trophic resource partitioning between two coexisting flatfish species off the North Coast of Anglesey, North Wales. *Neth. J. Sea Res.* **27(3/4)**: 325-335
- Chapman, D. G. and D. S. Robson (1960). The analysis of a catch curve. *Biometrics*
- Charles, A. (2001). Sustainable fishery systems. *Fish and Aquatic Resources Series 5. Blackwell Sciences*. 370 pp.
- Chuenpagdee, R. (1990). Population studies of female plaice (*Pleuronectes platessa* L.) in Anglesey: sexual maturity, growth and mortality. *M.Sc. Thesis, University of Wales*. 71 pp.
- Claussen, T. (1988). Characteristic levels and spatial distribution of trace elements in flatfish (dab, *Limanda limanda* L.) from the German Bight and the southern North Sea. *Mitt. Geol.-Palaontol. Inst. Univ. Hamburg* **65**: 115-131
- Colwell, R. K and D. J. Futuyma (1971). On the measurement of niche breadth and overlap. *Ecology* **52(4)**: 567-576
- Costello M. J. (1990). Predator feeding strategy and prey importance: a new graphical analysis. *J. Fish Biol.* **36**: 261-263
- Coyle, T. (1998). Stock identification and fisheries management: the importance of using several methods in a stock identification study. *Australia Society for Fish Biology. Fish and Resource Management Association Stock*. pp.173-182
- Crecco, V. and W. J. Overholtz (1990). Causes of density-dependent catchability for Georges Bank haddock, *Melanogrammus aeglefinus*. *Can. J. Fish. Aquat.* **47**: 385-394
- Creech, S. (1992). A multivariant morphometric investigation of *Atherina boyeni* (Teleostei; Atherinidae): Morphometric evidence in support of the two species. *J. Fish Biol.* **41**: 341-353
- Crisp, D. J. (1971). Energy flow measurements. In: methods for the study of marine benthos (Eds; M.A. Holmes and A.D. McIntyre). *IBP Handbook No. 16. Blackwell Scientific Publications*. 334pp.
- Crisp, D. T., R. H. K. Mann and J. C. McCormack (1978). The effects of impoundment and regulation upon the stomach content of fish at Cow Green, Upper Teesdale. *J. Fish Biol.* **12**: 287-301.
- Cushing, D. H. (1981). Fisheries biology: A study in population dynamics. *The University of Wisconsin Press. 2nd edition*, 295 pp.

- Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **25**: 249-293
- Daan, N. (1973). A quantitative analyses of the food intake of North Sea cod, *Gadus morhua*. *Neth. J. Sea Res.*, **6**: 479-517
- Daan, N., P. J. Bromley, J. R. G. Hislop and N. A. Nielsen (1990). Ecology of the North Sea fish. *Neth. J. Sea Res.* **26**: 343-386
- Dawson, A. S. and A. S. Grimm (1980). Quantitative changes in the protein, lipid and energy contents of the carcass, ovaries and liver of adult female plaice, *Pleuronectes platessa* L. *J. Fish Biol.*, **16**: 493-504
- de Groot, S.J. (1971). On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces; Pleuronectiformes). *Neth. J. Sea Res.* **5**: 121-196
- de Veen, J. F. and L. K. Boerema (1959). Distinguishing southern North Sea populations of plaice by means of otolith characteristics. *Cons. Intern. Explor. Mer. Near Northern Seas Comm., Pap. No. 91*: 5 pp.
- Deniel, C. (1990). Comparative study of growth of flatfishes on the West Coast of Brittany. *J. Fish Biol.* **37**: 149-166
- Dethlefsen, V. (1984). Diseases in North Sea fishes. *Helgo. Meeresunters.*, **37**: 353-374
- Disbrey, B. D and J. H. Rack (1970). Histological laboratory methods. *E & S Livingstone, Edinburgh and London. Longman Group Ltd.*: 414 pp.
- Donaldson, E.M. (1977). Bibliography of fish reproduction 1963-1974 (3 parts): Research and resource services, 4160 marine drive, West Vancouver, British Columbia: *Fisheries and Marine Service Technical Report No. 732*
- Downing, J. A., C. Plante and S. Lalande (1990). Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aquat. Sci.* **47**: 1926-1936
- Dreves, T., V. Kadakas, T. Lang and S. Møllergaard (1999). Geographical variation in the age/length relationships in Baltic flounder (*Platichthys flesus*). *ICES J. Mar. Sc.* **56**: 134-137
- Durbin, E. G., A. G. Durbin, R. W. Langton and R. E. Bowman (1983). Stomach contents of Silver Hake, *Merluccius bilinearis*, and Atlantic Cod, *Gadus morhua*, and estimation of their daily rations. *Fishery Bulletin*, **81(3)**: 437-454
- Dutil, J.-D. (1986). Energy constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia* **1986**: 945-955

- Ebeling, A. W. and D. R. Laur (1986). Foraging in surfperches: Resource partitioning or individualistic responses? *Environ. Biol. Fish* **16**: 123-133
- Edwards, R. S., D. M. Finlayson and J. H. Steel (1969). The ecology of O-group plaice and common dab at Loch Ewe. II. Experimental studies on metabolism. *J. Exp. Mar. Biol. Ecol.* **3**: 1-17
- Edwards, R. S and J. H. Steel (1968). The ecology of O-group plaice and common dab at Loch Ewe. I. Population and Food. *J. Exp. Mar. Biol. Ecol.* **2**: 215-238
- Elliott, J. M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshwater Biol.* **2**: 1-8
- Elliott, J. M. and L. Persson (1978). The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.*, **47**: 977-993
- Ellis, T. (1994). Production and mortality of early life stages of flatfishes. *PhD thesis. University of Liverpool.*
- Ellis, T. and R. N. Gibson (1995). Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Mar. Ecol. Prog. Ser.* **127**: 27-37
- Erickson, D. L., M. J. Harris and G. D. Grossman (1985). Ovarian cycling of tile fish, *Lepholatilus chamaeleonticeps* Goode and Bean, from the South Atlantic Bight, U. S. S. *J. Fish Biol.* **27**: 131-146
- Everhart, W. R., A. M. Eipper and W. D. Young (1953). Principles of fisheries science. *Cornell University Press, Ithaca and London*, 288 pp.
- Fange, R. and D. J. Grove (1979). Digestion. In: *Fish Physiology* (W.S. Hoar, D.J. Randall and J.R. Brett, eds.), *Vol. VIII*, pp. 161-260. *New York and London: Academic Press.*
- FAO, (1981). Methods of collecting and analysing size and age data for fish stock assessment. *FAO Fish. Cir.*, **736**: 100 pp.
- FAO, (1995). Fisheries Yearbook of fisheries statistics: catches and landings (1993). *Vol. 76*: 688 pp.
- FAO, (1998). Fisheries Yearbook of fisheries statistics: Capture production (1998). *Vol. 86/1*: 713 pp.
- Fleming, I. A. and M. R. Gross (1989). Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* **43**: 141-157
- Fleming, I. A. and M. R. Gross (1990). Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Ecology* **71**: 1-11

- Flowerdew, M. W. and D. J. Grove (1980). An energy budget for juvenile thick-lipped mullet, *Crenimugil labrosus* (Risso). *J Fish Biol.* **17**: 395-410
- Fonds, M., R. Cronie, A. D. Vethaak and P. Van der Puyl (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Neth. J. Sea Res.* **29**: 127-143
- Ford, E. (1933). An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *J. Mar. Biol. Ass. UK.* **19**: 305-384
- Forster, J. R. M and P. Gabbott (1971). The assimilation of nutrients from compounded diets by the prawns, *Palaemon serratus* and *Pandalus platyceros*. *J. Mar. Bio. Ass. UK.* **51**: 943-961
- Fossen, L., O. T. Albert and E. M. Nilssen (1999). Back-calculated individual growth of long roughdab (*Hippoglossoides platessoides*) in the Barents Sea. *ICES J. Mar. Sci.* **56**: 689-696
- Fox, M. G. (1994). Growth, density, and interspecific influences on pumpkinseed sunfish life histories. *Ecology*, **75**: 1157-1171
- Francis, M. P. (1994). Growth of juvenile snapper, *Pagrus auratus*. *New Zealand J. Mar. Freshwater Res.*, **28**: 201-218
- Frid, C. L. J. and S. J. Hall (1999). Inferring changes in North Sea benthos from fish stomach content analysis. *Mar. Ecol. Prog. Ser.* **184**: 183-188
- Fritz, E. S. (1974). Total diet composition in fishes by Spearman Rank Correlation Coefficients. *Copeia* **1**: 210-214
- Frost, W. E. (1977). The food of Charr *Salvelinus willughbii* (Gunther) in Windermere. *J. Fish Biol.* **11**: 531-547
- Garcia-Berthou, E. (1999). Food of introduced mosquitofish: ontogenetic diet shift and prey selection. *J. Fish Biol.* **55**: 135-147.
- Gauld, J. A. and J. R. Hutcheon (1990). Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* Rautt, in the north-western North Sea. *J. Fish Biol.* **36**: 611-613
- Gayanilo Jr., F. F., P. Sparre and D. Pauly (1996). The FAO-ICLARM Stock Assessment Tools (Fisat) User's Guide. *FAO Computerised Information Series (Fisheries). No. 8. Rome, FAO. 1995.* 126 pp.
- George, E. L. and W. F. Hadley (1979). Food and habit partitioning between rock bass (*Amploplites rupestris*) and small mouth bass (*Micropterus dolomieu*) young of the year. *Trans. Am. Fish. Soc.* **108**: 253-261

- Gerking, S. D. (1994). Feeding ecology of fish. San Diego: *Academic Press*
- Gibson, R. N., A. D Ansell and L. Robb (1993). Seasonal and annual variations in abundance and species composition of fish and microcrustacean communities on a Scottish sandy beach. *Mar. Ecol. Prog. Ser.* **98**: 89-105
- Gibson, R. N. and I. A. Ezzi (1987). Feeding relationships of a demersal fish assemblage on the West Coast of Scotland. *J. Fish Biol.* **31**: 55-69
- Gordon, J. D. M. (1977). The fish populations in inshore waters of the west coast of Scotland. The biology of the Norway pout (*Trisopterus esmarkii*). *J. Fish Biol.* **10**: 417-430
- Goulding, M. (1980). The fishes and the forest: exploitations in Amazon Natural History. Los Angeles, *University of California Press*.
- Gray, E. V. S., J. M. Boltz, K. M. Kellog and J. R. Stauffer Jr. (1997). Food resource partitioning by nine sympatric darter species. *Trans. Amer. Fish. Soc.* **126**: 822-840
- Greenstreet, S. P. R. (1996). Estimation of the daily consumption of production by fish in the North Sea in each quarter of the year. *Scottish Fisheries Research Report* **55**.
- Greenstreet, S. P. R and S. J. Hall (1996). Fishing and the ground-fish assemblage structure in the North Sea; an analysis of long-term and spatial trends. *J. Anim. Ecol.* **65**: 577-598
- Grosslein, M. D., R. W. Langton and M. P. Sissenwine (1980). Recent fluctuations in pelagic fish stocks of the northwest Atlantic, Georges Bank Region, in relation to species interactions. *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **177**: 374-404
- Grove, D. J., L. G. Loizoides and J. Noh (1978). Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri*. *J. Fish Biol.* **12**: 507-516
- Guenette, S., T. J. Pitcher and C. J. Walters (2000). Marine reserves for the management of northern cod in Newfoundland. *Bull. Mar. Sc.* **66**(3): 831-852
- Gulland, J. A. (1968). The concept of the maximum sustainable yield and fishery management. *FAO Fish. Biol. Tech. Pap. No. 70*
- Gulland, J. A. (1970). Food chain studies and some problems in world fisheries. In: *Marine food chains* (J. H. Steel, ed.), pp. 296-315. *Edinburgh: Oliver Boyd*
- Gulland, J. A. (1975). Manual of methods of fisheries resource survey and appraisal. Part 5. Objectives and basic methods. *FAO Fish. Tech. Pap.* **145**: 29 pp.
- Gulland, J. A. (1983). Fish stock assessment: a manual of basic methods. *J. Wiley and Sons* . 233p.
- Gulland, J. A. (1984). Advice on target fishing rates. *Fishbyte* **2**(1): 8-11

- Gulland, J. A. and S. J. Holt (1959). Estimation of growth parameters for data at unequal time intervals. *J. Cons. CIEM*, **25** (1): 47-49
- Gunderson, D. R. and P. H. Dygert (1988). Reproductive effort as a predictor of natural mortality rate. *J. Cons. CIEM*; **44**: 200-9
- Gwyther, D. (1978). The control of appetite in the dab, *Limanda limanda* L. *Ph.D. thesis, University of Wales.*
- Gwyther, D. and D. J. Grove (1981). Gastric emptying in dab, (*Limanda limanda* L.) and the return of appetite. *J. Fish Biol.* **18**: 245-259
- Hall, S. J., D. Basford, D. J. Robertson and M. R. Freyer (1990). The feeding relationships of the larger fish in a Scottish Seas Loch. *J. Fish Biol.* **37**: 775-791
- Harding, D. and J. H. Nicols (1987). Plankton surveys off the north- east coast England in 1976: An introductory report and summary of the results. *Fish. Res. Tech. Rep. 86, MAFF Direct. Fish. Res., Lowestoft*, 56 pp.
- Harding, D., J. H. Nicols and D. S. Tungate (1978). The spawning of the plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. *Rapp. Proces. Verb. Cons. Intern. Explor. Mer*, **172**: 102-113
- Hayward, P., T. Nelson-Smith and C. Sheilds (1996). Sea shore of Britain and Europe. *HarperCollins Publishers, London*. 352 pp.
- Hedgepeth, J. B., V. F. Gallucci, F. O'Sullivan and R. E. Thorne (1999). An expected maximisation and smoothing approach for indirect acoustic estimation of fish size and density. *ICES J. Mar. Sci.*, **56**: 36-50
- Hellawel, J. M. (1974). The ecology of population of dac, *Leuciscus leuciscus* (L). from two tributaries of the river Herefordshire, England. *Freshwater*, **4**: 467-468
- Hempel, G. (1964). Some observations on tidal effects on the catch of plaice, *Pleuronectes platessa* L., and dab, *Limanda limanda* L. in the German Bight. *Rapp.P.-V. reum. cons. perm. int. Explor. Mer.*, **155**: 65 pp.
- Hemri, G. I., O. Karlsen, G. Lehman, J. C. Holm and L. Lie (1993). Utilisation of protein, fat and glycogen in cod (*Gadus morhua*) during starvation. *Fiskeridirektorats skrifter Srie Emaring*, **6**: 1-9
- Henderson, P. A. and R. H. M. Seaby (1994). On the factor influencing juvenile flatfish abundance in the Lower Severn Estuary, England. *Neth. J. Sea Res.* **32(3/4)**: 321-330
- Henderson, B. A., J. L. Wong and S. J. Nepszy (1996). Reproduction of Walleye in Lake Erie: allocation of energy. *Can. J. Fish. Aqua. Sci.* **53**: 127-133
- Henderson, B. A., T. Trevedi and N. Collins (2000). Annual cycle of energy

