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Population dynamics of plaice *Pleuronectes platessa* L in the inshore waters of North West Wales and Eastern Anglesey

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**Population dynamics of plaice *Pleuronectes platessa* L. in the
inshore waters of North West Wales and Eastern Anglesey.**

Thesis submitted for the degree of Doctor of Philosophy

By

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Abstract

This study examines the population dynamics of juvenile and adult plaice *Pleuronectes platessa* L. in the coastal inshore area of North West Wales and Eastern Anglesey. The population dynamics of the adult population were studied by conducting autumnal otter trawl surveys in 2004/05. The data obtained were compared with an earlier study conducted in the same area in 1974/77 and with current data for other plaice stocks in North West Europe. The size/age structure, length/weight relationship, growth rate, mortality rate and size/age at first maturity (L_{50}/A_{50}) were described for male and female plaice. The results of the survey showed that the size/age structures of male and female fish were different with the older, larger and heavier fish comprising predominately female fish. The length/weight relationships were different for male and female fish with males exhibiting isometric growth ($b=3.02$) and females exhibiting positive allometric growth ($b=3.20$). Growth patterns, described using the von Bertalanffy growth model, were significantly different between male ($K=0.62 \text{ year}^{-1}$; $L_{\infty}=26.4 \text{ cm SL}$) and female ($K=0.25 \text{ year}^{-1}$; $L_{\infty}=43.8 \text{ cm SL}$) plaice. The instantaneous rate of total mortality was higher for male plaice than for females ($Z: \text{♂} = 1.05 \text{ year}^{-1} \text{ cf. } \text{♀} = 0.64 \text{ year}^{-1}$). Male plaice matured at a significantly smaller size and younger age than female plaice ($L_{50}, \text{♂}=16 \text{ cm SL cf. } \text{♀}=20 \text{ cm SL}$; $A_{50}, \text{♂}=1.33 \text{ years cf. } \text{♀}=2.11 \text{ years}$). A comparison of the results of the 2004/05 survey with the earlier 1974/77 survey showed differences in the size/age structure, growth rate and maturity ogives between the two surveys. A meta-analysis of the population dynamics of plaice stocks in North West Europe revealed consistent similarities in the size-structure and patterns of growth and maturation between the populations.

A detailed analysis was conducted of the population dynamics of plaice in the coastal inshore area of North West Wales and Eastern Anglesey, based on the autumnal RV *Prince Madog* fisheries surveys, for the time period 1970-2006. A cyclical trend in abundance (number of plaice hour⁻¹) was apparent in the catch data which was significantly correlated with the winter North Atlantic Oscillation Index (wNAOI). The results indicated no significant changes in the size composition of the plaice catch during the 4 decades (average sizes; $\text{♂}=24.0 \text{ cm SL cf. } \text{♀}=29.1 \text{ cm TL}$) but a decline in the proportion of older age classes (≥ 5 years old) in the catch (average ages; $\text{♂}=2.6 \text{ years cf. } \text{♀}=3.1 \text{ years}$). Analysis of the sex-ratio data between 1970 and 2006

indicated a decrease in the proportion of male plaice caught in the fisheries surveys over the last 4 decades. Male and female plaice both showed contrasting changes in growth patterns between 1970 and 2006. For female plaice, L_{∞} tended to increase over time with no change in K values. In contrast, male plaice showed no long term change in L_{∞} over time, but an increase in K-values post-1990. The L_{50}/A_{50} datasets were limited but analysis of the available data indicated a decrease in L_{50}/A_{50} values for male and female plaice over time. The population biology data for plaice (currently underexploited but historically overexploited in the 1970s and 1980s) for the time period 1970-2006 were compared with comparable data for dab *Limanda limanda* L. (an unexploited species in the Irish Sea) and whiting *Merlangius merlangus* L. (an overexploited species in the Irish Sea) obtained from the same fisheries surveys. Analysis of the time series data revealed changes in the size and growth patterns for the three species that were consistent with their level of exploitation (*i.e.* no changes for dab *cf.* changes for plaice and whiting). A similar analysis of the L_{50}/A_{50} data was more limited but suggested decreases in the maturity ogive values of plaice and dab. The results were suggestive of fisheries-induced evolution in plaice and whiting in the South East Irish Sea. The population dynamics of plaice were examined in relation to summer/winter/annual sea surface temperatures (SST) and wNAOI to examine whether any changes were related to recent climate change. This analysis indicated a correlation between abundance and wNAOI with higher abundances (number plaice hour⁻¹) recorded in the survey when the wNAOI was in negative phase. A simple model outlining the effects of increased/decreased SST on size and growth was proposed. For male plaice, the correlations between L_{∞}/K and SST/ wNAOI followed those predicted by the model, but the response was not observed for female plaice.

A detailed three year survey of the growth, length/weight relationship and condition of juvenile plaice on two nursery grounds (Conwy and Red Wharf Bays) between April 2004 and March 2007 are reported. Modal progression analysis was used to follow the growth of the 2004, 2005 and 2006 year classes with the average size increasing from 1.5-2.0 cm SL in April/May to *ca.* 8-10 cm SL the following February/March. Seasonal variations in the length/weight relationships and in condition factors were observed on both nursery grounds. Condition was lowest in the winter/spring and increased in the summer/autumn as a result of increased food availability and growth opportunity. No differences were observed between the two nursery grounds.

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Chapter 1:

General Introduction.

1.1.1 General Introduction

Fisheries and fish are both highly significant to human society. Fish are a major source of animal protein with current estimates of per capita food consumption of fish at 16.7 kg per year (FAO, 2009). The capture fisheries industry, currently estimated at 2.1 million motorised fishing vessels, that supplies these fish currently lands 90-95 million tonnes per annum, with the majority of these landings (80-85 MT) derived from marine capture fisheries (FAO, 2009). Both fish as food and the fisheries that supply them are recognised as particularly important to the developing world where they play a significant role in poverty alleviation and food security. However, in developed nations, although catches remain high, the fishing industry is reducing.

The North East Atlantic is currently the 4th most productive region of the world for fisheries, with 9.1 million tonnes landed in 2006 (FAO, 2009), although bycatch and discarding are recognised as serious issues in this region and the actual rate of fishing mortality, and thus the impact on the fish stocks in this region, is much greater (ICES, 2008a, 2008b; FAO, 2009). The North East Atlantic has a long history of commercial fisheries exploitation dating back over 500 years (*e.g.* Bolle *et al.*, 2004). The coastal shelf seas of the North East Atlantic are areas of high biological productivity and support a high biomass of fish (Jennings *et al.*, 2001) and major fisheries take place for pelagic species such as herring *Clupea harengus* L. and mackerel *Scomber scombrus* L. and demersal species such as gadids (cod *Gadus morhua* L., haddock *Melanogrammus aeglefinus* L., whiting *M. merlangus* L.) and flatfishes (*e.g.* plaice *P. platessa* L., sole *Solea solea* L, turbot *Psetta maximus* L.). The European plaice *P. platessa* L. is one of the most important commercial fish species landed in Europe (FAO, 2009). In this thesis, attention will be focussed on the study of plaice in the inshore coastal waters of North West Wales and Eastern Anglesey in order to provide current data on the population dynamics of adult plaice (Chapter 2), to examine changes in the population dynamics of adult plaice over a 36 year period (Chapter 3) and to examine seasonal changes in growth and condition of juveniles on two major nursery grounds in this area (Chapter 4). In the following sections of this chapter a number of key areas are reviewed: the study area – the Irish Sea in general and the inshore coastal waters of North West Wales and Eastern Anglesey in particular; the study species – the European plaice *P. platessa* L.; and the study of population dynamics on fishes.

1.1.2 The study area: the Irish Sea

The Irish Sea is an arm of the North East Atlantic Ocean that is approximately 410 km long and 240 km wide (at its widest point) separating the islands of Ireland and Great Britain. It is one of the smaller regional seas in UK coastal waters (Figure 1.1) with a surface area of approximately 58,000 km² (Vincent *et al.*, 2004). It is connected to the Atlantic Ocean from the south by St. George's Channel (which leads into the Celtic Sea) and by the North Channel to the north (Figure 1.1). Both channels allow the movement of water into the Irish Sea, and the two water bodies meet to form a standing wave and weak currents to the south-west of the Isle of Man (Vincent *et al.*, 2004). However, the predominant water movement is from the south with inshore coastal currents usually carrying water from the Celtic Sea through St George's Channel northwards to the North Channel where it mixes with water from the Outer

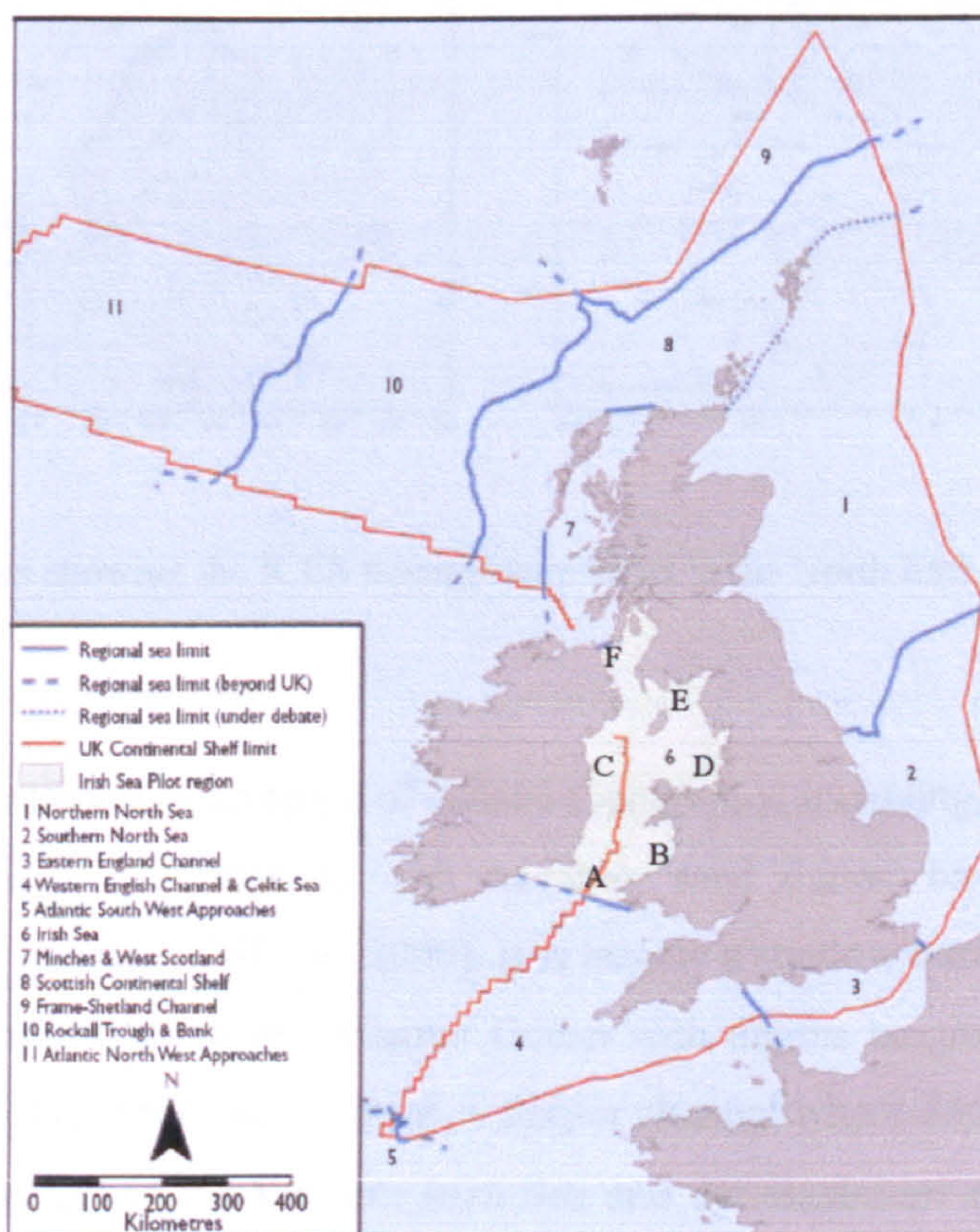


Figure 1.1: An outline of the eleven regional seas delineated within UK coastal waters. The Irish Sea (region 6) is highlighted in green. A = St George's Channel, B = Cardigan Bay, C = Western Irish Sea, D = South East Irish Sea, E = North East Irish Sea, F = North Channel. (Modified from Vincent *et al.*, 2004; original chart from JNCC, Crown Copyright).

Clyde as it exits the Irish Sea (ICES, 2008a). For fisheries stock assessment and management purposes, the International Council for the Exploration of the Sea (ICES) has divided up the waters of the North east Atlantic into management areas (Figure 1.2) and the Irish Sea is coded as a single management unit - division VIIa, although the Irish Sea can be subdivided geographically into 4 main areas: St, George's Channel and Cardigan Bay, North East, Western, and South East Irish Sea (Figure 1.1).

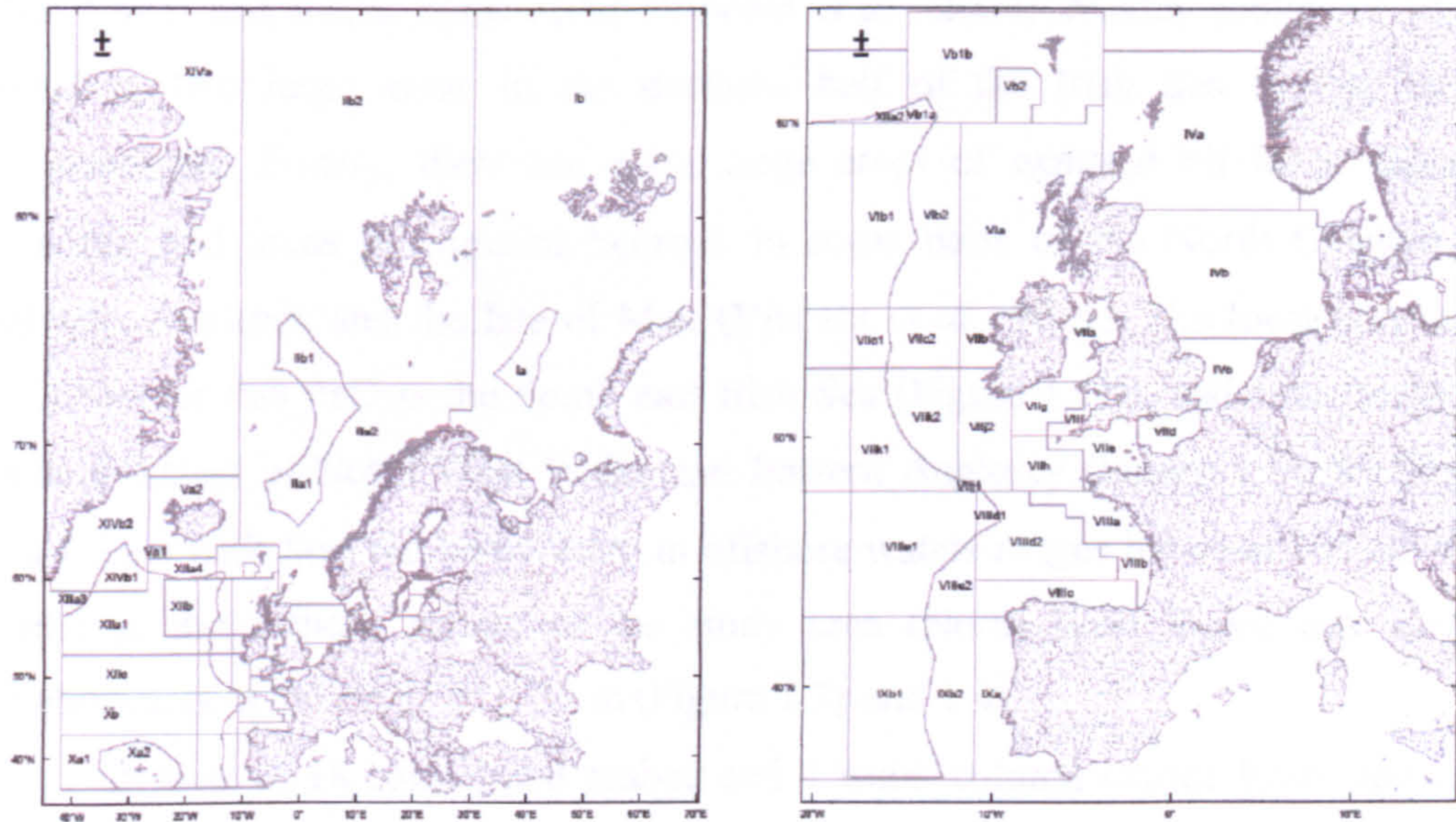


Figure 1.2: Maps showing the ICES management areas in the North East Atlantic Ocean (Source URL1).

The Irish Sea contains a wide range of coastal topography, including fjordic sea lochs, rocky headlands, cliff formations, salt marshes, sand dunes, bays, estuaries and numerous sandy beaches (OSPAR, 2000). It is largely a shallow basin, sheltered from the wind and currents from the Atlantic Ocean with depths ranging from 20-100m (Vincent, *et al* 2004). There is, however, a deeper channel where depths exceed 100m extending north-south in the Western Irish Sea and the maximum depth is 315 m in the Beaufort's Dyke (Vincent, *et al* 2004).

Although it differs in some details, in terms of bathymetry and substrate characteristics, the Irish Sea has many similarities to other UK regional seas on the continental shelf such as the Eastern Celtic Sea, the English Channel and the North

Sea. However, the Irish Sea does have the deep (>100m) north-south channel extending in the western part of the sea (Figure 1.3a), which other UK shelf seas do not have (ICES, 2008a). Vincent *et al.* (2004) provides a broad description of the substrate characteristics of the Irish Sea which are also summarised in Figure 1.3b. The broad “central belt” of the Irish Sea consists of extensive gravelly sediments in the areas subject to tidal currents. Areas of sandy substrate, often moderately mobile, also occur fairly extensively. In some parts of the Irish Sea, such as north of the Isle of Man, in Liverpool Bay, Cardigan Bay and in some parts of St. George's Channel, sand waves and megaripples occur (Vincent *et al.*, 2004). Muddy sediments can be found in two large areas in the northern half of the Irish Sea in low energy environments. Finally, there are some large areas of exposed till in St George's Channel, and areas of exposed bedrock in some parts of the North Channel and between Anglesey and the Isle of Man (Vincent *et al.*, 2004). The focal part of the Irish Sea for this PhD is the South east Irish Sea (Figure 1.1D), and specifically the inshore waters of North West Wales and Eastern Anglesey (Figure 1.4). Within the South East Irish Sea, the bathymetry in offshore waters ranges between 30 and 90 m, whilst in the inshore waters of the study area (North West Wales and Eastern Anglesey), is in the range of 0-30 m (Figure 1.3a and 1.4).

A total of 18 coastal and seabed and 4 water column marine landscape types have been identified in the Irish Sea (Table 1.1; Vincent *et al.*, 2004) and the distribution of these geographical and hydrographical groupings are shown in Figure 1.3b. The concept of marine landscapes was first proposed by Roff and Taylor (2000) who showed that geophysical and hydrographical information (*e.g.* seabed factors such as water temperature, depth/light, substratum type, exposure and slope, and water column factors such as water temperature, depth/light and the stratification/mixing regime), which are often available over larger geographical areas and in better detail than biological information, can be used in lieu of biological information to classify marine habitats and to inform marine conservation strategies. This is based on the very strong relationship that exists between the hydrographic and geophysical factors of the seabed and the composition of biological communities found in that location (Roff and Taylor, 2000). This classification approach has been used to classify marine habitats coastal waters of the EU (*e.g.* Vincent *et al.*, 2004; Al-Hamdi *et al.*, 2007; McBreen *et al.*, 2008) and elsewhere (*e.g.* Beaman and Harris, 2005; Harris *et al.*, 2008). For the Irish Sea, details of the biological characteristics

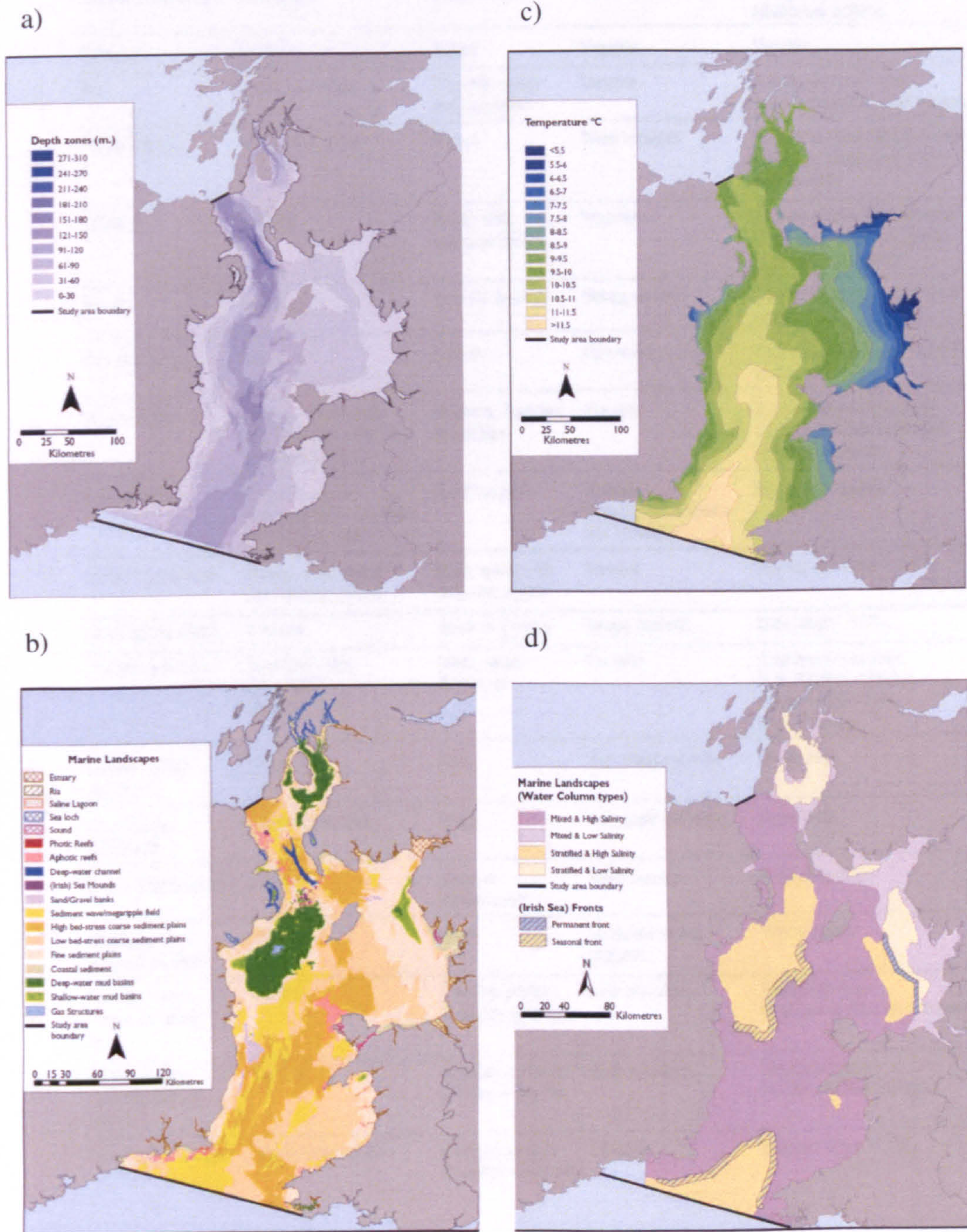


Figure 1.3: Irish Sea data maps on: a) bathymetry; b) landscapes & substrata; c) bottom temperature (Dec-Feb); d) number of biodiversity complexes. (Copied from Vincent *et al.*, 2004; original chart from JNCC, Crown Copyright).

Table 1.1: Summary of physical characteristics of seabed and coastal marine landscape types in the Irish Sea (copied from Vincent *et al.*, 2004).

Marine Landscape	Depth (m)	Substratum	Bed-stress/ current	Topography/ slope & additional criteria
Estuary	0-30m	Mixed	Variable	Variable
Ria	Shallow: 0-20m	Typically rocky with sediment	Variable	A drowned river valley; often v-shaped in cross section
Saline Lagoon	V Shallow 0-5m	Mixed	Weak currents	Parallel to coast, limited water exchange, large surface area: volume ratio
Sea loch	0-200m	Rocky with sediment basins	Variable	Includes fjords (have shallow sill & deep basins) & fjards (generally shallower)
Sound	0-30m	Gravels & sands	Strong currents	Narrow channel, open at both ends
Gas structures	Variable	Mixed	Very weak currents	Pockmarks/ depressions (hard structures)
Photoc Reefs	Within photic zone (i.e. generally <10-20m for the Irish Sea)	Bedrock, boulders & cobbles	Variable	Rough/uneven topography Contains Littoral Rock and Infralittoral Rock
Aphotic Reefs	In aphotic zone (i.e. generally >10-20m for the Irish Sea)	Rock biogenic	Variable (not as pronounced as Sea Mounds)	Rough topography
(Irish) Sea Mounds	Rising >20m above surrounding seabed	Rock, often with sediment veneer	Variable	Sea Mound slope > 1-8%
Sand/ gravel banks	Variable	Sands & gravels	Strong currents	Bank slope >1-8%
Coastal sediment	Intertidal -50m (& no BGS sediment data)	Muds, sands & gravels	Variable	Adjacent to coastline N.B. 'Bucket' category, where no BGS data were available.
Shallow-water mud basin	0-50m	Muds	Very weak currents	Depression
Deep-water mud basin	Deeper than 50m	Muds	Very weak currents	Depression
Fine sediment plain	Variable	Sands & muddy sands	Weak currents	Negligible slope
Sediment wave/ megaripple field	Variable	Sands	Moderate/strong currents	Waves/ripples
Low bed-stress coarse sediment plain	Variable	Cobbles, pebbles & muddy gravels	Low bed-stress	Negligible slope Evidence of fines in sediment
High bed-stress coarse sediment plain	Variable	Boulders, cobbles, pebbles & gravels	High bed-stress	Negligible slope No fines within sediment
Deep-water channel	Deeper than 150m	Cobbles, gravels & mixed sediments	Variable	Channel slope > 1-8%

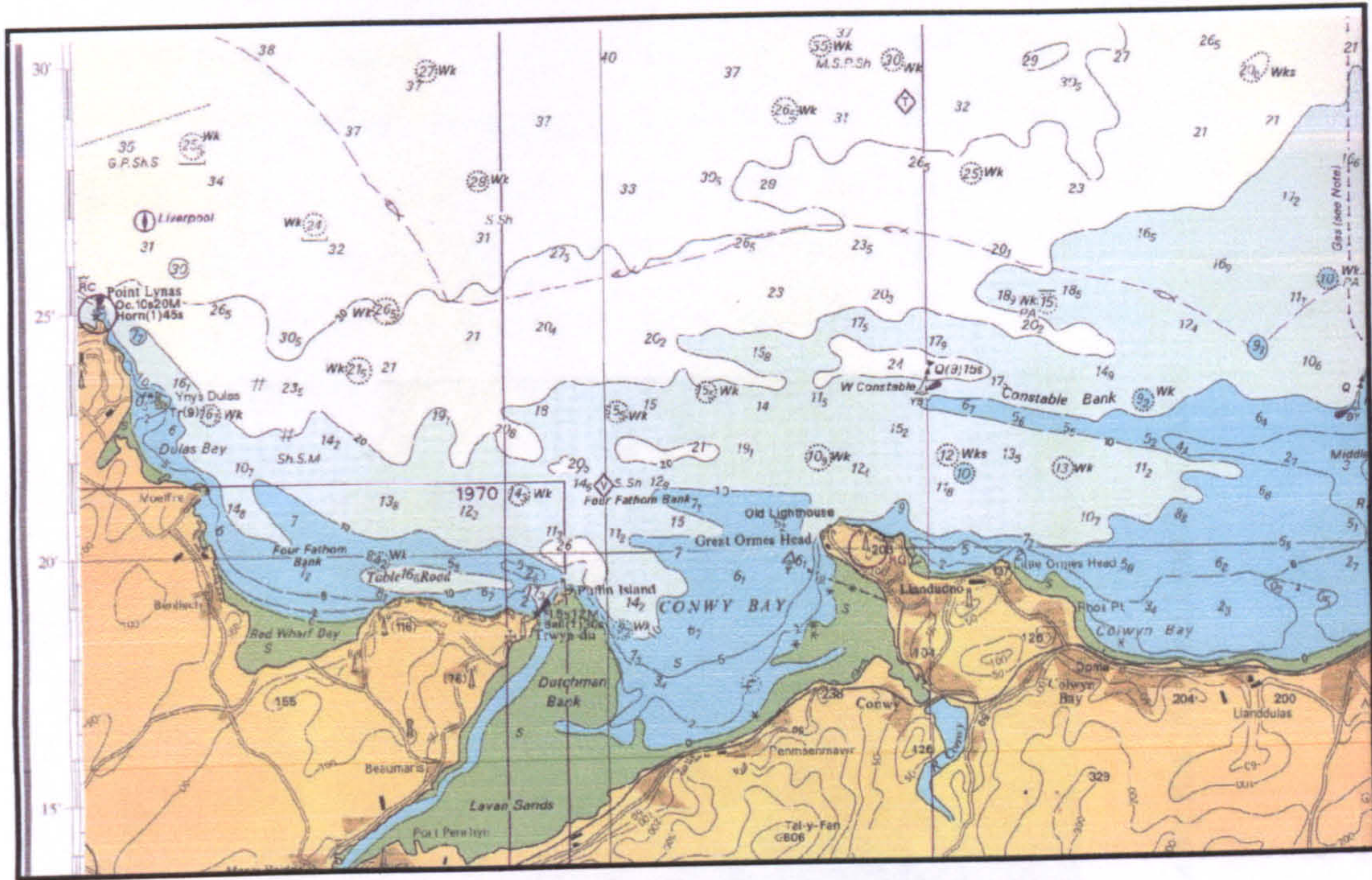


Figure 1.4: Admiralty chart of the coastal inshore waters of North West Wales and Eastern Anglesey. Note: depths on the chart are in fathoms (1 fathom = 1.83 m).

of each landscape type can be found in Vincent *et al.* (2004) (their Table 2). In general, the seabed sediments in the Irish Sea consist of rocky, gravelly, sandy and muddy substrates, or a mixture of two or more of these substrate types depending on the landscape type (Figure 1.3b, Table 1.1). The South East Irish Sea substrata are characterised by coastal sediments and fine sediment plains inshore, with a mixture of fine sediment plains and low/high bed-stress coarse sediment plains offshore (Figure 1.3b; Vincent, *et al.*, 2004). The sand transport pattern is complex in the North East Atlantic Ocean and particularly in the Irish Sea, with a zone of divergence across the Irish Sea west of Anglesey (OSPAR, 2000). Figure 1.5 shows the sedimentary biotopes in Red Wharf Bay and Conwy Bay produced by Rees (2004). The predominant sediment types are muddy sands in the subtidal areas of these two bays transitioning through various sand/broken shell mixtures in the deeper coastal waters (Figure 1.5). Although not surveyed as part of the Rees (2004) study, Colwyn Bay contains similar sediment types (Rees, pers. comm.).

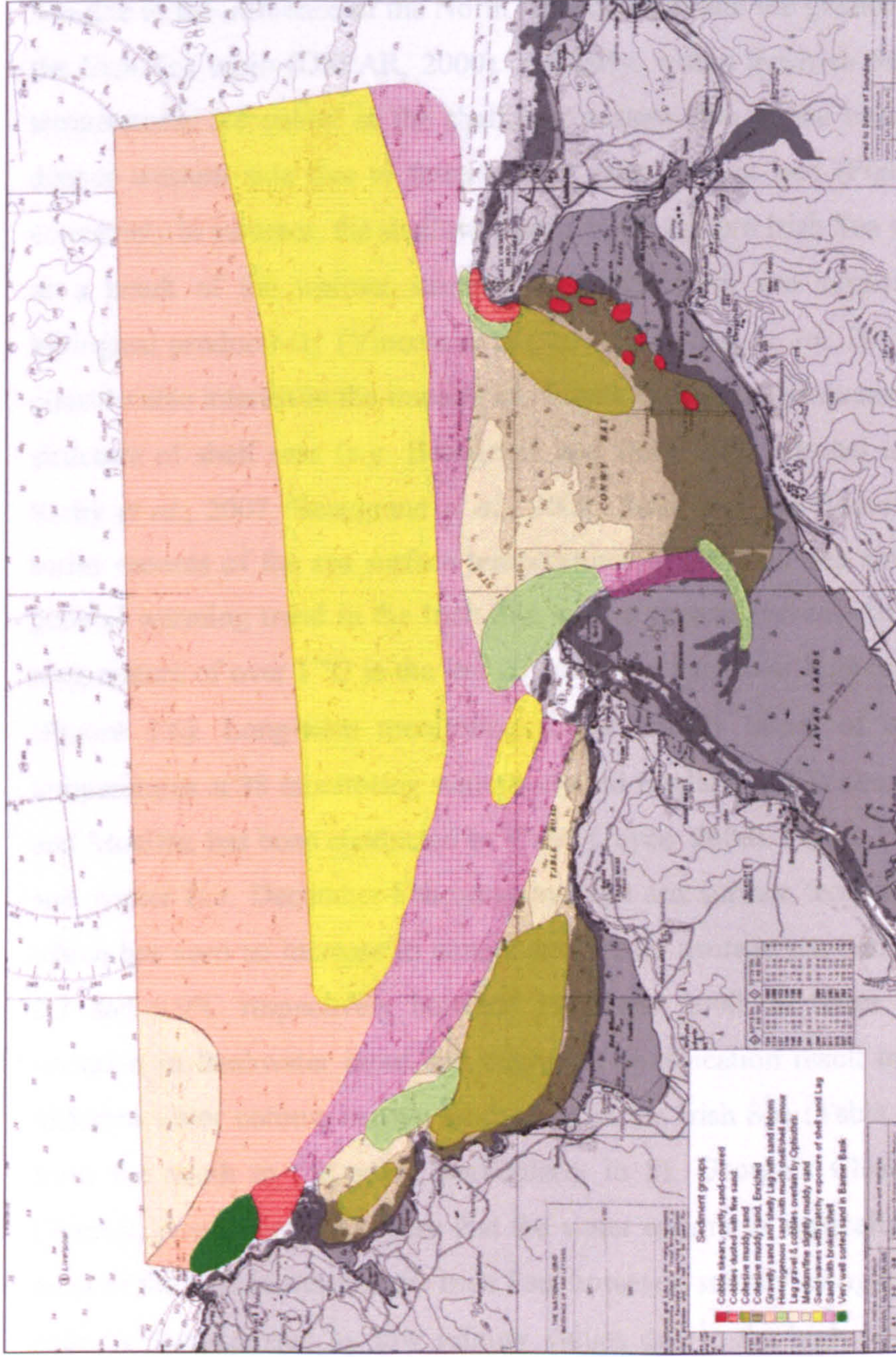


Figure 1.5: Sedimentary biotopes and their distributions in Red Wharf Bay and Conwy Bay. (Copied from Rees, 2004)

A plot of the winter (December-February) sea floor temperatures in the Irish Sea is presented in Figure 1.3c. The Irish Sea is isothermal (Tilstone, *et al.*, 2005), with winter floor temperatures ranging between $\sim 5.5 - 11.5^{\circ}\text{C}$ on a basin-wide basis and ranging between $\sim 3.5 - 10.5^{\circ}\text{C}$ in the South East Irish Sea (Figure 1.3c). Winter sea surface temperatures in the North East Atlantic to the west and south of Ireland are on average degrees warmer than those experienced in the comparatively shallow Irish

A plot of the winter (December-February) sea floor temperatures in the Irish Sea is presented in Figure 1.3c. The Irish Sea is isothermal (Tilstone, *et. al.*, 2005), with winter floor temperatures ranging between $< 5.5 - 11.5^{\circ}\text{C}$ on a basin-wide basis and ranging between $< 5.5 - 10.5^{\circ}\text{C}$ in the South East Irish Sea (Figure 1.3c). Winter sea surface temperatures in the North East Atlantic to the west and south of Ireland are several degrees warmer than those experienced in the comparatively shallow Irish Sea due to the influence of the North Atlantic Drift and the greater rate of heat loss in the Irish Sea basin (OSPAR, 2000). Similarly, within the Irish Sea, winter sea floor temperatures are colder in the shallower eastern side of the basin compared to the deeper western side due to faster/greater rates of heat loss (Figure 1.3). However, conversely in summer, the shallower parts of the eastern Irish Sea warm more quickly as a result of the warmer summer air temperature and support a high level of biological productivity (Vincent *et al.*, 2004; Tilstone, *et. al.*, 2005). There has been considerable interest in the impacts of climate change on productivity and community structure of shelf seas (*e.g.* Beaugrand and Reid, 2003; Brunel and Boucher, 2007; Kirby *et al.*, 2007; Beaugrand *et al.*, 2008; Reise and van Beusekom, 2008). Time-series records of the sea surface temperatures in the Irish Sea since 1960 indicate a general warming trend in the Irish Sea, with a general increase in annual sea surface temperature of over 1°C in the last 20 years and particular high temperatures in 1998 (Figure 1.6). Long-term monitoring (on a weekly basis) of coastal sea surface temperatures at 38 monitoring stations around England and Wales, including Amlwch and Moelfre, has been conducted by Cefas (Joyce, 2006). Figure 1.7 shows the annual and winter (*i.e.* December-February) average sea surface temperatures for Moelfre, which has seen an increase in annual and winter average sea surface temperatures of 0.7 and 0.9°C respectively between 1970 and 2000. In terms of salinity, spatial variation in freshwater input and degree of stratification result in the presence of 4 different water column marine landscapes in the Irish Sea (Table 1.2). Tidal mixing, from the south to the north, particularly in St. George's Channel and the North Channel, is sufficient to ensure that the water column is vertically mixed throughout most of the year in most of the Irish Sea, however, salinity along the Eastern Irish Sea coast is characterised by low salinity values due to the high volume of freshwater inflow (Tilstone, *et. al.*, 2005). Within the South East Irish Sea, low salinity water masses (predominately mixed) are found to the east of the permanent Irish Sea front due to freshwater input from the Mersey and Dee estuaries, whilst high salinity water

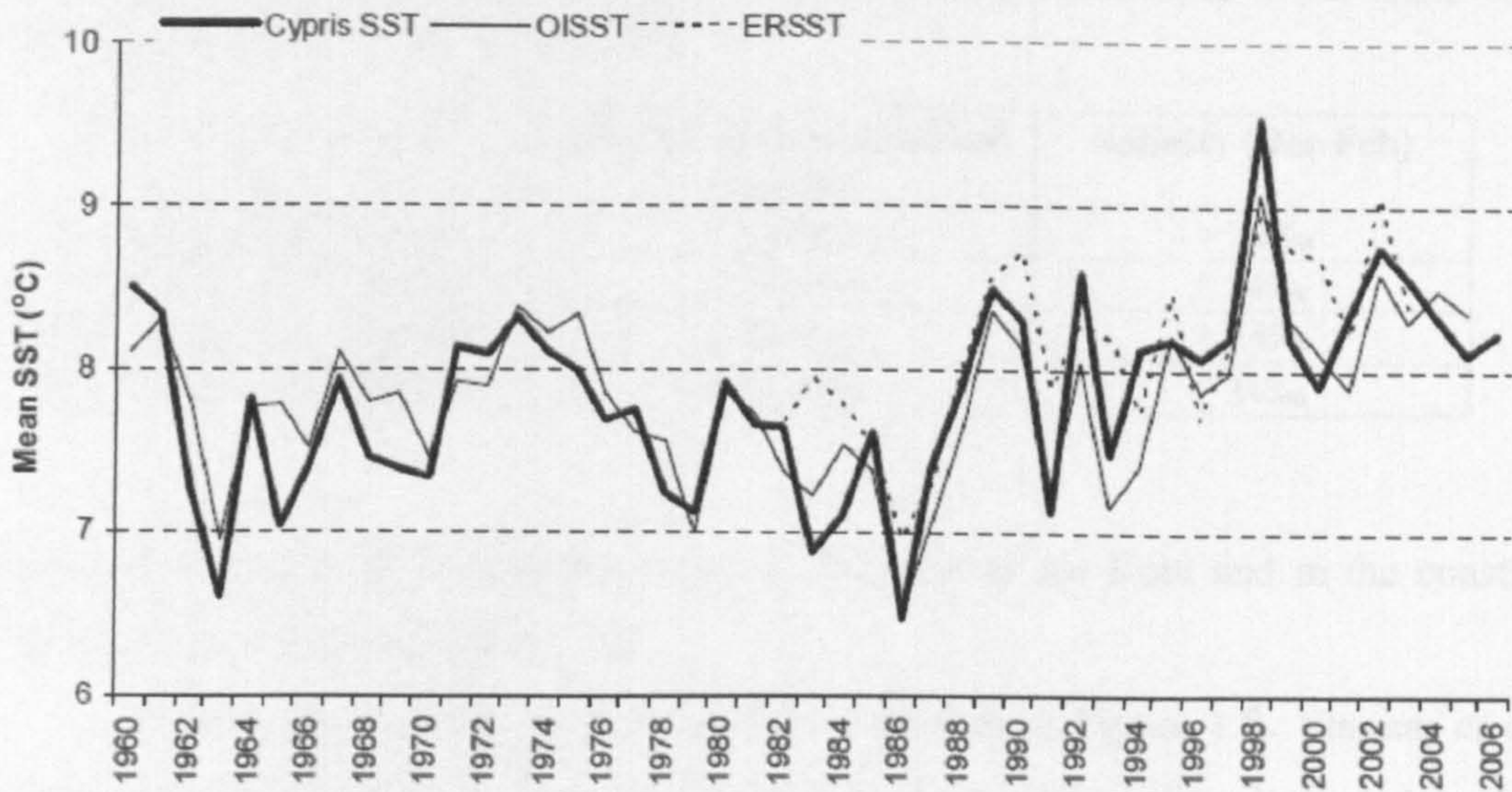


Figure 1.6: Annual sea surface temperature (SST, °C) for these stations in the Irish Sea since 1960. (copied from ICES, 2008a).

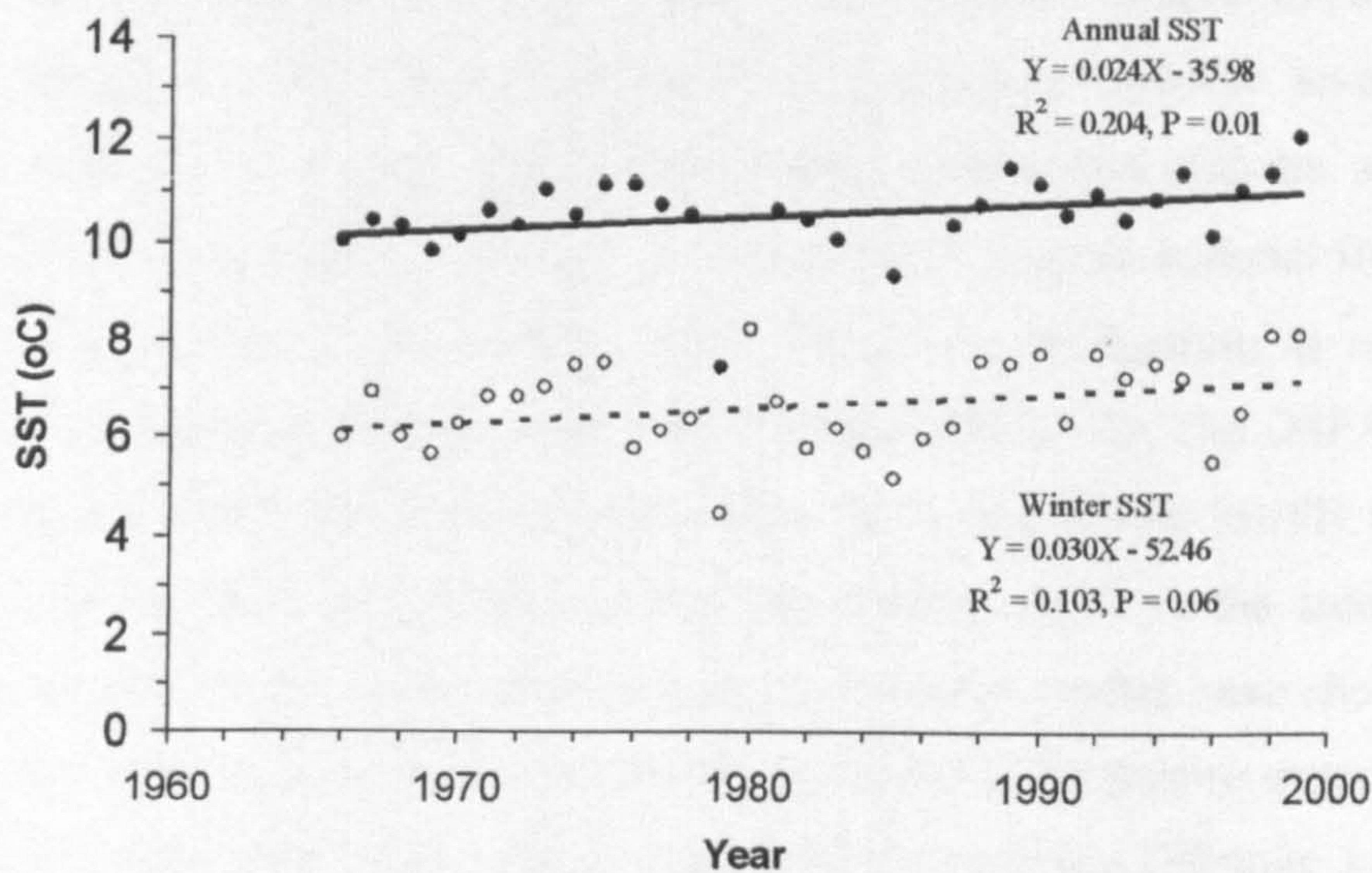


Figure 1.7: Annual (solid circles) and winter (December-February, open circles) sea surface temperature (SST, °C) for Moelfre station (53.350°N 4.233°W) in the Irish Sea for the period 1966-1999 (Date source: Joyce, 2006).