- allocation to growth and reproduction of yellow perch. *J. Fish Biol.* **57**: 122-133
- Hickling, C. F, and E. Ruthenberg (1936). The ovary as an indicator of spawning period in fishes. *J. Mar. Biol. Ass. UK*, **21**: 311-317
- Hilborn, R. and C. J. Waters (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Routledge, Chapman and Hall Inc. NY*. 569 pp.
- Hislop, E. J. (1980). Stomach content analysis – a review of methods and their applications. *J. Fish. Biol.* **17**: 411-429
- Hoar, S. W. (1966). General and comparative physiology. *Prentice Hall. , New Jersey*, 815 pp.
- Hoinés, A. S and O. A. Bergstad (1999). Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. *J. Fish Biol.* **55**: 1233-1257
- Holbrook, S. J. and R. J. Schmitt (1986). Food acquisition by competing surfperch on a patchy environmental gradient. *Environ. Biol. Fish* **16**: 135-146
- Hopkins, C. C. E, J.V. Seiring, O. Nyholmen and A. Hermannsen (1984). Ecological energetics from total lipid and total protein: Fact and artifact using a gravimetric method for lipid and a biuret method for protein. *Oceanogr. Mar. Biol. Ann. Rev.* **22**: 211-261. Margaret Barnes, Ed. *Aberdeen University Press*
- Horwood, J. W., M. G. Walker and P. Witthames (1989). The effect of feeding levels on the fecundity of plaice (*Pleuronectes platessa*). *J. Mar. Biol. Ass. U.K.* **69**: 81-92
- Horwood, J. W. and M. G. Walker (1990). Determination of fecundity in sole (*Solea solea*) from the Bristol Channel. *J. Mar. Biol. Ass. U.K.* **70**: 803-813
- Hom, H. S. (1966). Measurement of overlap in comparative ecological studies. *Am. Nat.* **100**: 419-423
- Hom, P. L. (1993). Growth, age structure and production of ling, *Genypterus blacodes* (Ophidiidae), in Zealand waters. *New Zealand J. Mar. Freshwater Res.*, **27**: 385-397
- Horppila J., J. Ruuhijarvi, M. Rask, C. Karpinen, K. Nyberg and M. Olin (2000). Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a lake. *J. Fish Biol.* **56**: 51-72
- Htun-Han, M. (1978a). The reproductive biology of the dab, *Limanda limanda* L., in the North Sea: gonosomatic index, hepatosomatic index and condition factor. *J. Fish. Biol.* **13**: 369-378
- Htun-Han, M. (1978b). The reproductive biology of the dab, *Limanda limanda* L., in

- the North Sea: seasonal changes in the ovary. *J. Fish Biol.* **13**: 351-359
- Htun-Han, M. (1978c). The reproductive biology of the dab, *Limanda limanda* L., in the North Sea: seasonal changes in the testes. *J. Fish Biol.* **13**: 361-367
- Huber, M. and D. A. Bengtson (1999). Interspecific differences in growth of somatic and reproductive tissues during the breeding season in *Menidia menidia* and *M. beryllina*. *J. Fish Biol.* **55**: 274-287
- Hunt, P. C. and J. W. Jones (1975). A population study of *Barbus barbus* L. in the River Severn, England. III. Growth. *J. Fish Biol.* **7**: 361-376
- Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-586
- Hurlbert, S. H. (1978). The measure of niche overlap and some relatives. *Ecology* **59**: 69-77
- Hutchings, J. A. (1993). Adaptive life histories effected by age-specific survival and growth rate. *Ecology*, **74**: 673-684
- Jennings, S., M. J. Kaiser and J. D Reynolds (2001). Marine fisheries ecology. *Blackwell Science, Oxford*, 424 pp.
- Jennings, S. and M. J. Kaiser (1999). The effect of fishing on marine ecosystems. *Adv. Mar. Biol. Vol. 34, ISBN: 0-12-026134-0*: pp. 203-314
- Jensen, A. J. C. (1937). The races of dab in the Danish waters. Rep. of Danish. *Biol. Stat., XLII*
- Jensen, A. J. C. (1939). Fluctuations in the racial characters of the plaice and dab. *J. Cons. Int. Explor. Mer*, **14 (XIV)**: 370-384
- Jepsen, D. B., K. O. Winemiller and D. C. Taphorn (1997). Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *J. Fish. Biol.*, **51**: 1085-1108
- Jobling, M. (1974). Feeding behaviour and food intake of the Dab, *Limanda limanda* L. *Unpublished M.Sc. Thesis, University of Wales*
- Jobling M. (1981). Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *J. Fish Biol.*, **19**: 245-258
- Jobling, M. (1982). Food and growth relationship for the Cod, *Gadus morhua* L., with special reference to Balsjorden, North Norway. *J. Fish Biol.* **21**: 357-371
- Jobling, M. (1993). Bio-energetics: feed intake and energy partitioning. In: J. C. Rankin and F. B. Jensen (eds.). *Fish eco-physiology. Chapman and Hall, London*:1-44

- Jobling, M. (1995). Environmental biology of fishes. *Chapman and Hall, London*, 455 pp.
- Jobling, M. and J. S. Johansen (1999). The lipostat, hyperphagia and catch-up growth. *Aquaculture Research*, **30**: 473-478
- Johnson, A. K, P. Thunur and R. R. Wilson Jr. (1998). Seasonal cycles in gonad development and plasma sex steroid levels in *Epinephelus morio*, a protogynous grouper in the Gulf of Mexico. *J. Fish Biol.* **52**: 502-518
- Johnson, F. H. (1977). Responses of walleye (*Stizostedion vitreum vitreum*) and Yellow perch (*Perca flavescens*) populations to the removal of White Sucker (*Catostomus commersoni*) from a Minnesota lake 1966. *J. Fish. Res. Bd. Can.* **34**: 1633-1642
- Jones, A. (1974). Sexual maturity, fecundity and growth of the turbot, *Scophthalmus maximus* L. *J. Mar. Biol. ASS. U.K.*, **54**: 109-125
- Jonsson, G. (1966). Contribution to the biology of the dab in Icelandic waters. *Rit. fiskideilar, vol. IV, no. 3*: 3-36
- Jonsson, N. and F. R. Gravem (1985). Use of space and food by resident and migrant brown trout, *Salmo trutta*. *Environmental Biology of Fishes* **18**: 281-293
- Jonsson, N. and B. Jonsson (1997). Energy allocation in polymorphic brown trout. *Functional Ecology II*: 310-317.
- Jonsson, N. and B. Jonsson (1998). Body composition and energy allocation in life-history stages of brown trout. *J. Fish Biol.* **53**: 1306-1316
- Jonsson, N. and B. Jonsson (1999). Trade-off between egg mass and egg number in brown trout. *J. Fish Biol.* **55**: 767-783
- Jorgensen, T. (1990). Long-term changes in age at sexual maturity of northeast Arctic cod (*Gadus morhus* L.). *J. du Cons. Per. Inter Int. Exp. Mer.* **46**: 235-248
- Joyeux, J. C., C. Aliaume and A. Zerbi (2001). An alternative to validation of otolith microincrementation (Brief communications). *J. Fish Biol.* **58**: 873-879
- Kaiser, M. J. and B. E. Spencer (1995). Survival of by-catch from a beam trawl. *Mar. Ecol. Prog. Ser.* **126**: 31-38
- Kaiser, M. J and B. E. Spencer (1996). Behavioural responses of scavengers to beam trawl disturbance. In: Greenstreet SPR, Tasker ML (eds.): Aquatic predators and their prey. *Blackwell Scientific Publications, Oxford*, pp. 117-123
- Kaiser, J. M. and K. Ramsay (1997). Opportunistic feeding by dabs within areas of trawl disturbance: possible implications for increased survival. *Mar. Ecol. Prog. Ser.* **Vol. 152**: 307-310

- Kandler, R. and W. Pirwitz (1957). Über die Fruchtbarkeit der Plattfische in Nordsee-Ostsee. *Raum. Kieler Meeresforsch.*, **13**: 11-13.
- Kandler, R. und Fr. Thurow (1959). On the stocks of flatfish and cod and the yields of the German fishery in the Baltic. *Rapp. Et Proc. Ver. Vol. 147*
- Kaperski, W. and J. Kozłowski (1993). The effect of exploitation on size at maturity in laboratory populations of guppies (*Poecilia reticulata*, Peters). *Acta hydrobiologia*, **35**: 65-72
- Karakiri, M., R. Berghahn and H. von Westernhagen (1989). Growth differences in 0-group plaice, *Pleuronectes platessa*, as revealed by otolith microstructure analysis. *Mar. Ecol. Prog. Ser.* **55**:15-22
- Karlsen, O., J. C. Holm and O. S. Kjesbu (1995). Effects of periodic starvation on reproductive investment in first time spawning Atlantic cod (*Gadus morhua* L.). *Aquaculture*, **133**: 775-784
- Kartavtsev, Y. P., K. A. Zgurovsky and Z. M. Fedina (1993). Spatial structure of the pink shrimp, *Pandalus borealis* kroyer, 1838 from the far-eastern seas as proved by methods of population genetics and morphometrics. *J. Shellfish Res.* **12**: 81-87
- Keast, A. (1965). Resource subdivision amongst co-habiting fish species in a bay, Lake Opinicon, Ontario. *Great Lakes Res. Div. Univ. Mich. Publ.* **13**: 106-132.
- Keast, A. (1977). Diet overlaps and feeding relationships between year-classes in the yellow perch (*Perca flavescens*). *Environmental Biology of fishes* **2**: 53-70
- Keast, A. (1978). Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Environmental Biology of fishes* **3**: 7-31
- Kerr, S. R. (1982). Estimating the energy budgets of actively predatory fishes. *Can. J. Fish. Aquat. Sci.* **39**: 371-379
- King, M. (1995). Fisheries Biology, Assessment and Management. *Fishing News Books*, London 341 pp.
- Kipling, C. and W. E. Frost (1969). Variation in the fecundity of pike (*Esox lucius* L.) in Windermere. *J. Fish Biol.* **1**: 221-237
- Kjesbu, O. S., J. Klungsoyr, H. Kryvi, P. R. Withames and M. G. Walker (1991). Fecundity, artresia, and egg mass of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Can. J. Fish. Aquat. Sci.* **48**: 2333-2343
- Knust, R. (1986). Food selection of dab (*Limanda limanda* (L.)): diel and seasonal changes. *International Council for the Exploration of the Sea CM1986/G*: 63
- Knust, R. (1987). Seasonal changes in feeding, condition and gonadosomatic

- index of dab (*Limanda limanda* L.): a comparison of two stations in the German Bight and on the Dogger Bank. *ICES C.M./G: 54. Demersal Fish Committee*. 13 pp.
- Knust, R. (1990). Ernährung der Kliesche (*Limanda limanda* L.) in der zentralen und südlichen Nordsee und die Bedeutung des Ernährungszustandes für Erkrankungen dieser Fischart. Veröff. Inst. Küsten- und Binnenfisch. *Hamburg. Nr. 102*: 184 pp.
- Knust, R. (1996). Food ecology of North Sea dab (*Limanda limanda* L.). Part 1: Seasonal changes in food uptake and condition in the German Bight and on Dogger Bank. *Arch. Fish. Mar. Res.* **44** (1/2): 1-12
- Koprivnjak, J.-F., K. R. Lum, M. M. Sisak and R. Saborowski (1996). Determination of α , γ (+ β)-, and δ -tocopherols in a variety of liver tissues by reverse-phase high pressure liquid chromatography. *Comparative Biochemistry and Physiology* **1113B**: 142-148.
- Kraus, G., A. Müller, K. Trella and F. W. Koster (2000). Fecundity of Baltic cod: temporal and spatial variation. *J. Fish Biol.* **56**: 1327-1341
- Krebs, C. J. (1989). Ecological methodology. *Harper and Row, NY*.
- Kroncke, I. and R. Knust (1992). Seasonal variation in macrofaunal abundance on the Dogger Bank in relationship to stomach content of dab (*Limanda limanda*). In: *Counc. Explor. Sea C.M./G 80*: 10 pp.
- Labropoulou, M. and A. Eleftheriou (1997). The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *J. Fish Biol.* **50**: 324-340
- Laevastu, T. and F. Favorite (1977). Preliminary report on dynamic numerical marine ecosystem model (Dynamics 11) for eastern Bering Sea. *U. S. Natl. Mar. Fish. Serv. Northwest and Alaska Fish. Cent. Seattle*.
- Lambert, Y. and J.-D. Dutil (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat.* **54** (Suppl. 1): 104-112
- Lande, R. (1976). Food and feeding habits of dab (*Limanda limanda* L.) in Borgenfjorden, North-Trondelag, Norway, Norw. *J. Zool.* **24**: 225-230
- Langton, R. W. (1982). Diet overlap between Atlantic cod, *Gadus morhus*, Silver Hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. *Fishery Bulletin U.S.* **80**: 745-759
- Langton, R. W. and R. E. Bowman (1980). Food of fifteen Northwest Atlantic Gadiform fishes-NOAA Technical Report NNFS SSRF-740: 1-23
- Larson, G. L. (1974). Liver weight of brook trout in a high-mountain lake in Washington State. *Progve Fish Cult.* **35**: 234-236

- Lee, C. K. C. (1972). The biology and population dynamics of the common dab (*Limanda limanda* L.) in the North Sea. *Ph.D. Thesis, Uni. East Anglia, U.K.*: 105 pp.
- Leslie, R. W. and W. S. Grant (1990). Lack of congruence between genetic and morphometric stock structure of the Southern African Anglerfish, *Lophius vomerinus*. *South African J. Mar. Sci.* **9**: 379-398
- Levins, R. (1968). Evolution in changing environments. *University press, Princeton, N.J.* 120 pp.
- Lie, O., E. Lied and O. Lambertsen (1988). Feed optimisation in Atlantic cod (*Gadus morhua*): fat versus protein content in the feed. *Aquaculture* **9**: 333-341
- Lockwood, S. J. (1974). The use of the von Bertalanffy growth to describe the seasonal growth of fish. *J. Cons. Int. Explor. Mer.*, **35(2)**: 175-179
- Lozan, J. L. (1988). Distribution, density and structure of the dab (*Limanda limanda* L.) population in the North Sea. *Archiv. Fuer. Fishch.* **38 (3)**: 165-189
- Lozan, J. L. (1989). Investigation on of the growth dab (*Limanda limanda* L.) in eight areas of the North Sea and comparisons with earlier findings. *Arch. Fischwiss.* **29 (2)**: 111-146
- Lozan, J. L. (1992). Sexual differences in food intake, digestive tract size, and growth performance of the dab, *Limanda limanda* L. *Neth. J. Sea Research*, **29 (1-3)**: 223-227
- MacArthur, R. H. and R. Levins 1967. The limiting similarity, convergence and divergence of co-existing species. *Am. Nat.*, **102**: 377-385
- Macer, C. T. (1967). The food web in Red Wharf Bay (North Wales) with particular reference to young Plaice, *Pleuronectes platessa* L. *Helgolander Wiss. Meeresunters.* **15**: 560-573
- Macer, C. T. (1972). The movements of tagged adult plaice in the Irish Sea. *Fish. Invest. Lond.* **11, 27(6)**: 41 pp
- MacLennan, D. N. (1990). Acoustic measurements of fish abundance. *ICES J. Acoust. Soc. Amer.*, **87**: 1-15
- Majkowski, J. and K. G. Waiwood (1981). A procedure for evaluating the food biomass consumed by a fish population. *Can. J. Aquat. Sci.* **38**: 1199-1208
- Man, H. S. H. and I. J. Hodgkiss (1977). Studies on the ichthyo-fauna in Plover Cove Reservoir, Hong Kong: feeding and food relations. *J. Fish. Biol.* **11**: 1-13
- Mann, R. H. K (1973). Observations of the age, growth, reproduction and food of the roach, *Rutilus rutilus* L. in two rivers in southern England. *J. Fish Biol.*, **5**: 707-736

- Mann, R. H. K. (1976). Observations of the age, growth, reproduction and food of the pike, *Esox lucius* L., in two rivers in southern England. *J. Fish Biol.* **8**: 179-197
- Marteinsdottir, G., A. Gudmundstottir, V. Thorsteinsson and G. Stefansson (2000). Spatial variation in abundance, size composition and viable egg production of spawning cod (*Gadus morhua* L.) in Icelandic waters. *ICES J. Mar. Sci.* **57**: 824-830
- Mazia, D., P. A. Brewer and M. Alfeat (1953). The cytochemic staining and measurement of protein with mercuric bromophenol blue. *Biol. Bull. Wood's Hole.* **104**: 57-67
- McFarlane, G. A. and M. W. Saunders (1997). Fecundity of pacific hake (*Merluccius productus*) for three stocks off of the west coast of North America. *Calif. Coop Oceanic. Fish. Invest. Rep.* **38**: 114-119
- Mcvoy, L. A. (1984). Ovulatory rhythms and over-ripening of eggs in cultivated turbot (*Scophthalmus maximus* L.) *J. Fish Biol.* **24**: 437-448
- Millner, R. S., C. Whiting, M. G. Walker and P. R. Witthames (1991). Growth increment, condition and fecundity in sole (*Solea solea* L.) from the North Sea and Eastern English Channel. *Neth. J. Sea Res.* **27(3/4)**: 433-439
- Minton, J. W. and R. B. McLean (1982). Measurement of growth and consumption of sauger, *Stizostedion canadense*: Implication for fish energetics studies. *Can. J. Fish. Aquat. Sci.* **39(10)**: 1396-1403
- Mookerji, N., C. Heller, H. J. Meng, H. R. Burgi and R. Muller (1998). Diel and seasonal intake of food intake and prey selection by *Coregonus* spp. In re-oligotrophic Lake Lucerne, Switzerland. *J. Fish Biol.* **52**: 443-457
- Morgan, M. J. and E. B. Colbourne (1999). Variation in maturity-age and size in three populations of american plaice (*Hippoglossoides platessoides*). *ICES J. Mar. Sci.* **56**: 673-688
- Morita, K. and Y. Takashima (1998). Effect of female size of fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. *J. Fish Biol.* **53**:1140-1142
- Morse, W. W. (1981). Reproduction of the summer flounder, *Paralichthys dentatus* L. *J. Fish Biol.*, **19**: 189-205
- Munk, P. (1997). Prey size spectra and small juvenile cod. *J. Fish Biol.*, **51 (Suppl. A)**: 340-351
- Nagahama, T. (1987). Gonadotropin action on gametogenesis and steroidogenesis in teleost gonads. *Zoological Society* **4**: 209-222

- Nash, R. D. M., A. J. Geffen and G. Hughes (1992). Winter growth of juvenile plaice on the Port Erin Bay (Isle of Man) nursery ground. *J. Fish Biol.* **41**: 209-215
- Nash, R. D. M., A. J. Geffen and G. Hughes (1994a). Individual growth of juvenile plaice (*Pleuronectes platessa* L.) on a small Irish Sea nursery ground (Port Erin Bay, Isle of Man, U.K). *Neth. J. Sea Res.* **32**: 369-378
- Nash, R. D. M., R. S. Santos, A. J. Hughes, and T. R. Ellis (1994b). Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin, Isle of Man and Port Pin Bay, Faial, Azores). *J. Fish. Biol.* **44**: 35-45
- Ney, J. J. (1990). Trophic economics in fisheries. Assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* **2**: 55-81
- Nichol, D. G. and E. I. Acuna (2001). Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the Eastern Bering Sea. *Fish. Bull.* **99(1)**: 108-122
- Nikolsky, G. V. (1963). The ecology of fishes. *Academic Press, London and New York*. 352 pp.
- Nikolskii, G. V. (1969). Theory of fish populations dynamics as the biological background for rational exploitation and management of fishery resources (translated by J.E.S Bradley), *Oliver and Boyd, London*.
- Nilsson, N. A. (1967). Interactive segregation between fish species. In: *The Biological Basis of Freshwater Fish Production* (Gerking, S.D., ed.), pp. 295-313. *Oxford, Blackwell*.
- Ortega-Salas, A. A. (1980). Seasonal changes in the common dab, *Limanda limanda* L., in the Isle of Man waters. *J. Fish Biol.*, **16**: 75-82
- Ortega-Salas, A. A. (1988a). Age and growth of the dab, *Limanda limanda* L. in the Isle of Man waters, U. K. *Anales del Instituto, de Ciencuas del Mar y Limnologia, Universidad Nacional Autonoma de Mexico. Mexico City; Vol. 15, No. 1*: 1-18
- Ortega-Salas, A. A. (1988b). Population structure of the dab, *Limanda limanda* L. in the Isle of Man waters, U. K. *Anales del Instituto, de Ciencuas del Mar y Limnologia, Universidad Nacional Autonoma de Mexico. Mexico City; Vol. 15, No. 1*: 19-30
- Ortega-Salas, A. A. (1988c). Diet, food consumption and growth of the dab, *Limanda limanda* L. in the Isle of Man waters, U. K. *Anales del Instituto, de Ciencuas del Mar y Limnologia, Universidad Nacional Autonoma de Mexico. Mexico City; Vol. 15, No. 1*: 31-40
- Paloheima, J. E and L. M. Dickie (1966). Food and growth in fishes. III. Relation among food, body size and growth efficiency. *J. Fish. Res. Bd. Can.*, **12**:1209-248
- Palsson, O. K. (1983). Feeding habits of demersal fish species in Icelandic Waters. *Rit Fisk.*, **7 (1)**: 38 pp.

- Parker, R. R. (1963). Effects of formalin on length and weight of fishes. *J. Fish. Res. Bd. Can.* **20**: 144-155
- Parrish, B. B. (1956). Cod, Haddock and Hake. In: Sea fisheries, their investigation in the United Kingdom (Graham, M. Ed). *Edward Arnold (Publishers) Ltd., London*
- Parrish, B. B., I. G. Blaxter and W. B. Hall (1964). Diurnal variations in size and composition of trawl catches. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer.:***155**: 27-37
- Parrish, C. C., J. S. Wells, Z. Yang and P. Dabinett (1999). Growth and lipid composition of scallop juveniles, *Placopecten magellanicus*, fed the flagellate *Isochrysis galbana*, with varying lipid composition and diatom *Chaetoceros muelleri* (1999). *Marine Biol. Vol. 133, 3*: 461-671
- Pauly, D. (1980). On the inter-relationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cons. CIEM, 39(1)*: 175-92
- Pauly, D. (1984). Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Stud. Rev. 8*: 325 pp.
- Pauly, D. (1994). A frame of latitudinal comparisons of flatfish recruitment. *Neth J. Sea Res. 32*: 107-113
- Pauly, D., V. Christensian, J. Dalsgaard, R. Froese and F. Torres Jr. (1998). Fishing down marine food webs. *Science 279*: 860-863
- Pauly, D. and G. Gaschutz (1979). A simple method for fitting oscillating length growth data, with a program for pocket calculator. *ICES C.M. 179/G, 24*: 26 pp., Mimeo.
- Pennington, M. (1985). Estimating the average food consumption by fish in the field from stomach contents data. *Dana, 5*: 81-86
- Pitcher, T. J. (2000). Ecosystem goals can reinvigorate fisheries management, help dispute resolution and encourage public support. *Fish and Fish. 1(1)*: 99-103
- Pitcher, T. J. and P. J. B. Hart (1982). Fisheries ecology. *Croom Helm Ltd.* 414 pp.
- Pitcher, T. J. and P. D. M. Macdonald (1973a). Two models for seasonal growth in fishes. *J. Appl. Ecol., 10*: 597-606
- Pitcher, T. J. and P. D. M. Macdonald (1973b). A numerical integration method for population fecundity. *J. Fish Biol. 5*: 549-553
- Pomory, C. and J. M. Lawrence (1999). Energy content of *Ophiocoma echinata* (Echinodermata: Ophiuroidea) maintained at different feeding levels during arm regeneration. *J. Exp. Mar. Biol. 238*: 139-150

- Poulsen, E. M. (1933). Biology of the dab in Danish waters. *Rep. Dan. Bio.* **XXXIII**: 9-30
- Powell, D. G. (1979). Estimation of mortality and growth parameters from the length frequency of a catch. *Rapp.P.- V. Reun. CIEM*, **175**: 167-169
- Power, M., M. J. Attrill and R. M. Thomas (2000). Environmental factors and interactions affecting the temporal abundance of juvenile flatfish in the Thames Estuary. *J. Sea Res.* **439(2)**: 135-149
- Prejs, A. and K. Prejs (1987). Feeding of tropical freshwater fishes: seasonality in resource availability and resource use. *Oecologia* **71**: 397-404
- Purchase, C. F. and J. A. Brown (2001). Stock-specific changes, food conversion efficiencies and energy allocation in response to temperature in Juvenile Atlantic Cod. *J. Fish Biol.* **58**: 36-52
- Ramsay, K., M. J. Kaiser and R. N. Hughes (1996). Changes in hermit crab feeding patterns in response to trawling disturbance. *Mar. Ecol Pro. Ser.* **144**: 63-72
- Ramsay, K. and P. Witthames (1996). Using oocyte size to assess seasonal ovarian development in *Solea solea* L. *J. Sea. Res.* **36**: 275-283
- Rasmusson, E. B., M. B. Salhauge and J. Boje (1999). The suitability of vertebral counts in stock delineation studies of Green halibut, *Reinhardtius hippoglossoides* (Walbaun), in West Greenland. *ICES J. Mar. Sci.*, **56**: 75-83
- Ricker, W. E. (1969). Effects of size-selective mortality and sampling bias on estimation of growth, mortality, production and yield. *J. Fish. Res. Bd. Can.*, **26**: 479-542
- Ricker, W. E. (1973). Linear regression in fishery research. *J. Fish. Res. Bd. Can.* **30**: 409-434
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish population. *Bull. Fish. Res. Can.* **191**: 382 pp.
- Ricker, W. E. (1979). Growth rates and models. In: Fish physiology, Vol. 8 (Hoar, W. S., D.J Randall, and J. R Brett, eds.) pp. 677-743. *New York, Academic Press.*
- Ricker, W. E. (1981). Changes in the average size and average weight of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **38**: 1636-1656
- Rijnsdorp, A .D. (1989). Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *J. Cons. Int. Explor. Mer*, **46**: 35-51
- Rijnsdorp, A.D. (1991). Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900. *ICES J. Mar. Sci.* **48**: 253-280

- Rijnsdorp, A. D. (1993). Fisheries as a large scale-experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, **96**: 391-401
- Rijnsdorp, A. D. (1994). Population-regulating processes during the adult phase in flatfish. *Neth. J. Sea Res.*, **32(2)**: 207-223
- Rijnsdorp, A. D., N. Daan, F. A. van Beek, H. J. L. Heessen (1991). Reproductive variability in North Sea cod, plaice and sole. *J. Cons. Inter. Explor. Mer.* **47**: 352-375
- Rijnsdorp, A. D. and R. S. Millner (1996): Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1880s. *ICES J. Mar. Sci.* **53**: 1170-1184
- Rijnsdorp, A. D. and P. I. van Leeuwen (1985). Annual variation in age and length at first maturity of North Sea plaice. *ICES CM 1985/G:56*
- Rijnsdorp, A. D. and P. I. van Leeuwen (1992). Density-dependent and independent changes in somatic growth of female North Sea plaice, *Pleuronectes platessa*, between 1930 and 1985 as revealed by back-calculation of otoliths. *Mar. Ecol. Prog. Ser.* **88**: 19-32
- Rijnsdorp, A. D and P. I. van Leeuwen (1996): Changes in growth on North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. . *ICES J. Mar. Sci.* **53**: 1199-1213
- Rijnsdorp, A. D., P. I. van Leeuwen, N. Daan and H. J. L. Heessen (1996): Changes in the Abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. *ICES J. Mar. Sci.* **53**: 1054-1062
- Rijnsdorp, A. D., P. I. van Leeuwen and T. A. M. Visser (1990). On the validity and precision of back-calculation from otoliths of the plaice (*Pleuronectes platessa* L.). *Fish. Res.* **9**: 97-117
- Rijnsdorp, A. D., A. D. Vethaak and P. I. Van Leeuwen (1992). Population biology of dab *Limanda limanda* in the south-eastern North Sea. *Mar. Eco. Prog. Ser. Vol. 91*: 19-35
- Rikhter, V. A. and V. N. Efanov (1976). On one of the approaches to estimation of natural mortality of fish populations. *ICNARF Res. Doc.* **76/VI/8**: 12 pp.
- Riley, J. D., D. J. Symonds and L. Woolner (1981). On the factors influencing the distribution of O-group demersal fish in coastal waters.-*Rapp. P.-v. Reun. Cons. Perm. Int. Explor. Mer* **178**: 223-228
- Robson, D. S. and D. G. Chapman, 1961. Catch curves and mortality rates. *Trans. Am. Fish. Soc.*, **90(1)**: 181-189