Table 1.2: Stratification period and salinity (‰; values measured in December-February in the Irish Sea) for the 4 different water column marine landscapes in the Irish Sea types. (copied from Vincent *et al.*, 2004).

Water Column types	Number of days stratified (annual)	Salinity (Dec-Feb)
Mixed and High Salinity	< 40 days	> 34‰
Mixed and Low Salinity	< 40 days	" 34‰
Stratified and High Salinity	≥ 40 days	> 34‰
Stratified and Low Salinity	≥ 40 days	" 34‰

masses (predominately mixed) are found to the west of the front and in the coastal waters of North Wales (Figure 1.3d).

The biotope richness in the Irish Sea is shown in Figure 1.8. Vincent, *et al* (2004) concluded that the biotope communities in the Irish Sea often depended on the fine structure of the habitat. The number of associated biotope complexes is considerably higher in the South East Irish (4-8) compared to most other regions (< 4), with the exception of Cardigan Bay which has similar biotope richness to the South East Irish Sea (Figure 1.8). Marine primary productivity, *i.e.* phytoplankton, forms the base of the food web as an important source of food directly for zooplankton with energy transferred up through the trophic levels to secondary consumers. In coastal waters, this primary production will be supplemented by macrophytic primary production and the input of organic material from land through freshwater run-off and offshore winds. Planktonic productivity is related to salinity and the degree of mixing in the water column (Table 1.3). The OSPAR (2000) report indicates that in the highly mixed waters, the spring bloom usually take place about one month later, and declines about two months earlier in the autumn, than in the more open waters to the north and south. Previous studies have shown significantly higher production rates in coastal areas compared with offshore waters, although there can be interannual and seasonal variation in the Irish Sea (Tilstone, *et. al.*, 2005). For example, Gowen and Bloomfield (1996) reported primary production values in spring 1992 of 2378 mg C m⁻² day⁻¹ and 4483 mg C m⁻² day⁻¹ during the summer respectively. In addition, Gowen and Bloomfield (1996) also report large differences in primary production over a 30 km spatial scale in the Irish Sea. The physical variability in the Irish Sea between the stratified waters west of the Isle of Man, the mixed waters in the Northern Channel and the southern Irish Sea and tidal terrestrial-

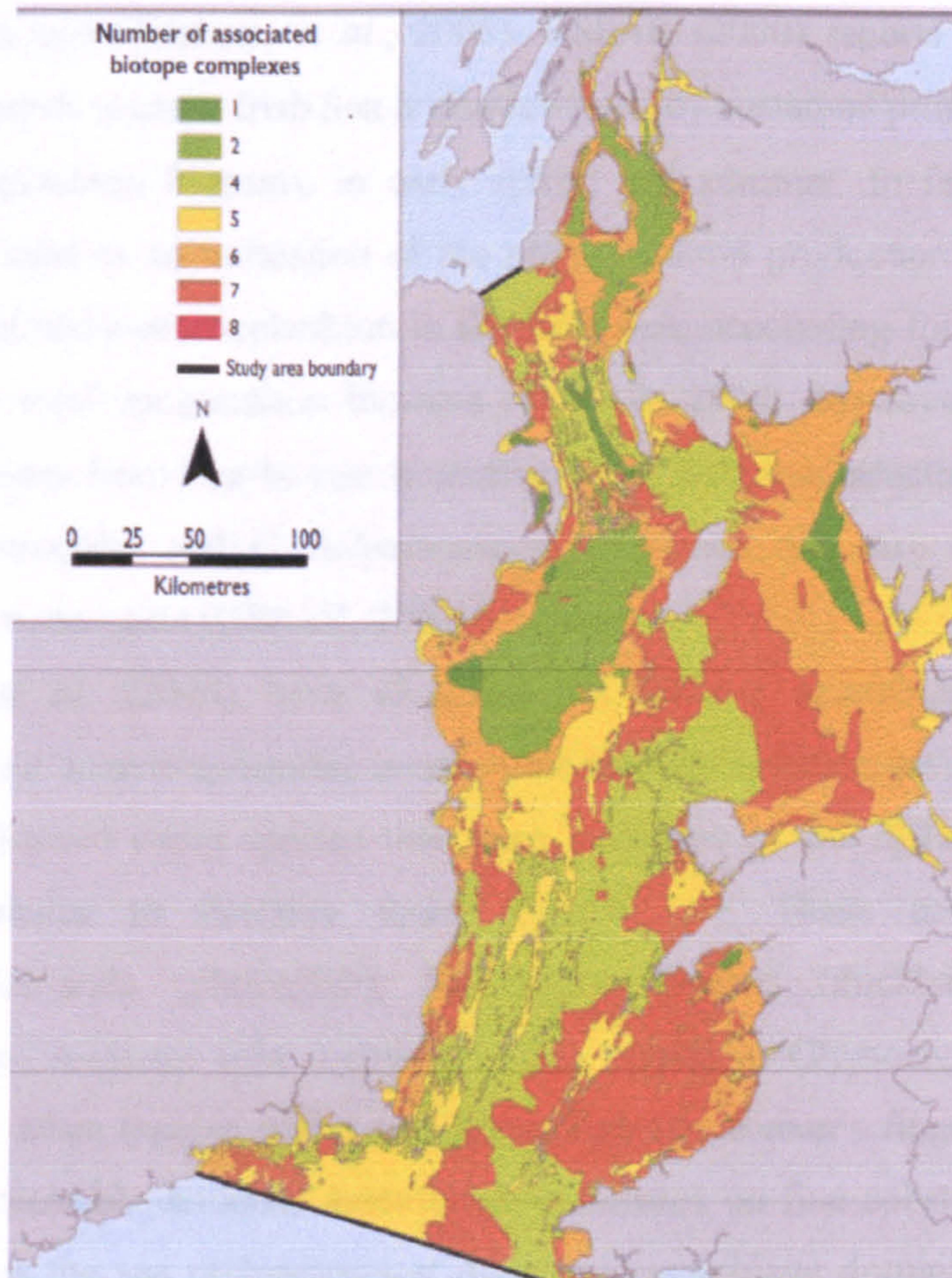


Figure 1.8: Biotope richness map for the Irish Sea showing the number of biotope complexes present within different regions of the Irish Sea (Copied from Vincent *et al.*, 2004; original chart from JNCC, Crown Copyright).

Table 1.3: Mean abundance (per 3 m³) of key plankton community features for the 4 water column marine landscapes found in the Irish Sea. (Copied from Vincent *et al.*, 2004).

Key plankton community Features	Water Column Types			
	Mixed & High Salinity	Mixed & Low Salinity	Stratified & High Salinity	Stratified & Low Salinity
	Mean abundance per 3 m ³			
Fish Larvae	1.19	1.24	1.17	1.23
<i>Dinophysis spp.</i>	1.13	1.38	1.52	1.61
Decapod larvae	1.98	2.80	2.14	3.07
Total adult Calanus	1.91	1.44	2.32	1.45
Coscinodiscus wailesii	1.06	1.23	1.08	1.31

influenced waters along the East coast result in high spatial variability in biomass and primary production (Tilstone, *et al.*, 2005). OSPAR (2000) reports that the coastal region of the north-western Irish Sea is characterised by sustained primary production, and high zooplankton biomass, in early spring and summer. In fact, zooplankton abundance is used as an indication of the phytoplankton production rate. Copepods are the most abundance zooplankton in the Irish Sea, accounting for up to 97% dry weight of the total zooplankton biomass (OSPAR, 2000). However, there can be strong fluctuations from year to year in terms of zooplankton production, for example, *Calanus finmarchicus* and *C. helgolandicus* abundance can vary by an order of magnitude between years (OSPAR, 2000).

Ellis *et al.* (2000) have identified six distinct assemblages of benthic communities (*i.e.* macro-epibenthic invertebrate and fish assemblages) in the Irish Sea and Bristol Channel using species that were indicative of the differences between these assemblages to describe them (Figure 1.9). These assemblages are: Pleuronectes-Limanda (plaice/dab), Microchirus-Pagurus (thickback sole/hermit crab), Echinus-Crossaster (sea urchin/sun star), Nephrops-Glyptocephalus (Norway lobster/witch), Maja (spider crabs) and Alcyonium (dead man's finger) (Ellis *et al.*, 2000). The Plaice/dab demersal assemblage dominates on fine substrates in inshore waters, whereas the sea urchin/sun-star demersal assemblage dominates the coarser substrates further offshore with the thickback sole/hermit crab demersal assemblage occurring in the transitional zone (Figure 1.9; Ellis *et al.*, 2000). The Norway lobster/witch demersal assemblage is typical of the muddy sediments in the central Irish Sea whilst beds of dead man's finger dominate on coarse substrates (Figure 1.9; Ellis *et al.*, 2000). The common spider crab demersal assemblage only dominates in the Bristol Channel (Figure 1.9; Ellis *et al.*, 2000). In addition, more recently Kaiser *et al.* (2004) found a distinct sandbank type habitat along the Welsh coastline (including parts of Red Wharf bay and Conwy bay) represented by low species diversity and shared by species such as the lesser weever fish *Echiichthys vipera*, the shrimp *Philocheras trispinosus*, and the hermit crab *Pagurus bernhardus*. In terms of fish diversity, more than 170 species of marine fish have been recorded from within the Irish Sea (ICES, 2008a). Trawl surveys in the Irish Sea, reported by Parker-Humphreys (2004a) have revealed that dab, plaice, solenette *Buglossidium luteum*, and common dragonet *Callionymus lyra* are the most abundant species, along with large numbers of poor-cod *Trisopterus minutus*, whiting *M. merlangus*, and sole.

Non-commercial fishes such as dab, solenette, red gurnard *Aspitrigla cuculus* and scaldfish (*Arnoglossus laterna*) have increased in abundance recently, whereas hake *Merluccius merluccius*, dragonets, and pogge *Agonus cataphractus* have become less abundant (ICES, 2008a).

In the inshore waters of North West Wales and Eastern Anglesey, Ellis *et al.* (2000) report that the plaice/dab demersal assemblage dominates (Figure 1.9) containing plaice, dab, sole *S. solea* and starfish *Asterias rubens* as the dominant species but also including common hermit crab, sand star *Astropecten iregularis* and solenette as discriminating species in comparison to some of the other assemblages. In addition, areas of Welsh sandbank habitat can be found in Red Wharf bay and Conwy Bay (Kaiser *et al.*, 2004). Rees (2004) conducted a more detailed survey of the subtidal

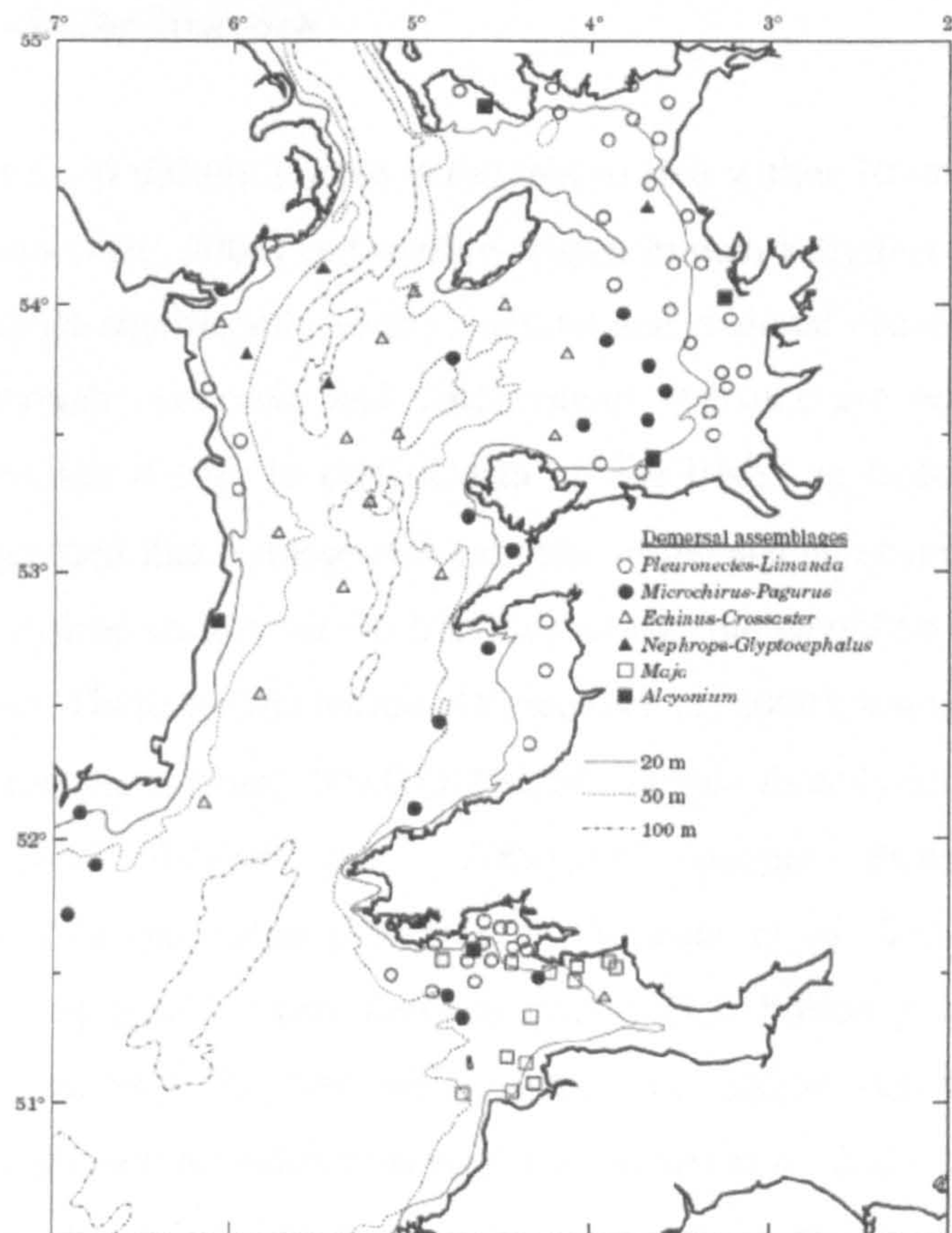


Figure 1.9: Distribution of six demersal assemblages types in the Irish Sea, St. George's Channel and Bristol Channel. 20, 50 and 100 m depth contours are also indicated. (Copied from Ellis *et al.*, 2000).

sediment biotopes in Red Wharf Bay and Conwy Bay and reported that both bays contain a wide range of shallow water sedimentary benthic biotopes containing various mixtures of mud, sand, gravel and broken shell (Figure 1.5). The prominent benthic invertebrate fauna include annelids such as *Lagis koreni* and *Sabellaria spinulosa*, bivalves such as *Abra alba* and *Spisula subtruncata*, and echinoderms such as starfish (*A. rubens* and *Astropecten irregularis*), sea potatoes *Echinocardium cordatum* and brittlestars (*Ophiura ophiura*, *Ophiothrix fragilis*) (Rees, 2004). Beam and otter trawl surveys conducted by the School of Ocean Sciences indicate that the dominant fish fauna in Red Wharf Bay and Conwy Bay are plaice, dab, solenette, whiting, grey gurnard *Eutrigla gurnardus* and small spotted catshark *Scyliorhinus canicula* (McCarthy, pers. comm.).

1.1.3 Fisheries in the Irish Sea

A population of *ca.* 6 million people is thought to live within 10 km of the Irish Sea coastline (Vincent *et al.*, 2004) and marine-related human activities dependent on the Irish Sea contribute significantly to the regional and national economies (Vincent *et al.*, 2004). Although economic and employment statistics are not compiled in a manner which makes it easy to extract data for the Irish Sea region, Vincent *et al.* (2004) have suggested that a reasonable estimate of the annual economic contribution of the principal marine sectors for the Irish Sea as a whole would be in the order of £6 billion per annum. These sectors include (Vincent *et al.*, 2004): tourism and recreation (value £2.5 billion per annum; 100,000-200,000 people directly employed), oil and gas (value £1.56 billion *p.a.*; 700-1,000 people directly employed), ports/shipping/ferries (no value presented by Vincent *et al.* 2004; 10,000-15,000 people directly employed), naval defence (value £1.0 billion *p.a.*; 10,000-20,000 people directly employed), renewable energy (a sector currently undergoing substantial development; no value presented by Vincent *et al.* 2004; potentially 1,500-6,000 jobs during the construction phase but longer term employment substantially lower), marine aggregates (value £1.8 million *p.a.*; < 100 people directly employed), mariculture (value £13 million *p.a.*; a few hundred people directly employed) and sea fisheries (a declining industry; value £60 million *p.a.*; 1,000-2,000 people directly employed).

The fisheries of the Irish Sea will be reviewed briefly in this section and the reader is referred to section 2.3.2 in Chapter 2 for a more detailed review. As mentioned earlier, the Irish Sea is coded as a single management unit - division VIIa – by ICES (Figure 1.2) for stock assessment and management purposes, although the Irish Sea can be subdivided geographically into 4 main areas, St. George’s Channel and Cardigan Bay, North East, Western, and South East Irish Sea (Figure 1.1) with spawning grounds for major fish species occurring in each of these areas (Figure 1.10a). OSPAR (2000) reported that catches are highest where fish aggregate for feeding or spawning and many of the commercially important fish found in Celtic and Irish Seas have relatively short migration routes between feeding and spawning areas (OSPAR, 2000).

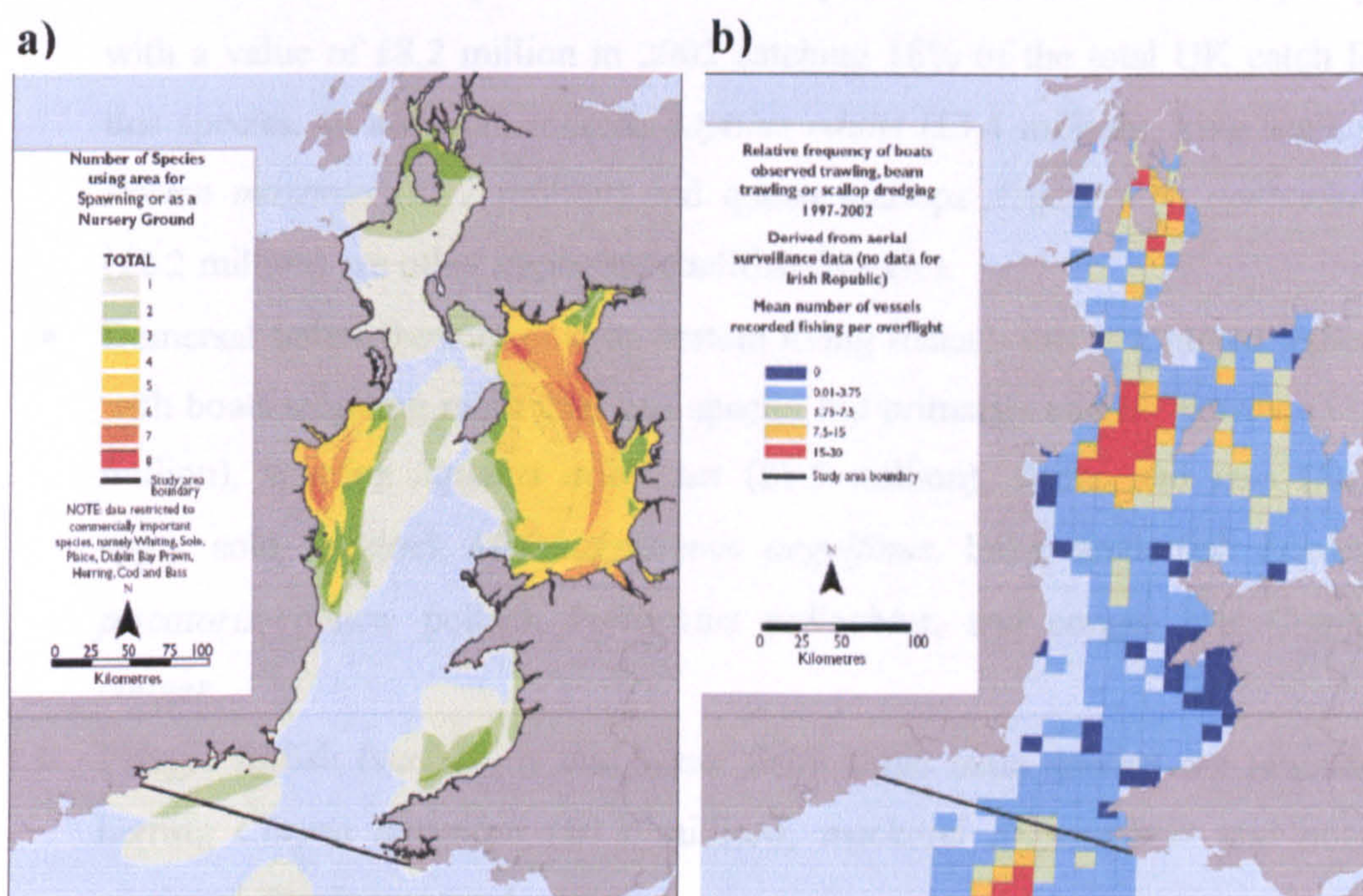


Figure 1.10: Locations of the main spawning grounds and main areas of fishing activity in the Irish Sea. (Copied from Vincent *et al.*, 2004).

The Irish Sea (ICES division VIIa) supports important fisheries for a number of important demersal and pelagic finfish and shellfish species, using beam, otter and *Nephrops norvegicus* trawling gears (Table 1.4). Figure 1.10b summarises the level of fishing activity in different parts of the Irish Sea. Fishing activity, in terms of the number of fishing vessels present in an area, is highest in the deep channel in the Western Irish Sea (where the main *Nephrops* fishery is located) and in the Firth of Clyde (*Nephrops* and scallop fishing areas). The beam/otter trawl mixed fishery for

demersal finfish is mainly carried out in the Eastern Irish Sea between the Isle of Man and the Cumbrian Coast (Figure 1.10b).

Table 1.4: A summary of the landings and value of the different sea fisheries in the Irish Sea in 2002. (Copied from Vincent *et al.*, 2004).

	Total weight (tonnes)	Value £ million	Value € million
Shellfish	52500	43.5	62.2
Demersal	11900	15.8	22.6
Pelagic	3900	0.6	0.8
Total	68300	59.5	85.6

Vincent *et al.* (2004) summarises the main fisheries in the Irish Sea as follows:

- Shellfish: the most important commercial species in the Irish Sea is *Nephrops* with a value of £8.2 million in 2002 catching 18% of the total UK catch for this species. In addition, mussels *Mytilus edulis* (£3.4 million), king scallops *Pecten maximus* (£3.2 million) and queen scallops *Aequipecten opercularis* (£2.2 million) are other important shellfish fisheries.
- Demersal fishes (bottom or near-bottom living fishes): this is a mixed fishery with boats targeting more than one species but primarily cod *G. morhua* (£1.8 million), spurdog *Squalus acanthias* (£1.5 million), skates and rays (*Raja* spp.), sole, haddock *Melanogrammus aeglefinus*, hake, anglerfish *Lophius piscatoris*, plaice, pollack *Pollachius pollachius*, and conger eels *Conger conger*.
- Pelagic finfish (surface or mid water fish): three main species are targeted, herring *Clupea harengus* (£0.3 million), mackerel *S. scombrus* and horse mackerel *Trachurus trachurus*.

A detailed summary of the history of the fisheries in the Irish Sea is provided in the reports by Parker-Humphreys (2004a) and ICES (2008a) and only a brief summary will be provided here. The majority of fishing vessels in the Irish Sea target *Nephrops* using either 70 mm diamond mesh with an 80 mm square-mesh panel or an 80 mm diamond mesh in their codends, and their landings must consist of at least 35% *Nephrops* by live weight. Bycatch is very high in the *Nephrops* fishery and most of this consists of juvenile whiting that are discarded (which has contributed to the decline of whiting stocks in the Irish Sea), haddock, cod and plaice (Enever *et al.*,

2007; ICES, 2008a). Twin-rig otter trawls, introduced in the early 1990s, are more efficient at catching *Nephrops* but have also increased the proportion of roundfish bycatch in the *Nephrops* fishery (ICES, 2008a). The beam trawl fishery commenced in the early 1960s, principally targeting sole but also landing plaice, rays, brill, turbot and anglerfish, with effort in this mixed fishery peaking in the late 1980s (Parker-Humphreys, 2004a). These beam trawl fisheries still fish in the Irish Sea and involve fleets from Belgium, the UK, Ireland, Holland and France, although catches these days are much lower (ICES, 2008a). The otter trawls fishing out of Ireland, Northern Ireland, England and Wales target plaice, haddock, whiting and cod, with small bycatches of anglerfish, hake, and sole (ICES, 2008a). Since 2001, they have adopted new mesh sizes of 100-120 mm and other gear modifications according to the requirements of the EU technical conservation regulations and national legislation.

The most lucrative finfish fishery in the Irish Sea is for cod which are caught throughout the year by otter trawlers that target spawning cod in spring and juvenile cod in autumn and winter in mixed-species fisheries, over a wide area but especially in the North West Irish Sea (Cefas, 2001; ICES, 2008a). Since the early 1980s, otter trawl fishing for cod has decreased and a semi-pelagic trawling method has been developed targeting both cod and whiting. Herring is the main pelagic species targeted in the Irish Sea, usually by Northern Ireland trawlers, but catches have declined to very low levels in recent years (ICES, 2008a). The UK demersal fishing fleet operating in the Irish Sea is very small and in 2003, 19 of the 237 demersal vessels working in the Irish Sea were permanently removed, representing a loss of 8% of the fleet (ICES, 2008a). Inshore fishing activity in the Irish Sea includes the deployment of gillnets and tangle nets in the inshore targeting cod, bass, grey mullet, sole, plaice and rays (Parker-Humphreys, 2004a). Long line fisheries targeting spurdog was a very lucrative fishery in the Irish Sea but catches have declined in recent years and the fishery is currently closed. In addition to the important fisheries for scallops off the Isle of Man and in the Firth of Clyde, an Irish Sea pot fishery for edible whelks crab and lobster whelks also exists. In terms of fishing activities in the inshore waters of North West Wales and Cardigan Bay, visiting beam and otter trawlers target demersal fishes within the 12 mile zone (Walmsley and Pawson, 2007). However, vessels within 3 miles of the coast are prevented from fishing between Rhyl and Haverigg Point if they exceed 13.7 m, and between Cemaes Head and Rhyl if they exceed 15.2 m (Walmsley and Pawson, 2007). Gill, tangle and trammel nets are also used for

demersal fishing in the inshore waters of North West and North Wales, with tangle and trammel nets with an inner section mesh size of between 100-120 mm used to catch sole, plaice and flounder *Platichthys flesus* and nets with a larger inner section mesh size of between 200-300 mm for rays, turbot *Psetta maxima* and brill *Scophthalmus rhombus*.

Discards are a continuing problem under the current EU Common Fishing Policy, with undersized target and non-target fish species returned to the sea, although dead or dying on capture. OSPAR (2000) estimated that approximately 65 % of the demersal fish discards from demersal fleets comprised of undersized whiting and haddock plus catsharks (OSPAR, 2000). A more recent survey by Enever *et al.* (2007) reported discard levels for the whole of ICES region VII (including Irish Sea, Celtic Sea, Bristol Channel and Western Ireland; Figure 1.2). Their research indicated that beam trawlers in ICES VII discard 71% of the fish that they catch (68.5 million fish; 12,500 tonnes) whilst otter trawlers discard 64% of the fish that they catch (41.6 million fish; 9000 tonnes). Discard rates in the pelagic fishery are much lower at 14% (7 million fish; 840 tonnes) with other fisheries in ICES region VII (netters, *Nephrops* trawlers, scallop dredgers, local pelagic trawlers, seiners, potters and long-liners) together contributing less than 4% of the total discards (Enever *et al.*, 2007).

1.1.4 The study species: plaice *P. platessa*

a) Plaice Taxonomy and Identification

The plaice *P. platessa* (Linnaeus, 1758) belongs to the Pleuronectidae family of flatfish (righteye flounders; 60 species) which also includes other commercially important flatfish such as dab, flounder, halibuts and sole. Nelson (2006) reports that the Pleuronectidae are classified in the order Pleuronectiformes (678 species), which are a very distinctive group of fishes characterized as having an asymmetrical body with one eye migrating onto the other side of the head, one pigmented side, dorsal and anal fins with long bases, and an absence of spiny rays and swim bladder in the adult fish. Larvae from this order are initially bilaterally symmetrical but towards the end of the larval phase and before settlement, one eye migrates onto the other side of the head (Nelson, 2006). The Pleuronectiformes consists of two suborders, the more primitive Psettoidae (the spiny turbot) and the Pleuronectoidei (Nelson, 2006). Within the suborder Pleuronectoidei are two major clades with four families

Scophthalmidae (turbot), Paralichthyidae (sand flounders), Pleuronectidae (right eye flounders) and Bothidae (left eye flounders) forming one clade and the Paralichthodidae (measles flounders), Poecilopsettidae (big eye flounders), Rhombosoleidae, Achiropsettidae (southern flounders) Samiridae (crested flounders), Achiridae (American soles), Soleidae (sole) and Cynoglossidae (tonguefishes) forming the other clade (Nelson, 2006). Within the Pleuronectidae are five subfamilies including the Pleuronectinae (13 genera, 42 species) which includes genera such as *Limanda* (dab, *L. limanda*), *Platichthys* (European flounder, *P. flesus*) and *Pleuronectes* (plaice, *P. platessa*). Many pleuronectid fish are commercially important food species with 10 species occurring in the North Atlantic (Gibson, 2004).

P. platessa is a laterally compressed flatfish that lies on its left hand side with the right hand side uppermost. The asymmetric head has both eyes close to each other and placed in the right hand side of the head (Figure 1.11). The plaice body is oval with a body width at its widest point of approximately half its body length. The body does not have a rough surface, like some flatfish such as the dab, because the scales have smooth edges. One identifying characteristic of plaice are the prominent orange-red spots that are obvious on the dorsal pigmented-side of the fish (Figure 1.11). Although plaice are well known for their bright orange-red spots, when the fish moves onto paler coloured substrate, for example sandy sediments, the red spots can become paler to match the fish's surroundings (Greenwood, 1975; Hayward, *at el*, 1996). The mouth is located in a terminal position on the plaice and appears small in size, however, it is highly protrusible enlarging widely (as a result of the articulation of the maxillary bones) and opens forwards and downwards to enable food to be taken from the surface sediments. Plaice possess a series of different-sized rounded bony tubercles running in a line from behind the eyes to the back of the head (Figure 1.10a) which are an identifying characteristic for this species. These tubercles make the lateral line slightly curved above the pectoral fin. The tail is rounded in shape (Figure 1.11a). Both the dorsal and anal fins in plaice have long bases and run along much of

the body and are sometimes referred to as "lateral" fins. The pectoral fins are small and thoracic in position. Plaice usually have sixty-five to seventy-five dorsal fin rays.

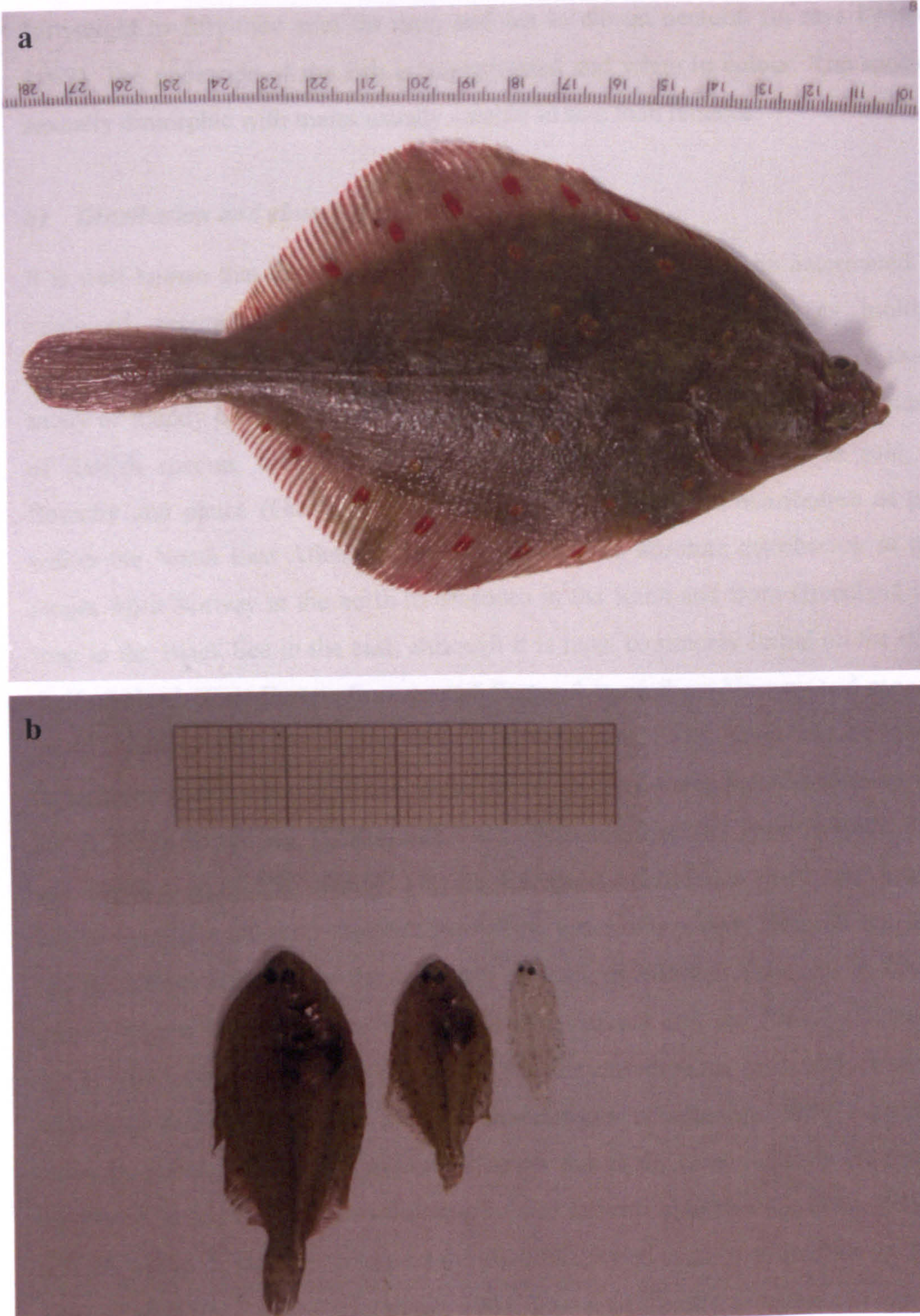


Figure 1.11: a) An adult plaice *P. platessa* caught from Conwy Bay, 2005. b) Juvenile plaice caught from Red Wharf Bay, 2005 (increasing in age/size from right to left from a newly settled juvenile).

the body and are sometimes referred to as “lateral” fins. The pectoral fins are small and thoracic in position. Plaice usually have sixty-five to seventy-nine dorsal fin rays; forty-eight to fifty-nine anal fin rays; and ten to eleven pectoral fin rays (Wheeler, 1969). The underside of the fish is unpigmented and white in colour. The species is sexually dimorphic with males usually smaller in size than females.

b) Distribution and abundance

It is well known that the distribution of any marine species will be determined by a range of geographical and hydrographical parameters as well as biological interactions (ICES, 2008a). The North East Atlantic provides a large area of shallow sandy or muddy continental shelf that is favourable habitats areas for a large number of flatfish species, including commercially important species such as sole, dab, flounder and plaice (Gibson, 2004). Figure 1.12 presents the distribution of plaice within the North East Atlantic Ocean (URL 2). The absolute distribution of plaice ranges from Norway in the north to Morocco in the south and from Greenland in the west to the Black Sea in the east, although it is most commonly found on the coastal shelf of North West Europe from central Portugal to northern Norway and especially in the regional seas around the British Isles (Figure 1.12). There are commercial fisheries for plaice where it is commonly found, in the Barents Sea (Kuznetsova *et al.*, 2004), Baltic Sea (ICES, 2008c), Irish/Celtic Seas and English Channel (ICES, 2008a) and North Sea (ICES, 2008b). On the European continental slope, the preferred habitat for plaice are sandy habitats in shallow water of less than 200m (ICES, 2008a, 2008b, 2008c) although in the far north of their distribution they can be found at greater depths in the Barents Sea and around Iceland and the Faroes (Wimpenny, 1953). Amezcua and Nash (2001) stated that the distributions of flatfish species are related to the sediment type and the invertebrate communities they support, for example, plaice prefer sandy and muddy areas due to the clear visibility for detecting their prey. In terms of the distribution of plaice according to size/age class, 0/1-group fish are found in inshore waters on the shallow coastal nursery grounds (*e.g.* Macer, 1967; Lockwood, 1974, Carter *et al.*, 1991; Fox *et al.*, 2007), 2-3 year old fish move offshore into deeper water whilst the oldest age groups (> 5 years old) tend to be found at the greatest depths (Rijnsdorp and Van Beek, 1991; Rijnsdorp and van Leeuwen, 1996; Gibson *et al.*, 2002).

The annual beam-trawl surveys conducted by Cefas in the Irish Sea have shown that plaice of less than two years old concentrate in large numbers in inshore areas such as found at the greatest depths (Rijnsdorp and Van Beek, 1991; Rijnsdorp and van Leeuwen, 1996; Gibson *et al.*, 2002).



Figure 1.12: The distribution of plaice *P. platessa* in the temperate waters of the North East Atlantic. The different colours relate to the relative probability of occurrence - within a species range, *i.e.* the relative probability (on a scale 0-1) that the species will be present in comparison to other areas within the range of occurrence (light yellow 0.01-0.19; dark yellow 0.20-0.39; orange 0.40-0.59; pink 0.60-0.79; red 0.80-1.00) (Source: URL 2).

Due to their commercial importance, the spawning and recruitment success and the abundance of plaice are monitored carefully by ICES (*e.g.* ICES 2008a, 2008b). This information is provided to ICES by member states, for example, data for the plaice stocks found in the regional seas around the U.K. are provided by the UK Government fisheries agency, Cefas who conduct annual beam trawl surveys to determine the abundance of commercially important fish species to inform management policies and to set annual catch quotas (*e.g.* Parker-Humphreys 2004a, 2004b, 2005). As an example, Figures 1.13 and 1.14 show the distribution and average abundance data for plaice in the Irish Sea from the 1993-2001 annual beam trawl surveys (Parker-Humphreys 2004a). These indicate that plaice in the Irish Sea

The annual beam-trawl surveys conducted by Cefas in the Irish Sea have shown that plaice of less than two years old concentrate in large numbers in inshore areas such as Red Wharf Bay, Conwy Bay, off Blackpool, off the river Ribble and off Abbey Head whilst older fish are found in the deeper waters of Liverpool Bay and off Morecambe Bay (Cefas, 2001; Parker-Humphreys 2004a).

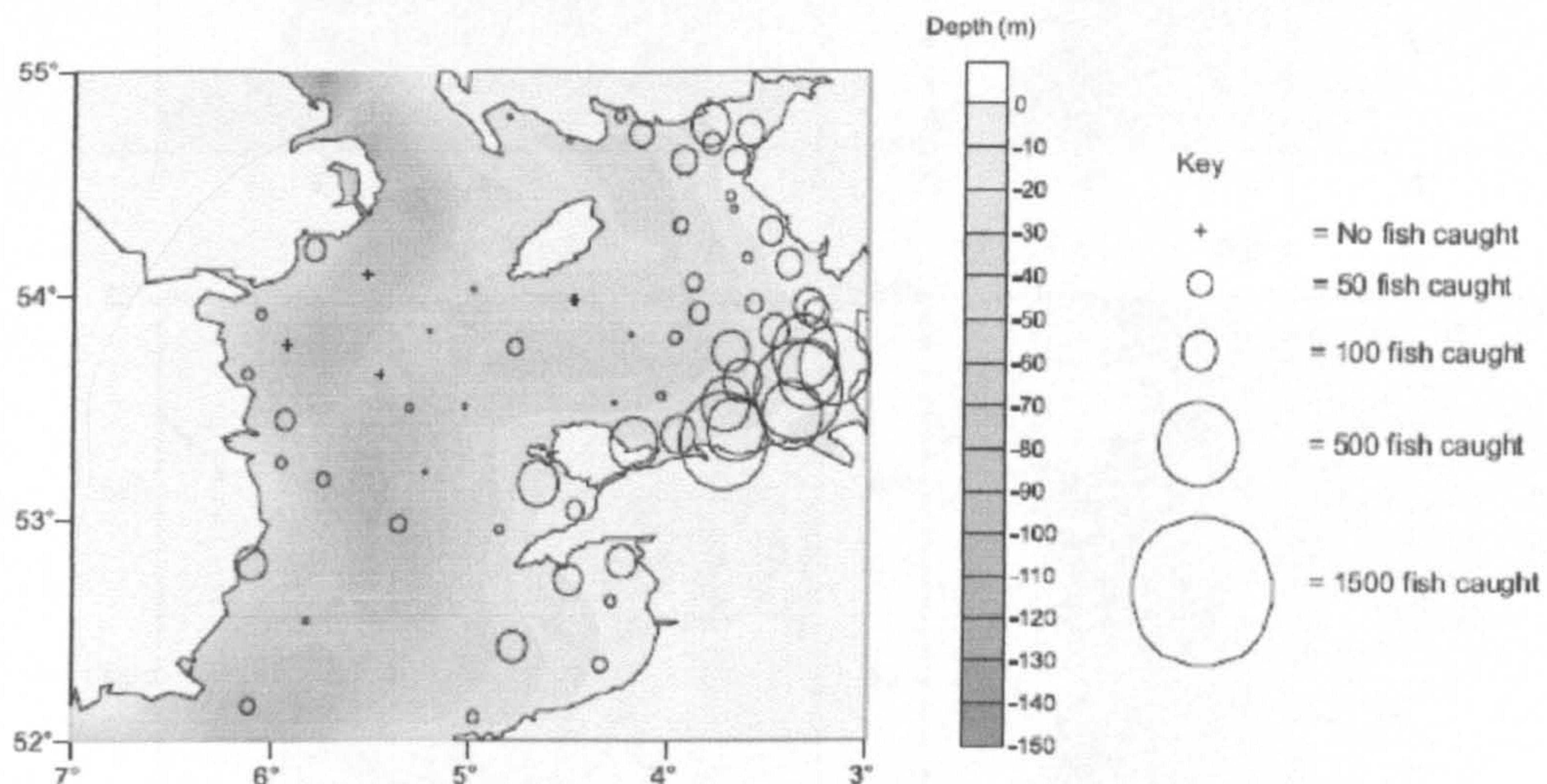


Figure 1.13: Abundance of plaice (number of fish caught hour⁻¹) in the Irish Sea in relation to depth. Data were collected in the Cefas annual beam trawl surveys for the time period 1993-2001. (Copied from Parker-Humphreys, 2004a).

By conducting regular (*i.e.* annual) surveys it is possible for Cefas and ICES to identify and model trends in important parameters such as adult spawning stock biomass, mortality rates and the number of recruits each year (e.g. ICES 2008a, 2008b) which are critical to the sustainable exploitation of commercial marine fish species.

c) Plaice Stock structure in the Irish Sea

There has been disagreement between various biologists concerning the plaice stock structure in the Irish Sea. Early studies assumed a single stock within the Irish Sea (*e.g.* Harden-Jones 1968) and ICES continue to manage plaice in the Irish Sea (ICES division VIIa; Irish Sea, Cardigan Bay, St George's Channel) and Celtic Sea/Bristol Channel (ICES division VIIf&g) as large, single management units (ICES, 2008a). However, tagging-recapture studies conducted by Cefas between 1979-1980 and

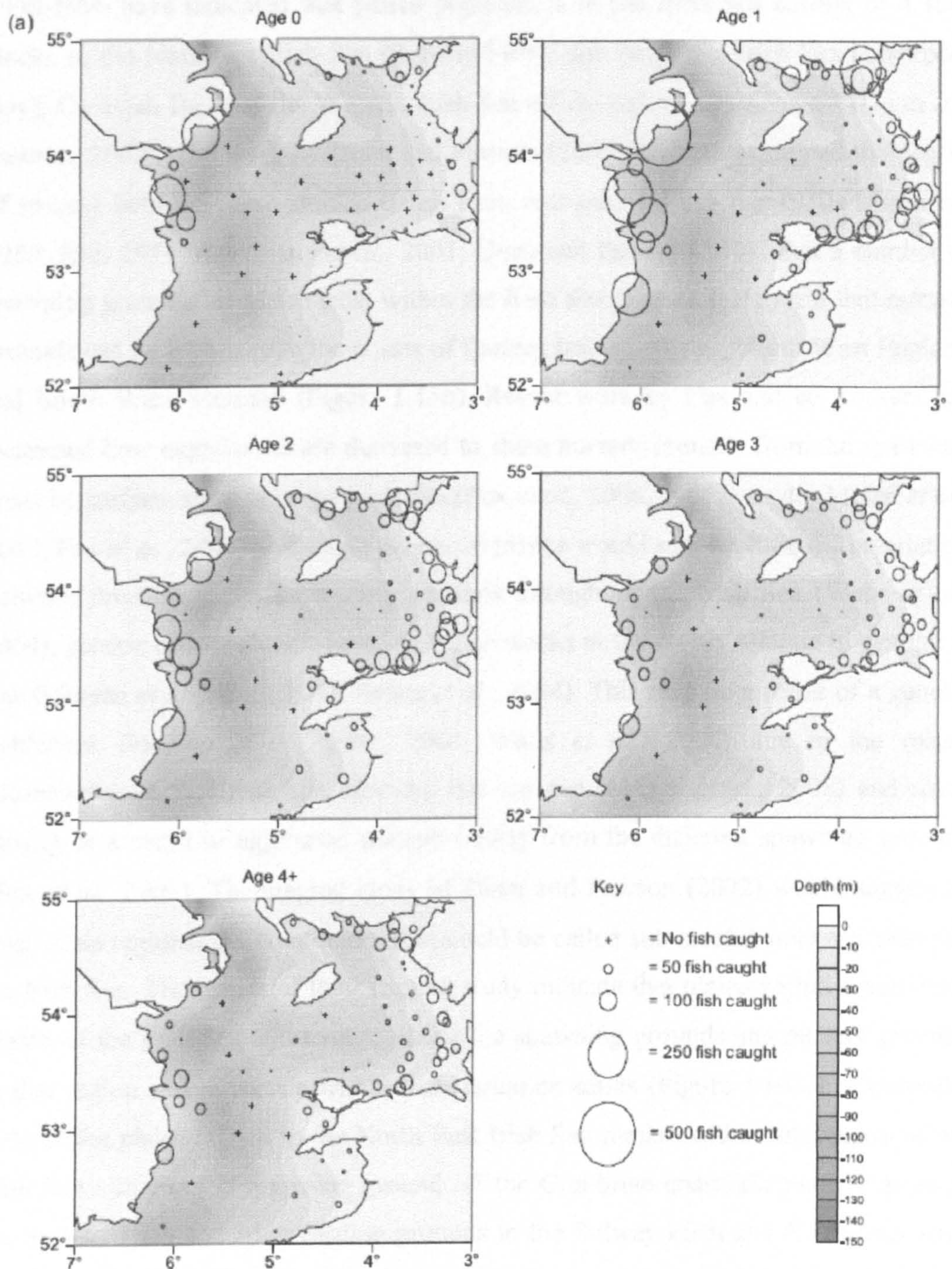


Figure 1.14: Abundance of plaice (number of fish caught hour⁻¹) in the Irish Sea in relation age group and depth. Data were collected in the Cefas annual beam trawl surveys for the time period 1993-2001. (Copied from Parker-Humphreys, 2004a).

1993-1996 have indicated that plaice populations in the Irish Sea consist of 4 sub-stocks in the Northeast Irish Sea (Solway Firth), the Southeast Irish Sea (Liverpool Bay), Cardigan Bay and the Western Irish Sea off the east coast of Ireland (Dunn and Pawson, 2002). The work by Dunn and Pawson (2002) has also examined the degree of mixing between these stocks. It has been recognized since the 1950s (Simpson, 1959; Hill, 1971; Armstrong *et al.*, 2001; Dunn and Pawson, 2002) that a number of spawning grounds for plaice exist within the Irish Sea (Figure 1.15a) and that nursery grounds can be found along the coasts of Eastern Ireland, Wales, North West England and South West Scotland (Figure 1.15b). Recent work by Fox and co-workers has examined how eggs/larvae are delivered to these nursery grounds from the spawning areas by surface currents in the Irish Sea (Fox *et al.*, 2006, 2007; van der Molen *et al.*, 2007; Fox *et al.*, 2009). Although genetic evidence would suggest little differentiation between juvenile plaice on nursery grounds throughout the Irish Sea (Watts *et al.*, 2004), genetic differentiation between plaice stocks in the North Atlantic in general is low (Horeau *et al.*, 2002, 2004; Watts *et al.*, 2004). This may be a result of a genetic bottleneck (Horeau *et al.*, 2002, 2004; Watts *et al.*, 2004) due to the recent colonization of the Irish Sea after the last ice age (Maggs *et al.*, 2008) and some mixing as a result of egg/larval transport away from the different spawning grounds (Fox *et al.*, 2009). The tagging study of Dunn and Pawson (2002) would suggest at least some regional differentiation (that could be called sub-stocks) between plaice in the Irish Sea. The results of their tagging study indicate that plaice within a particular region of the Irish Sea will tend to utilise the spawning grounds and nursery grounds in that region and to remain within that region as adults (Figure 1.16). For example, 99% of the plaice tagged in the North East Irish Sea remain within this region of the Irish Sea utilizing the spawning ground off the Cumbrian coast, the nursery areas in the Solway Firth and adult feeding grounds in the Solway Firth and North East Irish Sea (Figure 1.16). Similarly, the plaice within Cardigan Bay are thought to remain in the bay for their entire lifecycle (Figure 1.16). The South East Irish Sea plaice stock are interesting as approximately half the tagged adults remained within Liverpool bay to feed, whilst 43% undertook a migration south into the Celtic Sea (Figure 1.16). This stock would appear to utilise two spawning areas, one in the south of Liverpool Bay and the other of the coast of South East Ireland (Figure 1.16).

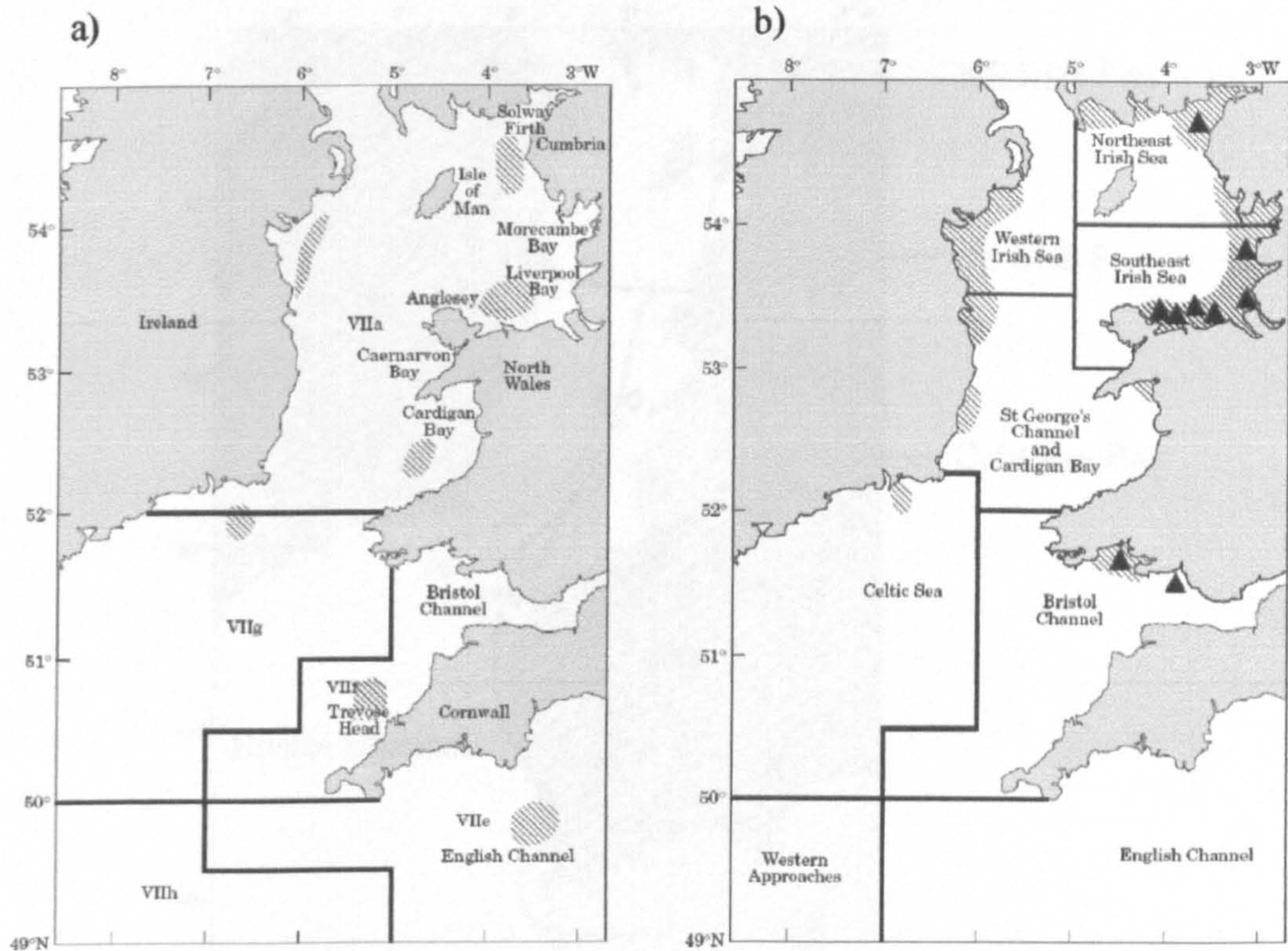


Figure 1.15: Location of (a) the main spawning grounds and (b) the main juvenile nursery areas for plaice *P. platessa* in the Irish Sea, Bristol Channel and English Channel. Spawning grounds identified by Simpson (1959) and Armstrong *et al.* (2001). Nursery grounds have been defined from Cefas beam trawl surveys 1986–2000 where the mean abundance of plaice <16 cm L_T was >50 fish hour⁻¹. (Copied from Dunn and Pawson, 2002).

Figure 1.16 does illustrate some degree of movement of adult fish between regions in the Irish Sea which may help to explain the lack of genetic differentiation, but also highlights the degree to which the regional plaice sub-stocks are “self-contained”, each with their own spawning, juvenile nursery and adult feeding areas. There are a number of earlier studies on the biological characteristics of plaice from different areas within the Irish Sea which would support Dunn and Pawson’s idea of regional sub-stocks. Earlier studies on the growth and maturity characteristics of plaice in the Irish Sea show differences between plaice in the western and eastern Irish Sea. Horwood (1990, 1993), Nash *et al.* (2001) and Parker-Humphreys (2004a, 2004b) all report similarities in the growth, age at maturation and fecundity for plaice in the

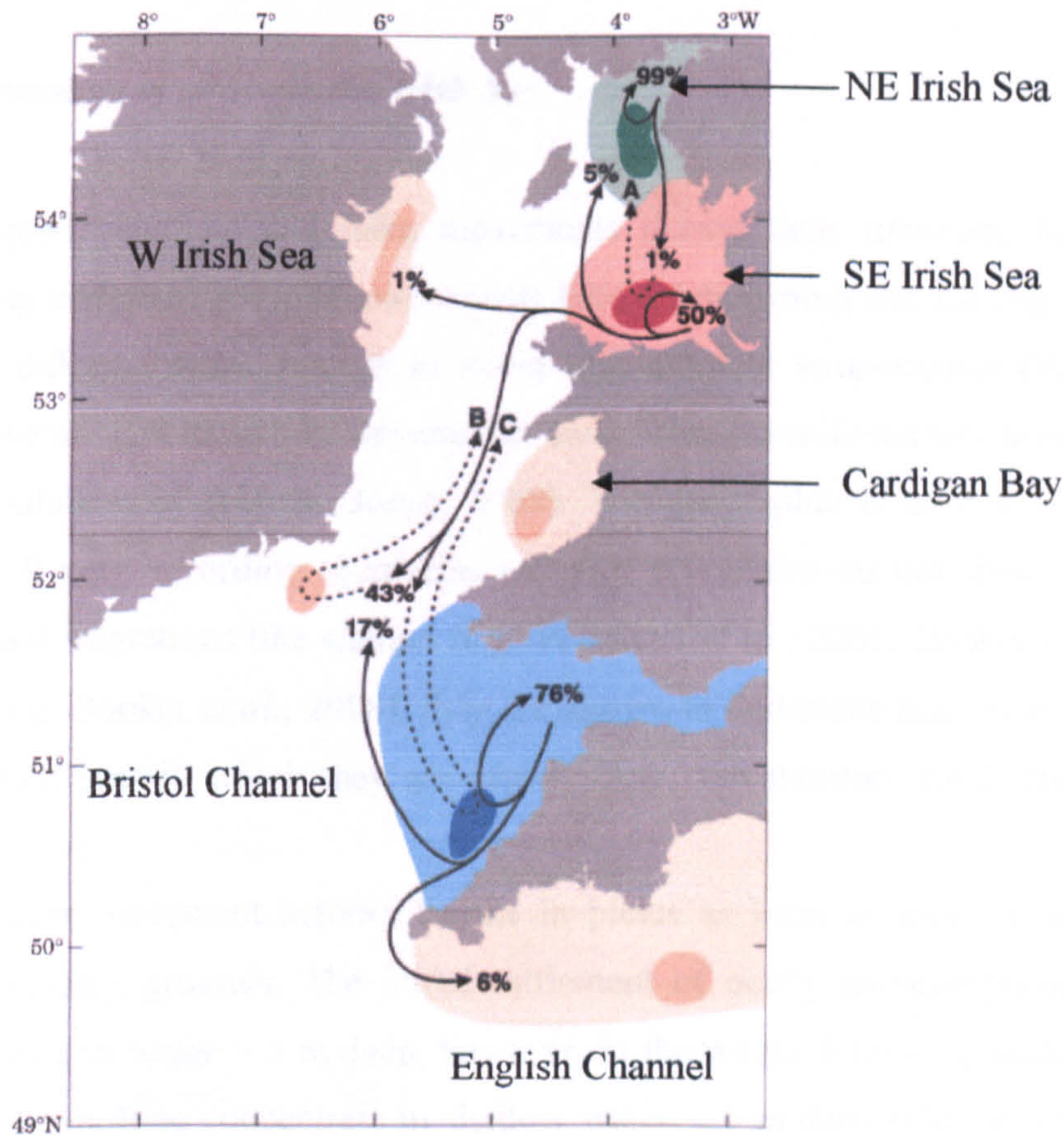


Figure 1.16: A schematic diagram showing principal stock areas and movements of plaice *P. platessa* L. in the Irish Sea with the main feeding area (light shading), and the main spawning area (dark shading) indicated for each stock. The arrows and percentage values represent the percentage of fish moving within, or away from, a stock area. A is estimated at c. 6%, and B+C together c. 46%. (Copied from Dunn and Pawson, 2002).

North East and South East Irish Sea and the Bristol Channel, but differences between these plaice populations and those found in the western Irish Sea and in Cardigan Bay. These differences in biological characteristics are unlikely to be due to differences in feeding and growth opportunity between the eastern and western sides of the Irish Sea but may be related to a lack of mixing between fish from both sides of the Irish Sea (Beggs and Nash, 2007). This lack of mixing could be the result of the strong tidal currents in the Irish Sea [see Dunn and Pawson (2002), their Figure 9] which could limit egg/larval exchange into Cardigan Bay and the Western Irish Sea but at the same time facilitate movement of eggs/larvae between the Bristol channel and the Eastern Irish Sea (excluding Cardigan Bay) (but see Fox *et al.*, 2009).

d) Movements of plaice in the Irish Sea

Many aquatic animals undertake movements during their lifecycle, for example, adults may undertake seasonal movements between spawning and feeding grounds, or between different water masses to avoid unfavourable temperatures (King, 2007), whilst juvenile can undertake movements away from juvenile nursery areas to recruit into the adult stock (Harden-Jones, 1968). The geographic area over which a fish moves will vary according to species and although plaice do not show large-scale, long-distant migrations like salmon (*e.g.* Friedland *et al.*, 2001; Booker *et al.*, 2008) or tuna (*e.g.* Rooker *et al.*, 2008), they are known to undertake migrations within the coastal shelf seas in which they are found (Dunn and Pawson, 2002; Hunter *et al.*, 2003).

Regular movement activity begins in plaice as soon as they recruit onto the juvenile nursery grounds. The initial settlement of newly metamorphosed juvenile plaice occurs in water > 5 m deep, however, in the weeks following settlement, they move shorewards to concentrate in shallow water < 1 m deep (Gibson *et al.*, 2002). However, these small juveniles do undertake small scale movements related to tidal and diurnal cycles (Gibson, 1973; Kuipers, 1973; Burrows *et al.*, 2002). As the juveniles increase in size, and attain a size refuge from predators such as brown shrimp *Crangon crangon*, they migrate into deeper water but continue to make regular tidal movements into shallower/deeper water according to the tide and time of day (Gibson *et al.*, 2002). Plaice can spend up to 24 months on the nursery grounds undertaking seasonal movements between the shallower and deeper water in the nursery grounds related to water temperature (Rogers, 1993; Dunn and Pawson, 2002), but once they attain a threshold size of *ca.* 16 cm total length, they will begin to move away from the nursery grounds into deeper water to associate with the adult stock (Nash *et al.*, 1992). Tagging studies have shown that adult plaice are known to undertake large-scale movements from the release areas once they achieve a length of 25 cm total length and that these movements are thought to be in relation to feeding or spawning depending on the time of year (Macer, 1967; Hill, 1971; Houghton and Harding, 1976; Rogers, 1993; Dunn and Pawson, 2002). The work of Dunn and Pawson (2002) provides an excellent example of the seasonal feeding and spawning migrations made by adult plaice from the different regional substocks in the Irish Sea.

For most adult fish, these movements are within a restricted geographical area of the Irish Sea (Figure 1.16), although some plaice from the South East Irish Sea can undertake a migration from Liverpool Bay south into the Celtic Sea and back, which will entail moving several hundred kilometres (Dunn and Pawson, 2002). A similar long distance migration has been observed for plaice in the North Sea (Hunter *et al.*, 2003; Metcalfe *et al.*, 2006). It is thought that the adult plaice utilise deep water currents in order to minimise the energetic costs of these long distance movements (Metcalfe *et al.*, 2006). Sex-specific seasonal movement patterns have been observed in plaice. For example, although adult fish will aggregate in coastal waters close to the spawning grounds during the winter in preparation to move offshore onto the spawning grounds, the male fish are known to move offshore earlier and remain on the spawning grounds whilst female plaice will make repeated movements on/off the spawning grounds as batches of eggs are matured and become ready to be released (Macer, 1967; Basimi and Grove, 1985c; Rijnsdorp, 1989; Dunn and Pawson, 2002; Solmundsson *et al.*, 2003).

e) Biology and life cycle of plaice

The majority of marine animals produce eggs which are released into the open sea: approximately 96% of all marine fish species follow this strategy by releasing eggs which are fertilized by sperm in the water column resulting in a pelagic larval stage (King, 2007). Although a range of reproductive strategies can be observed in marine fishes, from internal fertilization and placental viviparity to broadcast spawning and external fertilization, it is the latter strategy that dominates resulting in the production of thousands to millions of eggs per female per year depending on the species (Jennings *et al.*, 2001). Most flatfishes produce pelagic eggs, although some estuarine dwelling species lay demersal eggs (Gibson, 2004). Given the importance of understanding the size/age at maturation, reproductive behaviour and reproductive output of commercially exploited species, these aspects of the biology of plaice have received much research interest (*e.g.* Simpson, 1959; Houghton and Harding, 1976; Horwood *et al.*, 1986; Rijnsdorp, 1989; Horwood, 1990; Urban, 1991; Horwood, 1993; Bromley, 2000; Nash *et al.*, 2000; Dickey-Collas, *et al.*, 2003).

Plaice are iteroparous broadcast spawners that utilise defined spawning areas on the coastal shelf surrounding North West Europe (*e.g.* Figure 1.15a shows the spawning grounds in the Irish Sea). The spawning season for plaice usually runs from

January to late April/early May with peak spawning occurring from late-February to early-March, although the exact timings of the start/peak/end of the spawning season can vary from year to year depending on water temperature (Simpson, 1959; Harden-Jones, 1968; Nash and Geffen, 1999; Armstrong *et al.*, 2001; Dickey-Collas *et al.*, 2003; Fox *et al.*, 2007). It is believed that plaice prefer warm water (4 to 10 °C) for spawning, and water temperature is known to be the most important single factor in determining the timing of peak spawning activity and egg production (Harden-Jones, 1968). As mentioned earlier, male plaice will move onto the spawning ground and remain there for extended periods of time whilst the females make repeated movements on/off the spawning grounds every two to five days over a period of four to six weeks as batches of eggs are recruited into final maturation and ready for release (Rijnsdorp, 1989; Urban, 1991). The timing of peak egg production for plaice in the Irish Sea is known to be related to the mean autumnal water temperature (Nash and Geffen, 1999) whilst female fecundity is related to food availability in the autumn preceding the spawning season (Kennedy *et al.*, 2008). The annual fecundity of an individual female plaice appears to be determined before the onset of the spawning season (Urban, 1991). Individual fecundity is highly variable and is known to be a function of size (Simpson, 1959; Harden-Jones, 1968; Rijnsdorp, 1994) and nutritional state (Horwood *et al.*, 1989; Kennedy *et al.*, 2008). Female fecundity is known to vary between flatfish species and is a function of egg size for a particular species and the size range attained by females of that species (Urban, 1991). For example, female turbot *S. maximus* (1.1 mm egg diameter; 100cm) produce on average 8.5 million eggs and female flounder *P. flesus* (0.95 mm egg diameter; 60 cm) 1 million eggs whilst female sole *S. solea* (1.4 mm egg diameter; 70 cm) produce on average 570,000 eggs (Jenkins, 1936). Female plaice (1.8 mm egg diameter; 100 cm) produce on average 250,000 eggs (Jenkins, 1936), although fecundity varies between individuals depending on size and also between different plaice stocks. For example, Wimpenny, (1953) reported that fecundity in ripe female plaice in the North Sea increased from 10,000 to 500,000-700,000 eggs as size increased from 23 to 64 cm, whilst fecundity in Baltic Sea plaice increased from 60,000 eggs in a 23 cm female to 700,000 in a 40 cm female. Differences in fecundity between stocks can also be observed over much shorter geographical distances, for example, Horwood (1993) reported differences in fecundity between female plaice on either sides of St George's Channel: the average fecundity of a 35 cm female plaice off South Eastern

Ireland was 105,000 eggs but was 115,000 eggs for a 35 cm female plaice in the Bristol Channel. As for many fish species, food availability and subsequent female nutritional state has a strong influence on fecundity in plaice (Horwood, *et al.*, 1989). Egg development and maturation in the ovary occurs between July and December in female plaice (Rijnsdorp, 1989) and it has been observed that when food availability is low, female plaice have to breakdown muscle tissue in order to continue gonadal maturation (Rijnsdorp, 1989) which may impact the ability of the individual to migrate to the spawning ground, evade predators or escape fishing gear. Nash *et al.* (2000) have shown that overall regional egg production is dependent on food availability: in their study, egg production by plaice off the Cumbrian coast and in Liverpool Bay, is reduced in years when food availability is lower (Nash *et al.*, 2000). Determining the relationship between size and female fecundity is an important consideration in fisheries management as it allows annual egg production to be estimated which can provide some idea of subsequent juvenile production (King, 2007). A number of studies have examined total egg production for plaice (Houghton and Harding, 1976; Nash and Geffen, 1999; Armstrong *et al.*, 2001).

Once fertilised, plaice eggs float up into the pelagic surface waters where they are transported away from the spawning areas on surface water currents towards the coastal nursery grounds (Dunn and Pawson, 2002; Fox *et al.*, 2007, 2009). The rate of development in the egg and larval phase and the time taken to reach metamorphosis and settlement in plaice is known to be dependent on water temperature. For example, the time taken from fertilisation to hatch is 21 days at 5°C, 18.25 days at 6 °C, 12 days at 10 °C and 10.5 days at 12 °C (Wimpenny, 1953). In addition to temperature, developmental rate in flatfishes is also related to egg size. Among the pleuronectidae, the time taken from fertilisation to hatching at 10 °C is 4.5 days for flounder (egg diameter, 0.095 mm), 10 days for sole (egg diameter, 1.4 mm) and 12 days for plaice (egg diameter, 1.8 mm) (Jenkins, 1936). Given ambient sea surface water temperatures in the Irish Sea in February-April (the period when the majority of plaice eggs are produced), plaice eggs hatch after approximately 15 days (Nash, 1998). Once hatched the plaice larvae go through a series of developmental stages as a larva (Ryland *et al.*, 1975; Hyder and Nash, 1998; Fox *et al.*, 2003) until they metamorphose into juveniles and settle out on the nursery grounds. The time taken for the larval stage to be completed following hatching and for metamorphosis into the juvenile stage will vary from a few days to months depending on the species (King,

2007). After hatching, the time taken to metamorphosis in plaice is usually between 40 and 60 days, depending on water temperature, by which time the surviving nektonic plaice have reached the inshore nursery grounds (Ryland, 1966; Gibson, 2004). To begin with, larval plaice utilise their yolk-sac reserves but about one week after hatching, before the disappearance of the yolk-sac, plaice larvae commence feeding on the diatom *Coscinodiscus grani* and larval molluscs (Wimpenny, 1953). The plaice larvae, and newly metamorphosed juveniles usually remain in the surface waters within the nursery bays for a short period (Lockwood, 1974; Al-Hossaini *et al.*, 1989) before undergoing settlement onto the seabed in about 5m water depth (Lockwood, 1974; Gibson *et al.*, 2002). The size at metamorphosis and settlement for plaice is usually between 10 – 14 mm (Johnstone *et al.*, 1922; Lockwood, 1974; Hjörleifsson and Pálsson, 2001; Doggett, 2006). As a result of the batch spawning behaviour of the adult females and the pulsed delivery of larvae into the nursery grounds, settlement will occur over an extended time period during the summer, usually between April-July (Al-Hossaini *et al.*, 1989; Hyder and Nash, 1998; Hjörleifsson and Pálsson, 2001) but can extend as late as August (Macer, 1967). The timing and duration of the settlement period can vary from year to year, for example, Al-Hossaini and Pitcher (1989) recorded that plaice settlement in Red Wharf Bay (North Wales) occurred between mid-May and early June in 1986 and between late April and the end of May in 1987 respectively. During these time periods, several settlement cohorts were identified with variable growth and survival rates for each cohort (Al-Hossaini and Pitcher, 1989). Differences in growth and survival rates between settlement cohorts have also been recorded by Allen *et al.* (2008). Temperature has been identified as the main factor influencing numbers at metamorphosis and settlement patterns in plaice larvae (Hyder and Nash, 1998).

Once settled, as mentioned earlier, plaice larvae move shorewards into shallow water < 1.0 m deep in order to avoid predation and inter-specific competition for food with dab larvae that settle out in deeper water (Gibson *et al.*, 2002). The diets of juvenile 0-group and 1-group plaice are dominated by polychaetes such as *Pectinaria koreni*, *Nephtys* spp., and *Phyllodoce* spp., although other macrobenthos such as amphipods (*Ampelisca brevicornis*), copepods and molluscs (*A. alba* and *Macoma baltica*) can also be found in the diet (Macer, 1967; Basimi and Grove, 1985c; Carter *et al.*, 1991; Amara *et al.*, 2001). Larval polychaetes from the spionidae family

(chiefly *Polydora ciliata*) and *Pectinaria* often form the main food of newly metamorphosed flatfish in Red Wharf Bay, representing 60 to 70% of the diet of both 0-group plaice and dab but interspecific competition for food between the two species is avoided at this stage through spatial segregation on the nursery ground (Macer, 1967; Carter *et al.*, 1991). Initially, the small plaice undertake regular movements between the intertidal and the shallow subtidal areas of the shore in relation to daily tidal, diurnal and seasonal temperature cycles (Burrows *et al.*, 1994; Gibson *et al.*, 1998). Towards the end of their first summer, the plaice larvae are large enough to evade predation by *Crangon* (their main predator, Burrows *et al.*, 2001) and move into > 3 m water depth (Gibson *et al.*, 2002) where they feed on a variety of prey including bivalves, polychaetes, crustaceans and sand eels (Carter *et al.*, 1991). Interspecific competition with dab is avoided by trophic resource partitioning, since dab feed primarily on brittlestars and razor clams to avoid competition with juvenile plaice (Carter *et al.*, 1991). Juvenile plaice will remain on the nursery grounds for up to 2 years (Bowers, 1963; Nash *et al.*, 1992) before moving offshore into deeper water. The juvenile-adult transition for plaice and the offshore movement to recruit into the adult stock usually occurs between May and September (Rijnsdorp, 1989). Juvenile recruitment into the adult stock is a key input parameter in virtual population analysis (VPA) fisheries management and is monitored by ICES for commercially exploited stocks in order to assess annual year class strength and to assist in determining catch quota (e.g. ICES 2008a, 2008b, 2008c). Considerable variation in the annual recruitment estimates for juvenile plaice in ICES Division VIIa between 1964 and 2007 have been reported with estimates varying between 7 and 29 million (1965 peak recruitment value) individuals (ICES, 2008a). Following a period of strong year classes (> 15 million) in the mid/late 1980s, recruitment over the last 20 years has been steady at 8-10 million individuals (ICES, 2008a).

As adults, plaice will undertake feeding migrations within the continental shelf seas of North West Europe (Dunn and Pawson, 2002; Hunter *et al.*, 2003; Metcalfe *et al.*, 2006) and aggregate in coastal water over winter in advance of moving offshore to the regional spawning grounds (Basimi and Grove, 1985c; Dunn and Pawson, 2002). The diet of adult plaice continues to be dominated by polychaetes such as *Pectinaria*, *Nereis*, *Lanice* and *Magelona*, although the switch is made to feeding on adult polychaetes, in addition, molluscs such as *Spisula* spp. and *A. alba* also form a large proportion of the diet in large adult plaice (Braber and De Groot, 1973; Rijnsdorp and

Vingerhoed, 2001; Amezcua *et al.*, 2003). Seasonality diet composition has been observed for plaice with bivalves dominating the diet in the spring and summer and polychaetes in the spring and autumn (Basimi and Grove, 1985c; Rijnsdorp and Vingerhoed, 2001; Amezcua, *et al.*, 2003). In contrast, although a wide range of prey items are also taken by dab and sole, the primary components of the diet for these main competing flatfish species in the regional seas around the UK are brittlestars *Ophiura* spp, for dab (Saborowski and Buchholz, 1996; Seisay, 2001; Hinz *et al.*, 2005) and crustaceans for sole (Molinero and Flos, 1992; Cabral, 2000) respectively. Thus, the three main flatfish species in the coastal shelf seas of northern Europe avoid competition through dietary and habitat segregation. It is interesting to note that adult plaice, at least in the North Sea, may have undergone a shift in their main prey items. By comparing the historical literature from end of the 19th century (Cunningham, 1895) with the results of their study (1990s), Rijnsdorp and Vingerhoed (2001), suggest that a shift in primary food types from bivalve to polychaetes for sole and, to a lesser degree, for plaice. It is possible that this switch in primary prey type (*i.e.* bivalve to polychaete) is correlated with changes in the epibenthic macrofauna of coastal shelf seas as a result of intensive fishing activity. The effect of fishing gear on the community structure of the sea floor has been the focus of much investigation in recent decades. Although the action of trawling causes damage and disturbance to benthic communities (Jennings and Kaiser, 1998; Groenewold and Fonds, 2000; Kaiser and Hiddink, 2007; Hinz *et al.*, 2009), trawling can also enhance the food supply for some fish species by increasing the productivity of their principal prey (Rijnsdorp and Van Beek, 1991; Kaiser and Spencer, 1996; Millner and Whiting, 1996; Rijnsdorp and Van Leeuwen, 1996).

1.1.5 Fish Population dynamics

As the models used in fisheries management have developed over time since the first models proposed in the 1950s - Beverton and Holt's Dynamic Pool model and Schaeffer's surplus Production model (Jennings *et al.*, 2001; King, 2007) - an understanding of the ecology and population dynamics of an exploited fish species has become of critical importance in their management (King, 2007). This is because aspects of a species' population dynamics, such as abundance/recruitment, size/age structure, length-weight relationships, fecundity, growth and mortality rates and

age/size at maturity, often separate into data for males and females as sex-specific data for these parameters are common, and they are included in VPA models (King, 2007). In addition, the move away from single species fisheries models to ecosystem-based fisheries models has meant that an understanding of the interactions between the target commercial species and its predators and prey and the seasonal movement patterns of the target species are also needed in order to develop effective management plans to ensure sustainable exploitation (Jennings *et al.*, 2001; King, 2007). Given the importance of plaice as a food fish in Northern Europe (*e.g.* ICES, 2008a and 2008b), there has been much research into the population dynamics of the species over the last 100 years (*e.g.* Cunningham, 1895; Wallace, 1914; Wimpenny, 1953; Basimi and Grove 1985c). In this section, a brief review of key aspects of fish population dynamics in general and for plaice in particular are presented.

a) Growth and Size/Age

Growth in animals can be defined as an increase in the linear dimensions such as length, height and width resulting in a volume change and an increase in weight (King, 2007). In fisheries surveys, size is usually measured in terms of length (*e.g.* standard length, total length) as this parameter is easier and quicker to measure than weight. However, both the abundance and landings of target fish species are usually recorded in terms of biomass (*i.e.* weight) and therefore, length-weight calibrations are needed to convert size data from fisheries surveys into biomass data for inputting into VPA models. Previous studies have reported length-weight relations for different plaice stocks in the Irish Sea (*e.g.* Basimi and Grove, 1985c) and North Sea (Ruack, 1974; Rijnsdorp, 1989). Length-weight relationships in fishes are commonly described using a power curve equation, $W = aL^b$ (King, 2007) and once measurements of length and weight have been obtained it is possible to assess whether growth is isometric or allometric. Isometric growth occurs when all linear dimensions increase in proportion to each other and the b-value in the length-weight power curve is equal to 3 (King, 2007): this occurs since if an animal doubles in size, *i.e.* its length, width and height all double, then there will be an 8-fold, *i.e.* 2^3 , increase in volume (*i.e.* weight) (King, 2007). If the b-value in the length-weight relationship differs from 3 then growth is said to be allometric (King, 2007). Examination of seasonal, sex-specific and species-specific differences in the length-weight relationship can provide valuable information on the patterns of growth in fishes (Froese, 2006). In addition,

once the relationship between length and weight has been established then it is possible to calculate condition factors – these are a number of indices that relate length to weight for an animal and provide a numerical indication index of the “well-being”, *i.e.* how “fat” or “skinny” the animal is for a given length (Bolgor and Connolly, 1989; Jennings *et al.*, 2001; King, 2007). Previous studies have reported both seasonal and stock-dependent differences in condition factor for plaice (*e.g.* Rauck, 1975; Kuipers, 1977; Nash *et al.*, 1992)

If it is possible to age animals, then size (length/weight) can be related to age and growth curves (*i.e.* size at age relationships) can be constructed and growth rates determined for a species. In fishes, a number of hard parts such as the otoliths, vertebrae, opercular bones and scales, can be used for ageing (Panfili, *et al.*, 2002; King, 2007). Examination of these structures reveals a banding pattern (Figure 1.17) which occurs as growth in fishes is strongly influenced by food availability and water temperature (Gibson, 2004). For temperate water fish species, seasonal changes in food availability and water temperature influence growth rate and this is reflected in the body hard parts resulting in the formation of a regular banding pattern in scales, bones and otoliths (Figure 1.17) (King, 2007). Thus, relative growth rate at different periods of time can be assessed and the age of the fish can be determined (King, 2007). Since, temperate fish species will go through periods of fast growth (late spring – autumn) and slow/no growth (winter-early spring) each year, growth bands that differ in size and composition are usually discernible (Figure 1.17) with one pair fast/slow growth bands corresponding to one year’s growth. Thus, it is possible to age fish which allows various parameters such as size and maturation state to be related to age. The choice of hard part – bone, scale, otolith – used in the ageing process is dependent on the species under examination and whether a non-invasive sample is required. Scales can be taken non-invasively (*i.e.* without killing the fish to dissect and remove skeletal structures) and are also the ageing structure of choice for some fish species, *e.g.* sea bass *Dicentrarchus labrax*, as they allow age to be easily and clearly determined (Figure 1.17a). However, for many marine fish species, such as flatfish, the banding pattern on the scale is not clear and becomes hard to read in older fish and otoliths are the ageing structure of choice in most marine teleosts.

Given that growth in animals is periodic, it is possible to discern the presence of tidal, daily, lunar monthly and seasonal banding patterns in calcareous structures if the appropriate techniques are used (Panfili *et al.*, 2002; Easey and Millner, 2008).

However, for fisheries management purposes, where age is the parameter of interest, the large-scale seasonal banding patterns are used. During the warmer summer months, otolith growth is faster and translucent, widely-spaced bands (the hyaline zone) are laid down whilst in the cooler winter months, growth is slow and narrower, more densely packed, opaque bands (the opaque zone) are laid down (King, 2007). The difference in the composition/density of the hyaline and opaque

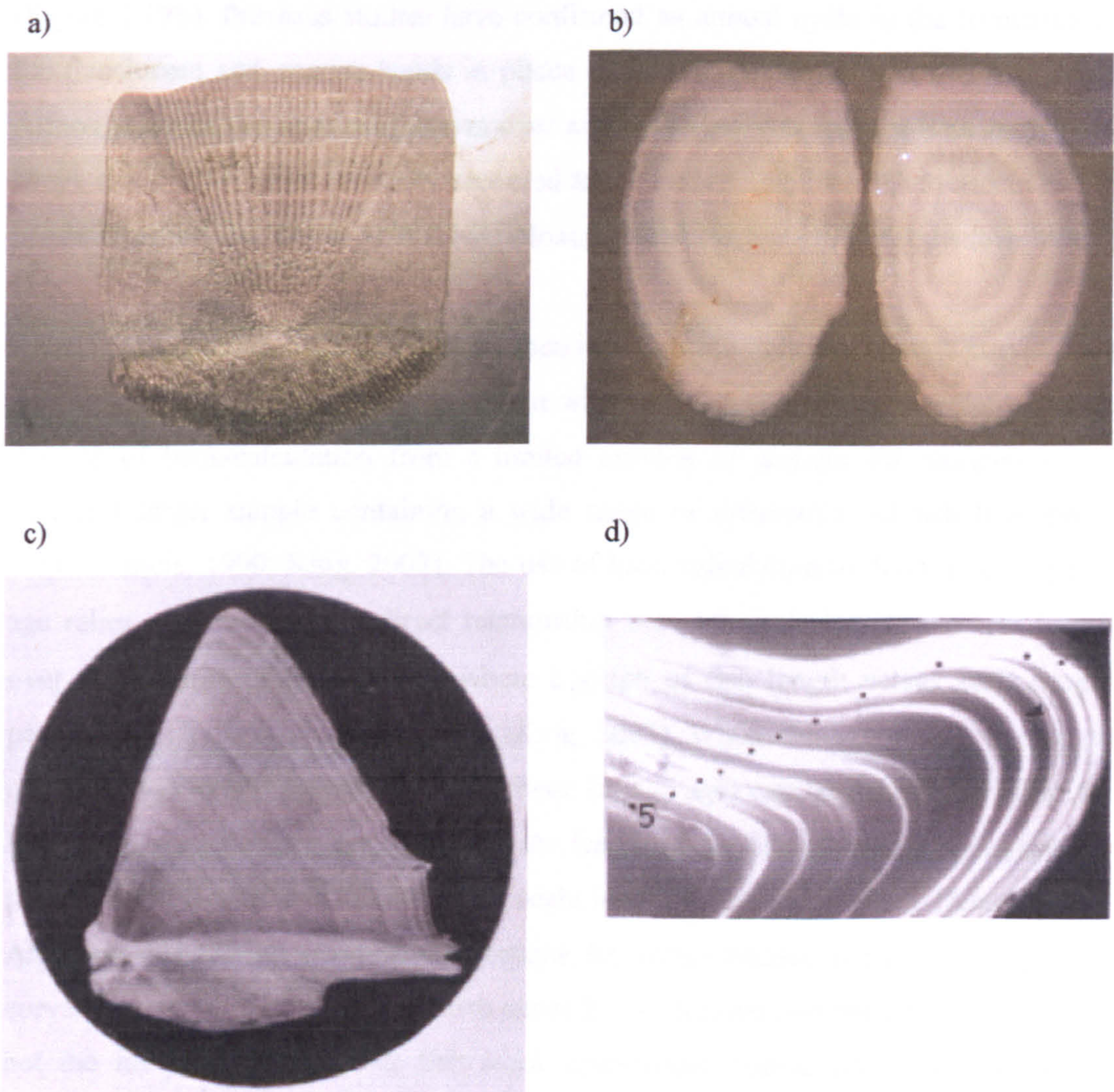


Figure 1.17: Examples of hard parts used for ageing in teleost fishes: (a) a scale from an 8 year old European sea bass *D. labrax* L. (McCarthy, unpublished photograph), (b) a pair of sagittal otoliths from a 4 year old plaice *P. platessa* L. (McCarthy, unpublished photograph), (c) an opercular bone from a 12 year old perch *Perca fluviatilis* (Le Cren, 1947), (d) a dorsal fin ray from a 15 year old ling cod *Ophiodon elongatus* (McFarlane and King, 2001).

zones of the otolith results in clear differences in their appearance under light microscopy which enables the bands to be identified, counted and an age assigned to the fish (Figure 1.17b). In some fish species, for example for gadoids and for many tropical fish species, the otoliths can be difficult to read without careful preparation using staining and sectioning techniques (*e.g.* Panfili *et al.*, 2002; Easey and Millner, 2008). However, for plaice, the sagittal otoliths are usually very easy to read using binocular microscopy as a result of their flattened structure and clear banding patterns (Figure 1.17b). Previous studies have confirmed an annual cycle in the formation of the translucent and opaque bands in plaice otoliths (*e.g.* Basimi and Grove, 1985c). Although plaice are known to spawn over a period of several months (late January to May), the 1st of April is generally accepted as the birth date of the fish to assign age in plaice (Basimi and Grove, 1985c; Al-Hossaini and Pitcher, 1989; Rijnsdorp, *et al.*, 1990).

Once age has been determined, then it is possible to derive growth curves for a particular species. There are two ways in which this can be achieved, either through the use of back-calculation from a limited number of scale/otolith samples or by ageing a larger sample containing a wide range of different-sized fish (Campana, 1990; Francis, 1990; King, 2007). The use of back-calculation to determine length at age relies on there being a direct relationship between scale length and fish length over the lifetime of the fish and where a graph of fish length versus scale length passes through the origin of the graph (King, 2007). Where this is the case, the length of a fish (L_x) at any previous growth check (x ; *i.e.* age) can be determined from the formula $L_x = L_p(S_x/S_p)$ where L_p equals the length of the fish at capture, S_p equals the present scale length and S_x equals the scale length at growth check x (King, 2007). Although this can be a valuable technique for reconstructing the estimated growth curves for individual fish, or a growth curve from a limited number of samples, this is not the favoured approach in fish stock assessment studies since back-calculated lengths are often less than actual measured fish lengths (Campana, 1990; King, 2007). The usual approach in fish stock assessment studies is to collect and age otoliths from a large size range of fish.

Several mathematical models have been proposed to express growth in fishes (reviewed in Jobling, 2002) but the most commonly used growth model is that proposed by von Bertalanffy (1938), probably due to its inclusion in the dynamic pool fisheries model developed by Beverton and Holt (1957). The von Bertalanffy growth

curve is an asymptotic growth curve, $L_t = L_\infty (1 - e^{-k(t-t_0)})$ where L_t is the length of a fish at age t , L_∞ is the theoretical maximum (or asymptotic) length for that species, k is the growth coefficient which describes the rate at which the asymptotic length is reached and t_0 is the theoretical age at zero length (King, 2007). Although there have been some criticisms about its use, especially since it is unlikely that a single model can be used to represent growth over the entire lifetime of a species where seasonal and ontogenetic changes in growth occur (e.g. Cloern and Nicholls, 1978; Lester *et al.*, 2004), the von Bertalanffy growth curve does provide a good general fit to length at age data and has been widely used by fish and fisheries biologists to describe growth in teleost fishes. Numerous studies have used the von Bertalanffy growth model to describe the pattern of growth in plaice, and to examine sex-dependent differences in growth, for example Basimi and Grove (1985c), Rijnsdorp and van Beek (1991), Bromley (2000) and Nash, *et al.* (2000).

b) Mortality

An understanding of the factors affecting mortality and an estimate of mortality rate is critical in understanding fish population dynamics and in fisheries management models. There are a wide range of factors that will result in the mortality of fishes, for example adverse environmental conditions, starvation and predation (Jennings *et al.*, 2001; King, 2007): all these factors are natural in origin and in fisheries science are commonly referred to as natural mortality and described by the parameter M , the instantaneous coefficient of natural mortality (King, 2007). In exploited fish stocks, in addition to natural mortality population size will also decrease as a result of fishing activities and this is commonly referred to as fishing mortality and described by the parameter F , the instantaneous coefficient of fishing mortality (King, 2007). By obtaining a large sample of fish and ageing them, it is possible to estimate mortality rates by determining the number of fish present in each age class, plotting an age-based catch curve [number of fish in age class (Y) versus age class (X)] and using the exponential decay equation $N_t = N_0 e^{-Zt}$ where N_t is the number of fish present in age class t , N_0 is the initial number of fish (in the case of the catch curve, the intercept on the y axis is a meaningless number) and Z is the instantaneous coefficient of total mortality where $Z = F + M$ (King, 2007). To make calculation of Z easier, the decay curve can be linearised by plotting $\ln N_t$ against age and fitting a linear regression

through the data where the slope of the line is Z (King, 2007). As King (2007) observes in exploited fish stocks it is easier to calculate total mortality than it is to calculate its sub-components, F and M . In reality it is difficult to calculate natural mortality, M , in fish stocks. Since fishing activities do not affect mortality rates in larval fishes and in small juveniles, estimates of natural mortality in these phases of the lifecycle can be obtained by repeated surveys over time to examine the changes in abundance for a particular cohort. The available data shows that natural mortality rates in the early life-history stages are very high (Houde, 2002). The egg/larval phase of the lifecycle has been described as the 'critical phase' of the lifecycle where in excess of 99% of the total mortality observed within a species will take place (Jennings *et al.*, 2001). This is the reason why so many fish species produce large numbers of eggs (King, 2007). There are some data available for natural mortality rates in plaice. For example, Dickey-Collas, *et al* (2003) report a daily instantaneous mortality rate of 0.15 - 0.29 day⁻¹ for plaice eggs in the Irish Sea in 1995 and 2000; Gulland (1977) estimated monthly mortality rates for plaice larvae in the North Sea at 80% month⁻¹. The daily mortality rates of egg and larval plaice in Irish Sea are increased at higher water temperatures (Pepin, 1991; Van der Land, 1991; Dickey-Collas, *et al*, 2003) and correlate with subsequent year class strength (Harding *et al.*, 1978; Van der Veer, *et al.*, 1990). Mortality rates in young plaice on their coastal nursery grounds have also been assessed by repeated surveys of cohorts of 0-group plaice (*e.g.* Macer, 1967; Al-Hossaini and Pitcher, 1989; Nash and Geffen, 2000; Allen *et al.*, 2008). Al-Hossaini and Pitcher (1989) demonstrated how survival was related to the timing of settlement for a particular cohort with mortality rates highest in early settling and late settling plaice. Examples of published mortality rates in juvenile plaice include work by Macer (1967) who estimated a monthly reduction in 0-group plaice numbers in Red Wharf Bay between September and December of 40% per month; Nash and Geffen (2000), calculated instantaneous mortality rates of 0-group plaice in Port Erin Bay for the period 1992 to 1998 of between 0.011 and 0.029 day⁻¹; and Hjörleifsson and Pálsson (2001) calculated daily instantaneous mortality rates of plaice in Iceland as 0.03 day⁻¹. In general, Iles and Beverton (1991) report mortality rates of 0-group plaice in nursery areas around the North Sea and in other British coastal waters to be between 0.007 and 0.052 day⁻¹. Mortality rates of juvenile plaice on nursery grounds will be dependent on factors such as food availability and predation pressure but will also correlate with water temperature. For

example, Nash (1998) reports that for the time period 1964-1994, the daily mortality rates of plaice in the Irish Sea ranged from 0.071 to 0.096 day⁻¹ during the pelagic phase and between 0.009 to 0.019 day⁻¹ on the nursery grounds and was significantly correlated with water temperature.