- Rodhouse, P. G., C. D Elvidge and P. N. Trathan (2001). Remote sensing of the global Light-Fishing Fleet: An analysis of interactions with Oceanography, other fisheries and predators. *Adv. Mar. Biol.* **39**: 261-303, ISBA 0-12-026139-1
- Roff, D. A. (1983). An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* **40**: 1395-1404
- Roff, D. A. (1984). The evolution of life history parameters in teleost. *Can. J. Fish. Aquat. Sci.* **41**: 989-1000
- Roff, D. A. (1992). The evolution of Life Histories; Theory and Analysis. London: Chapman and Hall
- Rogers, S. I., D. Maxwell, A. D. Rijnsdorp, U. Damm and W. Vanhee (1999). Fishing effects in Northeast Atlantic shelf areas: patterns in fishing effort, diversity and community structure. IV. Can compositions of species diversity be used to assess human impacts on demersal fish fauna. *Fisheries Research*, **40(2)**: 135-152
- Rogers, S. I. and R. S. Millner (1996). Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations, 1973-1995. *ICES J. Mar. Sci.* **53(6)**: 1094-112
- Rombards, M. D, J. F. Piatt and G. A. Rose (1999). Maturity, fecundity and intertidal spawning of pacific sand lance in the northern Gulf of Alaska. *J. Fish Biol.* **54**: 1050-1068
- Rose, G. A. and W. C. Leggett (1991). Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries; an example of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **48**: 843-848
- Rosenberg, R. and E. Selander (2000). Alarm signal response in the brittle star, *Amphiura filiformis*. *Marine Biology*, **136(1)**: 43-48
- Ross, S. T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia* **2**: 252-388
- Rothschild, B. J. (1986). Dynamics of marine fish populations. *Harvard University Press, Cambridge*: 1-277
- Rothschild, B. J., T. R. Osborn, T. D. Dockey and D. M. Farmer (1989). The physical basis for recruitment variability in fish populations. *J. Cons. Per. Int. Explor. Mer* **45**: 136-145
- Ruohonen, K. and D. J. Grove (1996). Gastrointestinal responses of rainbow trout to dry pellet and low-fat herring diets. *J. Fish Biol.* **49**: 501-513
- Saborowski, R. and F. Buchholz (1996). Annual changes in the nutritive state of North Sea dab. *J. Fish Biol.* **49**: 173-194

- Saborowski, R. and F. Buchholz (1997). Some observations on the seasonal distribution of dab, *Limanda limanda*, in the Southern North Sea. *Helgolander Meeresunters*, **51**: 41-51
- Sainsbury, K. J. (1986). Estimation of food consumption from field observations of fish feeding cycles. *J. Fish Biol.* **29**: 23-36
- Sala, E. and E. Ballesteros (1997). Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in Mediterranean rocky infralittoral ecosystem. *Mar. Ecol. Prog. Ser.* **152**: 273-283
- Sandheinrich, M. R. and W. A. Hubert (1984). Intraspecific resource partitioning by yellow perch (*Perch flavescens*) in a stratified lake. *J. Fish. Res. Bd. Can.* **29**: 755-764
- Sandstrom, O., E. Neuman and G. Thoresson (1995). Effects of temperature on life history variables in perch. *J. Fish Biol.* **47**: 652-670
- Santos, M. B., G. J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. P. Patterson, C. C. Kinze, S. Tougaard, R. Lick, U. Piatkowski and V. Hernandez-Garcia (1999). Stomach contents of sperm whales, *Physeter macrocephalus* stranded in the North Sea, 1990-1996. *Mar. Ecol. Prog. Ser.* **183**: 281-294
- Schnute, J. T. and L. J. Richards (2001). Use and abuse of fishery models. *Can. J. Fish. Aquat. Sci.* **58**: 10-17
- Schoener, T. W. (1974). Resource partitioning in natural communities. *Science* **185**: 27-39
- Schopka, S. A. and G. Hempel (1973). The spawning potential of populations of herring (*Clupea harengus*) L. and cod, *Gadus morhua* L. in relation to the rate of exploitation. *Rapp. P. -V. Reun. Cons. Int. Explor. Mer.* **164**: 178-185
- Scott, D. B. C. (1979). Environmental timing and the control of reproduction in fish. In: *Fish Phenology: anabolic adaptiveness in teleosts.* (Miller, P.J. ed.). 105-128. Academic press for the zoological society of London (*Symp. Zool. Soc. Lond. No. 44*).
- Scott, D. P. (1962). Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Can.*, **19**: 712-731
- Serventi, M., I. J. Hamison, P. Torricelli and G. Gandolfi (1996). The use of pigmentation and morphological characters to identify Italian mullet fry. *J. Fish Biol.*, **49**: 1163-1173
- Seyhan, K. (1990). A study of maturity, growth and mortality rates of Irish Sea plaice (*Pleuronectes platessa* L.) in Anglesey waters, North Wales. *M.Sc. Thesis, University of Wales*

- Seyhan, K. (1994). Gastric emptying, food consumption and ecological impact of whiting, *Merlangius merlangus* L. in the eastern Irish Sea Ecosystem. *PhD Thesis, University of Wales*
- Seyhan, K. and D. J. Grove (1998). Food consumption of whiting, *Merlangius merlangus*, in the eastern Irish Sea. *Fisheries Research* **38**: 233-245
- Siddeek, M. S. M. (1989). The estimation of natural mortality rate in Irish Sea Plaice, *Pleuronectes platessa* L., using tagging methods. *J. Fish Biol.*, **35 (Suppl.)**: 145-154
- Siegel S. and N. J. Castellan Jr. (1988). Non-parametric statistics for the behavioural sciences. 2nd. Ed. *Magraw-Hill International Editions, Statistic Series*. 399 pp
- Simpson, A. C. (1951). The fecundity of the plaice. *Fish. Invest. Lond., Ser. 2*, **17(2)**: 27 pp.
- Simpson, A. C. (1959a). The spawning of plaice, *Pleuronectes platessa*, in the North Sea. *Fish. Invest. Lond., Ser. 11*, **22(7)**:111 pp.
- Simpson, A. C. (1959b). The spawning of plaice, *Pleuronectes platessa*, in the Irish Sea. *Fish. Invest. Lond. Ser. 11*, **22(8)**:30 pp.
- Simpson, A. L. (1992). Differences in body size and lipid reserves between maturing and non-maturing Atlantic salmon parr, *Salmon salar* L. *Can. J. Zool.* **70**: 1737-1742
- Slotte, A., A. Johannessen and O. S. Kjesbu (2000). Effects of fish size on spawning time in Norwegian spring-spawning herring. *J. Fish Biol.* **56**: 241-459
- Smagula, C. M. and I. R. Adelman (1982). Day-to-day variation in food consumption by large mouth bass. *Trans. Am. Fish. Soc.* **111**: 543-548
- Smith, S. J., and F. H. Page (1996). Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. *ICES J. Mar. Sci.*, **53**: 597-614
- Sogard, S. M. and K. W. Able (1992). Growth variation in newly settled winter flounder (*Pseudopleuronectes americanus*) in New Jersey Estuaries as determined by otolith microstructure. *Neth. J. Sea Res.* **29(1-3)**: 163-172
- Soofiani, N. M. and A. D. Hawkins (1985). Field studies of energy budgets. In: *Fish Energetics New Perspectives* (Ed. P. Tytler and P. Calow). Croom Helm, London and Sydney. 349 pp.
- Sparholt, H. (1987). An estimate of the total biomass of fish in the North Sea, with special references on fish eating species not included in the MSVPA model. *ICES C.M.* **1987/G**: 52

- Sparre, P. and S.C. Venema (1998). Introduction to tropical fish stock assessment. Part 1. Manual. *FAO Tech. Pap. No. 306.1, Rev. 2, Rome, FAO*. 407 pp
- Specziar, A., L. Tolgy and P. Biro (1997). Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *J. Fish Biol.* **51**: 1109-1124
- Staples, D. J. (1975). Production biology of an upland bully *Philypnodon breviceps* Stokell in a small New Zealand lake. 1. Life history, food, feeding and activity rhythms. *J. Fish Biol.* **7**: 1-24
- Stearns, S. C. (1995). Life history tactics: a review of the ideas. *Quarterly review of Biology*, **51**: 3-47
- Stearns, S. C. and R. E. Crandall (1984). Plasticity for age and size at maturity: a life history response to unavoidable stress: In *Fish Reproduction*: Ed. by G. W. Plots and R. J. Wootton. *Academic Press, London*.
- Stefan, G., C. J. C. Camphysen and R. W. Furness (1996). Amount of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* **136**: 1-11
- Sutela, T. and A. Huusko (1997). Food consumption of vendace, *Coregonus albula* in Lake Lentua, Finland. *J. Fish Biol.* **51**: 939-951
- Swain, D. P., G. A. Poirier and A. F. Sinclair (2000). Effect of water temperature on catchability of Atlantic cod (*Gadus morhua*) to the bottom-trawl survey in the southern Gulf of St. Lawrence. *ICES J. Mar. Sci.*, **57**: 56-68
- Swenson, W. A. and L. L. Smith (1973). Gastric digestion, food consumption, feeding periodicity and food conversion efficiency in Walleye, *Stizostedion vitreum vitreum*. *J. Fish. Res. Bd. Can.*, **30**: 1327-1336
- Temming, A. and C. Hemming (1994). Sex specific consumption of dab (*Limanda limanda* L.) based on a 24 hour fishery. *Arc. Fish. Mar. Res.* **42(2)**: 123-136
- Templeman, W. (1981). Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947-71, and their use for delineating cod stocks. *J. Northwest Atlantic Fishery science* **2**: 21-45
- Thorpe, J. E. (1977). Daily ration of adult perch, *Perca fluviatilis* L. during summer in Loch Leven, Scotland. *J. Fish Biol.* **11**: 55-68
- Thorpe, J. E., M. S. Mills and D. S. Keay (1984). Development rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture* **43**: 289-305
- Thorpe, J. E., C. Talbot, M. S Miles and D. S. Keay (1990). Control of maturation in cultured Atlantic salmon, *Salmo salar*, in pumped seas water tanks, by restricting food intake. *Aquaculture* **86**: 315-326

- Tong, J. L. (1967). Endocrine studies on *Blennius pholis* L. *Phd. Thesis, University of Wales*, 136 pp.
- Townshead, T. J. and R. J. Wootton (1984). Effects of food supply on the reproduction of the convict cichlid (*Cichlasoma nigrofasciatum*). *J. Fish Biol.* **24**: 91-104
- Tsai, C.-F, M. Wiley and A.-L. Chai (1991). Rise and fall of the Potomac River striped bass stock: a hypothesis of the role of sewage. *Trans. Am. Fish. Soc.* **120**: 1-22
- Tveiten, H., I. Mayer, H. K. Johnsen and M. Jobling (1998). Sex steroids, growth and condition of Arctic charr broodstock, *Salvelinus alpinus* L., during an annual cycle. *J. Fish Biol.* **53**: 714-727
- Tyler, A. V. (1972). Food resource division among northern, marine, demersal fishes. *J. Fish. Res. Bd. Can.*, **29**: 997-1003
- Tyler, A. V. and R. S. Dunn (1976). Ration, growth and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypothesis regarding homeostasis. *J. Fish. Res. Bd. Can.* **33**: 63-75
- Van der Land, M. A. (1991). Distribution and mortality of flatfish eggs in the 1989 egg surveys in the southern North Sea. *Neth. J. Sea Res.* **27**: 277-286
- Van der Veer, H. W., R. Berghahn and A. D. Rijnsdorp (1994). Impact of juvenile growth on recruitment in flatfish. *Neth. J. Sea Research*, **32(2)**: 153-173
- Van der Veer, H. W., L. Pihl and R. Berghahn (1990). Recruitment mechanisms in North Sea plaice, *Pleuronectes platessa* L. *Mar. Ecol. Prog. Ser.* **64**: 1-12
- Van Eenennaam, J. P. and S. I. Doroshov (1998). Effect of age and body size on gonad development of the Atlantic surgeon, *Acipenser oxyrinchus*. *J. Fish Biol.* **53(3)**: 624-637
- Von Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology* **10(2)**: 181-213
- Walford, L.A. (1946). A new graphical method describing the growth of animals. *Biol. Bull. Mar. Biol. Lab. Woods Hole*, **90**: 141-147
- Walsh, S. J. (1994). Life history traits and spawning characteristics in populations of long rough dab (*Hippoglossoides platessa* F.) in the north Atlantic. *Neth. J. Sea Res.* **32**: 241-254
- Wang, Y-T. and W-N. Tzeng (1999). Differences in growth rates among cohorts of *Encrasicholina punctifer* and *Engraulis japonicus* larvae in the coastal waters off Tanshui River Estuary, Taiwan, as indicated by otolith microstructure analyses. *J. Fish Biol.* **54**: 1002-1016

- Ware, D. M. (1980). Bioenergetics of stock and recruitment. *Can. J. Fish. Aquat. Sci.* **39**: 1012-1024
- Ware, D. M. (1982). Power and evolutionary fitness of fish. *Can. J. Fish. Aquat. Sci.* **37**: 3-12
- Werner, E. E. and D. J. Hall (1979). Foraging efficiency and habitat switching in competing sunfishes. *Ecology* **60**: 256-264
- Wetherall, J. A., J. J. Polovina and S. Ralston, 1987. Estimating growth and mortality in steady state fish stocks from length frequency data. *ICLARM Conf. Proc.*, **13**:53-74
- Wheeler, A. W., 1969. The fishes of the British Isles and North West Europe. *Macmillan, London.*
- Wimpenny, R. S. (1953). The plaice. Arnold, London. 144 pp.
- Winberg, G. G. (1956). Rate of metabolism and food requirements of fishes. *Beloruss State University, Minsk (Fish. Res. Bd. Can. Transl. Ser. (194). pp.253 (1960)*
- Windell, J. T. and S. H. Bowen (1978). Methods for the study of fish diets based on analysis of stomach contents. In *Methods for Assessment of fish production in Fresh waters* (T. Bagenal, ed.), pp.219-226. *IBP Handbook No. 3. Oxford: Blackwell Scientific Publications*
- Woodhead, P. M. J. (1964). Diurnal catches in trawl catches of fishes. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer.* **155**: 35-44
- Wootton, R. J. (1973). The effect of size of food ration on egg production in the female three-spined stickleback, *Gasterosteus aculeatus* L. *J. Fish Biol.* **5**: 89-96
- Wootton, R. J. (1979). Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symposium of Zoological Society, London*, **44**: 133-159
- Wootton, R. J. (1990). *Ecology of teleost fishes.* London: Chapman and Hall
- Wyche, C. J. and S. E. Shackley (1986). The feeding ecology of *Pleuronectes platessa* L., *Limanda limanda* L. and *Scophthalmus rhombus* L. in Carmarthen Bay, South Wales, U.K. *J. Fish Biol.* **29**: 303-311
- Xie, S., Y. Cui, T. Zhang and Z. Li (2000). Seasonal patterns in feeding ecology of three small fishes in the Biandantang Lake. *J. Fish Biol.* **57**: 867-880
- Yaragina, N. A. and C. T. Marshall (2000). Trophic influences on interannual and seasonal variation in the liver condition of Northeast Arctic cod (*Gadus morhua*). *ICES J. Mar. Sc.* **57**: 42-55