Natural mortality can be harder to estimate in adult fish, unless the species/stock in question is unexploited. However, it is possible to estimate natural mortality rates in exploited fish populations: for example, if a stock has been fished over a period of time at a range of intensities and estimates of Z and fishing effort are available, a plot of effort (X-variable) versus Z (Y-variable) will produce a linear relationship and the intercept on the Y-axis will provide an estimate of M (i.e. the mortality rate when there is no fishing effort) (Jennings *et al.*, 2001). Since the natural mortality rate of a species will be related to its life history characteristics (e.g. r versus k strategies) as well as environmental parameters (such as temperature), there have been a number of attempts to relate published values of natural mortality to other, more easily measured life history parameters such as maximum size, growth rate and lifespan and environmental parameters such as temperature (e.g. Beverton and Holt, 1959; Beverton, 1963; Pauly, 1980; Hoenig, 1983; Gunderson and Dygert, 1988; Vetter, 1988). The equation most commonly used to estimate natural mortality is that of Pauly (1980) who conducted a multiple regression analysis based on data for fish stocks where natural mortality rates, the von Bertalanffy growth parameters and the mean annual sea surface temperature were known to derive an equation that allows M to be estimated ($\ln[M] = -0.0152 - 0.2790\ln[L_\infty] + 0.6543\ln[k] + 0.4634\ln[T]$; Pauly, 1980). There are some concerns over the use of this equation, however, for many species/stocks, the Pauly (1980) equation remains the best, or only, estimate of M (Vetter, 1988; Jennings *et al.*, 2001). There have been very few studies in adult plaice where natural mortality has been independently estimated: for example, natural mortality for adult plaice in the North Sea for the time period 1960-1971 has been predicted by Jensen, (1984) as 0.10 year⁻¹ for females and 0.15 year⁻¹ for males and Beverton (1964) estimated the annual natural mortality rate of mature male and female plaice to be 0.13 year⁻¹ and 0.08 year⁻¹ respectively. Instantaneous rates of fishing mortality in plaice will be discussed in a later section.

c) Length/age at sexual maturity

Successful reproduction is critical to the continuance of any species and the reproductive characteristics of exploited fish stocks are one area that has received a large amount of research interest by fisheries scientists. King (2007) states that most marine animals, including 96% of all fishes are external fertilisers releasing gametes into the water to produce large numbers of eggs/larvae. As stated earlier, mortality rates during this early phase of the lifecycle are extremely high: gametes may not encounter each to produce fertilised embryos, predation rates in the plankton are very high and those larvae that survive may not be carried by the surface currents into areas of high food abundance or into suitable nursery areas in inshore coastal waters (King, 2007). This is the reason why fecundity is so high in marine fishes: as stated earlier, fecundity in a large adult female plaice is *ca.* 700,000 eggs (Jenkins, 1936), however, large Atlantic cod can produce up to 9 million eggs (URL 3) and the most fecund vertebrate is the sunfish *Mola mola* which is through to produce *ca.* 300 million eggs (King, 2007).

There are a number of major reproductive life history events that are of interest to fisheries biologists: these are the cycle of maturation in the target species (*e.g.* is it an annual spawner? is it a semelparous or iteroparous spawner?), the timing of spawning (*i.e.* when during the year does spawning take place?) and the age and size at which fish first mature and therefore start to contribute to the adult spawning stock. It is well known that the rate and timing of gonadal development will be influenced by environmental factors such as temperature and photoperiod (Helfmann *et al.*, 2004; Bone and Moore, 2008) and will also vary between individuals. Fish must reach a certain size before they are capable of reproduction and as a result of biological variation this will vary between individuals as a result of individual genotypes and also between stocks. In fisheries science studies, the usual approach is to collect fish during the spawning season and to estimate the proportion of sexually mature fish in different length or age classes (King, 2007). The stage of sexual maturity is usually assessed by macroscopic examination of the gonads or through histological examination of gonadal tissue (*e.g.* West, 1990; Smith and Walker, 2004; Gerritsen and McGrath, 2006). From these data, the length or age at which 50% of the fish in that length or age class are sexually mature can be calculated – usually referred to as the L_{50} and A_{50} or maturity ogives (King, 2007). In fisheries, all fish that are

larger or older than the L_{50} or A_{50} value are assumed to be mature (King, 2007). The L_{50} or A_{50} values are usually determined by plotting the proportion of mature fish in a given size/age class (Y-axis) against the size/age class (X-axis) and fitting a logistic curve to the data such as $P = 1/(1 + e^{[-r(X-X_{50})]})$ where P is the proportion of sexually mature individuals in a given length or age class (X), X_{50} is the length or age at first maturity and r is the slope of the curve (King, 2007). These analyses are usually conducted separately for males and females since sex-specific differences in maturity ogives are very common amongst teleost fishes (King, 2007). Plaice is a good example of a species which displays differences in maturity ogives between males and females within a given stock and also differences in these male and female maturity ogives between stocks (e.g. Basimi and Grove, 1985c; Rijnsdorp, 1989; Horwood, 1990; Rijnsdorp, 1993a; Parker-Humphreys 2004a, 2004b, 2005). There is also evidence that changes in maturity ogives have occurred in plaice as an evolutionary response to fishing pressure (e.g. Rijnsdorp, 1993b). These differences are discussed in greater detail in Chapters 2 and 3 respectively.

1.1.6 Aims of this study

1. To conduct a detailed study of the population dynamics of adult plaice in the inshore waters of North West Wales and Eastern Anglesey utilizing data collected by otter trawl in October 2004-2005. Specifically, age-/size frequency distributions, growth rates, mortality rates and age-/size at maturity will be examined and compared with (i) data collected by a similar study 30 years ago conducted by Basimi (1978) and (ii) contemporary data for the other major plaice stocks of North West Europe.
2. To examine changes in the population biology of adult plaice in the inshore waters of North West Wales and Eastern Anglesey between 1970 and 2006 and to compare the results obtained with those for other local demersal fish stocks and in relation to fishing pressure and climate change.
3. Through monthly sampling, to describe the pattern of growth of plaice juveniles in Red Wharf Bay and Conwy Bay (2004-2006), two major nursery grounds for plaice in the South East Irish Sea.

Chapter 2:

Population biology of plaice *Pleuronectes platessa* L. in the coastal waters of Northwest Wales and Eastern Anglesey (2004-2005).

2.1 Introduction

Plaice *P. platessa*, a demersal pleuronectiform flatfish, is one of the main commercial species landed in Northwest Europe along with Atlantic herring *C. harengus harengus*, Atlantic cod *G. morhua* and Atlantic mackerel *S. scombrus* (ICES, 2008a, 2008b and 2008c). Fisheries for plaice have existed for centuries in Northwest Europe (Van Neer *et al.*, 2002; Bolle *et al.*, 2004) and due to its wide distribution and commercial importance, plaice catches were responsible for more than half of the total landings of flatfishes in the Northeast Atlantic during early twentieth century (Gibson, 2005). At the start of the 21st century, commercial fisheries for plaice can be found in the Barents Sea (Kuznetsova *et al.*, 2004), the Baltic Sea (Nielsen *et al.*, 2004; ICES, 2008c), and the coastal shelf seas of the Northeast Atlantic (Cefas, 2008; ICES, 2008a, 2008b). The average annual catch of plaice in Northwest Europe for the period 2000-2005 is *ca.* 88,500 tonnes (ICES, 2008a, 2008b and 2008c), with significant regional variation between different coastal areas (Table 2.1).

Around the UK, plaice are exploited in the North Sea, English Channel, Irish Sea and Celtic Sea (listed in order of landings, Table 2.1). Exploitation rates are highest in the North Sea since it is the largest shallow continental shelf sea surrounding the UK (570000 km² compared to 100000 km² for the Irish Sea) and most flatfish fisheries occur in water depths of less than 200m (Gibson, 2005). Given the commercial importance of plaice in the North Sea (where peak landings of >150000 tonnes *p.a.* were recorded in the 1980s; ICES, 2007), plaice stocks in the North Sea have been the focus of much research over the last 30 years to inform management policies (*e.g.* Rijnsdorp, 1989; Rijnsdorp and Van Leeuwen, 1996; Daan, 1997; Kell *et al.*, 1999; Bromley 2000; Grift *et al.*, 2003; Kell *et al.*, 2005; Cefas, 2008; ICES, 2008b).

In the Irish Sea, plaice are of minor commercial importance compared to Norway lobster *N. norvegicus* and sole *S. solea* (ICES, 2008a). Data on spawning stock biomass, recruitment and fisheries exploitation have been collected by ICES since 1964 (ICES, 2008a). These data show that the Irish Sea supports much lower numbers of plaice compared to the North Sea and hence exploitation rates have been lower (ICES, 2008a, 2008b). The long term average spawning stock biomasses in the two shelf seas are

Table 2.1: A summary of the average landings of plaice *P. platessa* from the coastal shelf seas of Northwest Europe for the period 2000-2005 (Source: ICES, 2008a, 2008b, 2008c).

Region	ICES code	Landings (tonnes)	Landings status (2000 – 2005)
Baltic Sea	Subdivisions 22-32	2500	Landings stable
Skagerrak/Kattegat	IIIa	9000	Landings stable
North Sea	IV	69500*	Declining landings
Irish Sea	VIIa	1400	Landings stable
Celtic Sea (W Ireland)	VIIb,c	73	Declining landings
Eastern Channel	VIIId	3900	Declining landings
Western Channel	VIIe	1200	Landings stable
Celtic Sea	VIIIf,g	600	Declining landings
Celtic Sea (SW Ireland)	VIIh-k	270	Declining landings
Total Plaice Landings		88443	

*Note: Discards for North Sea estimated as 50400 t/year for 2000-2005.

298276 tonnes (1957-2006) for the North Sea and 6200 tonnes (1964-2006) for the Irish Sea respectively. Both long term average recruitment and average landings differ by two orders of magnitude between the two seas: 1.04×10^9 Age 1 recruits and 110768 tonnes landed (plus 56767 tonnes discarded) in the North Sea compared to 1.3×10^7 Age 2 recruits and 3245 tonnes landed (discard levels unknown) in the Irish Sea (ICES, 2008a, 2008b). The lower exploitation rates in the Irish Sea have ensured that plaice in the Irish Sea are underexploited and at full reproductive capacity compared to the North Sea where ICES have assessed plaice as overexploited and at risk of reduced reproductive capacity (ICES, 2008a, 2008b). However, as ICES (2008a) highlight, discard rates of plaice in the Irish Sea have not been quantified and are thought to be substantial.

Although plaice in the Irish Sea (ICES division VIIa) are managed as a single stock by ICES, tagging-recapture studies conducted by Cefas between 1979-1980 and 1993-1996 have indicated that plaice populations in the Irish Sea consist of 4 sub-stocks in the Northeast Irish Sea (Solway Firth), the Southeast Irish Sea (Liverpool Bay), Cardigan Bay and the Western Irish Sea off the east coast of Ireland (Dunn and Pawson, 2002). Plaice in the Irish Sea have been less well studied compared to the North Sea. Although some studies have been conducted in the Northeast Irish Sea and Cardigan Bay (*e.g.* Simpson, 1959; Hill, 1971; Horwood, 1990; Nash *et al.*, 2000; Amezcua and Nash, 2001; Amezcua *et al.*, 2003), most research has focused around the Isle of Man and in the Southeast Irish Sea (*e.g.* Simpson, 1959; Macer, 1967, 1972; Basimi and Grove 1985a, 1985b, 1985c; Al-Hossaini and Pitcher, 1988; Carter *et al.*, 1991; Nash 1998; Nash *et al.*, 2000; Amezcua and Nash, 2001; Amezcua *et al.*, 2003; Watts *et al.*, 2004). In recent years, Cefas have conducted a series of studies modeling the dispersal patterns of eggs and larvae away from spawning grounds in the Irish Sea and the subsequent settlement of juveniles into nursery grounds in the eastern Irish Sea (Fox *et al.*, 2006, 2007; van der Molen *et al.*, 2007). In fact most of the research conducted on plaice in the Irish Sea has focused on egg/larvae distribution and on the ecology of juveniles on the nursery grounds (*e.g.* Macer, 1967; Hill, 1971; Basimi and Grove 1985b, 1985c; Al-Hossaini and Pitcher, 1988; Carter *et al.*, 1991; Rogers, 1993; Nash, 1998; Armstrong *et al.*, 2001; Gibson *et al.*, 2002; Dickey-Collas, *et al.*, 2003; Fox *et al.*, 2003; Watts *et al.*, 2004) and less is known about the ecology of the adults (*e.g.* Simpson, 1959; Macer 1972; Basimi and Grove, 1985b, 1985c; Horwood, 1990; Dunn and Pawson, 2002).

The southeast Irish Sea plaice stock is located within the greater Liverpool Bay area of the Irish Sea (Dunn and Pawson, 2002; Fox *et al.*, 2007). The main spawning ground for this stock is located in an area of Liverpool Bay (about 12 miles offshore from the Great Orme Llandudno) in North Wales (Simpson, 1959; Dunn and Pawson, 2002; Fox *et al.*, 2007). Spawning of plaice on the Great Orme spawning ground usually takes place between January and April with the main peak in spawning activity between late-February and late-March (Simpson, 1959). Following spawning, the fertilized eggs/larvae are transported on tidal currents (Fox *et al.*, 2006, 2007; van der Molen *et al.*, 2007) towards nursery grounds along the coast of Northwest England and North Wales (Dunn

and Pawson, 2002). Although the nursery grounds for the Southeast Irish Sea stock are thought to run along the Cumbrian/Lancashire/North Wales coast from Morecambe Bay to Eastern Anglesey (Nash, 1998; Dunn and Pawson, 2002; Fox *et al.*, 2007), the two main nursery grounds are thought to be Red Wharf Bay and Beaumaris Bay (Basimi and Grove, 1985c). Upon reaching the coastline, the post-larval juvenile fish will remain within the surface waters before undergoing metamorphosis and settling out on the seabed as small juveniles (Macer, 1967; Lockwood, 1974; Kuipers, 1977; Gibson *et al.*, 2002). The distribution of plaice along the Cumbrian/Lancashire/North Wales coast is not uniform with a preference for sandy/muddy areas (Amezcuca and Nash, 2001; Amezcuca *et al.*, 2003). The juvenile plaice remain on the nursery grounds for at least one year moving offshore into deeper water on the nursery ground as they increase in size (Lockwood, 1974; Kuipers, 1977; Gibson *et al.*, 2002). After 1 or 2 years, juvenile plaice move offshore and recruit into the adult stock. Tagging experiments by Cefas have shown that 50% of the adult plaice remain within the Liverpool Bay area whilst 50% undertake large-scale movements away from the Liverpool Bay Area with 43% moving south through the Irish Sea to Southeast Ireland before returning to Liverpool Bay (Dunn and Pawson, 2002).

Although various aspects of the ecology of adult plaice in the Southeast Irish Sea, such as growth rates, size/age at maturity and fecundity, have been studied individually (*e.g.* Nash *et al.*, 2000; Dunn and Pawson, 2002; Parker-Humphreys, 2004a), there has only been one detailed study where these various aspects of the population dynamics of the Southeast Irish Sea stock have been studied simultaneously. This work was conducted by Basimi in 1974-1977 for his PhD thesis (Basimi, 1978) producing several subsequent publications (Basimi and Grove, 1985a, 1985b, 1985c). Basimi's research focused on the plaice population in the inshore waters of Northwest Wales (Beaumaris Bay) and Eastern Anglesey (Red Wharf Bay) providing data on the size-/age-frequency distributions, feeding ecology, growth rates, mortality rates, size/age at first maturity and fecundity for this plaice population (Basimi, 1978; Basimi and Grove, 1985b, 1985c). This work was conducted during a period of time when fishing pressure on plaice in the Irish Sea was greater (1970-1979: average annual landing = 3900t, Mean F ages 3-6 = 0.70 year⁻¹; ICES, 2008a). Fishing pressure on plaice in the Irish Sea remained high through the

1980s (1980-1989: average annual landing = 4440t, Mean F ages 3-6 =0.64 year⁻¹; ICES, 2008a). However, there has been no detailed study that has examined the population dynamics of this plaice population since the introduction of a precautionary approach to fisheries management by ICES and a reduction in fishing pressure on plaice in the Irish Sea since the early 1990s (2000-2005: average annual landing = 1400t, Mean F ages 3-6 =0.23 year⁻¹; ICES, 2008a).

The aims of this chapter:

- 1) To conduct a detailed study of the population dynamics of adult plaice in the inshore waters of Northwest Wales and Eastern Anglesey utilizing data collected by otter trawl in October 2004/2005. Specifically, age-/size frequency distributions, growth rates, mortality rates and age-/size at maturity will be examined.
- 2) To examine whether sex-specific differences exist in these population parameters between male and female plaice.
- 3) To compare the population dynamics of plaice in the inshore waters of Northwest Wales and Eastern Anglesey in 2004/05 with the data collected by Basimi in the same areas in 1974/78.
- 4) To compare the population dynamics of plaice in the inshore waters of Northwest Wales and Eastern Anglesey in 2004/05 (part of the Southeast Irish Sea stock) with contemporary data for other plaice stocks in Northwest Europe.

2.2 Materials and methods

2.2.1 Sampling

Plaice, *P. platessa*, were caught from several locations in the coastal waters of North West Wales and Eastern Anglesey in the southeast Irish Sea in October 2004 and 2005. The trawl locations comprised three inshore sites [Conwy Bay, Colwyn Bay and Red Wharf Bay (including Moelfre)] and two offshore sites [offshore Colwyn Bay and offshore Point Lynas] (Figure 2.1). These sites have been fished by the School of Ocean Sciences using the RV *Prince Madog* in October/November on an annual basis since 1972. In total, 23 trawls were conducted in October 2004 and 2005. The trawl locations and directions are presented in Figures 2.1 and 2.2 and trawl details presented in Appendices 1a and 1b. Samples were collected using a rock-hopper otter trawl with a cod end stretched mesh size of 76 mm fished by the RV *Prince Madog*. The School of Ocean Sciences research vessel, the RV *Prince Madog* is a 34.9 m long shelf sea research vessel with a GRT of 390 tonnes. The duration of each trawl was approximately one hour and the trawl was towed at a speed of between 2 and 4 knots (dependent on whether towing with/against the tide) [see Appendices 1a and 1b]. After the net was hauled on deck, the whole catch was sorted and the key survey species [plaice, dab *L. limanda*, whiting *M. merlangus* and red, tub and grey gurnards (*A. cuculus*, *Trigla lucerna* and *E. gurnardus*)] retained. The total lengths (TL) of all plaice caught were measured to the nearest centimetre and the first three fish in each centimetre size class were retained as a length-stratified sub-sample (LSS) for more detailed dissection. For each trawl location, the plaice in the length-stratified subsample were divided into groups of circa 10 - 20 fish, stored and labeled in bags and frozen (-20°C). Due to the late return of the *Prince Madog* to Menai Bridge each day and the time required to dissect the plaice, the processing of measurements and data generation by dissection were conducted at a later date. The number of *P. platessa* caught using the RV *Prince Madog* and dissected in 2004 and 2005 were 514 fish (224 male, 287 female and 3 fish that could not be sexed) and 424 fish (141 male and 283 female) respectively.

2.2.2 Measurements

On the day of dissection, the frozen plaice were taken from the freezer to defrost them prior to dissection. As the thawing process took about two to three hours, the removal of fish from the freezer was staggered through the day to ensure that samples were not left for too long after thawing before dissection. King (2007) reports that the length of marine animals in fisheries studies is usually recorded as a “standard length” (SL), from tip of snout to the tip of the caudal peduncle, as this is easy and accurate to measure. This also avoids the problem of damaged caudal fins (damaged during trawling) introducing measurement error that can occur when total length is recorded. Therefore, the standard length of each fish in the stratified sub-sample was measured to the nearest millimetre and the body weight measured to the nearest gramme. The body organs were removed by opening up the peritoneal cavity and cutting the posterior intestine at the rectum and the stomach as close to the mouth as possible. The plaice were then sexed as male or female (if sex could be determined) and a maturity stage assigned by macroscopic examination of the gonads. Males are identifiable by lobular creamy-white colour gonads, whereas females have hollow, sac-like gonads, which are reddish/orangey in colour. Maturity stage was determined using the scale presented in Table 2.2 and Figure 2.3 (Anon., 2001; Bromley, 2000 and 2003) where maturity is determined based on the size, colour and appearance of the gonad. In October, female ovaries are usually at gonad stages two (‘developing’) or four (‘ripening’), with few fish having ovaries at any other stage of development. It was easier to determine maturity stage in female plaice as stage two in the female gonad is usually pink in colour and fills up to half the length of the ovarian cavity (see Table 2.2 and Figure 2.3) whereas, stage four gonads fill the ovarian cavity and tend to be yellow to orange in colour and it is clear to see individual oocytes by the naked eye (Figure 2.3). Determining the ‘ripening’ and ‘ripe’ maturity stages of the male gonads was a little more difficult, however, this was possible by cutting to look for sperm in the testes and spermaducts (Table 2.2 and Figure 2.3). In the final stage of dissection, the sagittal otoliths were extracted and stored in a labeled envelope until ageing at a later date. Fish were aged by counting the annual rings on the otolith which consist of alternating opaque and translucent rings. One pair of opaque ring and one translucent ring are deposited each year in the sagitta (Morales-Nin, 1992; Guillaud *et al.*, 2002). Plaice otoliths were read under a dissecting microscope (WILD, M3Z Heerbrugg) under reflected light and/or transmitted light using a

magnification of between 10 to 25x (with 10x eyepieces). The microscope contained a special port to which a digital camera could be attached. Otoliths were placed in a watch glass and submerged in 'Histoclear' which helped to clarify reading the otolith growth rings and increase the visual contrast. Once the rings had been counted and the fish aged, images of each otolith were captured using a digital camera (Nikon coolpix 4500, 4.0 Mega Pixels 4x Zoom) in order for any age reviewing later (see Figures 2.4 and 2.5). Because the otoliths of male fish tended to be smaller, it was more difficult to discern between the opaque and translucent rings and to age male fish compared to females and therefore a number of the male otoliths were unreadable using this ageing technique and were excluded from the age frequency and growth curve analyses (see Table 2.3). Figure 2.4 shows examples of otoliths that were easy to age whilst examples of unreadable otoliths are presented in Figure 2.5.

2.2.3 Data analysis:

Length frequency data and stock structure

Data on the length/age frequency distribution of males and females caught in 2004 and 2005 and for the combined 2004/2005 data were collated from the length-stratified sub-samples from each trawl. The total number of fish in a given age class and the average length-at-age for each age class were then calculated. From these data, the age-, length- and weight-percentage frequency distributions in the stratified sub-sample were calculated and the number of fish in different age and length classes compared using chi-square analyses (χ^2).

Length/weight relationship

The relationships between body weight and standard length for male and female plaice were determined from the sub-sample data using the following power function (King, 2007):

$$W = a L^b$$

Where:

W = wet weight (g)

L = standard length (cm).

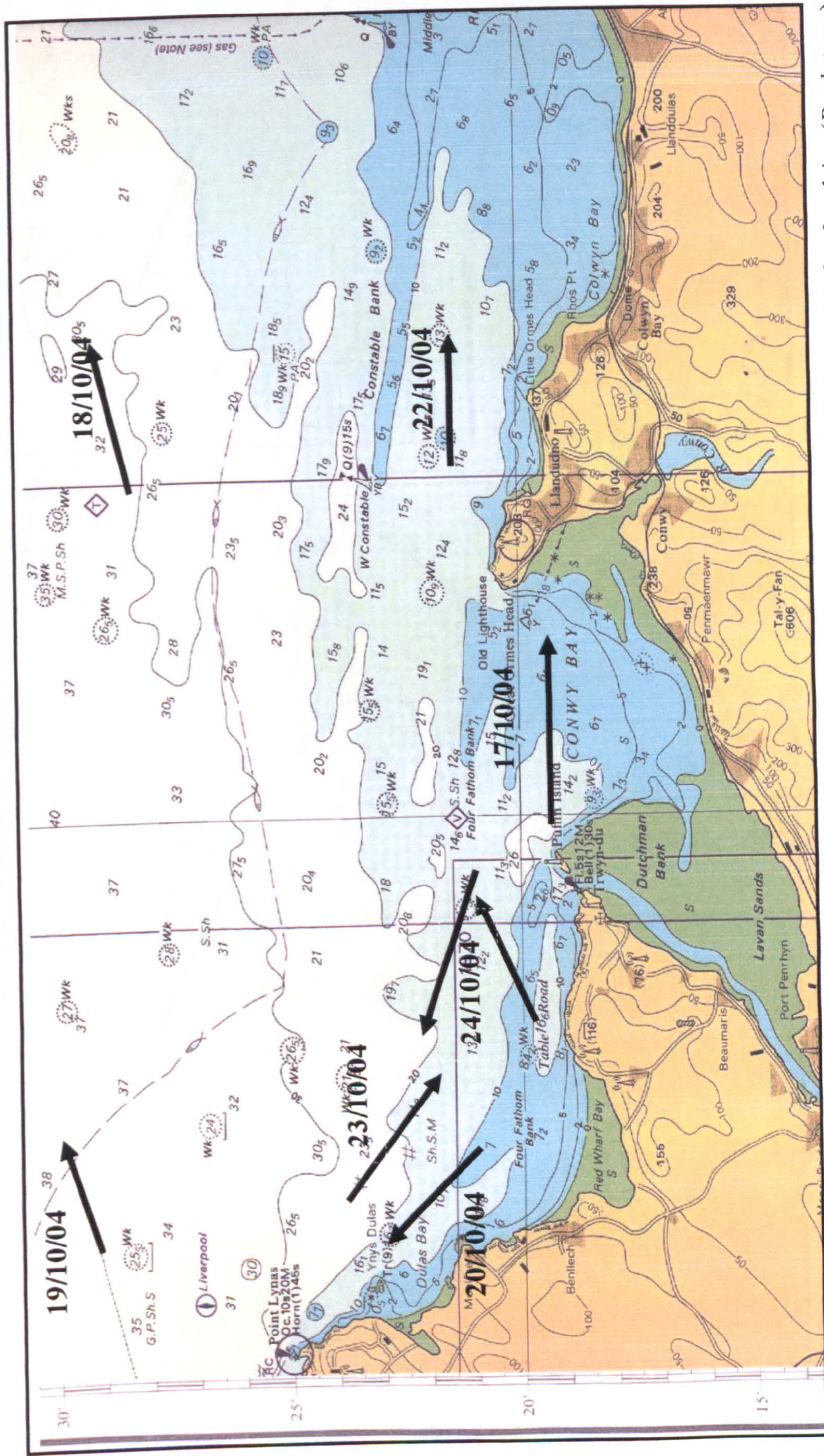


Figure 2.1: Map of Eastern Anglesey and North West Wales showing the locations trawled by the R.V. *Prince Madog* for plaice (*P. platessa*) in October 2004. Details on each trawl can be found in Appendix 1a.

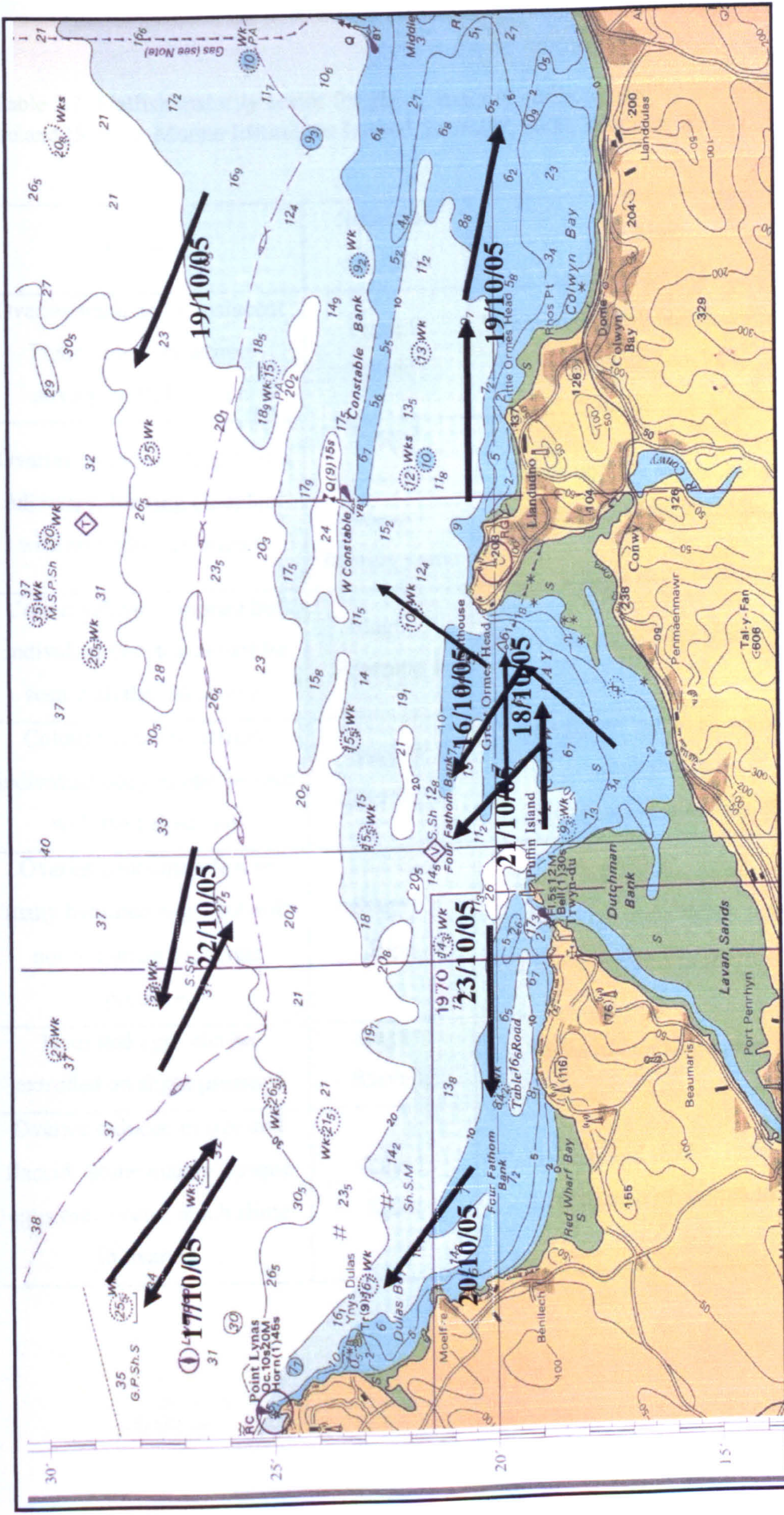


Figure 2.2: Map of Eastern Anglesey and North West Wales showing the locations trawled by the R.V. Prince Madog for plaice (*P. platessa*) in October 2005. Details on each trawl can be found in Appendix 1b.

Table 2.2: Flatfish maturity scales for plaice, megrim and sole used by the Marine Institute in Ireland [Source: Marine Institute in Ireland, Bromley, 2000; Bromley, 2003, (URL 4)].

Female	Stage and condition	Male
Ovaries small and translucent. Tunic lining sometimes silvery or dark colour.	Stage 1: Juvenile	Testes very small and translucent up to about 1 cm long.
Ovaries up to ½ of length of a full ovary. Pinkish colour with no yellow or orange.	Stage 2: Developing virgin / Resting spent	Testes up to ½ size of full testes grey to white in colour.
Colour yellow to orange but individual oocytes cannot be seen with the naked eye.	Stage 3: Ripening 1	No stage 3 for males.
Colour yellow to orange, individual oocytes can be seen with the naked eye.	Stage 4: Ripening 2	Testes filling but no sperm visible when they cut. No sperm in spermaducts.
Ovaries containing few or many hydrated eggs, but will not run under moderate pressure.	Stage 5: Ripe	Testes full but do not run under moderate pressure. When testes are cut some sperm is in spermaducts.
Hydrated eggs can be extruded on slight pressure	Stage 6: Running	Testes run on slight pressure
Ovaries reduced in size and flaccid. Some mainly opaque eggs may occur, much slime in ovaries.	Stage 7: Spent	Testes thin and flabby, little sperm may remain in spermaducts


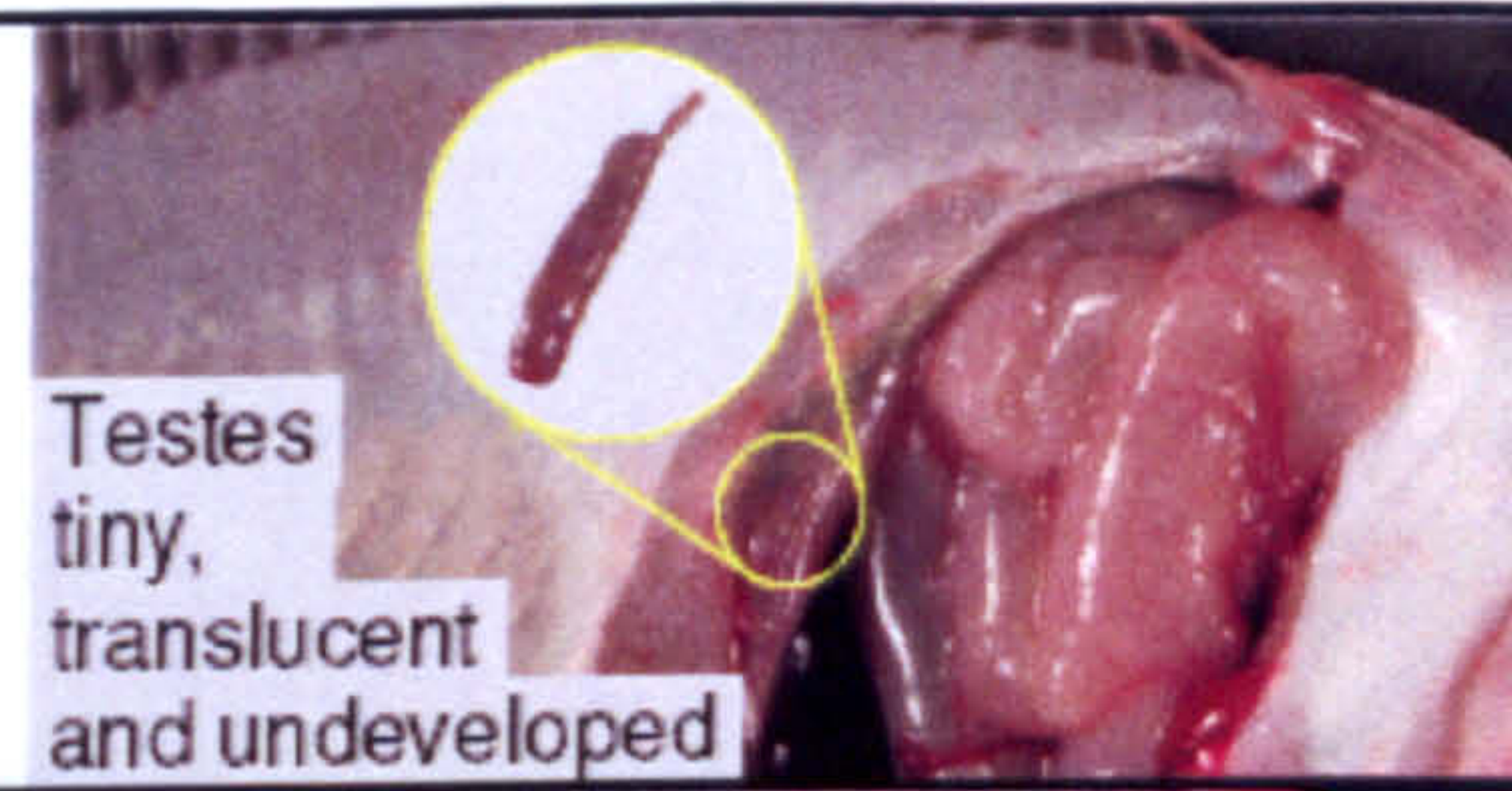

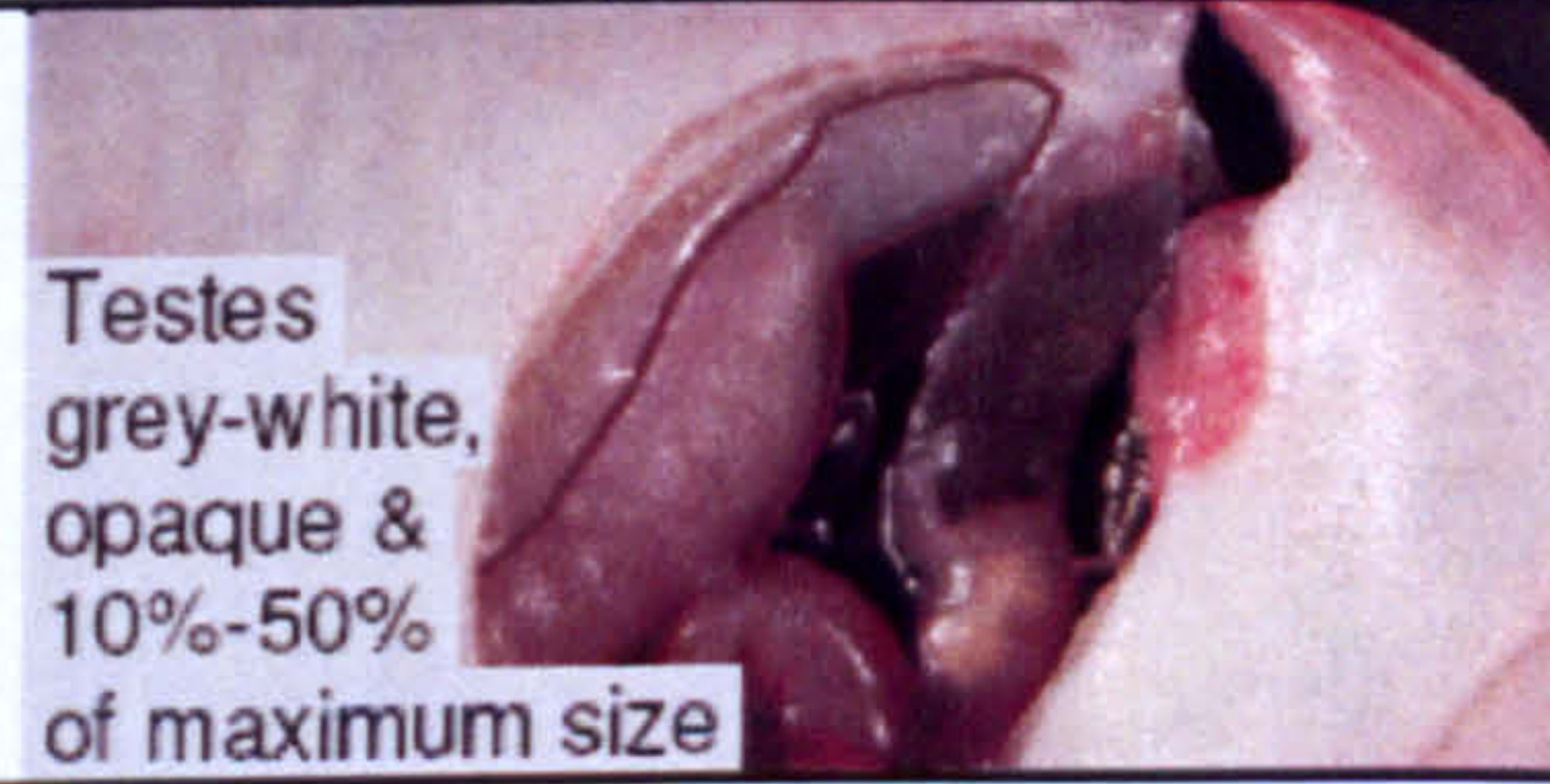
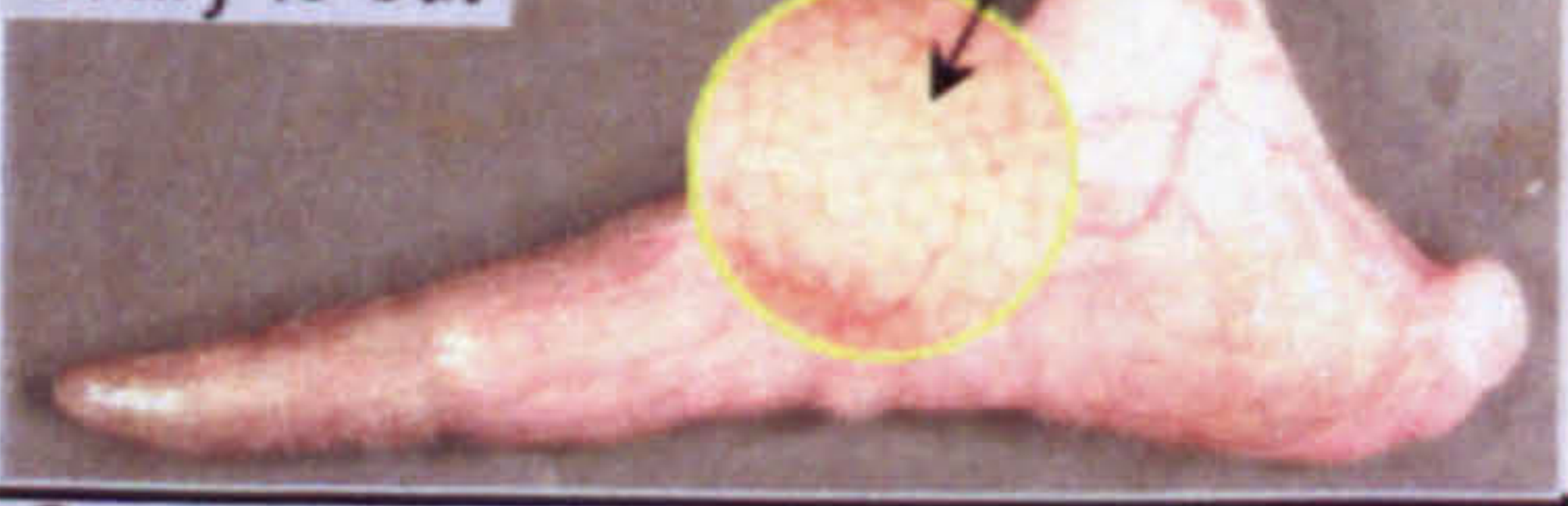

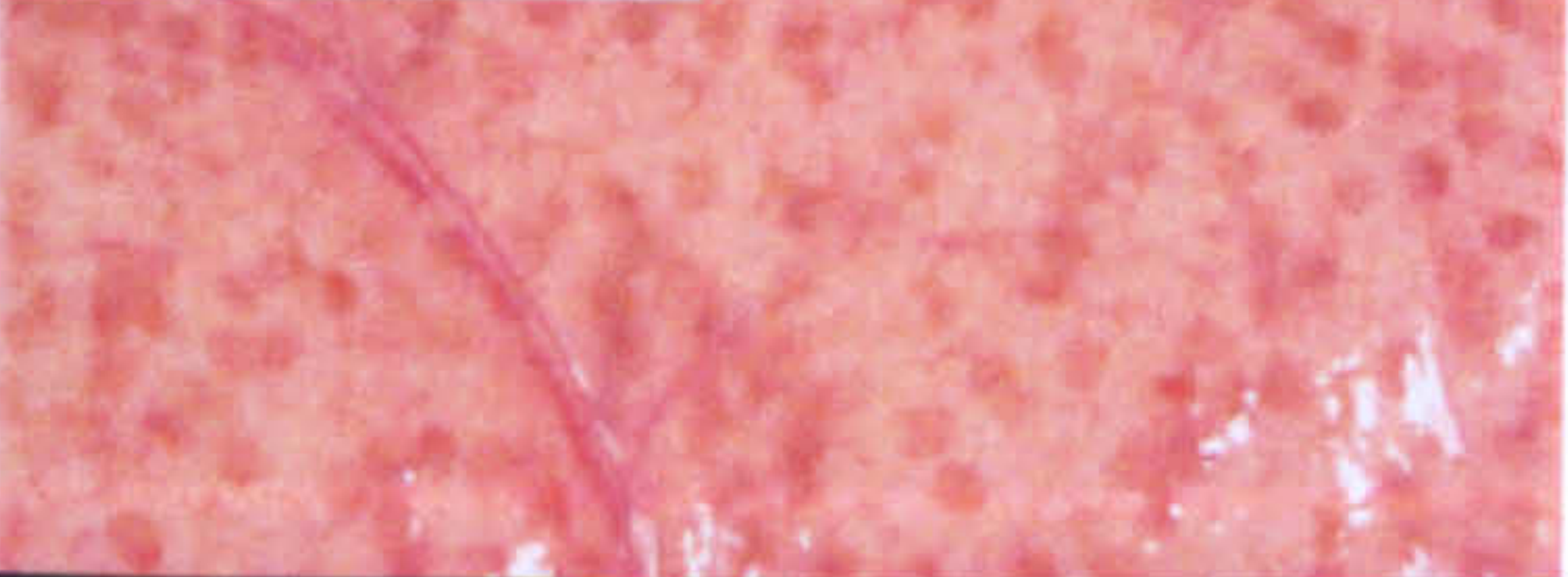

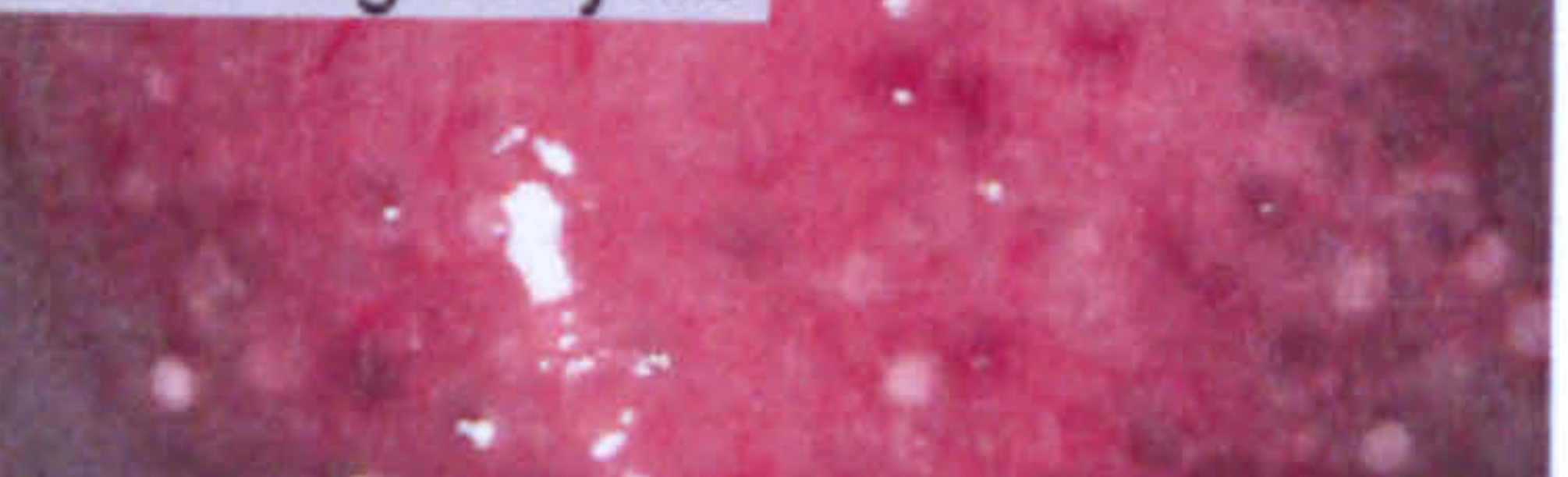

<p>Ovary small, contents translucent, nearly colourless</p> 	<p>1. virgin</p>	 <p>Testes tiny, translucent and undeveloped</p>
<p>Contents blurred translucent, pinkish, no oocytes visible</p> 	<p>2. early developing or resting spent</p>	 <p>Testes grey-white, opaque & 10%-50% of maximum size</p>
<p>no stage 3 in plaice</p>		
<p>Ovary contains opaque oocytes that are clearly visible when ovary is cut</p> 	<p>4. preparing</p>	 <p>Testes nearly full size but no sperm visible when cut</p>
<p>Ovary contains hydrated cells but does not run</p> 	<p>5. ripe</p>	 <p>Sperm visible when cut but testes do not run</p>
<p>Like stage 5 but ovaries run under moderate pressure</p>	<p>6. spawning</p>	<p>Like stage 5 but testes run under moderate pressure</p>
<p>Ovary slack, contains slime and sometimes remaining oocytes</p> 	<p>7. recently spent</p>	 <p>Testes can be quite small but with remaining sperm in duct</p>

Figure 2.3: Photographic key used to help identify maturity stage of male and female plaice in this study (Source: Marine Institute, Ireland; (URL 4)).

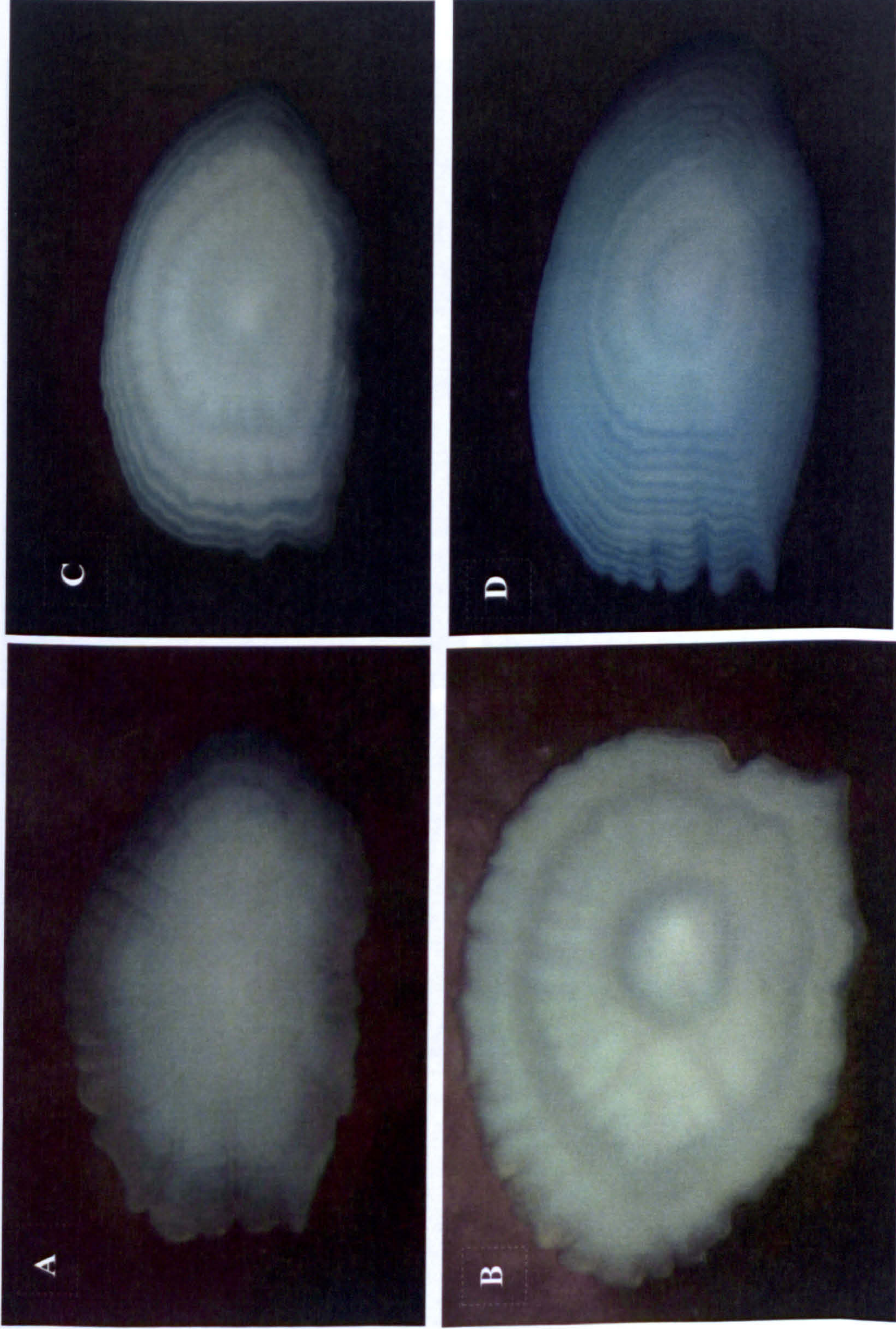


Figure 2.4: Plaice otoliths of various ages caught from Eastern Anglesey and North West Wales in 2004 and 2005, (A= otolith of age 0^{++} , B= age of 2^{++} , C= age of 6^{++} and D= age of 12^{++}).

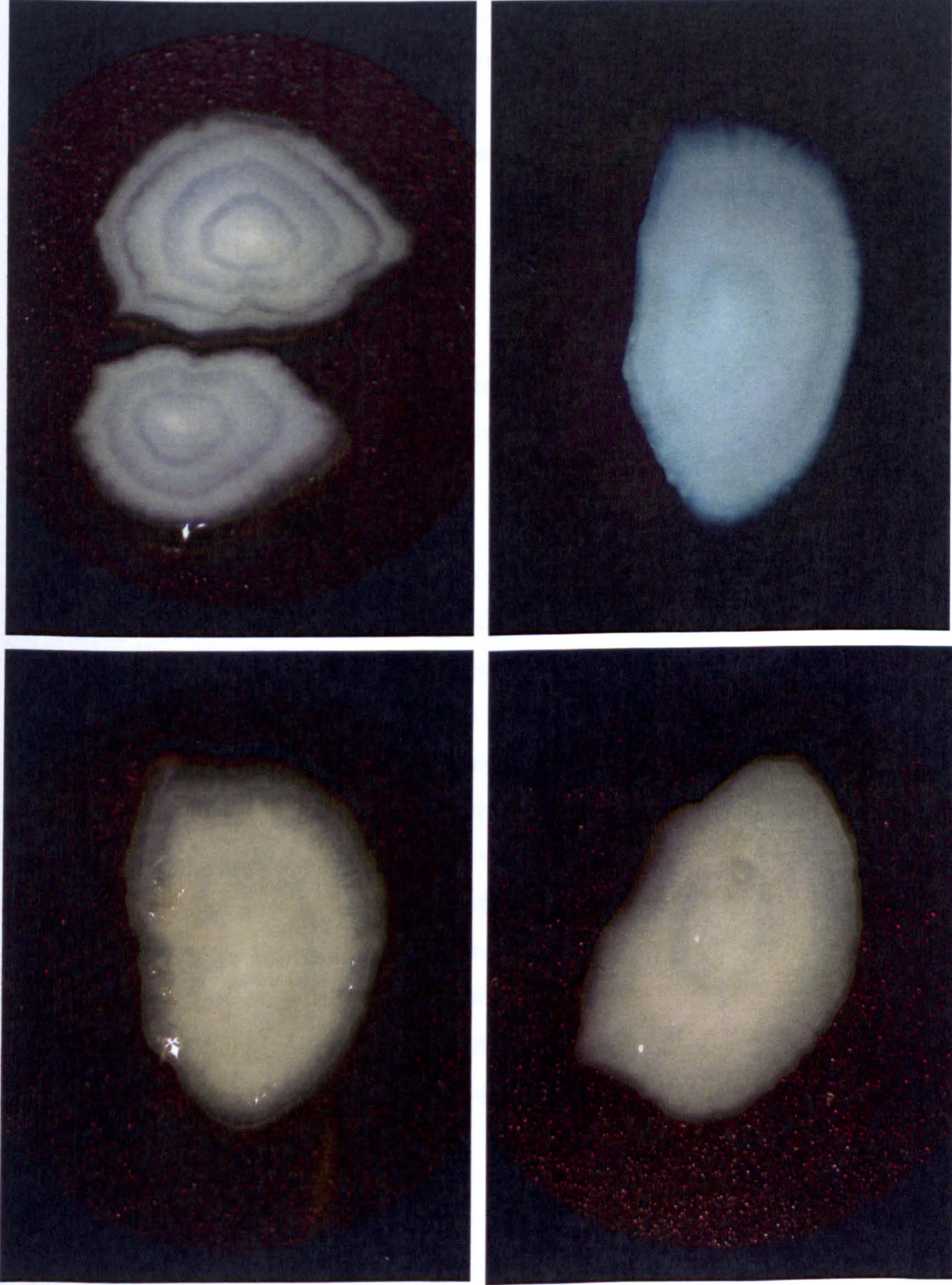


Figure 2.5: Examples of plaice otoliths that were unreadable, or where two dissimilar otoliths were obtained from the same fish, for plaice of various ages caught from Eastern Anglesey and North West Wales in 2004 and 2005.

and a and b are constants in the power function and $b = 3$ when growth is isometric (King, 2007). In order to compare the growth patterns of male and female plaice, the weight and length data were linearised by \log_{10} transformation (King, 2007). Least-squares linear regressions were then fitted to the transformed weight/length data as follows:

$$\text{Log}_{10} W = \text{Log}_{10} a + b \text{Log}_{10} L$$

To compare the two regression lines for male and female plaice, a general linear model (GLM) (Minitab Var. 13.20) was used to test for significant differences between the two slopes (b) and intercepts (a). GLM analysis was conducted on the data for 2004, 2005 and for 2004/2005 combined. As well as testing for differences between sexes, the slopes of the linear regressions for male and female plaice were compared to a slope value of $b=3$ using a t -test (Zar, 1984) to examine whether isometric or allometric growth patterns were observed:

$$t = \frac{\beta - b}{S_b}$$

Where:

β = the theoretical slope (= 3)

b = the calculated slope for male or female plaice

S_b = the standard error of the two slopes.

Age and growth

The selectivity of the sampling gear (stretched mesh size = 76 mm) resulted in smaller fish being under-represented in the length frequency distribution of the catch (King, 2007). Therefore, 0-group plaice that had been caught during the monthly push netting sampling in Red Wharf Bay and Llanfairfechen in October and November in 2004 and 2005 (see Chapter 4) were included in the construction of the growth curve: 17 0-group fish were added to the 2004 growth curve and 20 fish were added to 2005 growth curve. These data were included in order to derive a more accurate Von Bertalanffy growth curve (VBGC) and allow an accurate calculation of the coefficients for the growth curve. The omission of younger age classes from the curve (in this case, 0-group fishes) can result in errors in calculating k and t_0 values resulting in an underestimate of k and an erroneous negative value for t_0 (King, 2007).

The annual growth pattern in the sagittal otolith of plaice is represented by two bands, consisting of one highly calcified (opaque) band and one less-calcified (translucent) band (Troadek *et al.*, 2000). The first band (opaque), formed in the otolith core is laid down when a

flatfish undergoes metamorphosis and settles down on the sea bed and that is defined as a birth mark of age zero (Licandeo *et al.*, 2006). For plaice in the Irish Sea, this birth date is assumed to be 1st April (Macer, 1967; Hyder and Nash, 1998; Fox, *et al.*, 2006, 2007). Due to the clear banding pattern most plaice otoliths are easily readable (Figure 2.4). However, due to problems encountered in the reading of some otoliths, it was not possible to age some fish with confidence. For example, in some fish the two sagittal otoliths gave different ages, or the otoliths were crystallised and unreadable whilst in others alternate opaque/translucent bands were not discernible (Figure 2.5). As a result, a number of otoliths have been excluded from the ageing analysis. In 2004, 10 otoliths (6 male and 4 female) were unreadable and removed from the 514 fish in the LSS. In 2005, 6 female otoliths were unreadable and removed from the 424 fish in the LSS for that year. The growth rates of male and female plaice were determined by fitting a Von Bertalanffy growth function (VBG; von Bertalanffy, 1938) to the age-size data for 2004, 2005 and 2004/2005 combined using the non-linear regression function in SPSS (Var. 12.0). The VBG model fitted is as follows (King, 2007):

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

Where:

L_t = standard length (cm) at age t .

L_∞ = the theoretical maximum standard length (cm)

k = the growth coefficient

t_0 = the theoretical age when length is zero.

Since the plaice in this study were caught in October, during the second half of each year of growth, fish ages have been reported as ‘++’. So, for example, a 1⁺⁺ fish is approximately 18 months old, assuming a birth date of 1st April. The growth curves of male and female plaice in 2004, 2005 and 2004/2005 combined were compared using the likelihood ratio test (LR) as outlined by Kimura (1980). This analysis involves fitting VBG curves to the male and female data and to the combined data and noting the residual sum of squares for each growth curve. Growth curves are then fitted to the male and female data where L_∞ , k and t_0 are each constrained in turn to the value obtained for the combined VBG curve and the residual sum of squares noted for the male and female growth curves. Finally, growth curves are fitted to the male and female data where all three VBG coefficients are constrained and the residual sum of squares noted. Likelihood ratios (LR) were then

calculated as follows (Kimura, 1980):

$$LR = - N * \ln (\text{Res. SS}_{\text{no constraints}} / \text{Res. SS}_{\text{constrained}})$$

Where:

N = total number of observations (i.e. sum of male and female age classes) used in this test.

Res. SS_{no constraints} = sum of the male and female residual SS values without constraining any VBGF values.

Res. SS_{constrained} = sum of the male and female residual SS values when L_{∞} , k and t_0 or all three values were constrained.

Mortality rate

The instantaneous coefficient of total mortality (Z , year⁻¹) was calculated from the number of fish present in each age class in the length-stratified subsample by fitting an exponential decay curve (King, 2007) using the non-linear regression function in SPSS (Var. 12.0):

$$N_t = N_0 e^{(-Zt)}$$

Where:

N_t = Number of fish in a given age class.

N_0 = estimated number of fish at first sampling ($t = \text{zero}$).

Z = instantaneous rate of total mortality (year⁻¹).

t = time interval between sampling (in this study $t = 1$ year).

In order to compare the mortality rates of male and female plaice in 2004, 2005 and 2004/2005 combined, a semi-logarithmic plot of age vs. $\log_e(N_t)$ was constructed (King, 2007) and least-squares linear regressions were then fitted as follows:

$$\log_e N_t = \log_e N_0 + Zt$$

The slopes (Z values) of the two regression lines for male and female plaice were compared using a general linear model (GLM) (Minitab Var. 13.20). The instantaneous mortality rate was converted to percentage mortality (P) using the following equation (King, 2007):

$$P (\%) = 100 (1 - e^{-Z}).$$

Natural mortality (M , year⁻¹) was estimated using the equation of Pauly (1980):

$$\text{Log}_e M = 0.0152 - 0.279 \text{Log}_e L_\infty + 0.6543 \text{Log}_e k + 4634 \text{Log}_e T$$

where L_∞ and k are coefficients from the VBG curve and T is the average temperature (°C) for Moelfre in Red Wharf Bay (Joyce, 2006). The mean sea temperatures used were 7.35, 7.47 and 7.41 C° for 2004, 2005 and 2004/2005 combined respectively. Fishing mortality (F , year⁻¹) for the SE Irish Sea plaice stock was estimated as that reported by ICES for 3-6 year old plaice in Division VIIa for 2004 (0.143 year⁻¹) and 2005 (0.147 year⁻¹) respectively (ICES, 2008a).

Reproductive characteristics

Length and age at maturity

The maturity data for male and female plaice were sorted into 2 cm size class intervals or into age classes and the proportion of mature individuals in each size/age class was calculated. These data were used to calculate the length and age at first maturity by fitting logistic curves. The mean standard length (L_{50}) or age (A_{50}) at first maturity can be defined as the length or age at which 50 % of the animals become sexually mature and were estimated using the following equation (King, 2007):

$$P = 1 / (1 + e^{(-r(X - X_{50}))})$$

Where:

P = the proportion of mature individuals in a given length (cm) or age (years) class

X_{50} = length (cm) or age (years) at 50 % maturity.

X = length (cm) or age (years) class

r = slope of the logistic curve

Since the sample sizes used in the different analyses in this chapter varied depending on whether individual fish in the length-stratified subsample could be aged or sexed, a summary

of the numbers of fish used in the different data analyses are presented in Table 2.3.

In order to allow the size data from this thesis to be compared with other studies (see Discussion), it was necessary to convert the standard length (SL) measurements to total length (TL). To achieve this, SL and TL were measured (to the nearest millimetre) in 152 plaice (including males and females) and a calibration equation between SL and TL was determined (Figure 2.). Care was taken to ensure that the SL size range of plaice measured covered the majority of the size range of plaice recorded in the LSS in 2004 and 2005. The following calibration equation was determined:

$$TL = 1.2114 * SL - 0.0985 \quad (R^2 = 0.998, n=152, p<0.001)$$

Table 2.3: A summary of the sample sizes used for the different data analyses in the Results section based on the fish dissected in the length-stratified subsample (LSS) for 2004 and 2005.

Subject	Sex	2004	2005
Number of fish in LSS	Male	224	141
	Female	287	283
	Total	514*	424
Number of fish aged from LSS	Male	218	141
	Female	283	277
	Total	501	418
Number of 0 ⁺⁺ fish added to VBG curve	Male	8	10
	Female	9	10
Sample size for VBG curve	Male	226	151
	Female	292	287
Number of fish sexed from LSS	Male	221	140
	Female	286	277
	Total	507	417

* plus 3 fish that could not be sexed

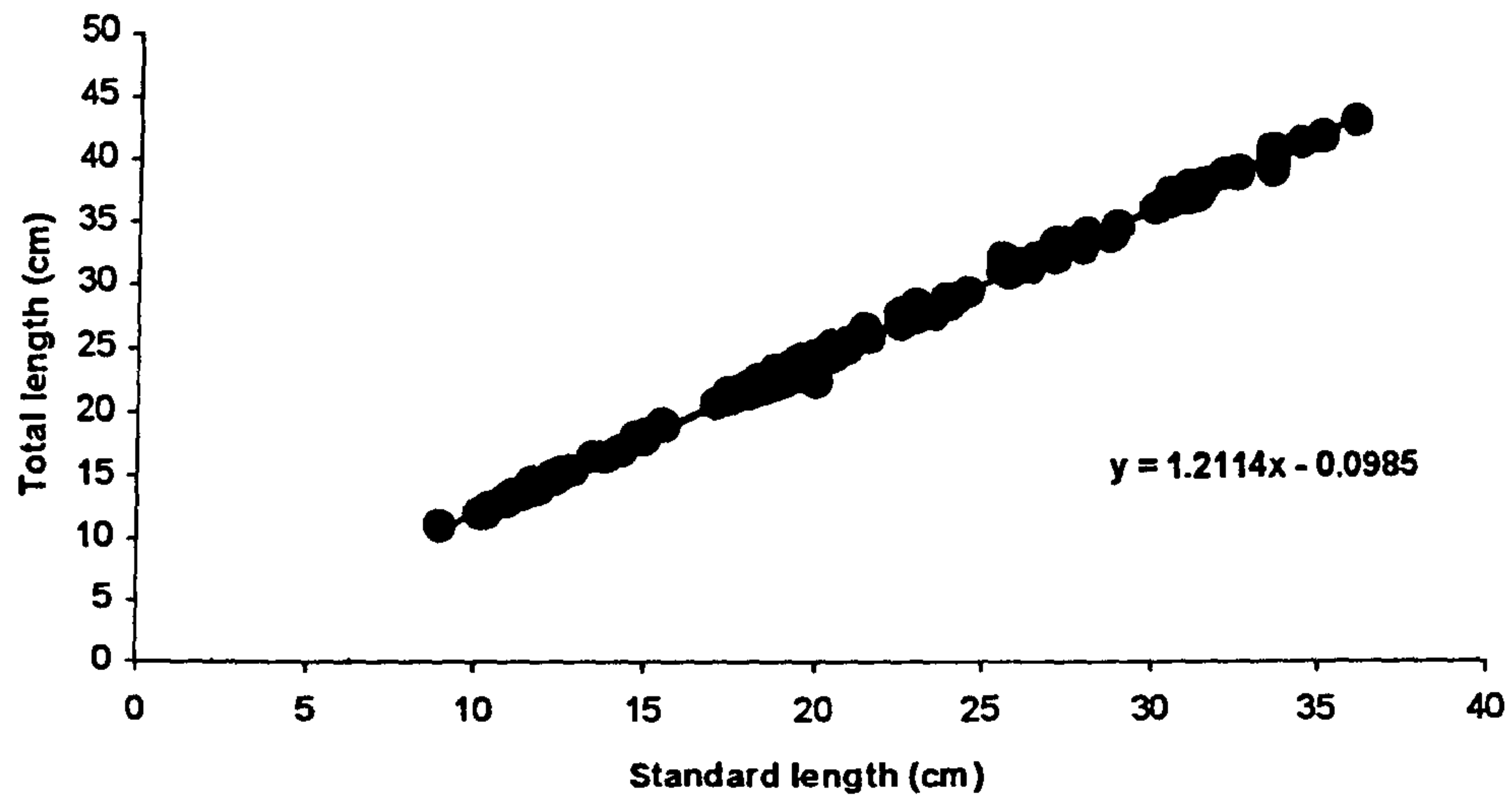


Figure 2.6: Calibration line for converting Standard Length (cm) to Total Length (cm) for combined of male and female plaice *P. platessa* caught in coastal waters off North West Wales and Eastern Anglesey.

2.3 Results

2.3.1 Size/Age frequency of the population

A total of 935 plaice were obtained in the length-stratified subsamples and dissected in this study: 511 plaice (224 male and 287 female, plus 3 unsexed fish) in 2004 and 424 plaice (141 male and 283 female) in 2005. The standard lengths of the plaice in the length-stratified subsamples ranged from 11.0 – 41.0 cm and 13.0 – 49.0 cm in 2004 and 2005 respectively (Tables 2.4 and 2.5). In both years, the largest and oldest plaice were females. For males, the length range in the sub-sample in 2004 was 13.0 – 32.4 cm SL (Table 2.4), however, a narrower length range, 13.0 – 31.0 cm SL, was caught in 2005 (Table 2.5). For females, the length ranges in 2004 and 2005 were from 11.0 to 41 cm SL (Table 2.4) and 14.0 to 49.0 cm SL (Table 2.5) respectively. The oldest male fish caught in 2004/2005 were 5⁺⁺/5⁺⁺ years old respectively whilst older female plaice were caught in both 2004 (7⁺⁺) and 2005 (12⁺⁺) (Tables 2.4 & 2.5). Very few 0⁺⁺ fish were caught in the rockhopper otter trawl: no 0⁺⁺ fish were caught in 2004 and ten 0⁺⁺ fish (5 male and 5 female) in 2005 (Tables 2.4 & 2.5). The age-length frequency data for male and female fish for both years combined are shown in Table 2.6. The mean average size at age, standard length (cm), and wet weight (g) for each year class of male and female plaice in 2004, 2005 and for 2004/2005 combined are shown in Tables 2.7-2.9. The weight data showed the same patterns as the length data, with the average size of female fish in the 2⁺⁺ age class and older being larger (*i.e.* longer and heavier) compared to male fish.

The age-frequency distributions for male and female plaice are shown in Figure 2.7. The majority of fish were between 1⁺⁺ and 3⁺⁺ years old: in 2004 the 1⁺⁺-3⁺⁺ age classes accounted for 89 % of male and 88 % of female plaice and in 2005 for 82 % of male and 69 % of female plaice respectively (Figure 2.7). When the data for 2004 and 2005 were combined, the most abundant age classes were 1⁺⁺ for male plaice (30 % of males) and 2⁺⁺ for female plaice (33 % of females). Chi squared analysis of the data for 2004, 2005 and for 2004/2005 combined showed that the age distributions of male and female plaice were significantly different (all $P < 0.01$) with more female plaice present in the older age classes. The length-frequency distributions for male and female plaice are shown in Figure 2.8 and indicate a bimodal size distribution between the sexes. The majority of male fish were between 19 and 25 cm SL: these size classes accounted for 78.8 %, 74.5 % and 77.1 % of male plaice in 2004, 2005 and 2004/2005 respectively (Figure 2.8). In comparison, the size distribution of female fish was wider with the majority of females found between 21 and 31

Table 2.4: Standard length (cm)/age frequency distribution for male and female plaice in the length-stratified sub-sample caught in October 2004 in coastal waters off Eastern Anglesey and North West Wales. (SL= standard length; N= number of fish; L_t = average length at age).

SL	Male						Female						
	1++	2++	3++	4++	5++	Total	1++	2++	3++	4++	5++	6++	7++
10						0							
11						1	1						
12						0							
13	1	2				4	1						
14	2	2				4							
15	1	0				4	2	1					
16	1	0				4		3					
17	5	2				13	4	2					
18	6	6	1			24	4	4	3				
19	14	3	4			31	4	4	2				
20	20	4	3			44	8	3	4	2			
21	7	13	8	1		50	12	4	4	1			
22	8	7	7	2		48	10	7	5	2			
23	2	10	14	4		55	10	9	4	2			
24	5	6	4	2		33	1	6	5	2	2		
25	2	2	6	3	3	43	4	16	7	0	0		
26	0	4	2	6	1	34	2	8	9	1	1		
27	1	1	1	1	0	24	1	8	10	1	0		
28		0	1	0	0	21		8	10	2	0		
29		0	1	1	0	11		4	5	0	0		
30		1	1		0	9		2	3	2	0		
31			0		1	12		2	7	2	0		
32			2			7		2	3	0	0		
33						7		1	3	2	1		
34						2			1	0	0		1
35						5			1	2	1	1	
36						1			1	0	0	0	
37						6			2	3	0	1	
38						2			1		1		
39						0					0		
40						0					0		
41						2					2		
N	75	63	55	20	5	501	64	94	90	24	8	2	1
L_t	20	21.35	23.2	24.6	26.4		20.9	24	26.7	28.2	33	36	34

Table 2.5: Standard length (cm)/age frequency distribution for male and female plaice in the length-stratified sub-sample caught in October 2005 in coastal waters off Eastern Anglesey and North West Wales. (SL= standard length; N= number of plaice; L_t = average length at age).

SL	Male						Total	Female													
	0++	1++	2++	3++	4++	5++		0++	1++	2++	3++	4++	5++	6++	7++	8++	9++	12++			
9		1					1														
10	2	0					4		2												
11	1	1					5	3	0												
12	1	4					7	1	1												
13	0	2					5	0	3												
14	1	2	2				11	1	5												
15		4	1	1			18		11	1											
16		6	5	0			19		4	4											
17		8	5	3			22		5	0	1										
18		4	10	4	1		26		0	5	2										
19		3	7	3	4		27		3	6	1										
20		0	1	5	3		15		1	4	1										
21		2	6	4	2		25		0	9	1	1									
22			0	6	3	1	19		1	5	3	0									
23			0	5	0	3	21		1	6	6	0									
24			3	1	1	1	22			12	3	1									
25			2	1	0	1	28			12	9	3									
26			0	1	1		23			8	8	3	2								
27			1	1			29			8	8	10	1								
28							29			7	9	12	1								
29							18			1	5	9	3								
30							16			1	7	5	2					1			
31							5					2	3					0			
32							7					1	5	1				0			
33							1					1	0	0				0			
34							4						3	0	1			0			
35							2							2	0			0			
36							3							1	1			0	1		
37							1							0	0			0	0	1	
38							2							0	1			0	1		
39							0							0				0			
40							0							0				0			
41							1							1				0			
42							0							0				0			
43							1							0				1			
44							0							0							
45							1							1							
N	5	37	43	35	15	6	418	5	37	89	64	48	20	6	3	2	2	1			
Lt	11	16	19	21	21	23		11.8	16	23.2	25.7	28	31	37	36	36.5	37	37			

Table 2.6: Standard length (cm)/age frequency distribution for male and female plaice in the length-stratified sub-sample caught in October 2004 and 2005 (data for both years combined) in coastal waters off Eastern Anglesey and North West Wales. (N= number of plaice; L_t = average length at age).

SL	Male							Female											
	0++	1++	2++	3++	4++	5++	Total	0++	1++	2++	3++	4++	5++	6++	7++	8++	9++	12++	
9		1					1												
10	2	0					4		2										
11	1	1					6	3	1										
12	1	4					7	1	1										
13	0	3	2				9	0	4										
14	1	4	4				15	1	5										
15		5	1	1			22		13	2									
16		7	5	0			23		4	7									
17		13	7	3			35		9	2	1								
18		10	16	5	1		50		4	9	5								
19		17	10	7	4		58		7	10	3								
20		20	5	8	3		59		9	7	5	2							
21		9	19	12	3		75		12	13	5	2							
22		8	7	13	5	1	67		11	12	8	2							
23		2	10	19	4	3	76		11	15	10	2							
24		5	9	5	3	1	55		1	18	8	3	2						
25		2	4	7	3	4	71		4	28	16	3	0						
26		0	4	3	7	1	57		2	16	17	4	3						
27		1	2	2	1	0	53		1	16	18	11	1						
28			0	1	0	0	50			15	19	14	1						
29			0	1	1	0	29			5	10	9	3						
30			1	1		0	25			3	10	7	2				1		
31				0		1	17			2	7	4	3				0		
32				2			14			2	3	1	5	1			0		
33							8			1	3	3	1	0			0		
34							6				1	0	3	0	2		0		
35							7				1	2	1	3	0	0	0		
36							4				1	0	0	1	1	0	1	0	1
37							7				2	3	0	1	0	0	0	0	1
38							4				1		1	0	1	0	1	0	1
39							0						0	0			0		
40							0						0	0			0		
41							3						2	1			0		
42							0							0			0		
43							1							0			1		
44							0							0					
45							1							1					
N	5	112	106	90	35	11	919	5	101	183	154	72	28	8	4	2	2	1	
L_t	11.4	18.6	20.4	22.2	23	24.7		12	18.9	23.7	26.3	28	31.1	37	35.5	36.5	37	37	

Table 2.7: Mean (\pm SD) standard length (SL, cm) and weight (Wt, g), for male and female plaice of different ages, caught in October 2004 in coastal waters off Eastern Anglesey and North West Wales. N = number of plaice.

Age	Female			Male		
	N	SL (cm)	Wt (g)	N	SL (cm)	Wt(g)
0 ⁺⁺	0	0	0	0	0	0
1 ⁺⁺	64	20.9 \pm 3.8	11.2 \pm 7.7	75	20.0 \pm 5.6	85.2 \pm 34.6
2 ⁺⁺	94	24.2 \pm 3.7	99.5 \pm 39.5	63	21.4 \pm 3.7	107.6 \pm 49.8
3 ⁺⁺	90	26.7 \pm 2.9	173.8 \pm 90.1	55	23.2 \pm 3.8	126.6 \pm 51.9
4 ⁺⁺	24	28.2 \pm 1.0	235.8 \pm 133.9	20	24.6 \pm 1.9	153.6 \pm 46.7
5 ⁺⁺	8	32.8 \pm 0.7	439.6 \pm 283.6	5	26.4 \pm 1.1	192.0 \pm 66.9
6 ⁺⁺	2	36.0 \pm 0.6	609.0 \pm 96.2			
7 ⁺⁺	1	34.0	426.0			

Table 2.8: Mean (\pm SD) standard length (SL, cm) and weight (Wt, g), for male and female plaice of different ages, caught in October 2005 in coastal waters off Eastern Anglesey and North West Wales. N = number of plaice.

Age	Female			Male		
	N	SL (cm)	Wt (g)	N	SL (cm)	Wt (g)
0 ⁺⁺	5	11.8 \pm 1.3	24.4 \pm 9.9	5	11.4 \pm 2.3	30.2 \pm 12.8
1 ⁺⁺	37	15.6 \pm 4.2	75.5 \pm 45.1	37	15.8 \pm 3.6	84.8 \pm 44.3
2 ⁺⁺	89	23.2 \pm 4.7	270.2 \pm 125.6	43	19.0 \pm 4.3	134.3 \pm 76.1
3 ⁺⁺	64	25.7 \pm 4.2	365.4 \pm 134.1	35	20.8 \pm 3.8	159.3 \pm 68.6
4 ⁺⁺	48	28.0 \pm 3.7	471.7 \pm 113.0	15	20.8 \pm 2.8	165.3 \pm 62.7
5 ⁺⁺	20	30.5 \pm 2.7	603.9 \pm 173.0	6	23.3 \pm 1.3	228.0 \pm 34.3
6 ⁺⁺	6	37.3 \pm 5.2	877.3 \pm 126.0			
7 ⁺⁺	3	36.0 \pm 2.0	974.7 \pm 173.1			
8 ⁺⁺	2	36.5 \pm 9.2	1044.0 \pm 693.0			
9 ⁺⁺	2	37.0 \pm 1.4	1030.0 \pm 53.7			
12 ⁺⁺	1	37.0	1234.0			

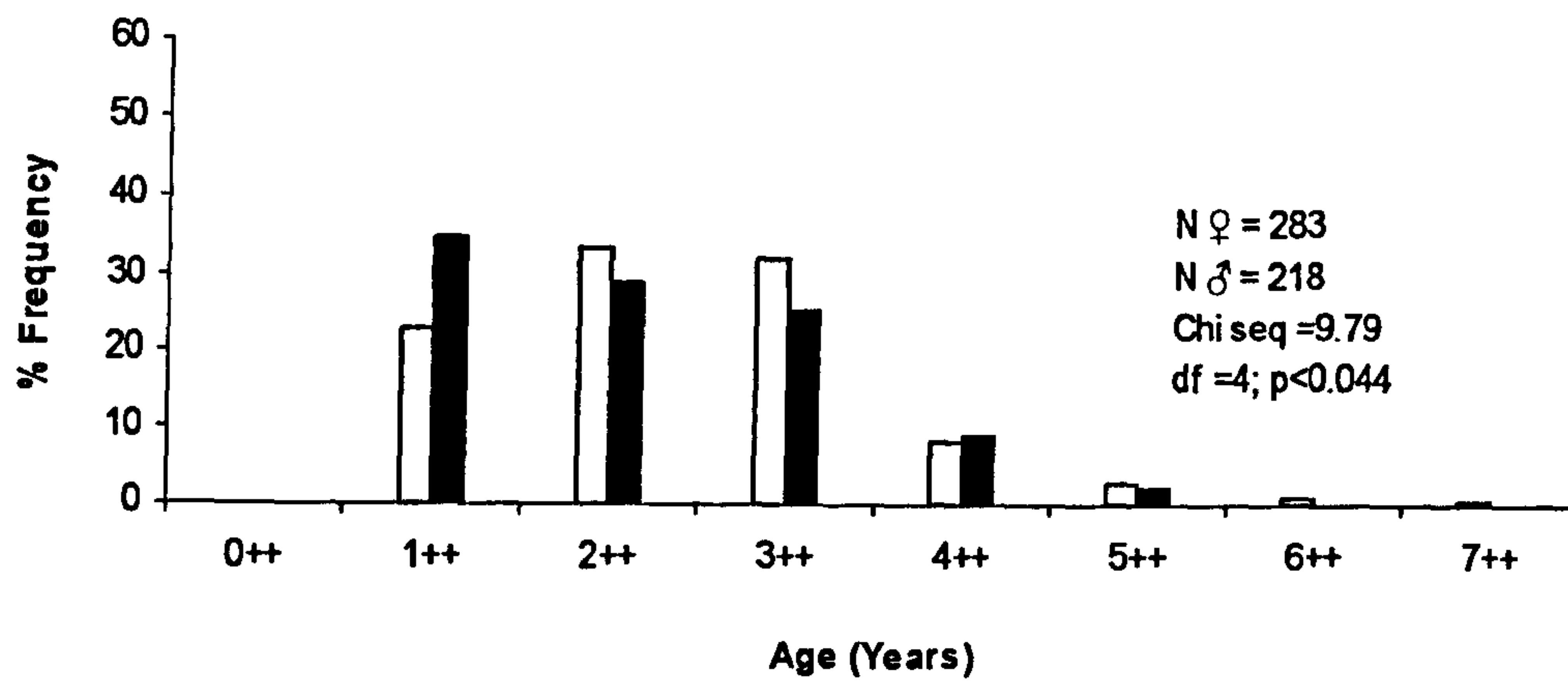
Table 2.9: Mean (\pm SD) standard length (SL, cm) and weight (Wt, g), for male and female plaice of different ages, caught in October 2004/2005 (data for both years combined) in coastal waters off Eastern Anglesey and North West Wales. N = number of plaice.

Age	Female			Male		
	N	SL (cm)	Wt (g)	N	SL (cm)	Wt (g)
0.5	5	12.0 \pm 1.3	14.2 \pm 9.2	5	11.0 \pm 0.7	16.3 \pm 12.4
1.5	101	18.9 \pm 4.2	90.7 \pm 43.0	112	19.0 \pm 5.8	85.1 \pm 37.8
2.5	183	23.7 \pm 7.3	220.7 \pm 119.0	106	20.0 \pm 5.3	118.5 \pm 62.9
3.5	154	26.3 \pm 6.0	289.6 \pm 148.1	90	22.2 \pm 5.2	143.2 \pm 62.2
4.5	71	28.4 \pm 3.4	410.8 \pm 161.3	35	23.0 \pm 2.0	158.6 \pm 53.6
5.5	28	31.1 \pm 1.4	557.0 \pm 218.2	11	24.7 \pm 1.4	211.6 \pm 52.2
6.5	8	37.0 \pm 0.9	810.3 \pm 167.6			
7.5	4	35.5 \pm 0.8	837.5 \pm 308.6			
8.5	2	36.5 \pm 0.4	1044.0 \pm 693.0			
9.5	2	37.0 \pm 0.6	1030 \pm 53.7			
12.5	1	37.0	1234.0			

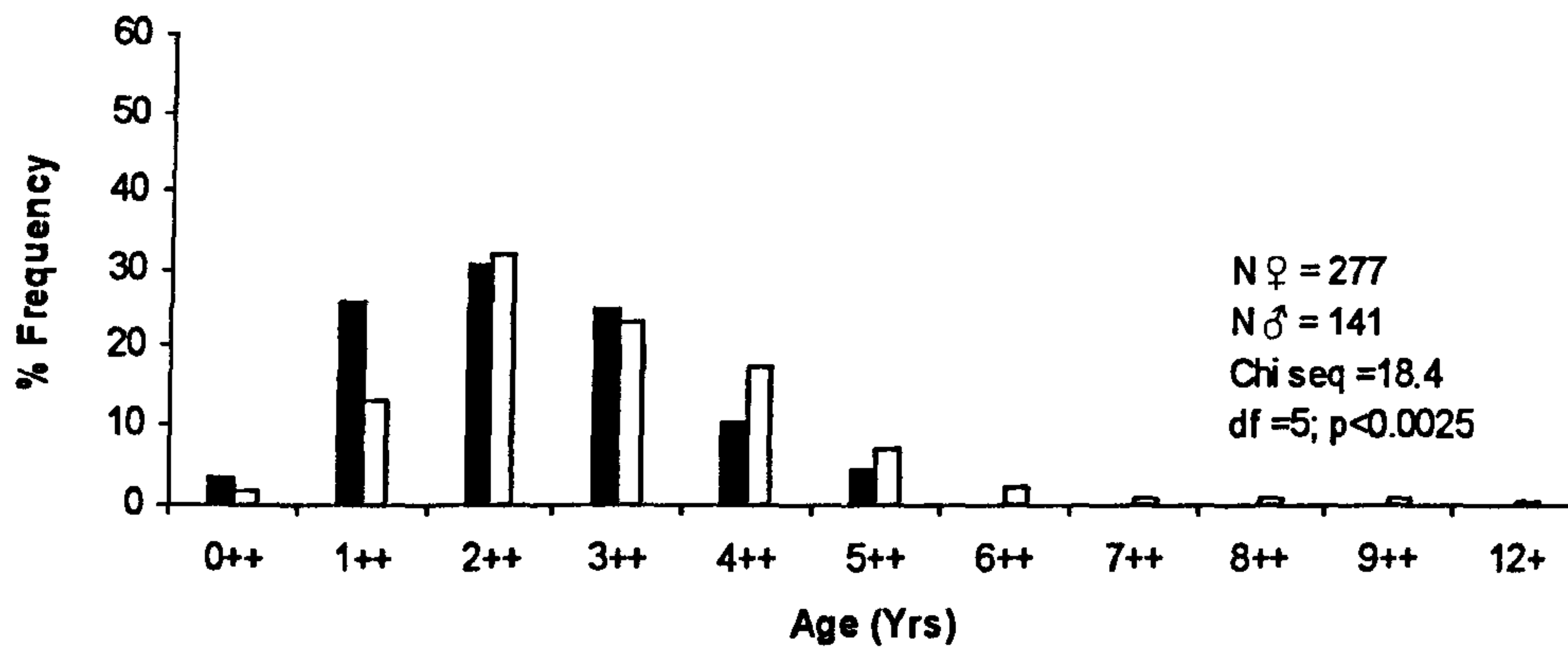
cm SL: these size classes accounted for 71.7 %, 64.3 % and 56.1 % of female plaice in 2004, 2005 and 2004/2005 respectively (Figure 2.8). Chi squared analysis of the data for 2004, 2005 and for 2004/2005 combined showed that the length distributions of male and female plaice were significantly different (all $P < 0.001$) with more female plaice present in the larger size classes (Figure 2.8). The average standard length for male and female plaice (2004/2005 data combined) were 22.0 ± 3.4 cm and 26.6 ± 5.7 cm respectively.