- Yoneda, M., M. Tokimura, H. Fujita, N. Takeshita, K. Yakeshita, M. Matsuyama and S. Matsuura (1998). Reproductive cycle and sexual maturity of the anglerfish, *Lophiomus setigerus*, in the East China Sea with a note on specialised spermatogenesis. *J. Fish Bio.* **53**: 164-178
- Zaret, T. H and A. S. Rand (1971). Competition in tropical stream fishes; support for the competitive exclusive principle. *Ecol.*, **52**: 336-342

9.0 APPENDICES

Appendix 1. Length/Age Matrix of total population number of dab estimated from the study area based on surveys 1999 and 2000

A. Male

Age yrs	0	1	2	3	4	5	Total
Length cm							
5	727.67						727.67
6	6873.43						6873.43
7	3150.95						3150.95
8	1224.81						1224.81
9	5085.97	2542.98					7628.95
10	27605.11						27605.11
11	3078.89	9236.67					12315.55
12		12411.75	12411.75				24823.5
13		9237.35	13856.03				23093.38
14		68086.66					68086.66
15		112301.2	20418.40				132719.60
16		82495.21	20623.80				103119
17		92795.14	30931.71				123726.8
18			132967.9	22161.32			155129.2
19			154807.4				154807.4
20				33755.06	11251.69		45006.75
21				57548.56	11509.71		69058.28
22					18791.45		18791.45
23					5883.88	5883.88	11767.77
24					3041.4	3041.4	6082.80
25						2854.99	2854.99
26						1122	1122
Total N	47746.85	389106.9	386017	113464.9	50478	12902.28	999716

B. Female

Age yrs	0	1	2	3	4	5	6	7	Total
Length cm									
5									
6	9164.58								9164.58
7	8751.55								8751.55
8	2428.51								2428.51
9	2107.81								2107.81
10	2391.1								2391.1
11	4827.52	3078.89							7906.41
12	7488.03								7488.03
13		32221.63							32221.63
14		19453.33	9726.67						29180
15		40836.80							40836.8
16		12342.80							123742.8
17		140280							140280
18		66483.95	88671.97						155155.92
19			154807.4						154807.4
20		67510.12	78761.81	22503.37					168775.3
21			92077.7	11491.01					103568.7
22			75165.81	37582.91					112748.7
23		5875.49	47003.9	29377.44					82256.82
24			21289.81	24331.21	9124.20				54745.22
25			11419.97	17129.86	5709.99				34259.92
26			4528.47	6792.70	12453.28	2264.23	1132.12		27170.79
27				2197.53	2329	8790.13	2197.53		15514.19
28					2149.99	3224.98	1074.99		6449.96
29						6887.77			6887.77
30							4282.04		4282.04
31						382.63	1208.57		1591.12
32									
33								585.84	585.84
34								585.84	585.84
35									
36									
37								477.83	477.83
Total N	37159.18	499483	583453.5	151406.1	31766.46	21549.74	9885.25	1649.51	1336353

Appendix 2. The estimation of area covered in 24-hour fishing surveys, 1999-2000. The catch (in numbers) km^{-1} is given per haul number and time of fishing

Diel periodicity in catch rates in 24-hour fishing surveys

November 1999						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	h	km^2	N km^{-2}
1	10:00 hr	16	5.4	0.93	0.156	102.77
2	14:00 hr	212	5.4	1.27	0.211	1003.37
3	18:00 hr	589	5.4	1.12	0.186	3162.13
4	22:00 hr	652	5.4	1.13	0.189	3448.88
5	02:00 hr	1704	5.4	1.10	0.183	9286.78
6	06:00 hr	585	5.4	1.30	0.217	2697.74
February 2000						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	hour	km^2	N km^{-2}
1	10:00 hr	19	5.4	1.217	0.203	93.62
2	14:00 hr	80	5.4	1.167	0.195	411.08
3	18:00 hr	177	5.4	1.117	0.186	950.25
4	22:00 hr	237	5.4	1.217	0.203	1167.79
5	02:00 hr	208	5.4	1.233	0.206	1011.05
6	06:00 hr	168	5.4	1.167	0.195	863.28
March 2000						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	hour	km^2	N km^{-2}
1	10:00 hr	79	5.4	1.150	0.192	410.53
2	14:00 hr	80	5.4	1.217	0.203	393.21
3	18:00 hr	88	5.4	1.217	0.203	434.60
4	22:00 hr	190	5.4	1.133	0.189	1002.93
5	02:00 hr	326	5.4	0.967	0.161	2023.62
6	06:00 hr	43	5.4	0.950	0.158	271.35
April 2000						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	hour	km^2	N km^{-2}
1	10:00 hr	21	5.4	1.033	0.172	121.83
2	14:00 hr	86	5.4	1.217	0.203	423.76
May 2000						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	hour	km^2	N km^{-2}
1	10:00 hr	87	5.4	1.067	0.178	488.97
2	14:00 hr	75	5.4	1.250	0.209	359.70
3	18:00 hr	400.5	5.4	1.250	0.209	1920.79
4	22:00 hr	585	5.4	1.117	0.186	3140.66
5	02:00 hr	588	5.4	1.150	0.192	3065.26
6	06:00 hr	42	5.4	0.800	0.133	314.74
July 2000						
Haul	Time	Catch	Vessel speed	Trawl duration	Area trawled	Catch rate
		N	Km h^{-1}	hour	km^2	N km^{-2}
1	10:00 hr	102	5.4	1.333	0.222	458.62
2	14:00 hr	259	5.4	1.233	0.206	1257.73
3	18:00 hr	143	5.4	1.200	0.200	714.40
4	22:00 hr	663	5.4	1.150	0.192	3456.24
5	02:00 hr	1080	5.4	1.083	0.181	5976.54
6	06:00 hr	77	5.4	1.233	0.206	374.28

Appendix 3. Percentage maturity at length and age in male and female dab, autumn 1999 and 2000

Female 1999				Male 1999			
Length cm	Total female	Number mature	% mature	Length Lt(cm)	Total male	Number mature	% Mature
9	1	0	0.00	6	2	0	0.00
10	3	0	0.00	7	2	0	0.00
11	0	0	0.00	8	0	0	0.00
12	0	0	0.00	9	2	0	0.00
13	41	0	0.00	10	2	0	0.00
14	33	2	6.87	11	5	0	0.00
15	71	25	35.25	12	49	16	32.65
16	102	18	17.32	13	32	6	19.38
17	119	35	29.12	14	88	28	32.01
18	132	75	56.64	15	98	71	72.26
19	210	120	57.25	16	106	72	67.86
20	173	109	62.68	17	124	124	100.00
21	127	103	80.60	18	153	153	100.00
22	113	93	82.36	19	85	85	100.00
23	87	53	60.92	20	70	70	100.00
24	59	56	94.73	21	59	59	100.00
25	44	29	65.03	22	36	36	100.00
26	33	28	87.03	23	12	12	100.00
27	18	18	100.00	24	3	3	100.00
28	10	10	100.00	25	2	2	100.00
29	10	10	100.00	26	1	1	100.00
30	3	3	100.00				
31	4	4	100.00				

Female 1999				Male 1999			
Age years	Total female	Number mature	% mature	Age years	Total female	Number mature	% mature
0.5	12	1	8.65	0.5	16	3	18.88
1.5	502	96	19.05	1.5	392	224	57.14
2.5	570	401	70.31	2.5	379	298	78.57
3.5	147	125	85.37	3.5	116	116	100.00
4.5	33	33	100.00	4.5	49	49	100.00
5.5	27	27	100.00	5.5	12	12	100.00
6.5	11	11	100.00				
7.5	3	3	100.00				

Appendix 3 continued.

**Female
2000**

Length cm	Total female	Number mature	% Mature
5	0	0	0.00
6	0	0	0.00
7	2	0	0.00
8	0	0	0.00
9	3	0	0.00
10	12	0	0.00
11	20	0	0.00
12	51	1	2.51
13	86	10	11.82
14	162	37	22.75
15	263	83	31.68
16	310	119	38.39
17	368	131	35.54
18	430	173	40.22
19	453	294	64.97
20	402	277	68.78
21	342	233	68.03
22	339	305	90.05
23	242	228	94.25
24	174	174	100.00
25	208	208	100.00
26	128	124	96.98
27	136	136	100.00
28	103	103	100.00
29	63	63	100.00
30	41	41	100.00
31	11	11	100.00
32	19	19	100.00
33	3	3	100.00
34	7	7	100.00
35	3	3	100.00
36	0	0	0.00
37	0	0	0.00

**Male
2000**

Length	Total male	Number mature	% Mature
5	0	0	0
6	0	0	0
7	0	0	0
8	1	0	0.00
9	5	0	0.00
10	15	0	0.00
11	24	2	9.33
12	39	8	21.01
13	96	39	40.65
14	147	97	65.82
15	128	122	95.91
16	165	151	91.81
17	197	190	96.74
18	165	165	100.00
19	125	125	100.00
20	104	104	100.00
21	99	99	100.00
22	89	89	100.00
23	28	28	100.00
24	0	0	0
25	0	0	0
26	0	0	0
27	0	0	0
28	0	0	0
29	0	0	0
30	0	0	0
31	0	0	0
32	0	0	0
33	0	0	0
34	0	0	0
35	0	0	0
36	0	0	0
37	0	0	0

Female 2000

Age years	Total female	Number mature	% mature
0.5	527	53	10.00
1.5	1450	326	22.45
2.5	1043	672	64.37
3.5	522	374	71.74
4.5	264	228	86.67
5.5	154	154	100.00
6.5	83	83	100.00
7.5	52	52	100.00

Male 2000

Age years	Total female	Number mature	% mature
0.5	92	21	22
1.5	744	459	62
2.5	530	442	83
3.5	349	349	100
4.5	72	72	100
5.5	27	27	100

Appendix 4. Variation in fecundity with length, age, somatic and ovary weight in dab, 1999-2001

Length cm	Age yrs	Somatic weight g	Ovary weight g	Number eggs	Length cm	Age yrs	Somatic weight g	Ovary weight g	Number eggs
24.5	4	168.00	2.50	354400	22.8	3	104.37	17.63	263200
24.8	4	173.00	9.66	861600	21.8	2	82.14	20.86	381200
25.6	6	188.00	7.61	820000	17.0	1	53.87	4.13	208800
24.4	3	152.00	6.44	296400	15.7	2	38.37	4.63	51200
27.8	6	230.30	5.78	962800	24.2	4	130.90	9.10	416000
24.3	5	151.62	4.93	541200	23.3	3	134.42	24.58	670933
29.6	7	281.54	4.38	598400	22.8	3	113.73	20.27	261600
27.5	6	233.72	17.28	271200	17.9	2	49.25	7.75	64800
22.2	4	103.83	7.17	444000	18.5	1	53.82	7.18	146800
25.5	5	164.75	6.25	468267	13.0	1	21.06	3.94	68400
24.4	4	162.62	8.38	532267	12.4	1	20.12	0.88	81600
21.9	3	109.52	4.48	326800	23.1	3	123.48	11.52	413600
22.4	4	110.35	4.65	278800	18.9	2	64.68	7.32	118000
24.1	4	153.64	12.36	173333	22.8	3	104.37	17.63	444000
28.5	7	239.33	7.67	541333	18.2	1	57.92	9.08	124000
25.6	6	169.38	6.62	491200	28.3	6	230.15	47.85	393600
23.7	4	130.36	6.64	285867	23.0	3	120.96	17.04	484000
27.0	6	192.71	10.29	588267	23.9	4	134.43	30.57	341600
25.5	4	195.98	12.02	425067	18.5	2	61.64	14.36	153600
26.9	6	190.14	6.86	393600	22.8	3	86.81	6.19	376400
25.6	5	180.90	10.10	429333	19.4	2	69.88	14.12	263200
26.7	5	201.18	12.82	508800	21.8	3	107.27	27.76	405600
23.0	4	122.20	8.80	276800	24.0	4	140.42	19.58	227200
22.1	3	128.01	4.99	292400	27.8	6	252.74	55.26	854222
25.0	5	144.68	6.32	323200	23.4	4	158.32	50.69	446667
23.0	4	143.65	10.35	373600	23.1	3	63.51	9.49	282667
24.6	6	157.58	9.42	640533	24.2	3	152.28	28.72	519111
23.9	4	144.67	6.33	533200	28.4	6	252.12	28.88	414222
21.9	3	120.53	6.47	400400	27.4	6	205.33	35.67	962667
25.5	5	166.69	10.31	332267	24.0	3	156.05	29.95	202667
24.0	4	140.16	5.84	370667	26.7	5	173.93	16.07	656000
26.6	5	202.45	11.55	410133	26.8	6	202.18	6.82	382667
23.6	4	145.42	7.58	340000	25.2	4	154.47	14.53	382667
25.8	4	186.02	10.98	174933					
20.7	4	100.08	4.94	312000					
29.4	8	274.91	11.09	526933					
22.8	3	126.60	7.40	315600					
22.3	4	116.41	7.59	222000					
22.4	3	128.87	22.13	161200					
15.1	1	30.49	4.51	92800					
19.5	2	74.72	13.28	298000					

Appendix 5. Diel variation in gut condition in 24-hour feeding cycle in dab, 1999-2000

		November 1999					
Fishing time	10:00 hr	14:00 hr	18:00 hr	22:00 hr	02:00 hr	06:00 hr	
Gut fullness	%	%	%	%	%	%	
SO	0.00	0.00	0.00	2.27	0.00	3.28	
SI	31.25	45.24	82.98	88.64	95.92	78.69	
I	62.50	47.62	10.64	9.09	4.08	11.48	
E	6.25	7.14	6.38	0.00	0.00	6.58	
Total (N)	16	42	47	44	49	61	
		February 2000					
Fishing time	10:00 hr	14:00 hr	18:00 hr	22:00 hr	02:00 hr	06:00 hr	
Gut fullness	%	%	%	%	%	%	
SO	0.00	2.17	4.00	0.00	1.85	0.00	
SI	47.62	76.09	72.00	92.16	74.07	77.78	
I	38.10	21.74	18.00	7.84	16.67	20.00	
E	14.29	0.00	6.00	0.00	7.41	2.22	
Total (N)	21	46	50	51	54	45	
		March 2000					
Fishing time	10:00 hr	14:00 hr	18:00 hr	22:00 hr	02:00 hr	06:00 hr	
Gut fullness	%	%	%	%	%	%	
SO	0.00	2.38	0.00	6.00	1.85	0.00	
SI	79.07	85.71	66.67	66.00	72.22	96.88	
I	18.28	9.52	31.11	28.00	18.52	3.13	
E	4.65	2.38	2.22	0.00	7.41	0.00	
Total (N)	43	42	45	50	54	32	
		May 2000					
Fishing time	10:00 hr	14:00 hr	18:00 hr	22:00 hr	02:00 hr	06:00 hr	
Gut fullness	%	%	%	%	%	%	
SO	0.00	4.55	0.00	10.94	3.28	7.32	
SI	68.52	68.18	37.88	65.63	85.25	65.85	
I	24.07	25.00	40.91	17.19	8.20	19.51	
E	7.41	2.27	21.21	6.25	3.28	7.32	
Total (N)	54	44	66	64	61	41	
		July 2000					
Fishing time	10:00 hr	14:00 hr	18:00 hr	22:00 hr	02:00 hr	06:00 hr	
Gut fullness	%	%	%	%	%	%	
SO	2.94	4.41	0.00	8.00	0.00	0.00	
SI	52.94	69.12	63.38	66.67	91.89	89.29	
I	36.76	26.47	29.58	12.00	5.41	7.14	
E	7.35	0.00	7.04	13.33	2.70	3.57	
Total (N)	68	68	71	75	74	28	

Appendix 6. Mean stomach content \pm SE (g) of dab by time of day, sex and length, 1999-2000

North Wales Coast (From present study)

Female Month: November

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥ 31	N
10:00 hr	-	-	0.059 \pm 0.041	6	0.462 \pm 0.298	4	0.000	1		
14:00 hr	0.010 \pm 0.006	5	0.013 \pm 0.013	7	0.193 \pm 0.150	14	0.296 \pm 0.296	4		
18:00 hr	0.161 \pm 0.012	2	0.468 \pm 0.119	12	0.502 \pm 0.182	14	0.354 \pm 0.151	8		
22:00 hr	0.286 \pm 0.115	4	0.494 \pm 0.114	10	0.858 \pm 0.204	14	1.271 \pm 0.615	4		
02:00 hr	0.154 \pm 0.040	7	0.513 \pm 0.094	10	0.944 \pm 0.368	13	1.055 \pm 0.411	7		
06:00 hr	0.000	1	0.312 \pm 0.090	16	0.399 \pm 0.272	16	1.255 \pm 0.423	7		
Mean	0.122		0.330		0.560		0.705			
Median	0.154		0.390		0.482		0.704			

Male Month: November

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥ 31	N
10:00 hr	0.000	2	0.071 \pm 0.071	2	-					
14:00 hr	0.087 \pm 0.054	3	0.079 \pm 0.055	7	-					
18:00 hr	0.083 \pm 0.043	4	0.453 \pm 0.079	5	0.000	1				
22:00 hr	0.163 \pm 0.045	6	0.243 \pm 0.083	5	0.251	1				
02:00 hr	0.197 \pm 0.039	4	0.234 \pm 0.075	6	0.444 \pm 0.110	2				
06:00 hr	0.157 \pm 0.046	6	0.699 \pm 0.279	14	1.662	1				
Mean	0.115		0.297		0.589					
Median	0.122		0.239		0.347					

Statistical comparison in mean stomach contents between male and female in November 1999

Size group	Test	P-value	Normality Test
11-15	1-Way Anova	0.897	Normally distributed
16-20	1-Way Anova	0.800	Normally distributed
21-25	1-Way Anova	0.930	Normally distributed

The results show no significant difference ($P > 0.05$) in the mean stomach content between male and female dab in length classes 11-15 cm and also 16-20 cm. Also there is no significant difference ($P > 0.05$) in the mean value (stomach content) between male and female dab of length class 21-25 cm.

All sex Month: November

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥ 31	N
10:00 hr	0.000	2	0.062 \pm 0.033	2	0.462 \pm 0.298	4	0.000	1		
14:00 hr	0.039 \pm 0.023	8	0.046 \pm 0.029	7	0.193 \pm 0.150	14	0.296 \pm 0.296	4		
18:00 hr	0.109 \pm 0.032	6	0.464 \pm 0.086	5	0.469 \pm 0.173	15	0.354 \pm 0.151	8		
22:00 hr	0.212 \pm 0.053	10	0.411 \pm 0.085	5	0.817 \pm 0.194	15	1.271 \pm 0.615	4		
02:00 hr	0.170 \pm 0.029	11	0.408 \pm 0.072	6	0.878 \pm 0.320	15	1.055 \pm 0.411	7		
06:00 hr	0.135 \pm 0.045	7	0.493 \pm 0.141	14	0.474 \pm 0.163	17	1.255 \pm 0.423	7		
Mean	0.111		0.314		0.549		0.705			
Median	0.122		0.410		0.472		0.704			

Female Month: February

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥ 31	N
10:00 hr	-	-	0.288 \pm 0.136	10	0.255 \pm 0.152	6	-			
14:00 hr	0.050 \pm 0.020	11	0.321 \pm 0.087	18	0.910 \pm 0.268	11	0.000	1		
18:00 hr	0.257 \pm 0.054	12	0.424 \pm 0.090	27	0.807 \pm 0.279	9	-			
22:00 hr	0.212 \pm 0.083	9	0.339 \pm 0.091	16	0.900 \pm 0.148	16	1.598 \pm 0.678	3		
02:00 hr	0.137 \pm 0.047	8	0.512 \pm 0.117	25	0.429 \pm 0.099	16	4.276 \pm 4.276	2		
06:00 hr	0.127 \pm 0.036	15	0.536 \pm 0.150	21	0.299 \pm 0.299	3	-			
Mean	0.138		0.403		0.600		1.906			
Median	0.123		0.382		0.618		1.600			

Appendix 6 continued.

Male Month: February

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26.30	N	≥31	N
10:00 hr	0.035±0.035	2	0.000	1	0.056±0.056	2				
14:00 hr	0.013±0.013	2	0.360±0.360	2	0.101	1				
18:00 hr	0.000	2	0.000	1	-					
22:00 hr	0.060±0.024	5	0.000	1	1.029	1				
02:00 hr	0.178	1	0.389±0.389	2	0.521	1				
06:00 hr	0.038±0.018	4	0.156±0.156	2	-					
Mean	0.054		0.151		0.427					
Median	0.037		0.078		0.311					

Statistical comparison in mean stomach contents between male and female in February 2000

Size group	Test	P-value	Normality Test
11-15	1-Way Anova	0.077	Normally distributed
16-20	1-Way Anova	0.015**	Normally distributed
21-25	1-Way Anova	0.487	Normally distributed

The results show no significant difference ($P>0.05$) in the mean stomach content between male and female dab in length classes 11-15 cm and also 21-25 cm. **There was however a significant difference ($P<0.05$) in the mean stomach content between male and female dab in length class 16-20 cm.

All sex Month: February

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.035±0.035	2	0.262±0.126	11	0.05±0.117	8	-			
14:00 hr	0.044±0.017	13	0.325±0.083	20	0.843±0.254	12	0.000	1		
18:00 hr	0.220±0.053	14	0.408±0.088	28	0.807±0.263	9	-			
22:00 hr	0.158±0.057	14	0.319±0.088	17	0.908±0.140	17	1.598±0.678	3		
02:00 hr	0.142±0.042	9	0.503±0.110	27	0.434±0.093	17	4.276±4.276	2		
06:00 hr	0.105±0.030	19	0.503±0.139	23	0.299±0.299	3	-			
Mean	0.117		0.387		0.583		1.960			
Median	0.124		0.367		0.620		1.600			

Female Month: March

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.318±0.083	13	0.331±0.105	11	0.170±0.115	7	7.512	1		
14:00 hr	0.203±0.099	10	0.646±0.159	18	1.306±0.696	6	-			
18:00 hr	0.061±0.034	8	0.309±0.088	12	0.341±0.161	7	0.000	2		
22:00 hr	0.250±0.051	12	0.292±0.094	13	0.422±0.160	11	0.000	2		
02:00 hr	0.086±0.040	10	0.406±0.112	19	0.681±0.255	12	-			
06:00 hr	0.241±0.065	7	0.524±0.102	11	0.705±0.354	5	4.003	1		
Mean	0.193		0.418		0.604		2.880			
Median	0.222		0.369		0.552		2.002			

Male Month: March

Time of day	Length class (cm)									
	11-15	N	16-20	N	21.25	N	26.30	N	≥31	N
10:00 hr	0.101±0.048	6	0.351±0.185	4						
14:00 hr	0.142±0.066	6	0.155±0.155	2						
18:00 hr	0.147±0.046	5	0.169±0.169	2						
22:00 hr	0.117±0.048	11	-							
02:00 hr	0.049±0.022	9	0.107±0.107	3						
06:00 hr	0.279±0.063	6	0.087±0.087	2						
Mean	0.139		0.174							
Median	0.130		0.155							

Appendix 6 continued.

Statistical comparison in mean stomach contents between male and female in March 2000

Size group	Test	P-value	Normality Test
11-15	1-Way Anova	0.077	Normally distributed
16-20	1-Way Anova	0.011**	Normally distributed

The results show no significant difference ($P>0.05$) in the mean stomach content between male and female dab in length classes 11-15 cm. **There was however a significant difference ($P<0.05$) in the mean stomach content between male and female dab in length class 16-20 cm.

All sex Month: March

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.250±0.063	19	0.336±0.088	15	0.170±0.115	7	7.512	1		
14:00 hr	0.180±0.066	16	0.595±0.147	20	1.306±0.696	6	-			
18:00 hr	0.094±0.029	13	0.297±0.081	24	0.341±0.161	7	0.000	2		
22:00 hr	0.187±0.037	23	0.292±0.094	13	0.422±0.160	11	0.000	2		
02:00 hr	0.069±0.023	19	0.365±0.100	22	0.681±0.255	12	-			
06:00 hr	0.259±0.044	13	0.457±0.097	13	0.705±0.354	5	4.003	1		
Mean	0.173		0.390		0.604		2.880			
Median	0.184		0.351		0.552		2.000			

Female Month: May

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.058±0.036	3	0.389±0.098	13	1.352±0.946	10	3.211±0.983	14	0.000	1
14:00 hr	0.282±0.115	8	0.189±0.072	6	0.614±0.327	7	1.502±1.298	4	1.046±0.706	2
18:00 hr	0.018±0.012	6	0.251±0.146	16	0.169±0.115	13	1.260±0.474	11	0.217	1
22:00 hr	0.339±0.180	7	1.481±0.381	22	1.578±0.720	12	1.438±1.124	6	-	
02:00 hr	0.172±0.096	3	0.762±0.223	12	1.670±0.469	17	4.366±1.415	10	5.470	1
06:00 hr	0.062±0.062	2	1.031±0.307	14	1.162±0.408	9	0	1	-	
Mean	0.155		0.685		1.091		1.963		1.680	
Median	0.117		0.580		1.257		1.470		0.630	

Male Month: May

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.055±0.055	3	0.109±0.089	7	0.663±0.663	3				
14:00 hr	0.176±0.071	10	0.006±0.006	4	0.010±0.010	3				
18:00 hr	0.030±0.021	5	0.100±0.059	13	0.086±0.046	2				
22:00 hr	0.170±0.126	6	0.215±0.105	9	1.655±0.820	3				
02:00 hr	0.289±0.106	7	0.654±0.145	10	-					
06:00 hr	-		0.528±0.181	11	2.117±1.536	4				
Mean	0.144		0.269		0.906					
Median	0.170		0.162		0.663					

Statistical comparison in mean stomach contents between male and female in May 2000

Size group	Test	P-value	Normality Test
11-15	1-Way Anova	0.882	Normally distributed
16-20	1-Way Anova	0.103	Normally distributed
21-25	1-Way Anova	0.882	Normally distributed

The results show no significant difference ($P>0.05$) in the mean stomach content between male and female dab in length classes 11-15 cm, 16-20 cm and 21-25 cm.

Appendix 6 continued.

All sex Month: May

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.056±0.029	6	0.291±0.076	20	1.193±0.735	13	3.211±0.983	14	0.000	1
14:00 hr	0.223±0.064	18	0.116±0.051	10	0.433±0.242	10	1.502±1.298	4	1.046±0.706	2
18:00 hr	0.024±0.011	11	0.184±0.085	29	0.158±0.099	15	1.260±0.474	11	0.217	1
22:00 hr	0.261±0.111	13	1.114±0.292	31	1.594±0.587	15	1.438±1.124	6	-	
02:00 hr	0.254±0.078	10	0.713±0.136	22	1.670±0.469	17	4.366±1.415	10	5.470	1
06:00 hr	0.062±0.062	2	0.810±0.193	25	1.458±0.524	13	0	1	-	
Mean	0.147		0.538		1.084		1.963		1.680	
Median	0.143		0.502		1.325		1.470		0.630	

Female Month: July

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.096±0.059	8	0.084±0.049	17	1.372±0.714	13	1.519±0.576	12	0.706±0.384	2
14:00 hr	0.025±0.010	4	0.692±0.166	20	1.139±0.391	15	3.063±0.886	11	-	
18:00 hr	0.059±0.047	3	0.895±0.237	18	0.677±0.207	12	1.430±0.540	15	0.000	1
22:00 hr	0.049±0.022	5	0.430±0.132	25	0.409±0.147	14	0.347±0.252	9	2.560±1.561	4
02:00 hr	0.091±0.024	11	0.580±0.135	19	1.677±0.398	16	0.608±0.195	12	0.000	1
06:00 hr	0.208±0.091	10	0.639±0.376	6	2.124±0.479	11	0.103±0.103	4	0.488±0.488	3
Mean	0.088		0.553		1.233		1.178		0.751	
Median	0.075		0.609		1.255		1.019		0.488	

Male Month: July

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.050±0.021	7	0.828±0.563	6	0.705±0.705	3				
14:00 hr	0.104±0.074	10	0.847±0.289	7	0.000	1				
18:00 hr	0.120±0.105	9	0.774±0.213	10	0.121±0.121	3				
22:00 hr	0.078±0.027	6	0.209±0.092	10	0.021	1				
02:00 hr	0.138±0.028	9	0.312±0.148	6	-					
06:00 hr	0.024±0.010	8	0.721±0.217	8	0.000	1				
Mean	0.857		0.615		0.169					
Median	0.091		0.747		0.021					

Statistical comparison in mean stomach contents between male and female in July 2000

Size group	Test	P-value	Normality Test
11-15	1-Way Anova	0.943	Normally distributed
16-20	1-Way Anova	0.708	Normally distributed
21-25	1-Way Anova	0.008**	Normally distributed

The results show no significant difference ($P>0.05$) in the mean stomach content between male and female dab in length classes 11-15 cm and 16-20 cm. The mean stomach contents of male and female dab of length class 21-25 cm are however significantly different ($P<0.05$).