The weight-frequency distributions for male and female plaice are shown in Figure 2.9 and indicate a bimodal size distribution between the sexes. The majority of male fish were between 22 and 165 g: these size classes accounted for 95 %, 82 % and 90 % of male plaice in 2004, 2005 and 2004/2005 respectively (Figure 2.9). In comparison, the size distribution of female fish was wider with the majority of females found between 22 and 465 g: these size classes accounted for 95 %, 78 % and 87 % of female plaice in 2004, 2005 and 2004/2005 respectively (Figure 2.9). The median weights for male/female fish were 106/160 g in 2004, 119/345 g in 2005 and 109/136 g in 2004/2005 respectively. The median weights of female fish were significantly larger than the median weights of the male fish in 2004, 2005 and 2004/2005 respectively (Mann Whitney U-test, all $P < 0.001$).

2004



2005



2004/2005

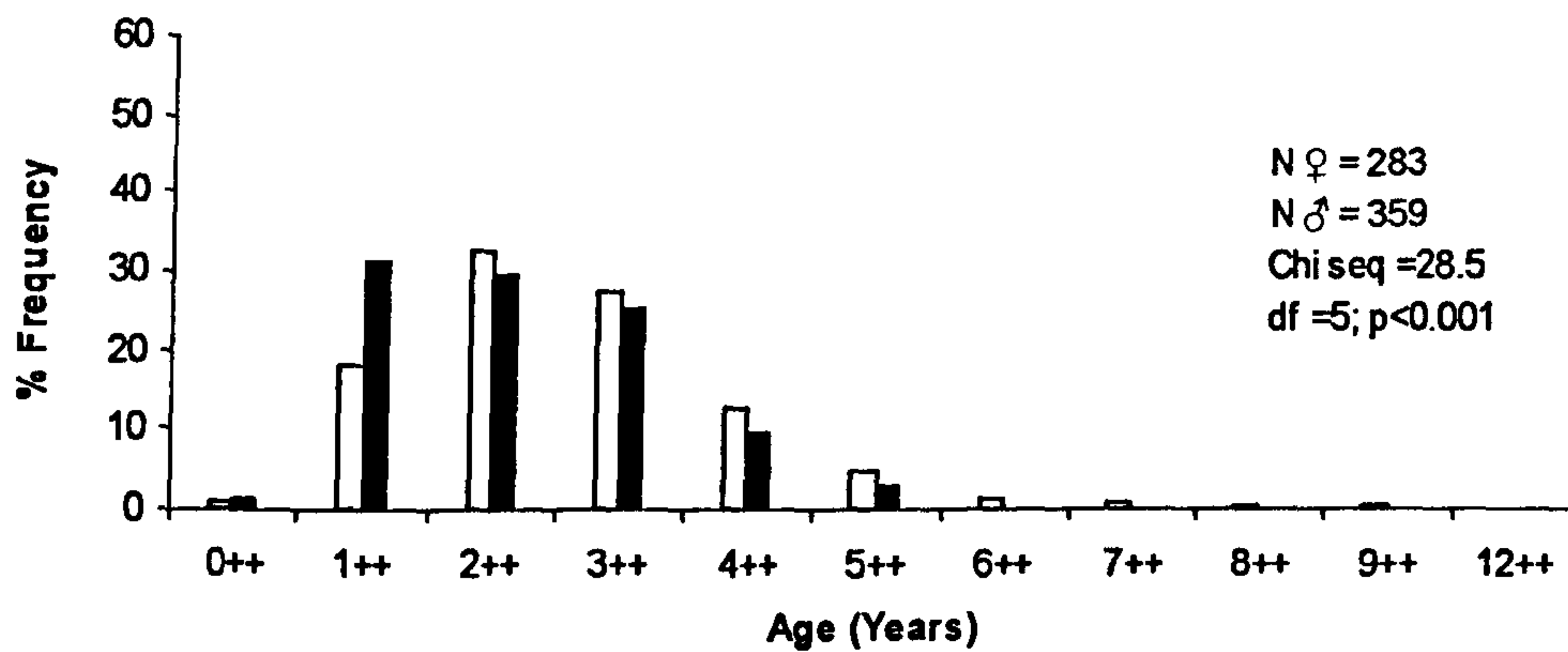


Figure 2.7: Age percentage frequency distributions of male (solid columns) and female (open columns) plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

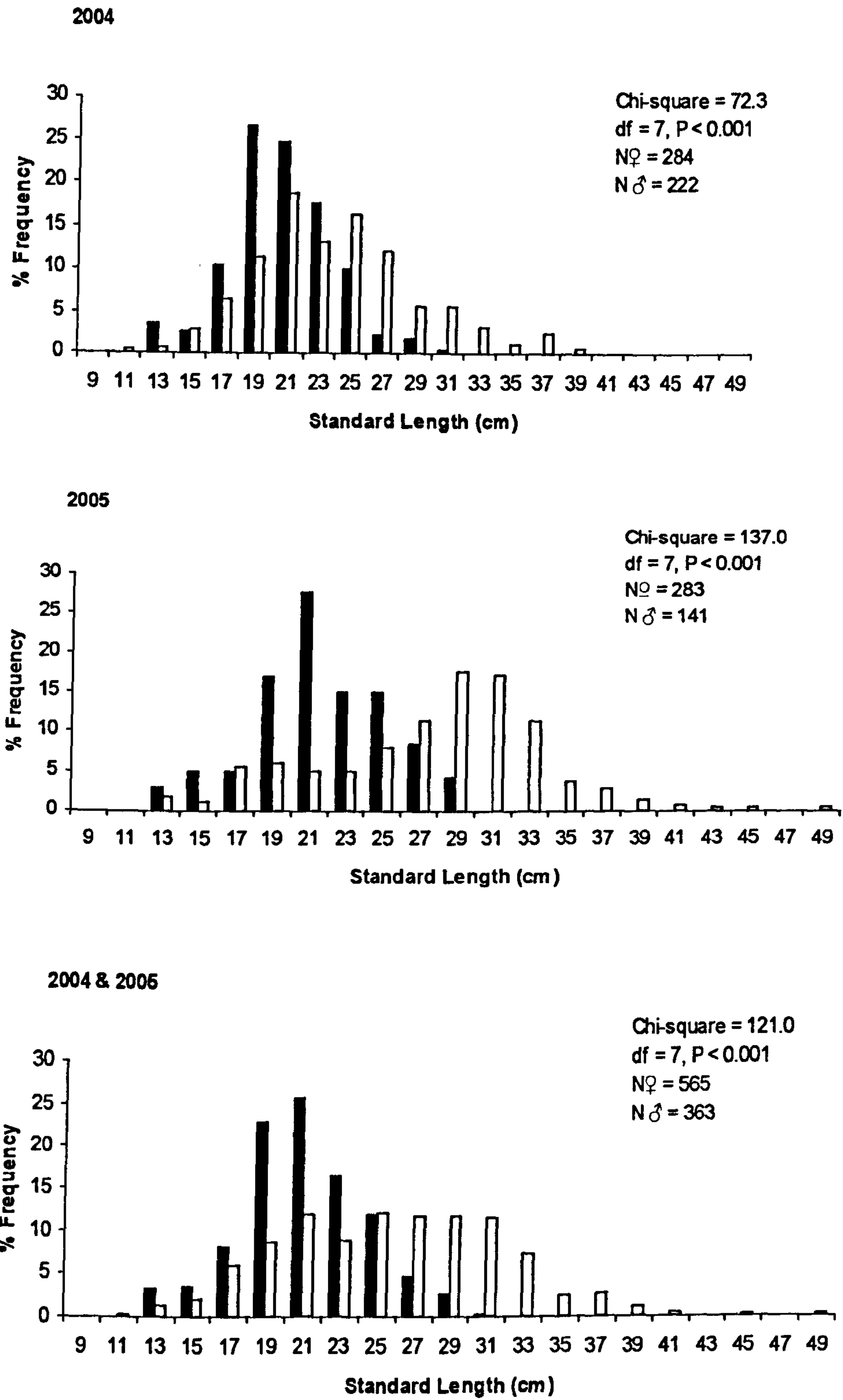


Figure 2.8: Length percentage frequency distributions of male (solid columns) and female (open columns) plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

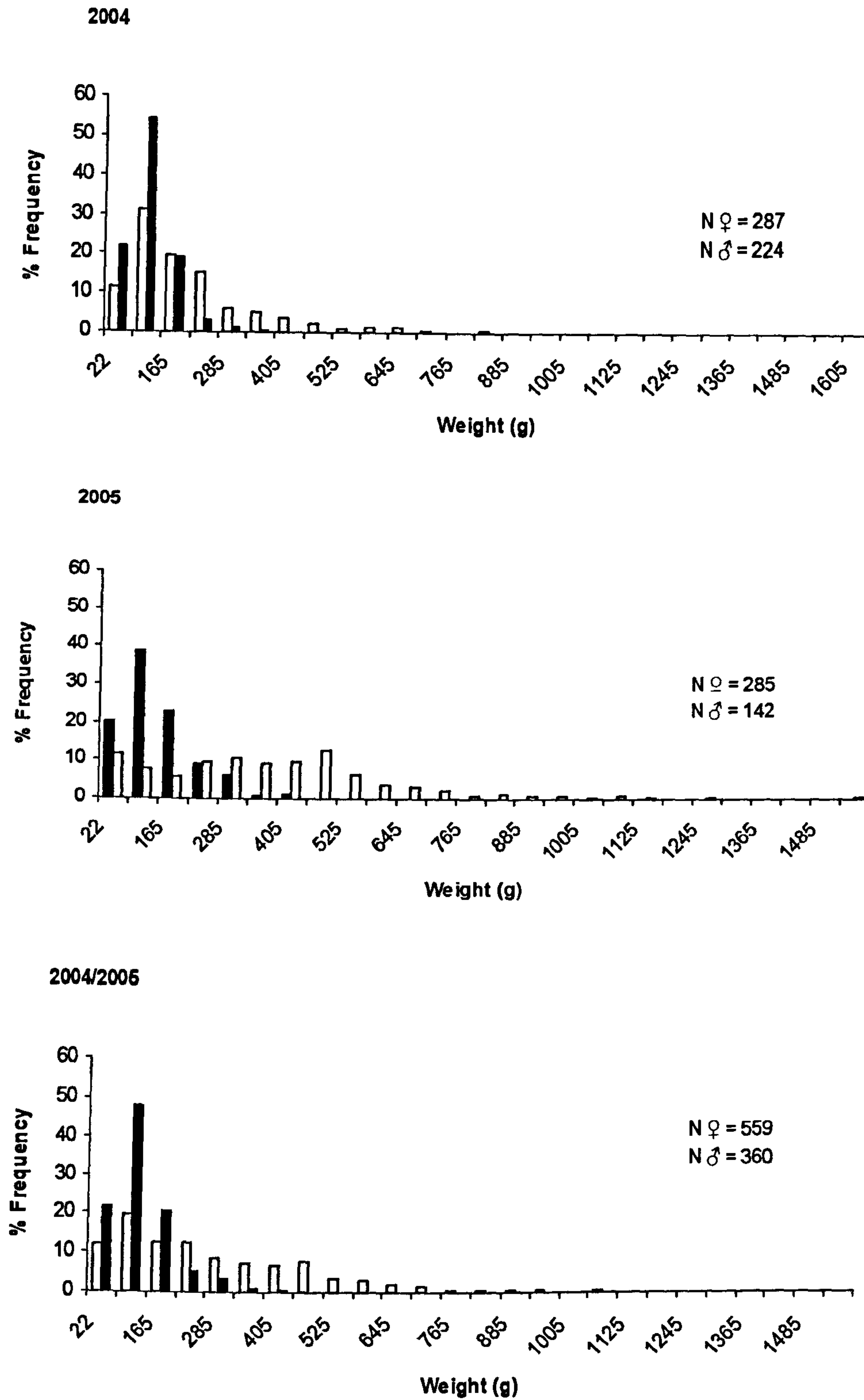


Figure 2.9: Weight percentage frequency distributions of male (solid columns) and female (open columns) plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

2.3.2 Length/weight relationship

The relationships between standard length and wet weight for male and female plaice caught in the coastal waters off E. Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined are shown in Figure 2.10 and the logarithmic plots of Log_{10} SL vs. Log_{10} Wt are shown in Figure 2.11. As expected, the length/weight relationship was curvilinear before log-transformation (Figure 2.10) and linear after log-transformation (Figure 2.11) and the plots suggested that female plaice were heavier than male plaice for a given length. This was especially apparent in the larger sized plaice where females had larger maturing gonads at the time of capture compared to males. The regression coefficients for the Log_{10} SL vs. Log_{10} Wt regression line are presented in Table 2.10. The slope values in 2004 and 2005 and for the combined 2004/2005 data were similar for both male ($b \approx 3.0$ for each data set) and female plaice ($b \approx 3.2$ for each data set). Comparison of the slope values (2004, 2005 and 2004/2005) for male and female plaice with a value of $b = 3$ indicated that male plaice exhibited isometric growth ($t = 0.33-1.00$, all $P > 0.05$) whilst female plaice exhibited positive allometric growth ($t = 7.0-12.5$, all $P < 0.0001$). A General Linear Model was conducted to compare the regression slopes of male and female plaice in 2004, 2005 and for the combined 2004-2005 data sets (Table 2.11). This analysis indicated that there was a significant effect of sex and a significant sex x length interaction indicating that the slope values for the Log_{10} SL and Log_{10} Wt regressions for male and female are significantly different (all $P < 0.001$). Thus, male and female plaice exhibit significant differences in their length-weight relationships.

2.3.3 Age and growth

The relationship between age and growth was asymptotic for both male and female plaice in 2004, 2005 and for the combined 2004/05 data set (Figure 2.12). The von Bertalanffy growth coefficients are presented in Table 2.12. There was some variation in the von Bertalanffy growth coefficients calculated for male and female fish in 2004 and 2005 and for the combined data set, but the same growth patterns were observed: male plaice exhibited higher growth rates (*i.e.* $k \approx 0.6-0.88$) and attained a smaller maximum size (*i.e.* $L_{\infty} \approx 25-27$ cm SL) compared to female fish ($k \approx 0.3$, $L_{\infty} \approx 36-44$ cm SL). Comparison of the growth curves for male and female plaice using the likelihood ratio test of Kimura (1980) indicated significant differences in the growth curves for both sexes in 2004, 2005 and for the combined data set (Table 2.13). Thus, male and female plaice exhibit significant differences in their growth patterns

Table 2.10: Parameters for the standard length (cm)/wet weight (g) relationship ($W = aL^b$) for male and female plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales. Parameters 'a' and 'b' are presented \pm SE values together with the coefficient of determination (R^2) for each regression line.

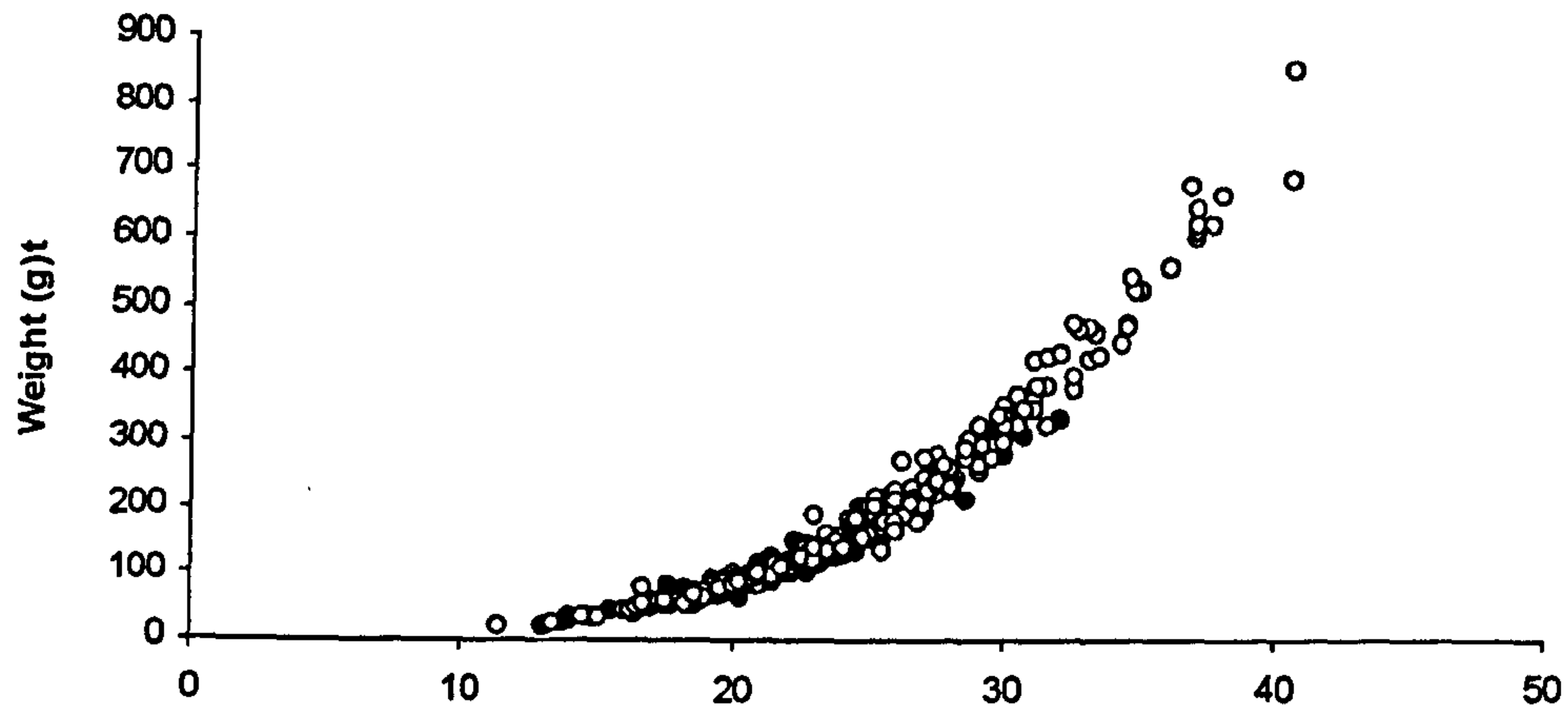
Year	Sex	N	$\text{Log}_{10}a \pm \text{SE}$	$b \pm \text{SE}$	R^2	P
2004	Male	224	-2.03 ± 0.05	3.04 ± 0.04	0.968	< 0.001
	Female	287	-2.25 ± 0.04	3.21 ± 0.03	0.982	< 0.001
2005	Male	141	-2.94 ± 0.06	2.99 ± 0.04	0.990	< 0.001
	Female	283	-1.75 ± 0.05	3.25 ± 0.02	0.989	< 0.001
2004/2005 combined	Male	365	-2.40 ± 0.05	3.02 ± 0.06	0.982	< 0.001
	Female	570	-2.02 ± 0.03	3.20 ± 0.02	0.989	< 0.001

Table 2.11: General Linear Models to compare the slopes and intercepts of the regression lines describing the relationships between Log_{10} standard length (cm) and Log_{10} wet weight (g) for male and female plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

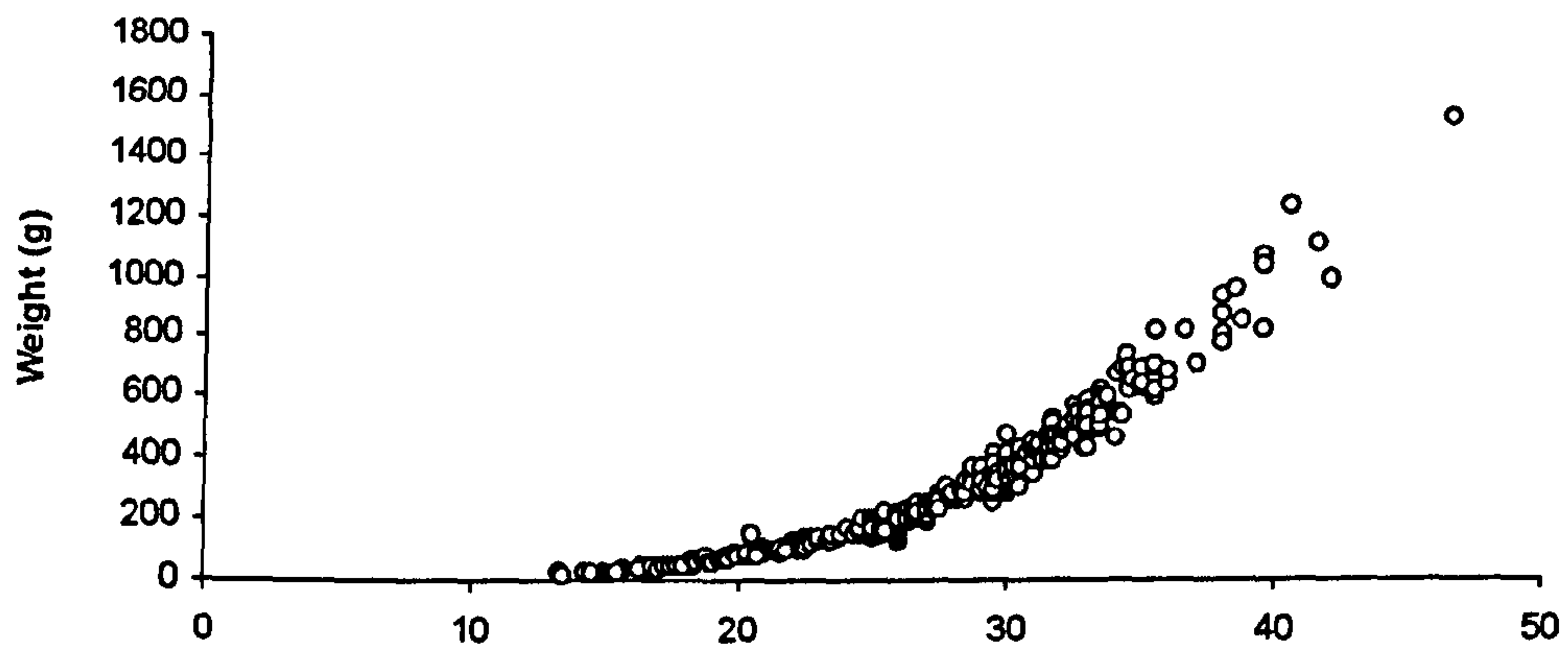
Years	Source	Df	Seq SS	Adj SS	Adj Ms	F	P
2004	Sex	1	5.191	0.017	0.017	11.85	0.0006
	Log_{10} SL	1	31.835	26.511	26.511	18539	<0.0001
	Interaction	1	0.021	0.021	0.021	14.96	0.0001
	Error	507	0.719	0.719	0.001		
	Total	510	37.766				
2005	Sex	1	13.167	0.047	0.047	32.85	<0.0001
	Log_{10} SL	1	49.419	33.534	33.534	23615	<0.0001
	Interaction	1	0.052	0.052	0.052	36.33	<0.0001
	Error	420	0.591	0.591	0.591		
	Total	423	63.330				
2004/2005 combined	Sex	1	19.143	0.099	0.099	41.34	<0.0001
	Log_{10} SL	1	87.775	62.585	62.585	26235	<0.0001
	Interaction	1	0.110	0.110	0.110	46.31	<0.0001
	Error	931	2.202	2.202	0.002		
	Total	934	109.231				

Note: Df = degrees of freedom, Seq SS= Sequential sum of squares, Adj SS & Adj Ms = Adjusted sum of squares and Adjusted mean squares respectively, F= Variance ratio, P = probability values and (SL)= standard length.

2004



2005



2004&2005

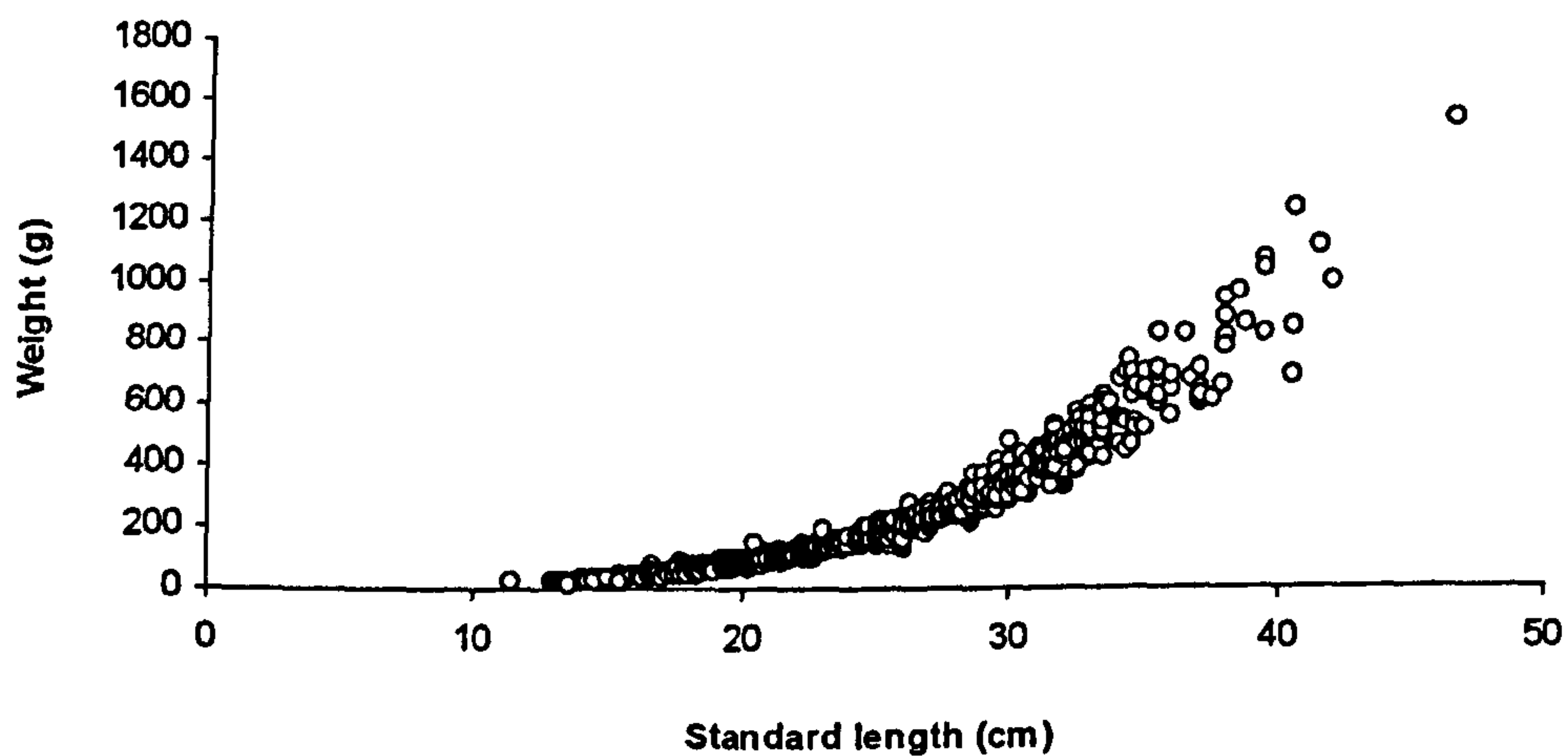


Figure 2.10: Relationships between standard length (cm) and wet weight (g) for male (solid circles) and female (open circles) plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

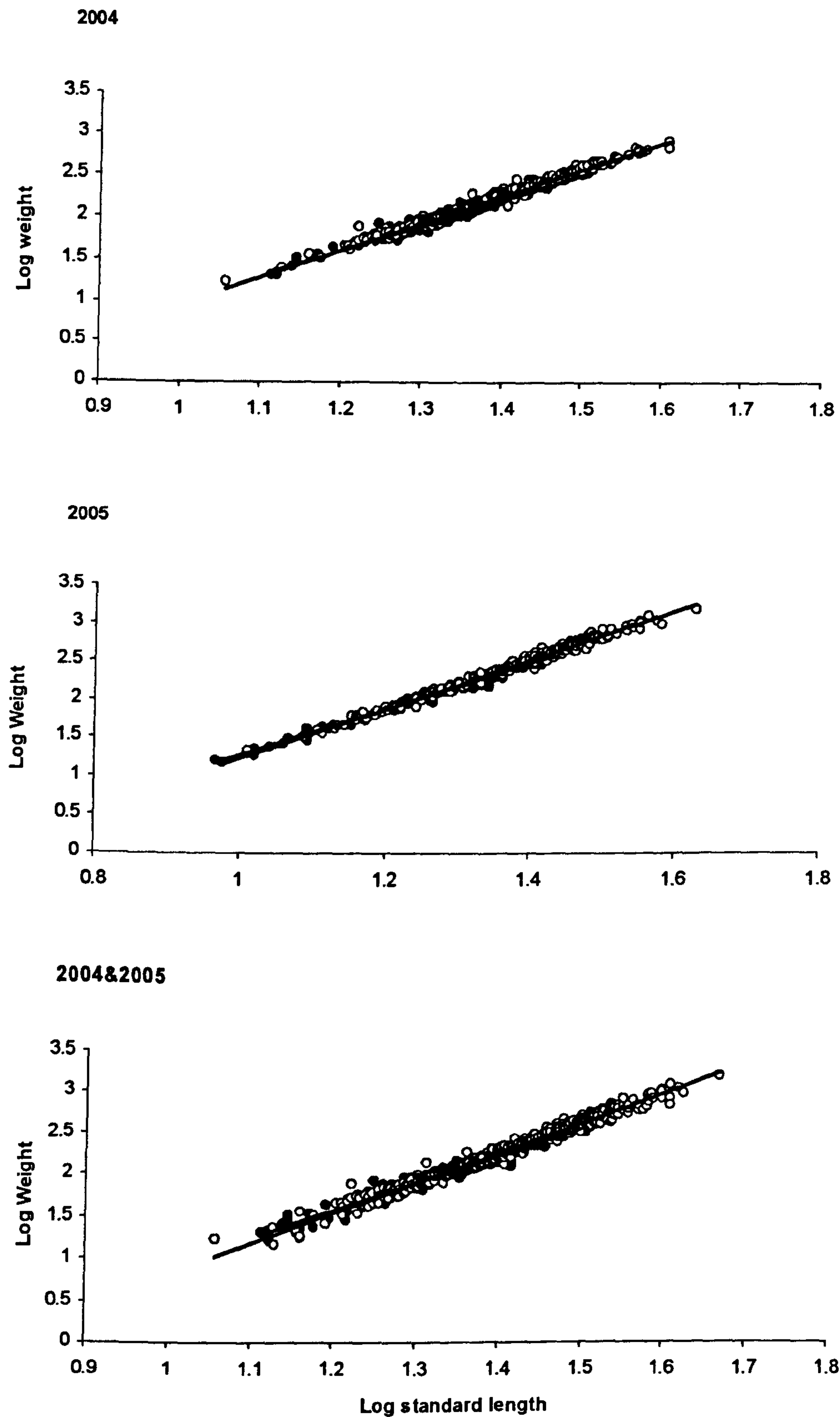


Figure 2.11: Relationships between \log_{10} standard length (cm) and \log_{10} wet weight (g) for male (solid circles) and female (open circles) plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales. Linear regression details are presented in Table 2.10.

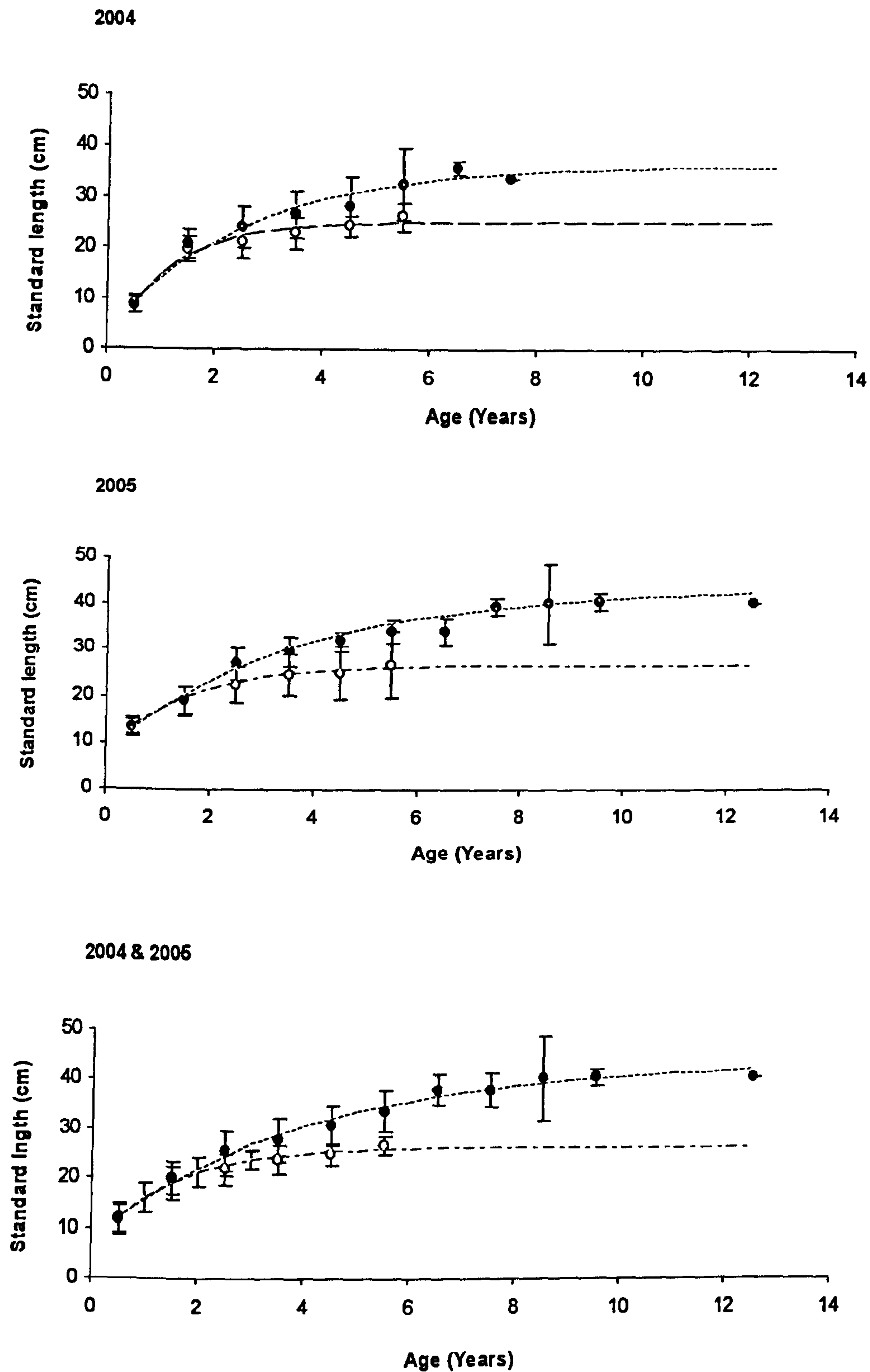


Figure 2.12: Von Bertalanffy growth curves based on standard length (cm) and age (years) for male (○ and dashed line) and female (● and dotted line) plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined. Length data are presented ± SD values (Note: No SD for 12⁺⁺ age of female as it comprise a single datum point).

Table 2.12: Von Bertalanffy growth parameters (\pm SE) for male and female plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales. The L_{∞} values presented are for standard length (cm) and the coefficient of determination (R^2) and the samples sizes (N) for each curve are also presented.

Years	Parameters	Male	Female
2004	L_{∞}	25.3 \pm 1.1	36.4 \pm 2.8
	K	0.88 \pm 0.25	0.38 \pm 0.11
	t_0	-0.02 \pm 0.18	-0.33 \pm 0.33
	R^2	0.970	0.961
	N	218	283
	Res SS	5.8422	21.3986
2005	L_{∞}	27.0 \pm 1.0	43.6 \pm 1.7
	K	0.62 \pm 0.15	0.280 \pm 0.05
	t_0	- 0.61 \pm 0.27	-0.75 \pm 0.29
	R^2	0.982	0.976
	N	141	277
	Res SS	2.2069	22.1844
2004/2005	L_{∞}	26.4 \pm 1.2	43.8 \pm 1.5
	K	0.66 \pm 0.17	0.25 \pm 0.03
	t_0	-0.43 \pm 0.27	-0.80 \pm 0.24
Combined	r^2	0.977	0.985
	N	359	560
	Res SS	3.312	13.6899

2.3.4 Mortality rate

Age-based catch curves showing the number of male and female fish in each age class in the length-stratified subsamples from 2004, 2005 and for 2004/2005 combined are presented in Figure 2.13. The youngest age classes (i.e. 0^{++} to 2^{++}) were under-represented in the catch and were omitted from the calculation of instantaneous rates of total mortality (Z , year⁻¹). The catch curves were linearised using a semi-log plot (Figure 2.14) allowing the calculation of instantaneous rates of total mortality (Table 2.14). Mortality rates were higher in 2004

compared to 2005 and compared to the combined data set. However, analysis of the slopes values using GLM indicated that there were no significant differences in the mortality rates of male and female plaice in either year or for the combined 2004/2005 data set (Table 2.15). The average instantaneous rate of total mortality for plaice was $Z=0.76 \text{ year}^{-1}$ which was equivalent to an annual percentage mortality of 53%.

Table 2.13: Comparison of von Bertalanffy growth curves for male (M) and female (F) plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined, using the likelihood ratio test (Kimura, 1980).

	Constraint	L_{∞} M	L_{∞} F	k M	k F	t_0 M	t_0 F	Res. SS	LR	df	P
2004 (N=14)	None	25.3	36.4	0.88	0.38	0.02	-0.33	26.401	-	-	-
	$L_{\infty}M=L_{\infty}F$	29.1	29.1	0.42	0.85	-0.56	-0.09	94.216	17.81	1	<0.001
	k M=k F	26.2	32.6	0.64	0.64	-0.24	-0.04	39.86	5.77	1	<0.05
	t_0 M= t_0 F	25.4	34.7	0.79	0.47	-0.11	-0.11	28.57	1.10	1	>0.05
	All above	29.1	29.1	0.64	0.64	-0.11	-0.11	124.83	21.75	3	<0.001
2005 (N=17)	None	27.0	43.6	0.62	0.28	-0.61	-0.75	17.91	-	-	-
	$L_{\infty}M=L_{\infty}F$	37.5	37.5	0.17	0.43	-2.33	-0.42	66.43	22.31	1	<0.001
	k M=k F	30.6	41.2	0.32	0.32	-1.45	-0.63	23.23	4.42	1	<0.05
	t_0 M= t_0 F	27.9	42.6	0.48	0.27	-0.88	-0.88	18.00	0.08	1	>0.05
	All above	37.5	37.5	0.32	0.32	-0.88	-0.88	173.37	38.59	3	<0.001
2004/2005 combined (N=17)	None	26.4	43.8	0.62	0.25	-0.43	-0.80	14.09	-	-	-
	$L_{\infty}M=L_{\infty}F$	34.7	34.7	0.21	0.54	-1.79	-0.21	163.12	41.63	1	<0.001
	k M=k F	29.3	40.3	0.36	0.36	-1.11	-0.35	30.55	13.15	1	<0.001
	t_0 M= t_0 F	27.1	42.9	0.51	0.27	-0.71	-0.71	14.81	0.84	1	>0.05
	All above	34.7	34.7	0.36	0.36	-0.71	-0.71	268.99	50.13	3	<0.001

None = no constraints

Res. SS = Residual sum of squares.

LR = Likelihood ratio; (LR= $-N * \ln (\text{Res. SS}_{\text{no constraints}} / \text{Res. SS}_{\text{constrained}})$).

N = total number of observations

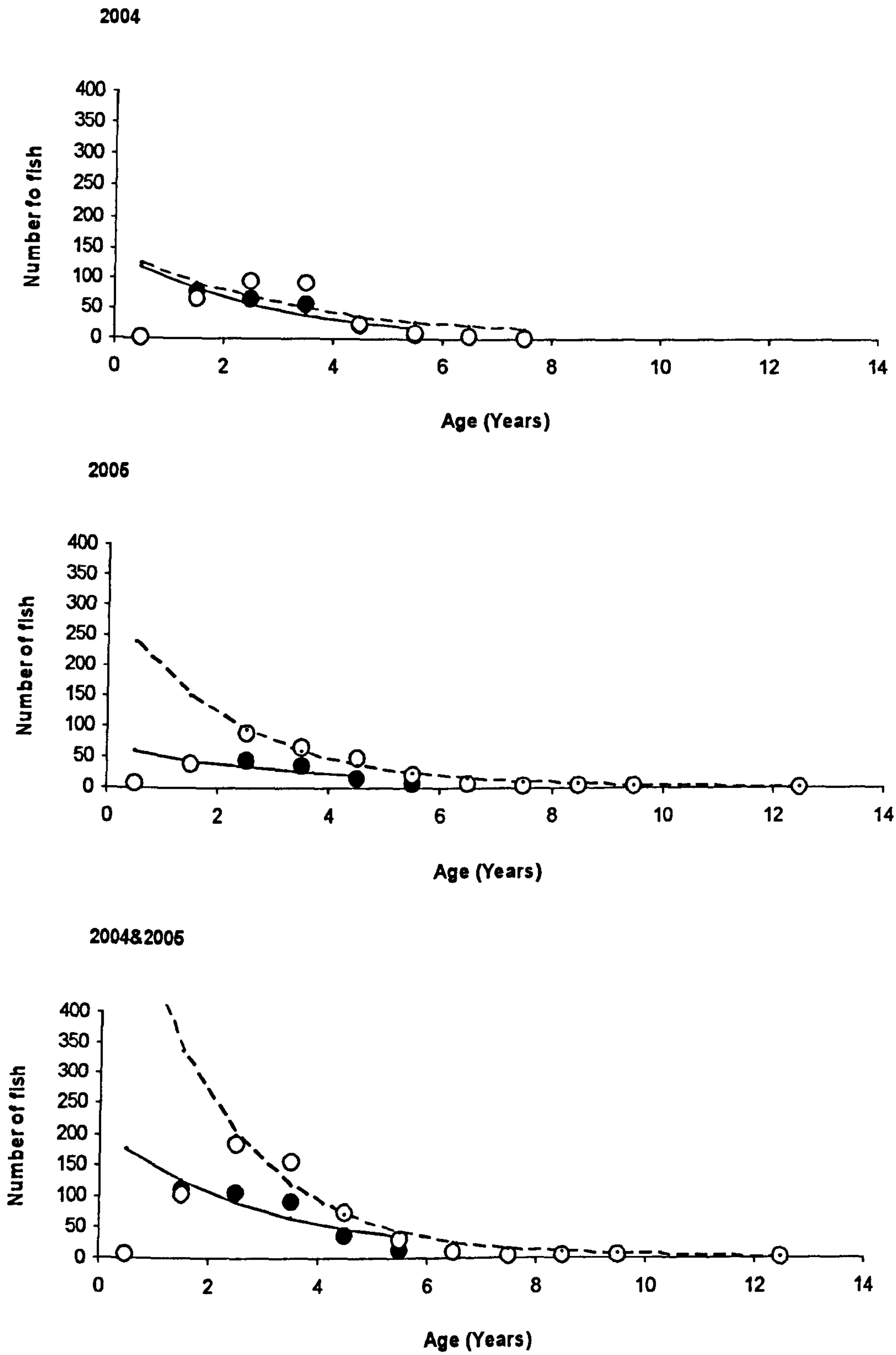


Figure 2.13: Age-based catch curves for male (solid circles, solid lines) and female (open circles, dashed lines) plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

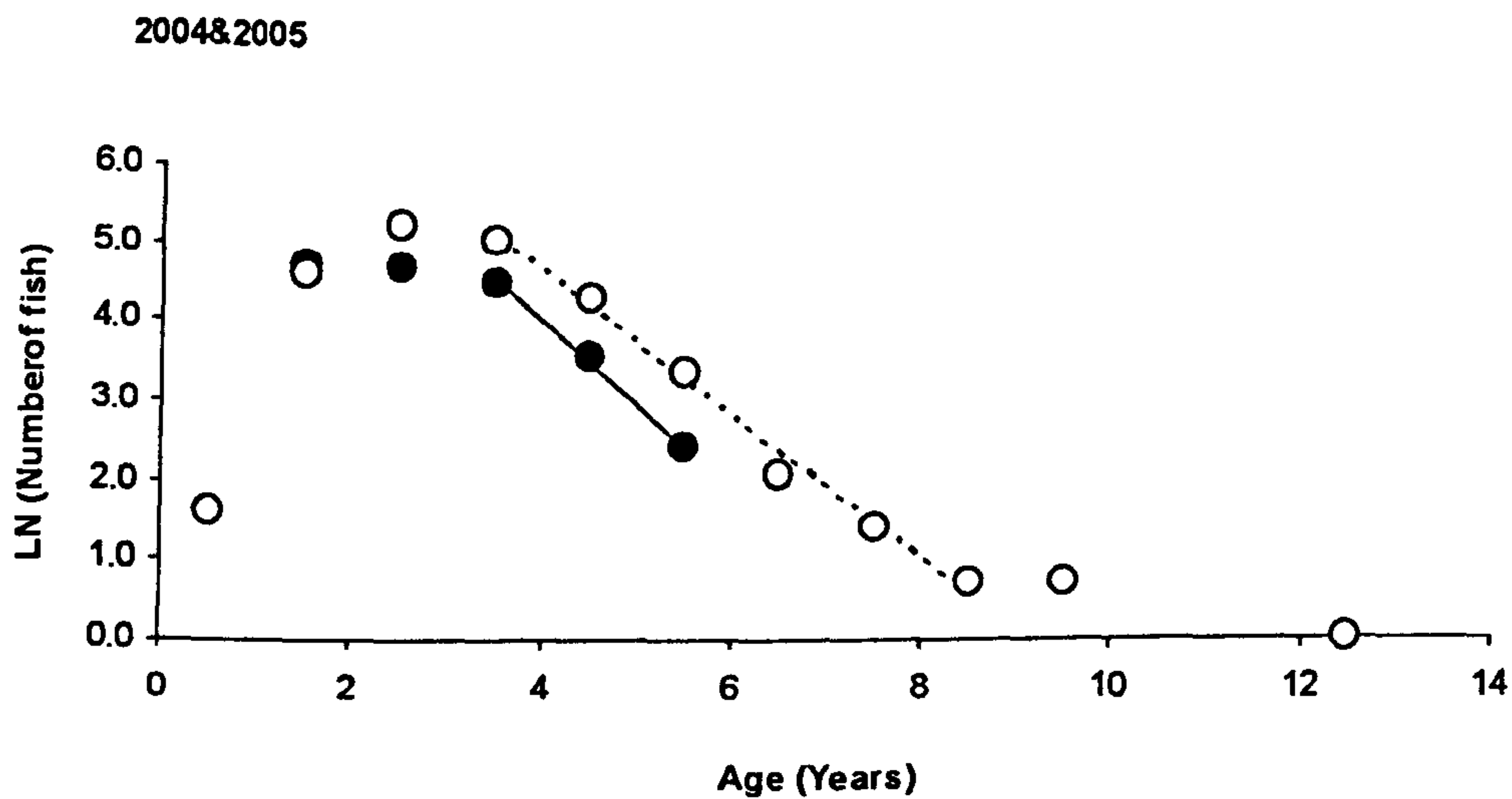
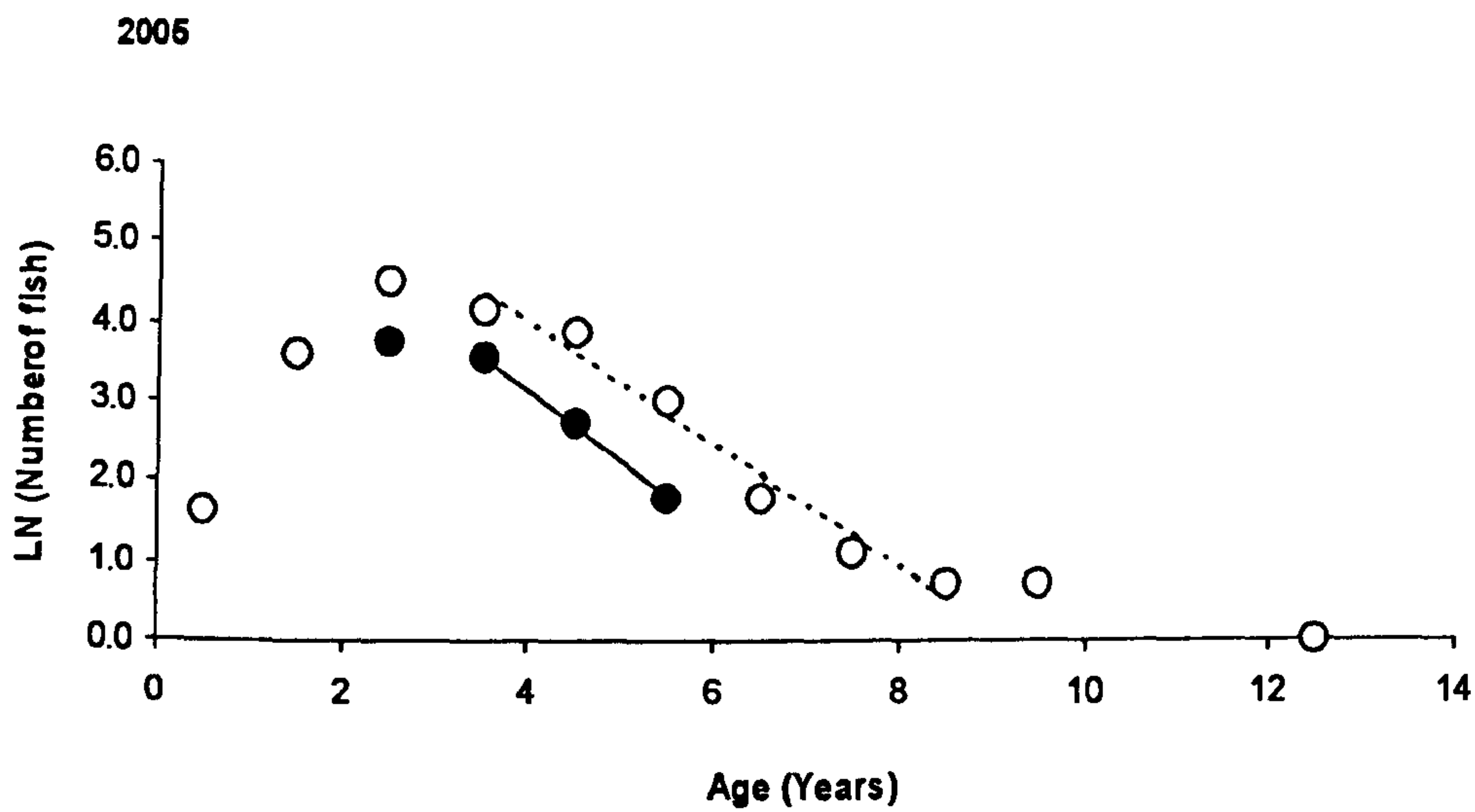
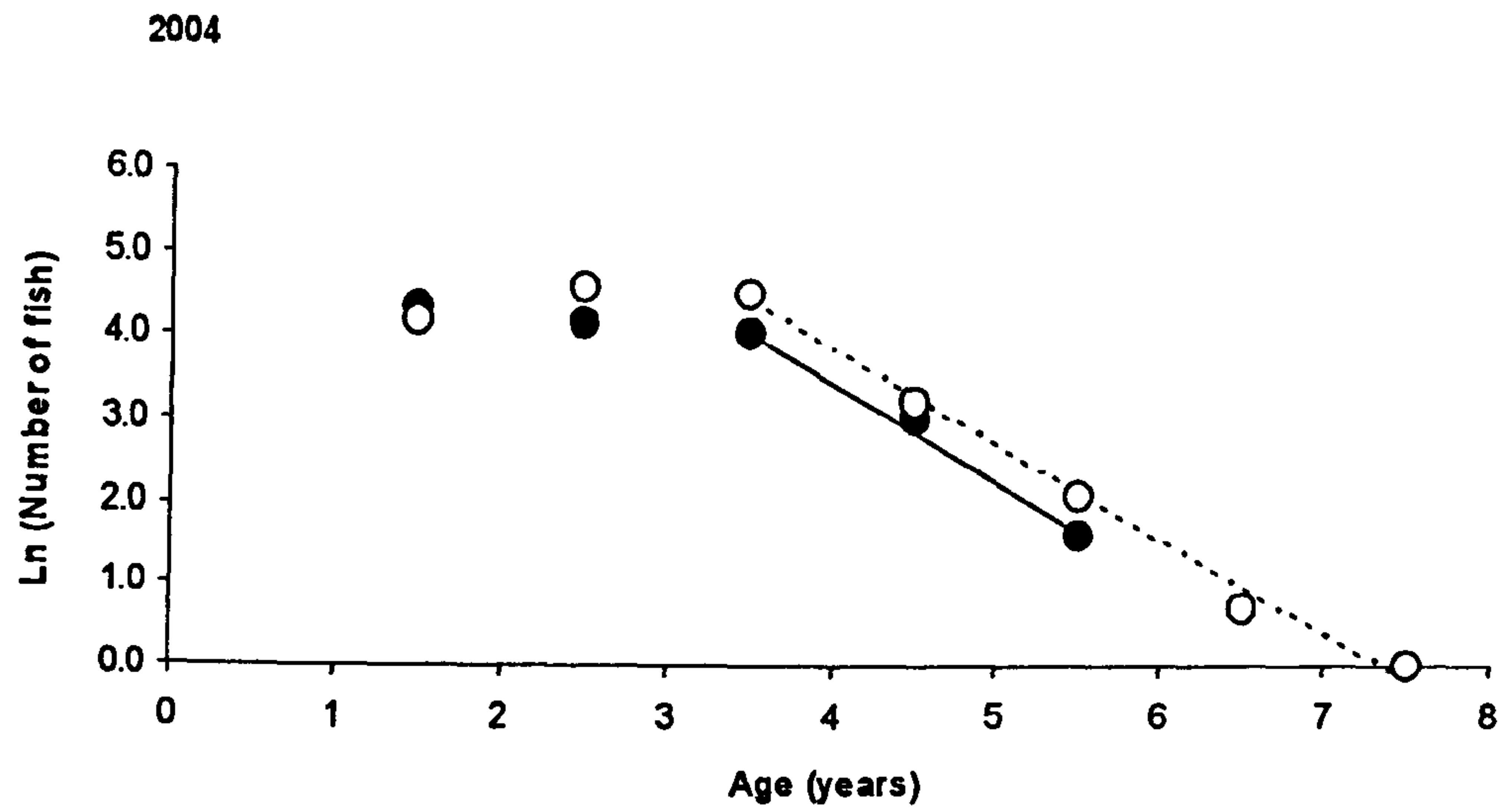


Figure 2.14: Semi-logarithmic plot of the numbers of male (solid circles, solid lines) and female (open circles, dashed lines) plaice of different ages caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

Table 2.14: Instantaneous rates of total mortality (Z , year⁻¹) for male and female plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined. Regression coefficients (\pm SD) for the equation $\text{Log}_e N_t = \text{log}_e N_0 + Z_t$ are presented together with the associated coefficient of determination (R^2). P (%) = annual percentage mortality.

Years	Sex	N	$\text{Log}_e N_0 \pm \text{SE}$	Z	R^2	p	P (%)
2004	Male	218	8.27 ± 0.53	1.20 ± 0.12	0.995	< 0.061	69.9
	Female	283	8.88 ± 0.20	1.25 ± 0.04	0.998	0.001	71.4
2005	Male	141	5.74 ± 0.50	0.69 ± 0.12	0.970	0.030	50.2
	Female	277	7.10 ± 0.40	0.77 ± 0.06	0.974	< 0.001	53.7
2004/2005	Male	359	8.23 ± 0.40	1.05 ± 0.09	0.993	< 0.052	65.0
combined	Female	560	6.66 ± 0.00	0.64 ± 0.00	1.000	< 0.001	47.3

Table 2.15: General Linear Models to compare the slopes (Z , year⁻¹) and intercepts ($\text{Ln}N_0$) of the regression lines describing the Ln-transformed age-based catch curves for male and female plaice caught in October 2004, October 2005 and October 2004/2005 (data combined) in coastal waters off Eastern Anglesey and North West Wales.

Years	Source	Df	Seq SS	Adj SS	Adj Ms	F	p
2004	Sex	1	0.1143	0.0234	0.0234	1.87	0.265
	Age	1	10.7067	8.5807	8.5807	686.68	< 0.001
	Interaction	1	0.0040	0.0040	0.0040	0.32	0.611
	Error	3	0.0375	0.0375	0.0125		
	Total	6	10.8625				
2005	Sex	1	0.1252	0.0117	0.0117	0.21	0.669
	Age	1	11.8307	4.8803	4.8803	85.86	< 0.001
	Interaction	1	0.0236	0.0236	0.0236	0.42	0.548
	Error	5	0.2842	0.2842	0.0568		
	Total	8	12.2637				
2004/2005 Combined	Sex	1	0.9345	0.0000	0.0000	0.00	0.985
	Age	1	16.4742	6.8603	6.0603	268.00	< 0.001
	Interaction	1	0.0387	0.0387	0.0387	1.51	0.273
	Error	5	0.1280	0.1280	0.0256		
	Total	8	17.5754				

2.3.5 Length (L_{50}) and age (A_{50}) at first maturity

In the present study it was easier to assign maturity stage to female plaice compared to male plaice. In female fish, it was possible to see developing eggs with the naked eye whereas the testes of many male plaice were examined under the microscope to determine the presence of sperm. The majority of male and female plaice in the length-stratified subsample were in stages 2 or 4 at the time of capture in October. In both male and female plaice, the proportion of mature fish increased with increasing size class (Figures 2.15 and 2.16) and increasing age class (Figures 2.17 and 2.18). There was some variation in the L_{50} and A_{50} values calculated for male and female fish between years (Tables 2.16 and 2.17) but males matured at a smaller size ($L_{50} \approx 16$ cm SL) and a younger age ($A_{50} \approx 1.33$ years) compared to female plaice ($L_{50} \approx 20$ cm SL; $A_{50} \approx 2.11$ years).

Table 2.16: Parameter estimates for the logistic model ($Y = 1/(1 + e^{(-r(\text{Length}-L_{50})})$) used to estimate standard length (cm) at first maturity (L_{50}) for male and female plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

Year	Sex	L_{50}	r	R^2	P
2004	Male	17.3 ± 0.227	0.941 ± 0.181	0.9795	<0.0001
	Female	21.0 ± 1.285	0.522 ± 0.309	0.6653	<0.0001
2005	Male	18.8 ± 0.143	1.710 ± 0.587	0.9872	<0.0001
	Female	23.5 ± 0.116	0.698 ± 0.050	0.9964	<0.0001
2004/2005	Male	18.1 ± 0.178	0.854 ± 0.112	0.9892	<0.0001
Combined	Female	21.8 ± 0.117	0.554 ± 0.032	0.9966	<0.0001

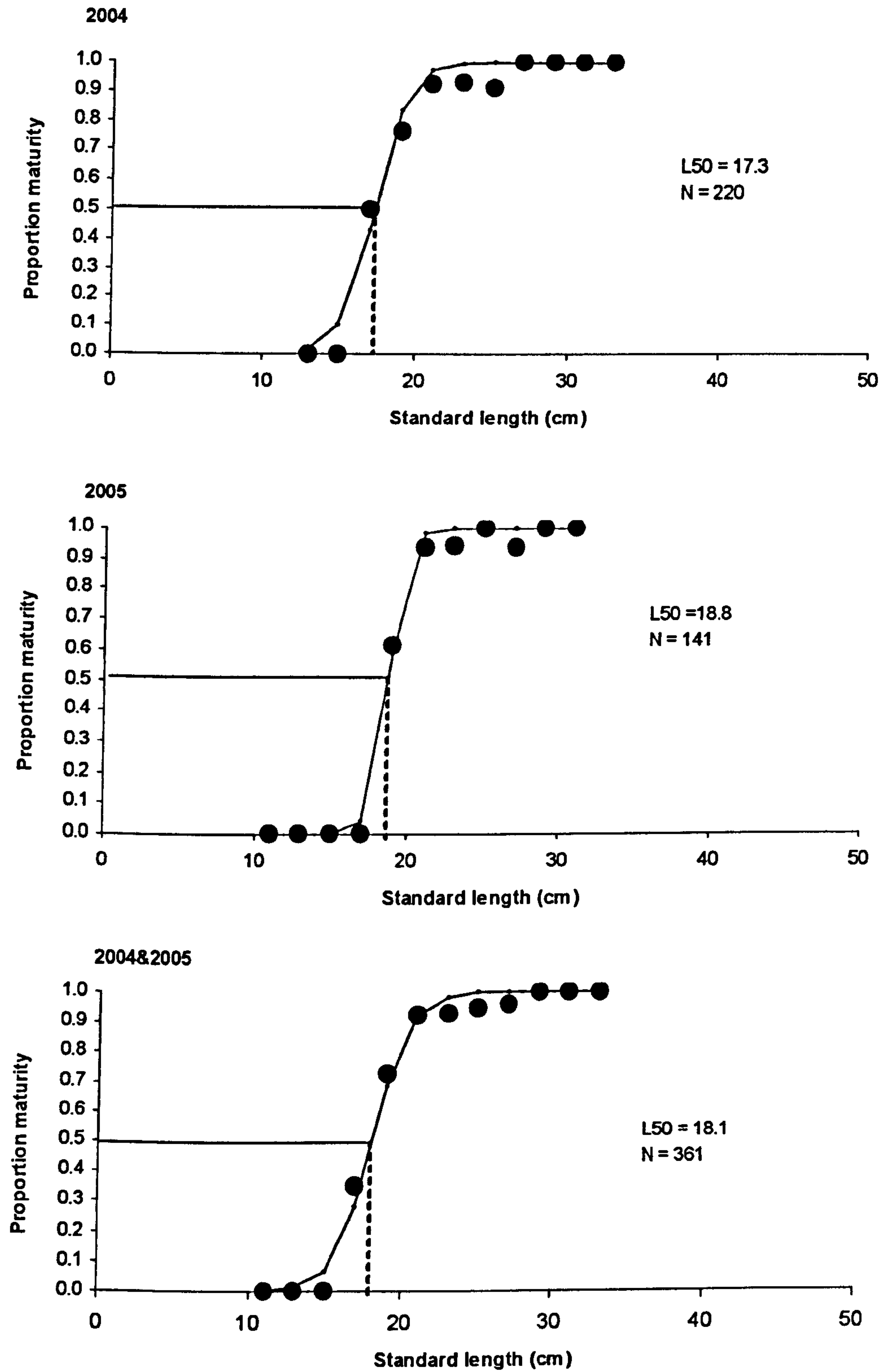


Figure 2.15: Standard length at first maturity (L_{50} , cm) for male plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

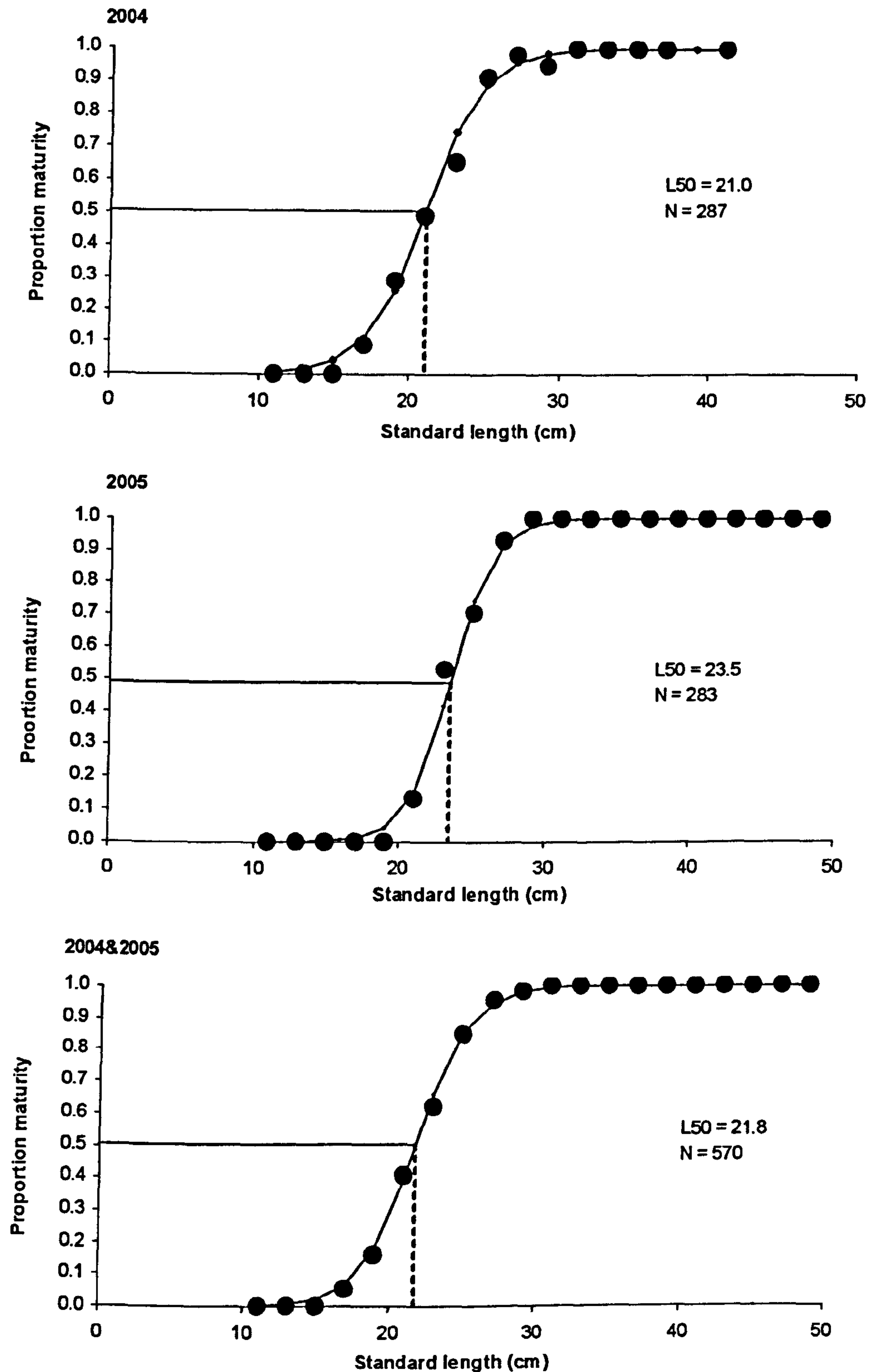


Figure 2.16: Standard length at first maturity (L_{50} , cm) for female plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

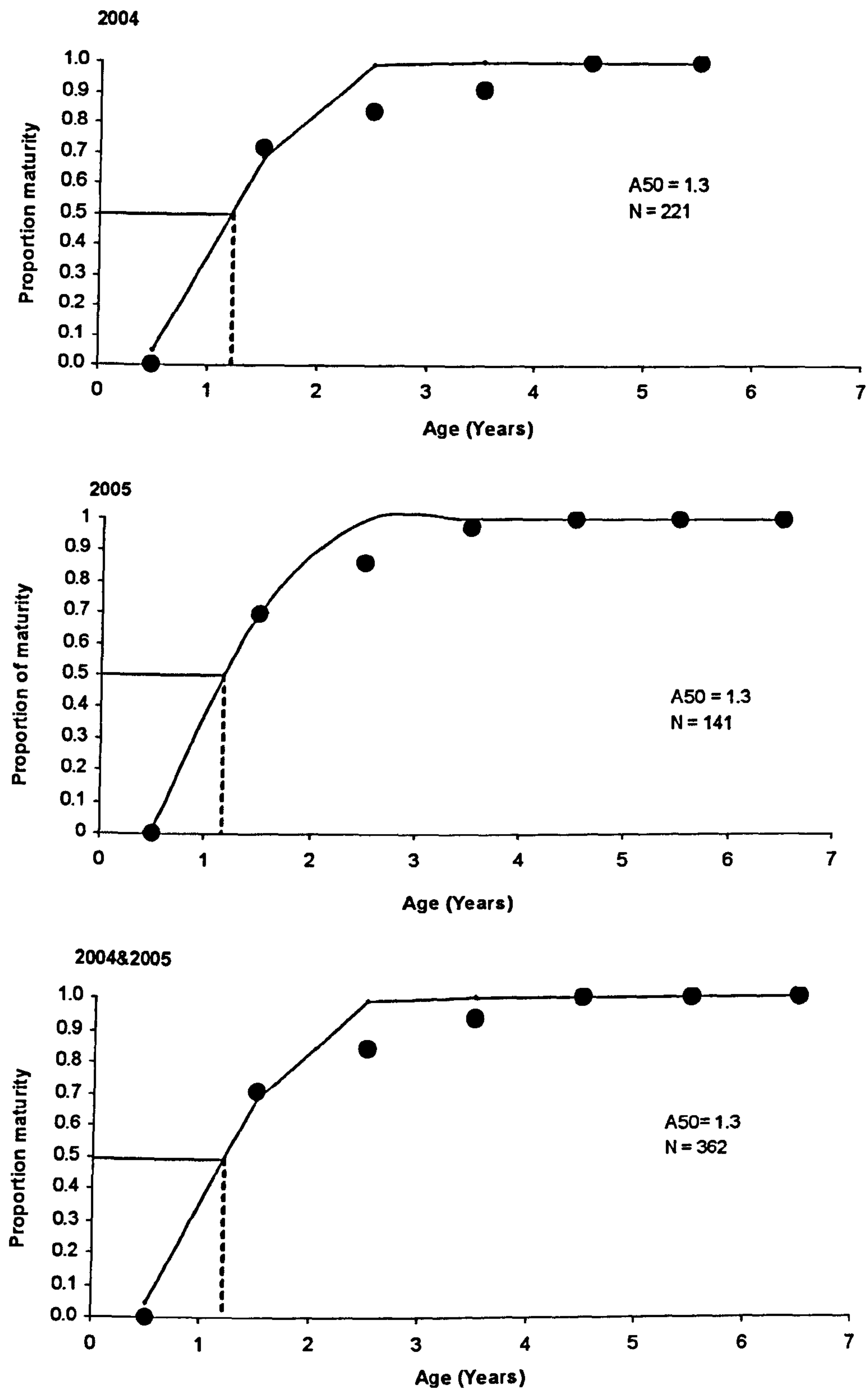


Figure 2.17: Age at first maturity (A_{50} , years) for male plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

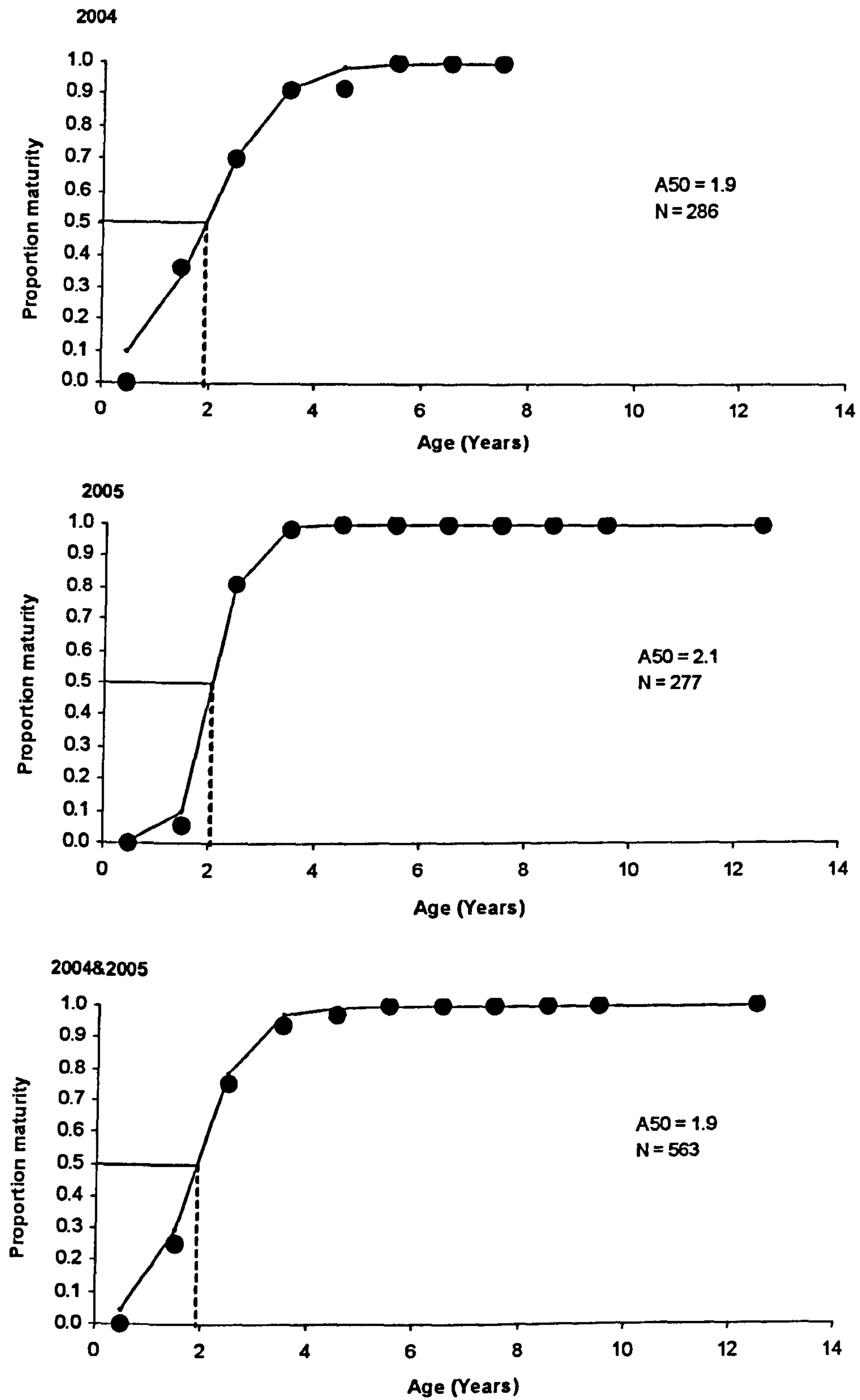


Figure 2.18: Age at first maturity (A_{50} , years) for female plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

Table 2.17: Parameter estimates for the logistic model ($Y = 1/(1 + e^{(-\tau(\text{Age}-A_{50}))})$) used to estimate age (years) at first maturity (A_{50}) for male and female plaice caught in the coastal waters off Eastern Anglesey and North West Wales in October 2004, October 2005 and for the 2004/2005 data combined.

Year	Sex	A_{50}	τ	R^2	P
2004	Male	1.3 ± 0.169	3.807 ± 2.508	0.9322	0.0002
	Female	1.9 ± 0.116	1.546 ± 0.248	0.9777	<0.0001
2005	Male	1.3 ± 0.092	4.785 ± 2.341	0.9882	<0.0001
	Female	2.1 ± 0.004	3.595 ± 0.032	0.9999	<0.0001
2004/2005	Male	1.3 ± 0.152	3.807 ± 2.243	0.9375	<0.0001
Combined	Female	1.9 ± 0.048	2.195 ± 0.188	0.9939	<0.0001

2.4 Discussion:

The results of this chapter provide detailed information on the population dynamics of plaice *P. platessa* L. in the inshore waters of North West Wales (Colwyn Bay, Beaumaris Bay) and Eastern Anglesey (Red Wharf Bay) in 2004-05 and comprise the second detailed study of this population. In this discussion, the results of the 2004-05 survey will be discussed in the general context of fish population dynamics, in relation to the survey of the same stock by Basimi (1978) 30 years ago and in relation to the contemporary population dynamics of plaice in North West Europe.

2.4.1 The population dynamics of plaice *P. platessa*

Modern virtual population analysis (VPA) fisheries models, also called cohort analysis (Hillborn and Walters, 1992), rely on deriving estimates for a number of biological parameters in order to model the effect of changes in fishing pressure on population structure/biomass and the yield to the fishery (Pope, 1972; Gulland, 1977; Jones, 1984; Hillborn and Walters, 1992; Nash, 1998; Nevarez-Martinez *et al.*, 1999; Jennings *et al.*, 2001; King 2007). These parameters include the age and size structure of the population, the length-weight coefficient (b), the VBG coefficients (k , L_{∞}), the instantaneous coefficient of natural mortality (M) and maturity ogives (L_{50}) (Cushing, 1975; Rijnsdorp, 1989; Rijnsdorp and van Beek, 1991; Jennings *et al.*, 2001; Erzini, *et al.*, 2006; Froese, 2006; King 2007; Raventos, 2007). Estimates of these values are derived by conducting detailed fisheries surveys (such as the one conducted in this present study) to obtain estimates for these population parameters. A good example of how the population parameters derived from a fisheries survey are incorporated into VPA models to inform fisheries management is the recent study by Al-Mamry (2006). In that study, samples of spangled emperor *Lethrinus nebulosus* and king soldier bream *Argyrops spinifer* were collected from artisanal and trawl fisheries for these species in Oman. Population parameters derived by analysis of the data obtained from these samples (size structure, length-weight relationship, k , L_{∞} , M and L_{50} ; Al-Mamry *et al.*, 2007 and 2009) were then used to model the population structure of each stock and VPA was used to determine how changes in fishing pressure (through the introduction of changes in mesh size or the length of the fishing season) would affect population structure (in particular SSB) and the yield to the artisanal and trawl

fisheries (Al-Mamry 2006). The results of the VPA modelling indicated that the spangled emperor and king soldier bream stocks in the Arabian Sea off Oman were underexploited and that fishing pressure on these two species could be increased without any significant impact on the SSB for either stock (Al-Mamry, 2006). VPA is also used by ICES in the management of plaice and other commercially important demersal fish stocks in the Northwest Atlantic (e.g. ICES, 2008a, 2008b, 2008c). In the latest management reports from ICES, management advice is derived by using multispecies VPA models, based on commercial catch data and separable for different species such as plaice, haddock *M. aeglefinus*, herring *C. harengus*, whiting *M. merlangus* and sole *S. solea* (e.g. ICES, 2008a, 2008b, 2008c).

The results of the present study have shown that the size- and age-frequency distributions of male and female plaice differ. Although the majority of fish of both sexes were found within a narrow range of age-, length- and weight-classes (Figure 2.7-2.9), the older, larger and heavier fish were predominately female: a common result in temperate water marine fishes [e.g. dab *L. limanda* (Rijnsdorp, 1992), roughscale sole *Clidoderma asperrimum* (Tokranov and Orlov, 2003); cod *G. morhua* (Shelton and Healey, 1999; Cefas, 2004; Moore *et al.*, 2007); barrelfish *Hyperoglyphe perciformis* (Filer and Sedberry, 2008); sculpin *Gymnocanthus pistiliger* (Hoff, 2000)]. However, the fact that male fish in these fisheries studies tend to be younger and smaller could be attributed to the sampling methods used and/or a patchy distribution of male/female fish inshore. Gerritsen and McGrath (2007) have suggested using a minimum sample size of 10 times the number of length classes in the sample to avoid under-representation of smaller sized individuals from the population within the sample. In the present study, this criteria was fulfilled with 31 size classes associated with a stratified sample size of 501 plaice in 2004 and 41 size classes representing 418 plaice in 2005.

The relationship between length and weight in fishes is best described by a power function of the form $W = a \cdot L^b$ where b is the weight exponent (King, 2007). When $b=3$, growth is described as isometric with positive or negative allometric growth occurring when b is significantly > 3 or < 3 respectively. The results of this study have shown that male plaice in the inshore waters of North West Wales and Eastern Anglesey exhibit isometric growth ($b \approx 3.0$) during October compared to female plaice that exhibit positive allometric growth ($b \approx 3.2$). These differences in the length-weight relationship are to be expected during October in the run-up to the

onset of the breeding season in late January. Reproductive investment is known to differ significantly between the sexes in fishes with the energetic investment and increase in gonad size being significantly greater in females than males (*e.g.* Coull *et al.*, 1989; Henderson *et al.*, 2000; Licandeo *et al.*, 2006). This sex-specific difference in the length-weight relationship between male and female fish depends on the time of year at which the sampling occurs in relation to the timing of the spawning season and the seasonal changes in gonad size in male and female fish [*e.g.* plaice (Basimi, 1978; Rijnsdorp, 1989), dab (Seisay, 2001); long rough dab (Bagenal, 1957), herring (Wilking, 1967; Slotte, 1999; Slotte *et al.*, 2000), cod (Love, 1960; Dambergs, 1964)]. At certain times of the year, both male and female fish can exhibit negative allometric growth, *i.e.* immediately after the spawning season when the gonads are spent and body condition is low (*e.g.* Dawson and Grimm, 1980; Henderson *et al.*, 2000; Mackinnon, 1972), or isometric growth (*e.g.* Rijnsdorp and Ibelings, 1989; Seisay, 2001). It is unusual for male fish to show positive allometric growth at some point during the year and this is usually only seen in females (*e.g.* Rijnsdorp and Ibelings, 1989; Seisay, 2001; Al-Mamry, 2006). Seisay (2001) reports that female dab in the South East Irish Sea exhibit positive allometric growth between October and February while male dab exhibit isometric growth during the same period. Seasonal changes in body weight for a given length have also been reported in other studies (Basimi, 1978; Ortega-Salas, 1980; Al-Mamry, 2006).

The most common model used to describe the relationship between size and age in fishes is the von Bertalanffy growth curve (von Bertalanffy, 1938; Jennings *et al.*, 2001; King, 2007). In this model, growth rates are high (k) when fish are young, slowing down as the fish gets older (as energy intake is switched from somatic growth to reproductive investment) until attaining an asymptotic maximum size (L_{∞}). The von Bertalanffy growth model has been used to describe the growth curves for many temperate marine fish species (*e.g.* Chen *et al.*, 1992; Fossen *et al.*, 1999; Dwyer *et al.*, 2001; Parker-Humphreys 2004a, 2004b, 2005; Vinarge *et al.*, 2008) and including plaice (Basimi and Grove 1985b; Bromley, 2000; Bolle *et al.* 2004; Parker-Humphreys 2004a, 2004b, 2005; this study). The results of this study have shown significant differences in the growth curves of male and female plaice (Figure 2.12, Tables 2.12 and 2.13). Male plaice exhibited significantly higher growth rates when younger (k : ♂ = 0.62 year⁻¹ *cf.* ♀ = 0.25 year⁻¹) and attained a significantly smaller L_{∞} compared to female plaice (L_{∞} : ♂ = 26.4 cm SL *cf.* ♀ = 43.8 cm SL). This sex-

specific difference in growth has been reported in other studies on plaice (*e.g.* Basimi and Grove, 1985b; Bromley, 2000; Parker-Humphreys 2004a & b, 2005) and is common in temperate water marine fishes (*e.g.* Arneri *et al.*, 2001; Seisay, 2001) and elasmobranchs (*e.g.* Conrath *et al.*, 2002; Whittamore and McCarthy, 2005).

As is common in studies of fish population dynamics, a semi-logarithmic plot of age vs. fish number was used to estimate the instantaneous rate of total mortality (Z , year⁻¹; King, 2007). The results of this analysis (Figure 2.14, Table 2.14) indicated that although Z tended to be higher for male plaice compared to female plaice (Z : ♂ = 1.05 year⁻¹ *cf.* ♀ = 0.64 year⁻¹) this difference was not significant (Table 2.15). In temperate marine fish species it is common for males to exhibit significantly higher Z values than females (*e.g.* Basimi and Grove, 1985c; Seisay, 2001), although other studies have shown no difference in total mortality rate between males and females (*e.g.* Dulčić *et al.*, 2008; this study). One possible answer for this discrepancy may be the sample sizes of fish collected in each study as this may determine the number of age classes that can be used in the analysis (*e.g.* see Figure 2.13). Seisay (2001) suggested that the higher mortality rate reported for male dab in the South East Irish Sea may be due to the males remaining in deeper water for longer periods of time and therefore are more vulnerable to capture by fishing gear compared to female dab that spend more time feeding in inshore waters. It is possible to estimate the instantaneous rates of natural mortality for male and female plaice in this study (2004/05 combined) using the equation of Pauly *et al.* (1980) incorporating the k/L_{∞} values for male/female plaice (Table 2.12) and using an average annual seawater temperature of 7.41°C (Moelfre; Joyce, 2006). This provides estimates of $M = 0.754$ year⁻¹ and $M = 0.361$ year⁻¹ for male and female plaice respectively in this study. Since $Z = F + M$ (King, 2007) it is possible to estimate instantaneous rates of fishing mortality of $F = 0.296$ year⁻¹ for male plaice and $F = 0.279$ year⁻¹ for female plaice respectively in this study. These values compare well with the measure of fishing mortality provided by ICES for plaice in the Irish Sea (based on the mean F for 3-6 year old plaice): the average F value for the period 2001-2005 is 0.220 ± 0.065 year⁻¹ (ICES, 2008a). The majority of plaice landed in the Irish are caught in the Eastern Irish Sea off the Cumbrian coast and in Liverpool Bay where landings of 12500 and 15000 kg day⁻¹ have been reported for the period 1979-2000 (Dunn and Pawson, 2002). Therefore, it would be expected for the values of fishing mortality estimated in this study to be similar to values reported by ICES for the Irish Sea as a whole since the majority of

fishing effort is concentrated within the region containing the South East Irish Sea plaice stock. The difference between the values calculated in this study ($F \approx 0.30 \text{ year}^{-1}$) and reported by ICES ($F \approx 0.22 \text{ year}^{-1}$) may be due to discarding.

Maturity ogives, representing the change in the proportion of mature fish in a sample with increasing size or age class, are used to estimate the length or age at 50% maturity (L_{50} and A_{50}) which in fisheries science is taken to be the length or age class for a species above which all individuals are considered to be mature in fisheries management models (King, 2007). Although maturity ogives can be expressed as either an L_{50} or an A_{50} , length at first maturity is more informative since key life history decisions such as the timing of first maturity are usually determined by growth rate and size rather than age (Rijnsdorp, 1989; King, 2007) and L_{50} values are used in VPA (and other fisheries models) for temperate marine fish species (Froysa *et al.*, 2002; Al-Mamry 2006; King, 2007). In this study, male plaice matured at a smaller size and younger age compared to female plaice (Figures 2.15-2.18; $L_{50} \text{ ♂} \approx 16 \text{ cm SL}$ *cf.* $\text{♀} \approx 20 \text{ cm SL}$; $A_{50} \text{ ♂} \approx 1.33 \text{ years}$ *cf.* $\text{♀} \approx 2.11 \text{ years}$). This sex-specific difference in size/age at first maturity is common in temperate water marine fishes (*e.g.* Seisay, 2001; Lorenzo *et al.*, 2002; Pajuelo and Lorenzo, 2004; Parker-Humphreys, 2004a & b, 2005; Pajuelo *et al.*, 2006; Grandcourt *et al.*, 2007) and elasmobranchs (*e.g.* Oddone *et al.*, 2005; Whittamore and McCarthy, 2005) and is related to difference in reproductive investment between the sexes. However, no differences in L_{50}/A_{50} values for male and female fish have been reported in some species, for example herring, sprat and whiting (Grygiel and Wyzsynski, 2003; Preston, 2007). In male fish, reproductive investment is low with gonadosomatic indices (gonad size expressed as a percentage of body weight) for temperate water fishes usually less than 1% (King, 2007). In contrast, reproductive investment in female fish is much greater and fecundity is positively correlated with female size in plaice (Bagenal, 1966; Basimi and Grove, 1985c; Rijnsdorp, 1993, 1994; Nash *et al.*, 2000) and many other marine fish species (King, 2007).

2.4.2 A brief review of fisheries in the Irish Sea, with emphasis on plaice fisheries

Vincent *et al.* (2004) reported that fisheries in the Irish Sea had a turnover of around £60 million in 2002 (Table 2.18).

Table 2.18. A summary of the composition and value of fisheries landings in the Irish Sea (ICES region VIIa) in 2002. Source: Vincent *et al.* (2004).

Marine animals	Total weight (tonnes)	Value £ million	Principal species
Shellfish	52,500	43.5	<i>Nephrops</i> , mussels, scallops, queen scallops
Demersal	11,900	15.8	Cod, sole, spurdog, plaice, haddock, hake, anglerfish, skates/rays
Pelagic	3,900	0.6	herring, mackerel
Total	68,300	59.5	

Fisheries in the Irish Sea have targeted principally several high value species: *N. norvegicus* (demersal otter trawls), sole *S. solea* (demersal otter and beam trawling) and spurdog *Squalus acanthus* (longlining) with several other high value species being landed in the demersal trawls as associated catch (see Table 2.19). In 2002, the *Nephrops* fishery in the Irish Sea (excluding the Clyde) was worth £8.2 million and landed 18% of the UK catch for this species (Vincent *et al.*, 2004). There are also important fisheries for shellfish (principally pectinids) around the Isle of Man. In 2002, these fisheries were worth £3.2 million (scallop) and £2.2 million (queen scallop) respectively (Vincent *et al.*, 2004). The mariculture of mussels is also an important shellfish industry in the Irish Sea, worth £3.2 million in 2002 (Vincent *et al.*, 2004), although this is mainly localised to the Menai Strait. Demersal finfisheries are of lesser importance in the Irish Sea compared to *Nephrops* and historically this has been a mixed fishery. Bottom-set longlines have targeted spurdog and in 2002 this fishery was worth £1.5 million (Vincent *et al.*, 2004) although this fishery has now been closed due to overexploitation (ICES, 2008a). Otter trawlers have principally targeted cod *G. morhua* (worth £1.8 million in 2002; Vincent *et al.*, 2004), haddock *M. aeglefinus*, whiting *M. merlangus* and plaice, with some important by-catch species such as anglerfish *Lophius piscatorius*, hake *M. merluccius*, sole and skates/rays (*Raja* spp.) (Parker-Humphreys, 2004a; Vincent *et al.*, 2004). The beam trawl fishery in the Irish Sea targets principally sole but also lands plaice, skates/rays, brill

Scophthalmus rhombus, turbot *P. maxima* and anglerfish (Parker-Humphreys, 2004a). Pelagic fisheries in the Irish Sea are limited (£0.6 million value in 2002; Table 2.18) and target principally herring *C. harengus* and mackerel *S. scombrus*.

Parker-Humphreys (2004a) reports the landings and values for the principal fish and shellfish species landed by the UK fishing fleet into ports in England and Wales for the period 1993-2001. These data are summarised in Table 2.19 to indicate the relative magnitude and value of the landings for these species in the Irish Sea. The data are divided up into different groups – flatfish, gadoids, other demersal fish, elasmobranchs, and invertebrates – and are listed within group according to the average value of their landings for the period 1993-2001. From Table 2.19, it is clear that finfisheries in the Irish Sea focus on a small number of target species: sole, plaice, cod, whiting, spurdogs plus skates/rays (these are not distinguished to species level in fisheries landings; ICES, 2008a). However, smaller landings of high value species such as brill, turbot, hake, haddock which are caught in association with the target species also contribute significantly to the value of landings (Table 2.19). The current status and management recommendations for each fish stock (derived from ICES, 2008a), where this information is known, are presented in Table 2.19. It is interesting to note that for many of the species presented in Table 2.19, the stock status (*e.g.* spawning stock biomass, annual recruitment, detailed information on exploitation rate and landings) is unknown and at best ICES has to guess from current catch statistics whether the stock is being under/overexploited (ICES, 2008a). However, based on the detailed data available for the most important species (*e.g.* sole, plaice, gadoids, spurdogs) plus the landing statistics presented by Parker-Humphreys (2004a), the recurrent pattern is for catches to be declining for most species (Table 2.19). This decline is probably due to a combination of two factors, overfishing and a reduction in the size of the fishing fleet in the Irish Sea.