All sex Month: July

Time of day	Length class (cm)									
	11-15	N	16-20	N	21-25	N	26-30	N	≥31	N
10:00 hr	0.074±0.032	15	0.278±0.158	23	1.247±0.590	16	1.519±0.576	12	0.706±0.384	2
14:00 hr	0.081±0.053	14	0.732±0.142	27	1.068±0.373	16	3.063±0.886	11		
18:00 hr	0.105±0.078	12	0.851±0.168	28	0.566±0.176	15	1.430±0.540	15	0.000	1
22:00 hr	0.065±0.018	11	0.367±0.099	35	0.383±0.139	15	0.347±0.252	9	2.560±1.561	4
02:00 hr	0.112±0.018	20	0.516±0.109	25	1.677±0.398	16	0.608±0.195	12	0.000	1
06:00 hr	0.126±0.054	18	0.686±0.195	14	1.947±0.471	13	0.103±0.103	4	0.488±0.488	3
Mean	0.094		0.572		1.148		1.178		0.751	
Median	0.093		0.601		1.158		1.019		0.488	

Appendix 7. Comparison of mean stomach contents by month and size in male and female dab

North Wales Coast (From present study)

Sex: Female Size class: 11-15 cm

Month	N	Mean stomach content (g)	Std	ANOVA		DF
				F-value	P-value	
November	5	0.122	0.012	0.880	0.493	4
February	5	0.138	0.075			
March	6	0.193	0.100			
May	6	0.155	0.132			
July	6	0.088	0.065			

There is no significant difference ($P>0.05$) in the mean stomach content in female dabs between the months.

Sex: Female Size class: 16-20 cm

Month	N	Median stomach content (g)	H-value	KRUSKALWALLIS		DF
				P-value		
November	6	0.390	3.78	0.436	4	
February	6	0.382				
March	6	0.369				
May	6	0.576				
July	6	0.610				

There is no significant difference ($P>0.05$) in the median stomach content in female dab between the months.

Sex: Female Size class: 21.25 cm

Month	N	Mean stomach content (g)	Std	ANOVA		DF
				F-value	P-value	
November	6	0.560	0.286	2.82	0.046	4
February	6	0.600	0.306			
March	6	0.604	0.400			
May	6	1.091**	0.587			
July	6	1.233**	0.634			

There is a significant difference ($P<0.05$) in the mean stomach content in female dab between the months. Tukey's multiple comparison test shows that the mean stomach contents in May and July are significantly higher.

Sex: Female Size class: 26-30 cm

Month	N	Median stomach content (g)	H-value	KRUSKAL-WALLIS		DF
				P-value		
November	6	0.705	2.51	0.644	4	
February	6	1.600				
March	6	2.002				
May	6	1.470				
July	6	1.019				

There is no significant difference ($P>0.05$) in the median stomach content in female dab between the months.

Sex: Male Size class: 11-15 cm

Month	N	Mean stomach content (g)	Std	ANOVA		DF
				F-value	P-value	
November	6	0.115	0.072	1.53	0.225	4
February	6	0.054	0.064			
March	6	0.139	0.077			
May	5	0.144	0.105			
July	6	0.086	0.043			

There is no significant difference ($P>0.05$) in the mean stomach content in male dab between the months.

Appendix 7 continued.

Sex: Male Size class: 16-20 cm

Month	N	Mean stomach content (g)	Std	ANOVA		DF
				F-value	P-value	
November	6	0.297	0.241	3.95	0.013	4
February	6	0.151	0.184			
March	5	0.174	0.105			
May	6	0.269	0.261			
July	6	0.615**	0.280			

There is a significant difference ($P < 0.05$) in the mean stomach content in male dab between the months. Tukey's multiple comparison test shows that the mean stomach content in July is significantly higher.

Sex: Male Size class: 21-25 cm

Month	N	Mean stomach content (g)	Std	ANOVA		DF
				F-value	P-value	
November	6	0.589	0.738	1.07	0.394	3
February	6	0.427	0.453			
May	5	0.906	0.944			
July	6	0.169	0.304			

There is no significant difference ($P > 0.05$) in the mean stomach content in male dabs between the months.

Appendix 8. Prey Number (%), Weight (%), Occurrence (%) and Index of Relative Importance of Food (IRIF) in the diet of dab, 1999-2000

Taxon	February 1999				March 1999			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
Hydrozoa								
<i>Obelia sp.</i>	8.96	0.50	13.95	7.80	5.56	0.74	2.17	2.82
<i>Gonothyrea sp.</i>	13.43	1.90	13.95	9.76	5.56	0.01	2.17	2.58
Others	4.48	8.30	4.65	5.81				
Crustacean								
Amphipoda								
<i>Ampelisca sp.</i>	38.81	0.90	6.98	15.56	5.56	0.02	2.17	2.58
<i>Caprella sp.</i>	8.96	0.25	4.65	4.61				
Others	4.48	0.10	4.65	3.07				
Decapoda								
<i>Crangon sp.</i>	1.49	4.71	2.33	2.84	11.11	1.48	4.35	5.56
<i>Upogebia sp.</i>					5.56	21.67	2.17	9.80
Echinodermata								
Ophiuroidea								
<i>Ophiura texturata</i>	10.45	8.68	11.63	10.25	5.56	0.38	2.17	2.70
Echinoidea								
<i>Echinocardium cordatum</i>					5.56	1.26	2.17	3.00
Polychaeta								
<i>Nereis spp.</i>	2.99	1.20	4.65	2.95				
Mollusca								
Bivalvia								
<i>Ensis ensis</i>	2.99	60.11	2.33	21.81	11.11	18.99	4.35	11.48
<i>Abra alba</i>	1.49	1.51	2.33	1.78				
Gastropoda								
<i>Patella sp.</i>					5.56	6.68	2.17	4.80
Sipuncula								
<i>Golfingia sp.</i>	1.49	11.85	2.33	5.22				
Algae								
<i>Bifurcaria bifurcata</i>					5.56	2.31	2.17	3.35
April 1999								
Taxon	N%	W%	F%	IRIF	May-June 1999			
Hydrozoa								
<i>Obelia sp.</i>	1.75	0.12	1.69	1.19				
<i>Gonothyrea sp.</i>	0.88	0.02	1.69	0.86				
<i>Sertularia sp.</i>	3.51	0.29	5.08	2.96				
Others	5.26	2.57	5.08	4.30				
Crustacean								
Amphipoda								
<i>Ampelisca sp.</i>	1.751	0.19	5.08	2.34				
Decapoda								
<i>Pagurus sp.</i>	0.88	0.07	1.69	0.88				
<i>Upogebia sp.</i>	2.63	1.99	5.08	3.24	0.88	1.48	4.35	2.23
<i>Carcinus maenas</i>	1.75	1.79	5.08	2.88				
<i>Cancer pagurus</i>	0.88	0.22	1.69	0.93	0.88	0.08	4.35	1.77
<i>Liocarcinus depurator</i>	0.88	3.03	1.69	1.87	0.88	0.45	4.35	1.89
<i>Corystes sp.</i>	1.75	4.38	3.39	3.17	2.63	27.70	13.04	14.46
Others	9.65	5.95	22.03	12.54	2.63	11.76	8.70	7.70

Appendix 8 continued.

Echinodermata

Ophiuroidea

<i>Ophiura texturata</i>	10.53	3.23	11.86	8.54	2.63	4.29	8.70	5.20
<i>Amphiura brachiata</i>	10.53	3.37	22.03	11.98	46.69	13.84	21.74	27.36
<i>Amphipholis sp.</i>	0.88	0.21	1.69	0.93	7.89	9.10	13.04	10.01
Others					20.18	5.04	13.00	12.75

Echinoidea

<i>Echinocardium cordatum</i>					3.51	10.80	17.39	10.57
-------------------------------	--	--	--	--	------	-------	-------	-------

Polychaeta

<i>Nereis sp.</i>	5.26	2.64	3.39	3.77	0.88	0.12	4.35	1.78
<i>Lagis koreni</i>	0.88	0.69	1.69	1.09				

Nemertine

					6.14	6.09	4.35	5.53
--	--	--	--	--	------	------	------	------

Mollusca

Bivalvia

<i>Ensis ensis</i>	7.89	10.41	11.86	10.06	2.63	3.55	13.04	6.41
<i>Abra alba</i>	0.88	0.62	1.69	1.08				
<i>Gari depressa</i>	1.75	0.87	3.39	2.00				
<i>Angulus sp.</i>	0.88	0.23	1.69	0.94	1.75	1.89	13.04	5.56
Others	14.91	17.19	32.20	21.44	0.00	2.81	0.00	0.94

Gastropoda

<i>Patella sp.</i>	0.88	0.58	1.69	1.05				
<i>Natica alderi</i>	1.75	0.79	3.39	1.98				
<i>Patina sp.</i>	4.39	2.17	1.69	2.75				
<i>Alvania cancellata</i>	0.88	0.44	1.69	1.01				
<i>Gibbula adonsoni</i>	0.88	0.27	1.69	0.95				
<i>Nassarius reticulatus</i>	0.88	1.16	1.69	1.25				
Others	0.88	0.03	1.69	0.87				

Algae

<i>Punctaria latifolia</i>	0.88	0.15	1.69	0.91				
<i>Jania rubens</i>	0.88	0.01	1.69	0.86				
Others	1.75	4.97	3.39	3.37				

Digested food

	-	29.36	25.42	18.26				
--	---	-------	-------	-------	--	--	--	--

Taxon	July 1999				August 1999			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>								
<i>Obelia sp.</i>					1.22	0.02	5.0	2.08
<u>Crustacean</u>								
Amphipoda								
<i>Ampelisca spp.</i>	0.79	0.02	1.47	0.76				
Cirripidia								
<i>Elminius modestus</i>	4.76	0.50	1.47	2.24				
<i>Balanus balanus</i>					1.01	1.39	2.00	1.47
Decapoda								
<i>Pagurus sp.</i>	3.17	8.25	5.88	5.77	5.27	6.24	9.00	6.84
<i>Upogebia sp.</i>	2.38	3.99	4.41	3.59	0.41	1.39	2.00	1.27
<i>Carcinus maenas</i>	2.38	3.40	4.41	3.40	0.61	1.03	4.00	1.88
<i>Cancer pagurus</i>	4.76	5.33	8.82	6.31	1.83	2.58	4.00	2.80
<i>Liocarcinus depurator</i>	32.54	16.52	16.18	21.74	25.96	13.93	31.00	23.63
<i>Corystes sp.</i>	2.38	4.61	4.41	3.80	5.48	5.97	7.00	6.15
<i>Pirimeta sp.</i>	0.79	0.11	1.47	0.79				
<i>Macropodia deflexia</i>					0.81	0.28	2.00	1.03
<i>Galathea dispersa</i>					0.41	0.06	2.00	0.82
<i>Maia squinado</i>					0.20	0.06	1.00	0.43
Others	3.17	0.86	5.88	3.31	2.63	11.76	8.70	7.70

Appendix 8 continued.

Echinodermata

Ophiuroidea

<i>Ophiura texturata</i>	4.76	1.89	7.35	4.67	4.67	2.78	11.00	6.15
<i>Amphiura brachiata</i>	1.59	1.17	2.94	1.90	1.62	0.45	1.00	1.03
Others	1.59	9.29	4.41	5.10	0.41	0.08	3.00	1.16

Echinoidea

<i>Echinocardium cordatum</i>	3.18	6.30	5.88	5.12				
-------------------------------	------	------	------	------	--	--	--	--

Polychaeta

<i>Nereis sp.</i>	0.79	0.26	1.47	0.84	3.04	4.63	7.00	4.89
<i>Lagis koreni</i>	1.58	0.42	2.94	1.64	0.61	1.27	3.00	1.63
Others					0.20	0.14	1.00	0.45
<u>Nemertine</u>	1.59	0.10	2.94	1.54	1.42	4.82	5.00	3.75

Mollusca

Bivalvia

<i>Ensis ensis</i>	7.94	24.12	16.18	16.08	1.83	23.41	8.00	11.08
<i>Pholas dactylus</i>	0.79	0.31	1.47	0.86				
<i>Pecten maximum</i>	0.79	0.36	1.47	0.88	1.83	0.22	3.00	1.68
<i>Angulus sp.</i>	3.97	0.67	4.41	3.02	1.83	0.89	9.00	3.91
<i>Mytilus edulis</i>	1.59	1.82	2.94	2.13	0.61	0.30	3.00	1.30
<i>Donax sp.</i>		0.79	0.68	1.47	0.98			
Others	4.76	2.62	8.82	5.40	0.20	0.21	1.00	0.47

Gastropoda

<i>Tritonalia sp.</i>	0.88	0.58	1.69	1.05				
<i>Urasalpinx cinera</i>					0.20	0.21	1.00	0.47
<i>Nucella sp.</i>					0.20	0.15	1.0	0.45
<i>Philine aperta</i>					30.43	12.33	23.00	21.92
<i>Lithorina sp.</i>					0.20	0.10	1.00	0.43
<i>Monodonta lineata</i>					0.61	0.53	3.00	1.38
Others	1.59	0.23	2.94	0.79				

Algae

<i>Prasiola stipitata</i>	0.79	0.15	1.47	0.80				
<i>Petalonia fascia</i>					0.41	0.20	2.00	0.87

Stone

	0.79	0.39	1.49	0.88	3.25	1.78	8.00	4.34
--	------	------	------	------	------	------	------	------

Digested food

	-	1.47	3.27	1.58	-	9.39	17.00	8.80
--	---	------	------	------	---	------	-------	------

Taxon	September 1999				October 1999			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>								
<i>Obelia sp.</i>	5.70	0.31	11.21	5.74	11.68	1.98	9.29	7.64
<i>Gonothyrea sp.</i>	0.17	0.01	0.43	0.20	2.05	0.32	1.64	1.34
<u>Crustacean</u>								
Decapoda								
<i>Pagurus sp.</i>	1.34	0.81	2.59	1.58	0.68	0.09	0.55	0.44
<i>Upogebia sp.</i>					2.74	4.29	2.19	3.07
<i>Crangon crangon</i>					0.67	0.19	0.55	0.47
<i>Cancer pagurus</i>	0.17	0.06	0.43	0.22				
<i>Liocarcinus depurator</i>	9.90	3.45	12.07	8.47	11.64	4.07	6.01	7.24
Others	1.17	0.47	4.31	1.99	1.37	0.36	1.09	0.94
<u>Echinodermata</u>								
Ophiuroidea								
<i>Ophiura texturata</i>	13.09	4.86	18.53	12.16	13.01	6.37	6.56	8.65
<i>Amphiura brachiata</i>	22.65	16.21	18.97	19.28	0.68	0.80	0.55	0.68
Others	1.01	0.65	1.29	0.98	-	15.21	2.73	5.98
Echinoidea								
<i>Echinocardium sp.</i>	1.68	4.17	4.31	3.39	0.68	0.31	0.55	0.51

Appendix 8 continued.

Polychaeta

<i>Nereis spp.</i>	1.01	0.76	2.16	1.31	2.05	1.26	1.09	1.47
<i>Lagis koreni</i>	2.52	2.21	4.74	3.16	6.85	1.13	4.37	4.12
<i>Nephtys spp.</i>	2.01	1.83	4.31	2.72				
<i>Phyllodoce sp.</i>					2.74	1.26	2.19	2.06
<i>Aphrodite aculeata</i>					0.68	2.86	0.56	1.37

<u>Nemertine</u>	1.34	0.02	0.86	0.74				
-------------------------	------	------	------	------	--	--	--	--

Mollusca

Bivalvia

<i>Ensis ensis</i>	2.18	7.51	5.60	5.10	4.79	22.49	3.83	10.37
<i>Abra alba</i>	7.55	1.66	8.19	5.80	0.68	0.37	0.55	0.53
<i>Donax sp.</i>	4.03	0.61	4.74	3.13	6.85	1.82	2.19	3.62
<i>Angulus sp.</i>	12.08	3.66	11.64	9.13	13.70	3.54	5.46	7.57
<i>Pecten maximum</i>	0.34	0.64	0.43	0.47				
<i>Mytilus edulis</i>	0.67	0.35	1.72	0.91				
<i>Scrobicularia sp.</i>	1.51	1.32	3.02	1.95				
<i>Acanthocardium sp.</i>	0.17	0.15	0.43	0.25				
<i>Solecurtis spp.</i>	0.17	0.22	0.43	0.27				
<i>Pholas dactylus</i>	0.17	0.02	0.43	0.21				
<i>Mya sp.</i>	0.17	0.79	0.43	0.47				
<i>Others</i>	6.88	1.93	14.22	7.68	13.01	9.88	10.38	11.09

Gastropoda

<i>Monodonta lineata</i>	0.17	0.01	0.43	0.20	0.68	1.23	0.55	0.82
<i>Others</i>					0.68	0.31	0.55	0.51

Algae

<i>Petalonia fascia</i>	0.17	0.01	0.43	0.20	2.05	0.56	1.64	1.42
-------------------------	------	------	------	------	------	------	------	------

Digested food

	-	45.31	44.40	29.90	-	19.30	18.03	12.44
--	---	-------	-------	-------	---	-------	-------	-------

Taxon	November 1999				December 1999			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>								
<i>Obelia sp.</i>	4.35	0.20	10.42	4.99	3.30	0.03	5.08	2.81
<i>Gonothyrea sp.</i>	0.64	0.02	1.54	0.74				
<i>Others</i>	0.16	0.01	0.39	0.18				

Crustacean

Decapoda

<i>Pagurus sp.</i>	0.16	0.40	0.39	0.32	4.95	2.07	5.08	4.03
<i>Crangon crangon</i>	0.16	0.23	0.39	0.26				
<i>Corystes sp.</i>					0.55	0.40	0.85	0.60
<i>Liocarcinus depurator</i>	0.81	0.19	1.93	0.98	4.40	4.19	5.08	4.56
<i>Others</i>	0.48	0.03	1.16	0.56	2.20	1.45	3.39	2.35

Amphipoda

<i>Ampelisca sp.</i>	1.45	0.01	1.54	1.00				
<i>Caprella sp.</i>	0.32	0.01	0.39	0.24				
<i>Others</i>	0.32	0.01	0.39	0.24				

Cirripedia

<i>Elminius sp.</i>					0.55	0.40	0.85	0.60
---------------------	--	--	--	--	------	------	------	------

Pcynoqonida

<i>Achelia sp.</i>	0.32	0.09	0.77	0.40	0.55	0.10	0.85	0.50
--------------------	------	------	------	------	------	------	------	------

Echinodermata

Ophiuroidea

<i>Ophiura texturata</i>	24.80	11.42	27.80	21.34	1.65	1.09	2.54	1.76
<i>Amphiura brachiata</i>	45.57	38.33	53.28	45.34				
<i>Others</i>	-	2.77	1.16	1.31	-	15.21	2.73	5.98

Echinoidea

<i>Echinocardium sp.</i>	0.16	0.08	0.39	0.21	1.65	1.29	2.54	1.83
--------------------------	------	------	------	------	------	------	------	------

Appendix 8 continued.

Polychaeta

<i>Nereis sp.</i>	1.13	0.08	2.70	1.30	1.65	1.33	2.54	1.84
<i>Lagis koreni</i>	7.41	0.46	8.49	5.46	46.70	45.05	47.46	46.41
<i>Nephtys sp.</i>					1.65	4.43	2.54	2.87
<i>Phyllodoce sp.</i>								
<i>Aphrodite aculeata</i>	0.16	0.14	0.39	0.23	1.65	3.22	2.54	2.47
Others	-	0.09	0.39	0.16	1.65	0.81	1.69	1.39

Nemertine

8.70	0.78	11.99	7.15	0.55	0.17	0.85	0.52
------	------	-------	------	------	------	------	------

Mollusca

Bivalvia

<i>Ensis ensis</i>	0.48	0.05	1.16	0.56	4.95	13.88	6.78	8.54
<i>Abra alba</i>	0.48	0.02	1.18	0.55				
<i>Donax sp.</i>	3.70	0.39	3.86	2.65				
<i>Angulus sp.</i>	2.09	0.20	3.86	2.05	1.65	0.29	1.69	1.21
<i>Mya sp.</i>	0.16	0.15	0.39	0.23				
Others	2.74	1.03	4.63	2.80	8.79	10.65	13.56	11.00

Gastropoda

<i>Philine aperta</i>	0.16	0.06	0.39	0.20	1.10	0.29	1.69	1.02
<i>Nucella sp.</i>	0.16	0.10	0.39	0.22				
<i>Monodonta lineata</i>	0.16	0.02	0.39	0.19				
Others					0.55	0.17	0.85	0.52

Algae

<i>Petalonia fascia</i>	1.13	0.07	2.70	1.30	8.79	4.74	13.56	9.03
-------------------------	------	------	------	------	------	------	-------	------

Stone

0.55	0.16	0.85	0.52
------	------	------	------

Digested food

-	43.28	54.05	32.44	-	3.79	25.42	9.74
---	-------	-------	-------	---	------	-------	------

Taxon	February 2000				March 2000			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>								
<i>Obelia sp.</i>	4.54	0.34	10.74	5.21	3.69	1.35	9.33	4.79
<u>Crustacean</u>								
<u>Decapoda</u>								
<i>Pagurus sp.</i>					1.13	2.51	2.61	2.09
<i>Upogebia sp.</i>	0.28	1.20	0.74	0.74				
<i>Liocarcinus depurator</i>	1.28	0.64	3.33	1.75	2.41	3.07	5.60	3.69
Others	0.28	0.86	0.74	0.62	0.14			
<u>Echinodermata</u>								
<u>Ophiuroidea</u>								
<i>Ophiura textura</i>	4.82	1.21	10.74	5.59	3.83	3.59	8.96	5.46
<i>Amphiura brachiata</i>	70.21	80.35	71.48	74.01	37.02	62.68	52.99	50.90
<u>Echinoidea</u>								
<i>Echinocardium sp.</i>	0.28	0.03	0.74	0.35	0.43	0.83	1.12	0.79
<u>Polychaeta</u>								
<i>Nereis spp.</i>	0.28	0.08	0.74	0.37	0.28	0.44	0.75	0.49
<i>Lagis koreni</i>	6.81	2.14	12.59	7.18	17.45	6.78	24.25	16.16
<i>Aphrodite aculeata</i>	0.28	0.70	0.74	0.57				
Others	0.14	0.02	0.37	0.18				

Appendix 8 continued.

Mollusca

Bivalvia

<i>Ensis ensis</i>	1.42	3.31	3.33	2.69	1.56	5.79	4.10	3.82
<i>Abra alba</i>	0.14	0.01	0.37	0.17				
<i>Donax sp.</i>	4.96	0.23	2.96	2.72	0.71	0.33	1.87	0.97
<i>Angulus sp.</i>	1.42	0.39	3.70	1.84	22.98	6.11	17.91	15.67
<i>Others</i>	2.84	1.44	5.93	3.40	8.23	2.68	8.58	6.50

Gastropoda

<i>Philine aperta</i>					0.14	0.08	0.37	0.20
-----------------------	--	--	--	--	------	------	------	------

Digested food

	-	7.07	18.52	8.53	-	3.00	16.42	6.47
--	---	------	-------	------	---	------	-------	------

Taxon	April 2000				May 2000			
	N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>								
<i>Obelia sp.</i>	0.57	0.29	1.89	0.92	2.54	0.32	4.82	2.56

Crustacean

Decapoda

<i>Pagurus sp.</i>	0.57	0.87	1.89	1.11	0.63	0.25	0.90	0.59
<i>Upogebia sp.</i>					2.06	4.68	3.31	3.35
<i>Liocarcinus depurator</i>	1.14	1.40	3.77	2.11	10.32	7.38	15.36	11.02
<i>Carcinus maenas</i>					0.16	0.12	0.30	0.20
<i>Cancer pagurus</i>					0.16	0.04	0.30	0.17
<i>Others</i>					0.79	0.59	1.51	0.97

Pcynogonida

<i>Achelia sp.</i>	0.28	0.03	0.94	0.42				
--------------------	------	------	------	------	--	--	--	--

Echinodermata

Ophiuroidea

<i>Ophiura texturata</i>	1.42	0.82	2.83	1.69	3.49	2.18	6.02	3.90
<i>Amphiura brachiata</i>	48.72	69.49	68.87	62.36	37.94	45.58	36.45	39.99

Echinoidea

<i>Echinocardium sp.</i>					0.16	0.09	0.30	0.18
--------------------------	--	--	--	--	------	------	------	------

Polychaeta

<i>Nereis sp.</i>	9.69	2.44	9.43	7.19	0.79	0.75	1.51	1.02
<i>Lagis koreni</i>	7.69	3.89	16.04	9.20	15.56	6.73	17.77	13.35
<i>Nephtys sp.</i>	0.85	1.38	2.83	1.69				
<i>Phyllodoce sp.</i>					0.32	0.67	0.60	0.53

Nemertine

					0.32	0.01	0.60	0.31
--	--	--	--	--	------	------	------	------

Mollusca

Bivalvia

<i>Ensis ensis</i>	3.70	10.56	9.43	7.90	3.81	14.37	6.33	8.17
<i>Abra alba</i>	2.28	0.88	4.72	2.83	1.59	2.38	3.01	2.33
<i>Donax sp.</i>	1.42	0.12	4.72	2.09	2.70	0.60	2.41	1.90
<i>Angulus sp.</i>	17.95	2.37	8.49	9.60	9.37	5.76	4.82	6.65
<i>Pecten maximum</i>	0.57	0.09	1.89	0.85				
<i>Mytilus edulis</i>					0.16	0.39	0.30	0.28
<i>Others</i>	2.28	2.70	5.66	3.55	5.87	5.76	6.63	6.09

Gastropoda

<i>Philine aperta</i>	0.28	0.13	0.94	0.45	0.16	0.01	0.30	0.16
-----------------------	------	------	------	------	------	------	------	------

Fish

<i>Sprattus sprattus</i>					0.95	0.36	0.90	0.74
--------------------------	--	--	--	--	------	------	------	------

Appendix 8 continued.

						0.16	0.01	0.30	0.16
<u>Stone</u>									
<u>Algae</u>									
	<i>Petalonia fascia</i>	0.57	0.26	1.89	0.90				
<u>Digested food</u>		-	2.30	12.26	4.85	-	1.00	4.82	1.94
		July 2000				October 2000			
Taxon		N%	W%	F%	IRIF	N%	W%	F%	IRIF
<u>Hydrozoa</u>									
	<i>Obelia sp.</i>	1.40	0.72	2.46	1.53	4.76	0.52	9.27	4.85
<u>Crustacean</u>									
<u>Decapoda</u>									
	<i>Pagurus sp.</i>	0.42	0.63	0.49	0.52	3.06	2.57	2.65	2.76
	<i>Upogebia sp.</i>	0.98	2.78	1.72	1.83	0.34	0.71	0.66	0.57
	<i>Liocarcinus depurator</i>	12.32	9.16	14.04	11.84	3.74	2.37	7.28	4.46
	<i>Corystes sp.</i>					0.34	0.26	0.66	0.42
	<i>Carcinus maenas</i>	0.14	0.10	0.25	0.16				
<u>Echinodermata</u>									
<u>Ophiuroidea</u>									
	<i>Ophiura texturata</i>	1.12	0.90	1.97	1.33	0.68	1.10	1.32	1.04
	<i>Amphiura brachiata</i>	16.67	24.32	22.41	21.13	41.84	59.71	47.02	49.52
	<i>Ophiothrix fragilis</i>	1.26	2.60	0.70	1.53				
<u>Echinoidea</u>									
	<i>Echinocardium spp.</i>	0.98	0.66	1.72	1.12	0.34	0.51	0.66	0.50
	<i>Echinus esculentus</i>				1.02	3.07	1.32	1.80	
<u>Polychaeta</u>									
	<i>Nereis sp.</i>	1.82	0.96	2.22	1.67	2.04	1.55	3.97	2.52
	<i>Lagis koreni</i>	35.29	21.25	38.67	31.74	22.79	11.13	26.49	20.14
	<i>Nephtys sp.</i>	0.14	0.15	2.71	1.55				
	<i>Phyllodoce sp.</i>					0.34	0.23	0.66	0.41
	<i>Arenicola sp.</i>					2.04	1.04	1.99	1.69
<u>Nemertine</u>		1.68	0.25	2.71	1.55				
<u>Mollusca</u>									
<u>Bivalvia</u>									
	<i>Ensis ensis</i>	6.58	21.27	11.08	12.98	2.04	4.79	3.97	3.60
	<i>Abra alba</i>	3.50	4.22	3.94	3.89	0.68	0.26	1.32	0.75
	<i>Donax sp.</i>	0.56	0.34	0.99	0.63	1.36	0.83	1.99	1.39
	<i>Angulus sp.</i>	9.52	4.57	6.40	6.83	2.04	0.49	3.31	1.95
	<i>Venus sp.</i>	0.14	0.17	0.25	0.19				
	<i>Mytilus edulis</i>	0.56	1.13	0.74	0.81				
	<i>Gibbula sp.</i>	0.14	0.05	0.25	0.15				
	<i>Mactra sp.</i>					0.34	0.35	0.66	0.45
	<i>Others</i>	4.34	2.89	6.90	4.71	3.06	1.38	5.96	3.47
<u>Gastropoda</u>									
	<i>Philina aperta</i>					2.72	3.02	1.99	2.58
	<i>Monodonta lineata</i>					0.34	0.32	0.66	0.44
<u>Fish</u>									
	<i>Sprattus sprattus</i>	0.42	0.30	0.74	0.49	0.68	0.33	0.66	0.56
<u>Stone</u>						3.40	0.59	0.66	1.55
<u>Digested food</u>		-	0.60	4.19	1.60	-	2.90	6.62	3.18