The main fishing nations involved in the demersal finfisheries in the Irish Sea have been the UK (England, Wales and Northern Ireland) and Ireland with Belgium, Holland and France also contributing to the landings (Parker-Humphreys, 2004a; ICES, 2008a). British and Irish vessels comprise the otter trawl fishery in the Irish Sea targeting mainly plaice, haddock, cod and whiting, with smaller associated catches of anglerfish, hake and sole (ICES, 2008a). The beam trawl fishery takes place mainly in the eastern Irish Sea and consists of Belgian, British and Irish vessels targeting mainly sole with important associated catches of plaice, rays, turbot, brill, anglerfish and cod

(ICES, 2008a). In inshore coastal waters there are some tangle net and gill net fisheries for sea bass, sole, plaice, rays, mullet and cod and some invertebrate fisheries for lobsters, whelks and scallops that are not assessed by ICES. There has been a decline in fishing effort and landings by beam trawl and otter trawl in the Irish Sea since a peak in the 1980s. For example, fishing effort by otter trawl in 1999-2004 had declined to 25% of the peak value in the 1980s (ICES, 2008a). There has been a decline in the number of vessels (11,108 in 1993 to 7,033 in 2002) and employment (19,044 in 1996 to 12,746 in 2002) in the UK fishing industry in recent years, and it is thought that this trend also applies to the Irish Sea (Vincent *et al.*, 2004).

Plaice in the Irish Sea have been landed in both the otter trawl and beam trawl fisheries (Dunn and Pawson, 2000; Parker-Humphreys, 2004a; ICES, 2008a). Although 4 separate stocks are known in the Irish Sea – North East Irish Sea, South East Irish Sea, Cardigan Bay and Western Irish Sea (Dunn and Pawson, 2002) – fishing effort and landings have been greatest in the beam trawl fishery in the eastern Irish Sea (Dunn and Pawson, 2002). ICES have collated data on plaice stocks in the Irish Sea (ICES region VIIa) since 1964 and the trends in the landings, fishing mortality, recruitment and spawning stock biomass are presented in Figure 2.19. Landings of plaice in the Irish Sea have never been high, with an average landing of 3245 tonnes for the period 1964-2006 (ICES, 2008a) and a peak landing of 6220 tonnes in 1989 (Figure 2.19a). In contrast, due to its higher productivity, the North Sea has supported landings of plaice in excess of 50000 tonnes since data collection started in ICES region IV in 1957 (ICES, 2008a). The trend has been for a steady decline in landings since the peak in 1969 with landings dropping below 1000 tonnes for the first time in 2006 (Figure 2.19a, 932 tonnes; ICES, 2008a). This decline in landings has been due to a decline in fishing effort rather than overfishing. Mean fishing mortality on the 3-6 year age classes (the predominant age classes in the adult stock) has declined steadily since the mid 1970s (peak $F = 0.92 \text{ year}^{-1}$ in 1976; Figure 2.19b) and the stock is currently classed as being harvested sustainably ($F \approx 0.1 \text{ year}^{-1}$ *cf.* $F_{pa} = 0.45 \text{ year}^{-1}$; ICES, 2008a) and is viewed by ICES as underexploited (ICES, 2008a). This level of underexploitation is reflected in the level of juvenile recruitment into the fishery (Figure 2.19c), which has showed little variation over time (average recruitment of 13.04 million fish per year for the period 1964-2006; ICES, 2008a),

Table 2.19. A summary of the average landings by all demersal gears for UK vessels landing into England and Wales for the period 1993-2001 (calculated from Parker-Humphreys 2004a). Data (mean \pm SD) are presented in terms of tonnes landed, values of the landings (£1000's) and landing price (£/kg). Species are listed by group (flatfish, gadoids, other demersal fish, elasmobranchs and invertebrates), within each group species are listed in order of monetary value. Data on the current status of fish stocks, where available, have been collated from ICES (2008a, 2008b).

	Value (£1000's)	Landings (tonnes)	Landing Price (£/kg)	Current status of Fish stocks *(ICES, 2008a, 2008b)
Flatfish				
Sole	1167 \pm 392	218 \pm 100	5.60 \pm 0.74	*Catches ↓, RRC, HU, OE, SSB < B _{lim} , F = F _{lim}
Plaice	682 \pm 208	673 \pm 200	1.01 \pm 0.11	*Catches ↓, FRC, HS, UE, SSB > B _{pa} , F < F _{pa}
Brill	177 \pm 43	48 \pm 11	3.71 \pm 0.44	Catches variable, Stock status unknown, stable?
Turbot	138 \pm 78	27 \pm 15	5.24 \pm 0.71	Catches ↓, Stock status unknown, stable?
Lemon Sole	44 \pm 18	19 \pm 8	2.32 \pm 0.34	Catches ↓, Stock status unknown, stable?
Megrim	27 \pm 38	11 \pm 15	2.08 \pm 0.68	*Catches ↓, Stock status unknown, stable?
Dab	12 \pm 7	41 \pm 16	0.26 \pm 0.07	Catches ↓, Stock status unknown, stable?
Flounder	9 \pm 4	49 \pm 17	0.19 \pm 0.03	Catches variable, Stock status unknown, stable?
Gadoids				
Cod	549 \pm 235	464 \pm 217	1.25 \pm 0.21	*Catches ↓, RRC, HU, OE, SSB < B _{lim} , F > F _{lim}
Hake	155 \pm 136	55 \pm 35	2.64 \pm 0.64	*Catches stable, FRC, HS, SSB = B _{pa} , F = F _{pa}
Haddock	136 \pm 115	108 \pm 61	1.14 \pm 0.36	*Catches ↓, Stock status unknown, OE?
Whiting	118 \pm 54	332 \pm 159	0.36 \pm 0.05	*Catches ↓, Stock status unknown, OE?
Pollock	40 \pm 19	37 \pm 18	1.08 \pm 0.16	Catches stable, Stock status unknown, stable?
Ling	28 \pm 11	36 \pm 18	0.79 \pm 0.12	Catches stable, Stock status unknown, stable?
Other Demersal Fish				
Anglerfish	97 \pm 71	65 \pm 40	1.58 \pm 0.56	*Catches stable, Stock status unknown, stable?
Sea bass	62 \pm 59	13 \pm 11	4.59 \pm 0.96	*Catches ↑, Stock status unknown, stable?
Mixed gurnards	27 \pm 7	85 \pm 15	0.32 \pm 0.05	Catches ↑, Stock status is unknown, stable?
Elasmobranchs				
Skates/Rays	720 \pm 433	713 \pm 141	1.01 0.07	*Catches ↓, Stock status unknown, recognised as OE, also large bycatch
Spurdogs	651 \pm 230	769 \pm 249	0.84 \pm 0.14	*Depleted and in danger of collapse, Fishery currently suspended
Dogfish, hounds, sharks	92 \pm 37	189 \pm 55	0.49 \pm 0.14	Fishery not assessed by ICES
Invertebrates				
Scallops	1166 \pm 738	701 \pm 413	1.62 \pm 0.13	Fishery not assessed by ICES
Nephrops	908 \pm 178	491 \pm 64	1.84 \pm 0.21	*Catches stable, Stock status unknown, stable?
Lobster	385 \pm 181	41 \pm 19	9.45 \pm 0.90	Fishery not assessed by ICES
Queen scallop	352 \pm 366	833 \pm 795	0.44 \pm 0.10	Fishery not assessed by ICES
Whelks	262 \pm 317	770 \pm 784	0.31 \pm 0.06	Fishery not assessed by ICES
Edible crabs	77 \pm 63	70 \pm 45	1.01 0.26	Fishery not assessed by ICES
Cockles ¹	254 \pm 262	603 \pm 614	0.44 \pm 0.34	Fishery not assessed by ICES
Mussels ²	1636 \pm 1281	5017 \pm 2605	0.29 \pm 0.11	

1 – harvested from shoreline 2 – Extensive mariculture rather than capture fishery
 HS – Harvested sustainably; HU – Harvested unsustainably; OE – Overexploited; UE – underexploited; FRC – Full reproductive capacity; RRC – Reduced reproductive capacity; B – Biomass; F – Instantaneous rate of fishing mortality; pa – precautionary approach; limiting value (i.e. minimum B or maximum F).

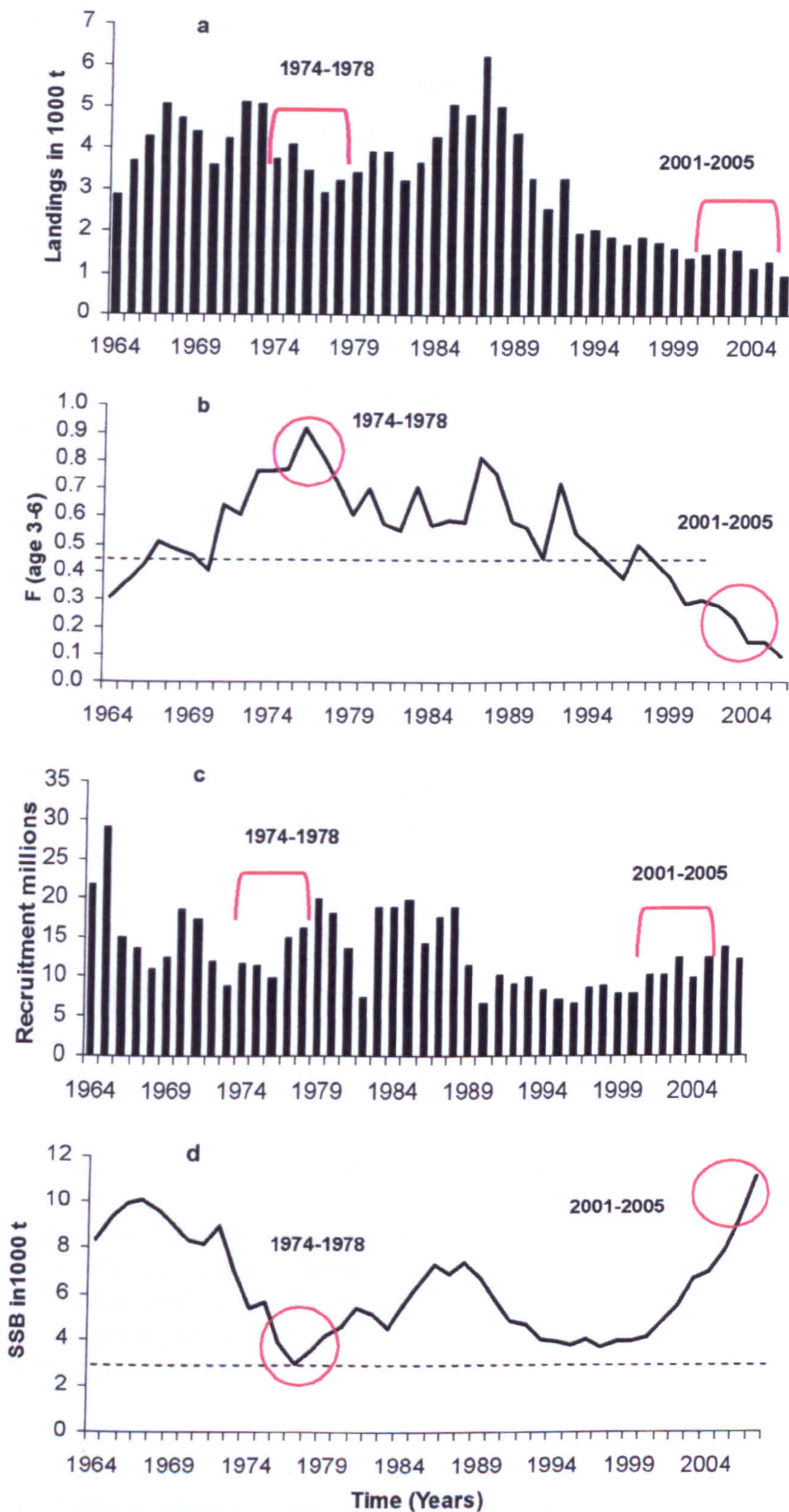


Figure 2.19: a) Landings (tonnes), b) fishing mortality (F , year⁻¹), c) recruitment (millions of fish) and d) spawning stock biomass (tonnes) for plaice *P. platessa* in the Irish Sea (ICES Division VIIa) between 1964 and 2006. Data redrawn from ICES (2008a).

and in the size of the adult spawning stock which is currently assessed as being at full reproductive capacity (ICES, 2008a). The target spawning stock biomass (B_{pa}) is 3100 tonnes and the estimated plaice spawning stock biomass in the Irish Sea has been at or in excess of this value since 1964 (Figure 2.19d). Since 2000, the spawning stock biomass has been increasing at an exponential rate ($Y = 3 \times 10^{-11} x e^{0.133X}$, $R^2 = 0.989$; Figure 2.19d) and is currently at the highest level on record since 1964 (11100 tonnes in 2007; ICES, 2008a). The underexploitation of the Irish Sea plaice can be seen in the ICES precautionary approach plot (Figure 2.20) which has shown that the stock has never been overfished (*i.e.* $SSB < B_{pa}$) although the plot would suggest that fishing pressure was high during the 1970s. Fishing mortality has been below the F_{pa} value of 0.45 year^{-1} since 1995 and Irish Sea plaice are currently well within the underfished quadrant (Beddington *et al.*, 2007) in the precautionary approach plot (Figure 2.20).

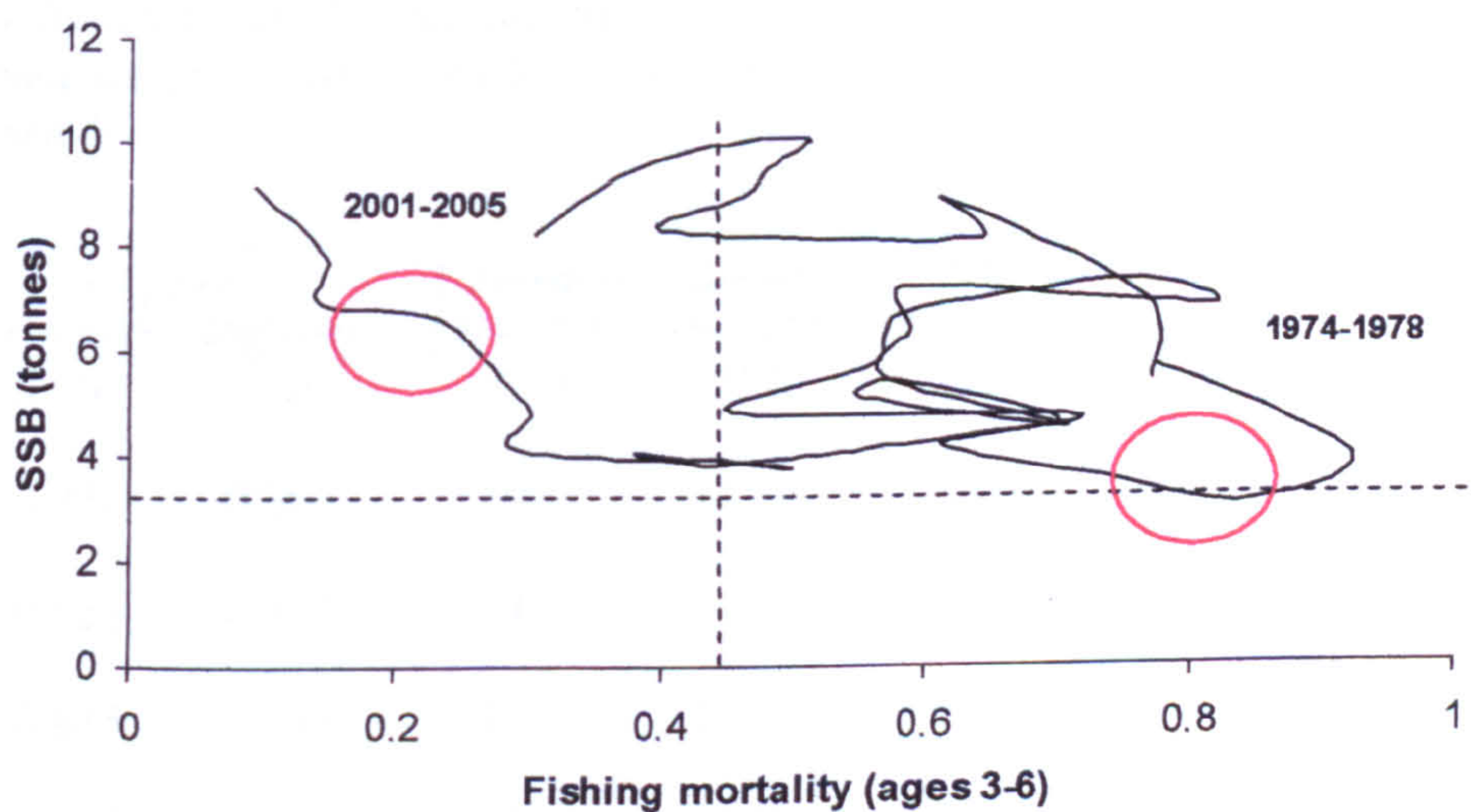


Figure 2.20. ICES precautionary approach plot for plaice *P. platessa* in the Irish Sea (ICES Division VIIa) between 1964 and 2006. F_{pa} ($F = 0.45 \text{ year}^{-1}$) and B_{pa} (3100 tonnes) are overlain on the plot for comparison. Data redrawn from ICES (2008a). The two time periods 1974-1978 (red oval) and 2001-2005 (red oval) are indicated on the figure.

2.4.3 Comparing the present study with Basimi (1978): 1974-77 vs. 2004-05

The results of the present study comprise a detailed survey of the population dynamics of plaice from the South East Irish Sea plaice stock located in the inshore

coastal waters of Beaumaris Bay and Red Wharf Bay in October/November 2004/05. Between 1974 and 1977, a similar study was conducted by Basimi (1978) in the same locations employing the same gear type (Rockhopper otter trawl) and using the same sampling methodologies as employed in the current study. Thus, the results of Basimi (1978) and this study are directly comparable and provide detailed information on the population ecology of the plaice population 30 years apart. It is interesting to note that these two studies have been conducted during two time periods with contrasting levels of fishing pressure on plaice in the Irish Sea. Basimi (1978) conducted his study at a time (1974-1978) when fishing mortality and landings were significantly higher (F , $t = 11.15$, 8 df, $p < 0.0001$; Landings, $t = 9.47$, 8 df, $p < 0.0001$) and the estimated spawning stock biomass was significantly lower ($t = 9.47$, 8 df, $p = 0.03$) compared to the present day (2001-2005) (Table 2.20, Figure 2.19a and d).

Table 2.20: A comparison of the instantaneous rates of fishing mortality (F , year⁻¹), Landings (tonnes) and estimated spawning stock biomasses (SSB, tonnes) for plaice in the Irish Sea for the periods 1974-1978 and 2001-2005. Source: ICES (2008a). Data are presented for each of the years plus the mean (\pm SD) values for each 5 year period.

F (year⁻¹)		Landings (tonnes)		SSB (tonnes)	
1974-1978	2001-2005	1974-1978	2001-2005	1974-1978	2001-2005
0.700	0.301	3715	1371	5427	4852
0.776	0.280	4063	1473	5669	5456
0.923	0.232	3473	1623	3903	6644
0.835	0.140	2904	1559	3003	6927
0.735	0.147	3231	1143	3541	7853
0.794	0.220	3477	1416	4309	6346
(\pm 0.088)	(\pm 0.065)	(\pm 444)	(\pm 188)	(\pm 1179)	(\pm 1180)

As highlighted in the ‘fishery history’ (Figure 2.19) and the ICES precautionary approach plots (Figure 2.20), Basimi assessed the population at a time when the stock could be considered to be overfished (1974-1977) whilst the present study was conducted on an underexploited stock (2004-2005). It is interesting to note that at the end of Basimi’s study, the estimated SSB for the stock attained its lowest value and fishing mortality attained its highest value since records began in 1964

(3003 tonnes in 1977; Table 2.20, Figure 2.19b and d). In contrast, in 2004-05, fishing mortality was the lowest to that date since records began in 1964 ($F \approx 0.145 \text{ year}^{-1}$) and SSB estimates were increasing (Table 2.20; Figure 2.19b and d).

The length-frequency distributions (1cm TL intervals) for 1974-1977 and 2004-2005 are presented in Figure 2.21 and show that the length profile of the plaice stock has changed over the 30 year time period. In Basimi's study, the modal size class was 20 cm TL (12 % of total catch) and 64% of the catch was between 18 and 24 cm TL, whilst in the present study, the modal size class was 23 cm TL with 58% of the total catch between 20 and 26 cm TL (Figure 2.21). When the data were divided into length classes (≤ 20 , 21-25, 26-30, 31-35, ≥ 36 cm TL; Figure 2.22a), there was a significant difference in the distribution of fish in the different size classes between 1974-77 and 2004-2005 ($\chi^2 = 154.4$, 4 df, $p < 0.0001$). The χ^2 analysis indicated that there were fewer plaice in the ≤ 20 cm TL size class (contribution of this size class to the $\chi^2 = 48.7$) and more fish in the 26-30 cm TL size class (contribution of this size class to the $\chi^2 = 82.8$) than expected in 2004/2005 compared to 1974-1977. This pattern can be clearly seen when the number of fish in each size class interval in 1974-77 (Basimi, 1978) and 2004-05 (this study) are expressed as a percentage of the total number of fish measured in each study and the Basimi value is subtracted from the value for the current study (Figure 2.22b). Thus, the results of these analyses clearly show that both as fishing pressure has decreased substantially the average size and proportion of larger fish in the stock have increased since Basimi conducted his study in 1974-77.

The age-frequency distributions (1 year intervals) for 1974-77 and 2004-05 are presented in Figure 2.23 and show that the age structure of the plaice stock has changed slightly over the 30 year time period. In Basimi's study, a wider age range was recorded in the catch compared to the present study (1^{++} to 15^{++} in 1974-77 *cf.* 1^{++} to 12^{++} in 2004-05) (Figure 2.23). Also, a greater percentage of the catch was comprised of older age classes (*i.e.* $\geq 5^{++}$ years old) of plaice in 1974-1977 (23 % of the total) compared to 2004-05 (6% of the total). When the data were divided into 5 age classes (*i.e.* 1^{++} , 2^{++} , 3^{++} , 4^{++} , $\geq 5^{++}$), there was a significant difference in the distribution of fish in the different age classes between 1974-77 and 2004-2005 ($\chi^2 = 119.4$, 4 df, $p < 0.0001$) due to the greater abundance of older fish in the 1974-1977

sample. When fish aged $\geq 5^{++}$ are removed from the χ^2 analysis, there was no difference in the age structure of the 1974-1977 and 2004-2005 data sets ($\chi^2 = 2.81$,

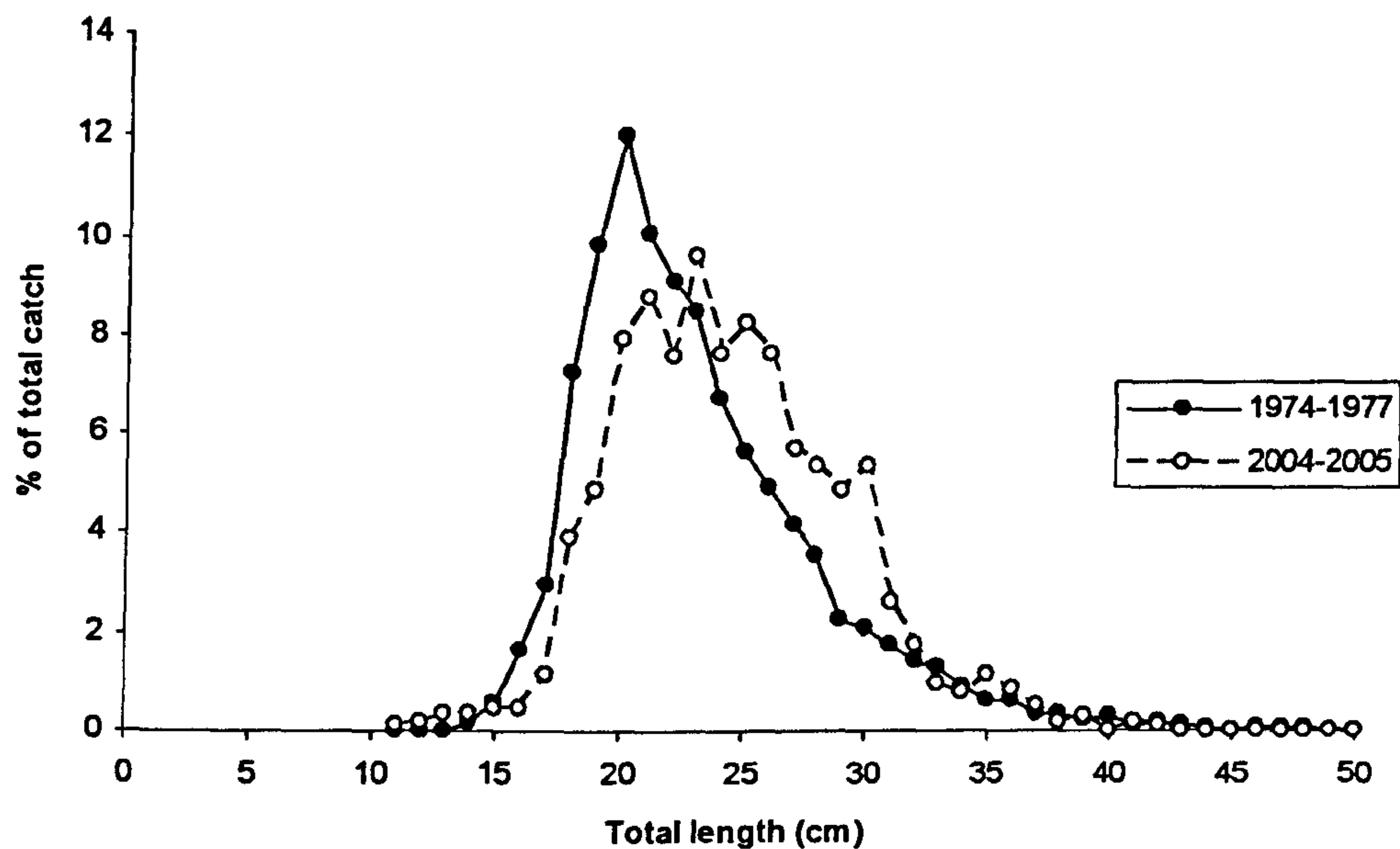


Figure 2.21: Length-frequency distribution (Total length, 1 cm length class intervals) for plaice *P. platessa* (data for males and females combined) plaice recorded by Basimi (1978) in 1974-1977 and in the current study (2004-2005).

3 df, $P=0.42$). Thus, the results of these analyses clearly show that both as fishing pressure has decreased substantially the average size and proportion of larger fish in the stock have increased since Basimi conducted his study in 1974-77. The variation in age structure may also be due to the difference in the amount of inshore/offshore sampling effort between the two studies. Both studies were conducted at similar times of the year, using similar gear, and a similar number of tows were conducted in both studies. However, the distribution of adult fish in the coastal waters of North Wales exhibits spatial variation (Basimi and Grove, 1985c) with fewer larger adult plaice being caught at the offshore sites (*i.e.* OPL and OCB) compared to the inshore sites (*i.e.* RWB, CON and ICB). If Basimi conducted more offshore tows in his 1974-1977 survey compared to the present study, this may also help to explain the greater abundance of larger/older fish in his study.

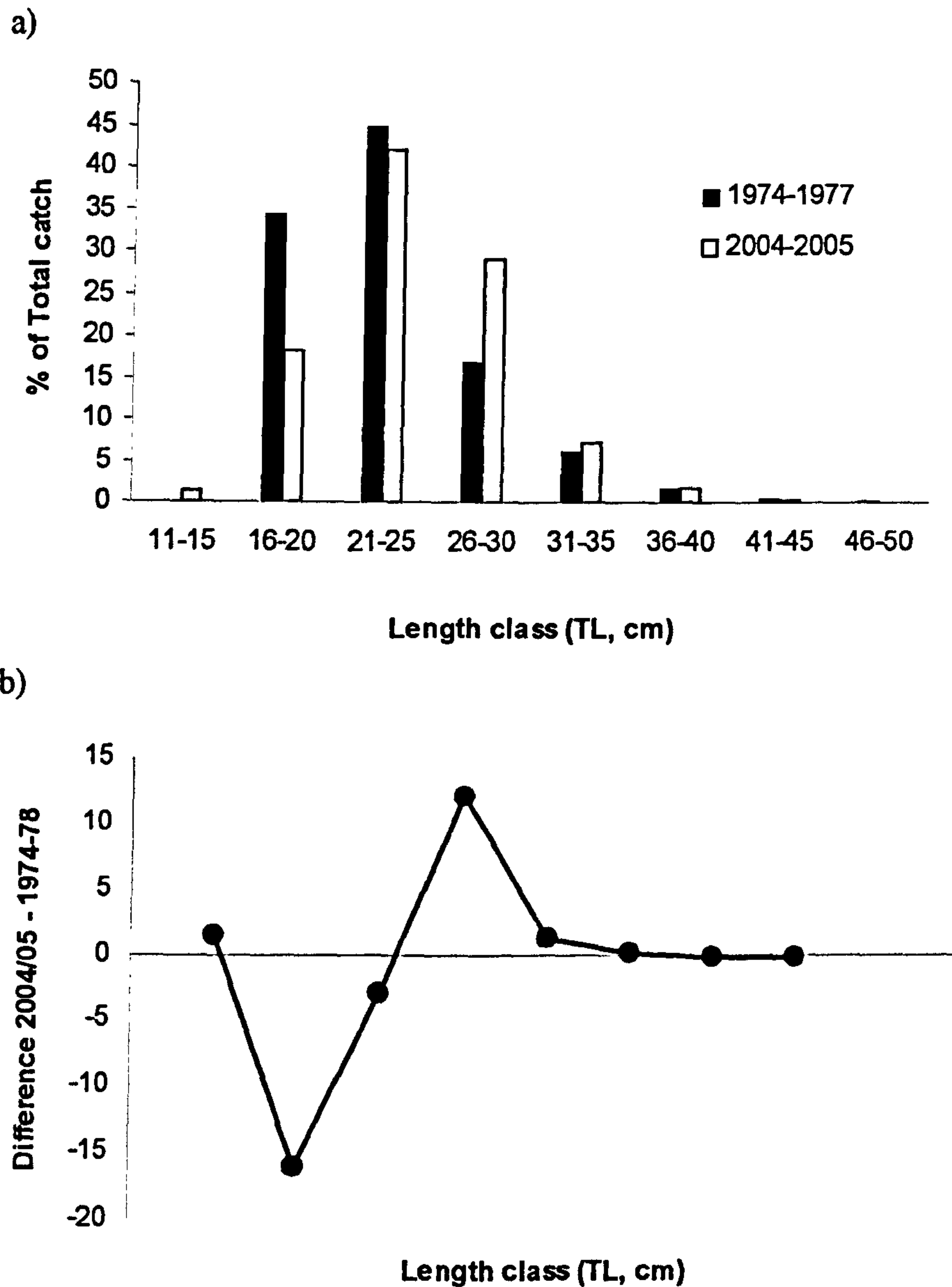


Figure 2.22. (a) Length-frequency distribution (Total length, 5 cm length class intervals) for plaice *P. platessa* (data for males and females combined) plaice recorded by Basimi (1978) in 1974-1977 and in the current study (2004-2005). (b) Relative difference between the percentage of plaice in each 5cm TL class interval (calculated as % in a given TL class in 2004-2005 minus % in a given TL class in 1974-1977).

The von Bertalanffy growth curves for plaice in the study area for 1974-1977 (using data from Basimi, 1978) and 2004-2005 are presented in Figure 2.24 with the growth coefficients presented in Table 2.21. In both studies, a similar sex-specific pattern in growth can be seen, with male fish growing faster and attaining a smaller theoretical maximum size at a younger age compared to female plaice (Figure 2.24,

Table 2.21). As discussed earlier, this difference in growth is common amongst temperate water marine teleost fishes (e.g. Chen *et al.*, 1992; Fossen *et al.*, 1999; Dwyer, *et al.*, 2001; Vinarge, *et al.*, 2008).

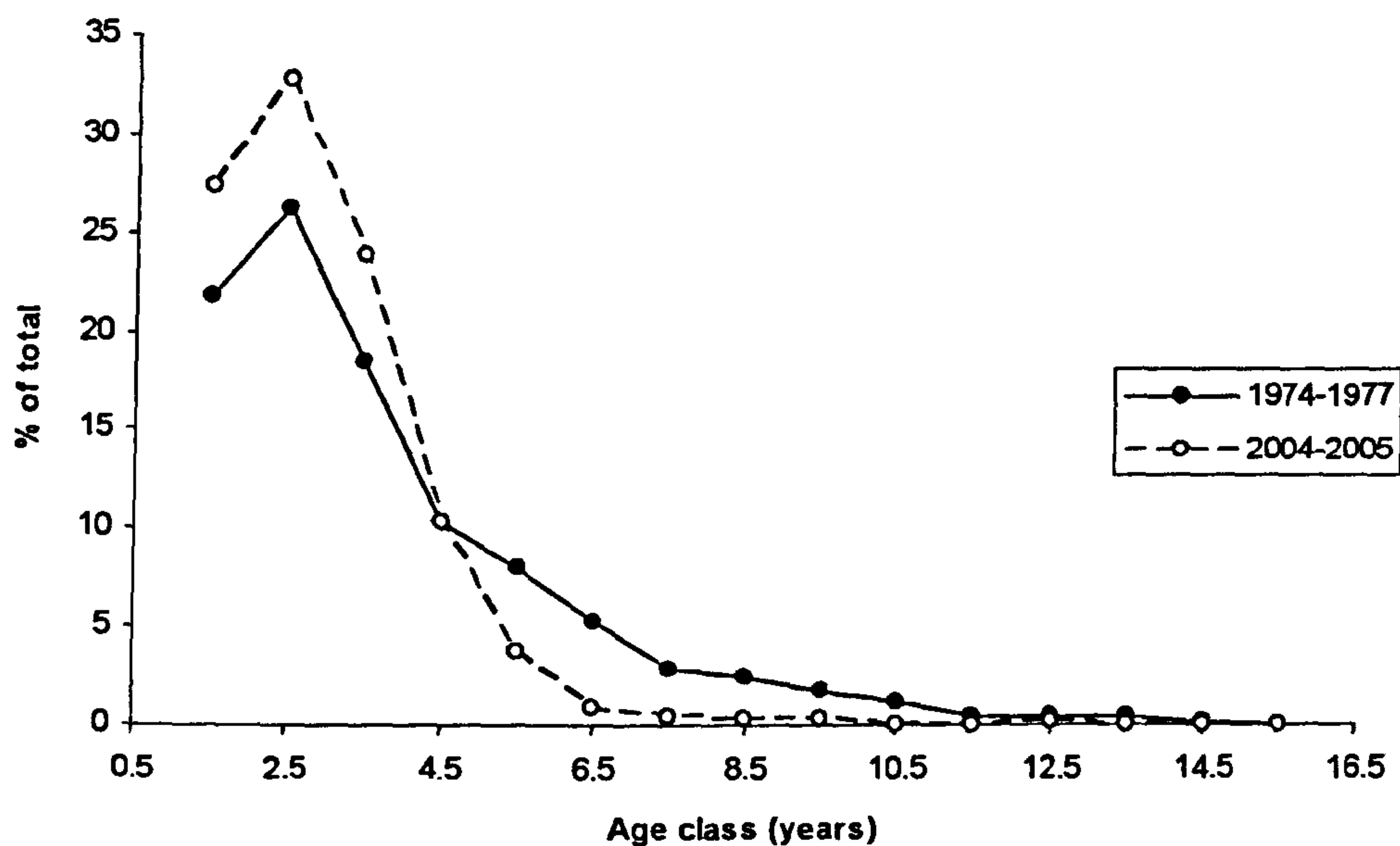


Figure 2.23: Age-frequency distributions for plaice *P. platessa* (data for males and females combined) plaice recorded by Basimi (1978) in 1974-1977 and in the current study (2004-2005).

Table 2.21. Von Bertalanffy growth parameters for male and female plaice reported by Basimi (1978) for 1974-1977 and in this study (2004-2005) caught in October/November in coastal waters off Eastern Anglesey and North West Wales. The L_{∞} values presented are for total length (cm).

Years	Parameters	Male	Female
1974-1977	L_{∞}	34.5 ± 0.795	47.6 ± 0.465
	K	0.336 ± 0.055	0.219 ± 0.012
	t_0	-1.003 ± 0.433	-0.970 ± 0.162
2004-2005	L_{∞}	31.1 ± 1.212	51.4 ± 1.690
	K	0.791 ± 0.188	0.282 ± 0.037
	t_0	-1.470 ± 0.184	-0.549 ± 0.220

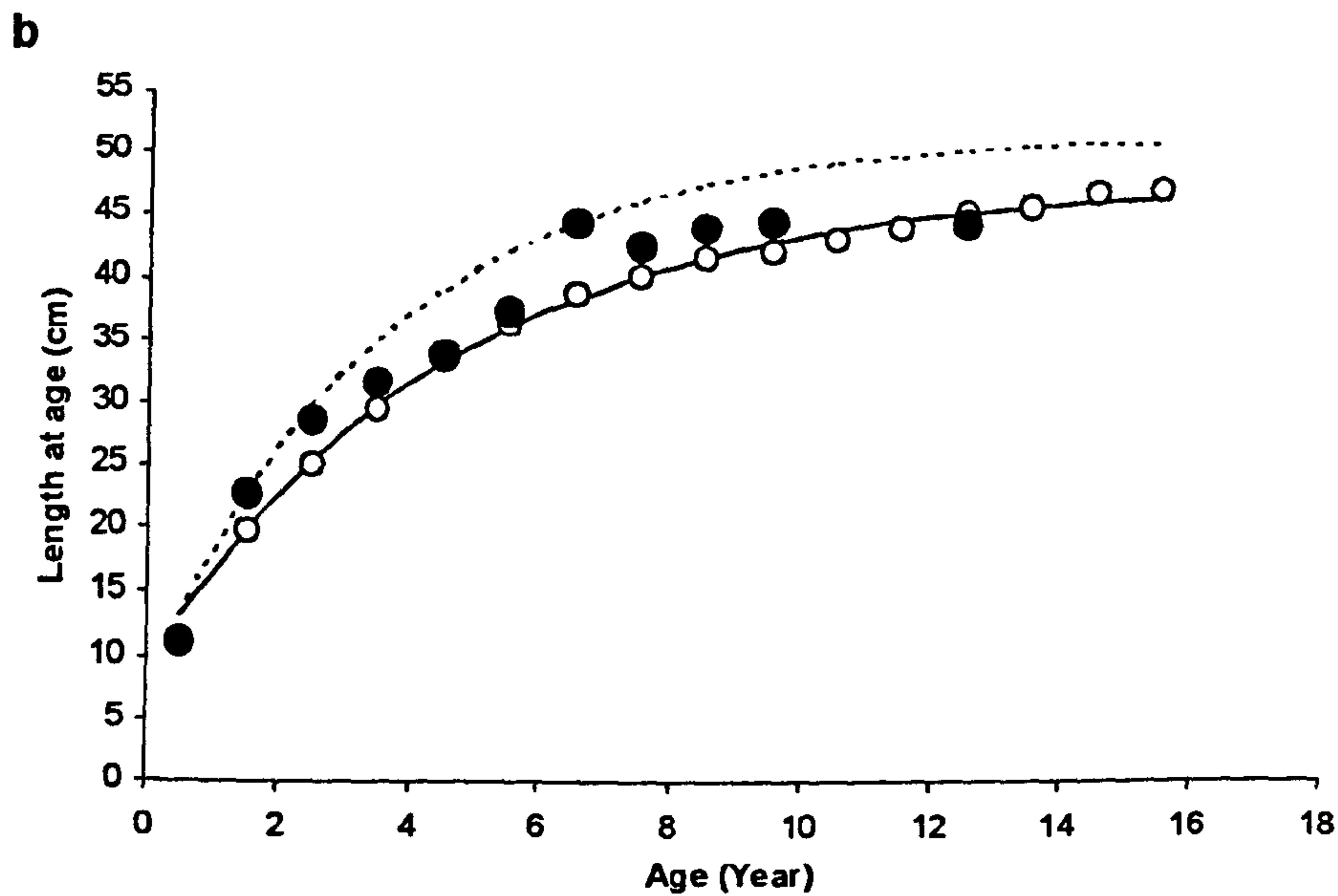
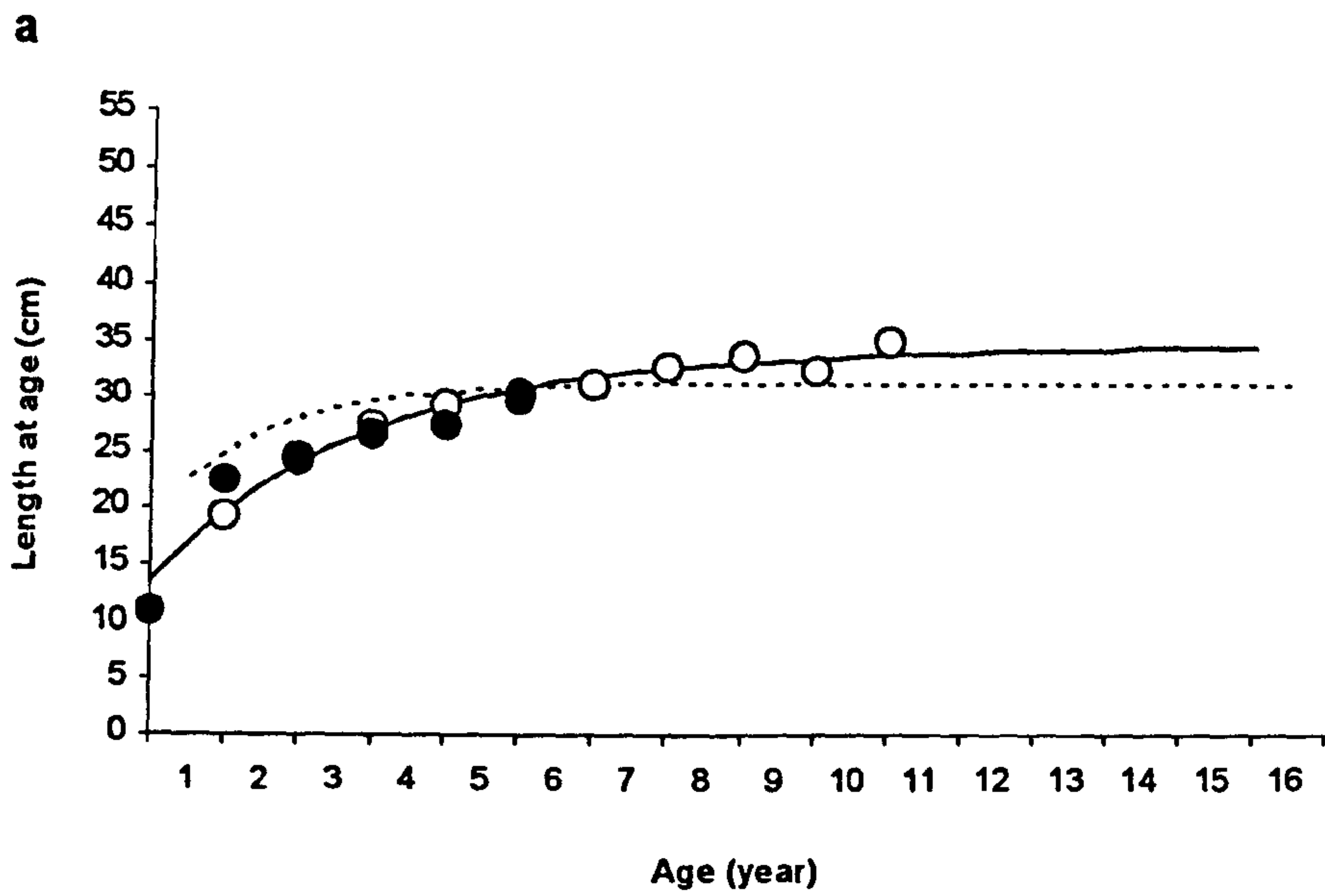


Figure 2.24: A comparison of growth curves of a) male and b) female plaice caught from South East Irish Sea, North West Wales by Basimi and Grove (1974-1977; open circles, solid line) and this study (2004 and 2005; solid circles, dotted line) for data collected from coastal waters off Eastern Anglesey and North West Wales.

From Table 2.21, it can also be seen that for male fish there has been a decrease in theoretical maximum size (L_{∞}) and a substantial increase in growth rate (k) between 1974-1977 and 2004-2005 whilst for female fish both of these values showed only a slight increase over time (Table 2.21). For both sexes, the von Bertalanffy growth curves for 1974-1977 and 2004-2005 were compared using the likelihood ratio test (Kimura, 1980) to examine whether there had been any significant changes in the growth pattern of either male fish or female fish over the 30 year time period. The results of the likelihood ratio test are presented in Table 2.22. For male fish, this analysis showed that all 3 von Bertalanffy coefficients were significantly different between the 1974-1977 and 2004-2005 growth curves and the overall shapes of the two growth curves were significantly different ($P < 0.0001$; Table 2.22). For female fish, significant differences in theoretical maximum size were found between the 1974-1977 and 2004-2005 growth curves, and marginally insignificant differences between the two growth coefficients ($P = 0.06$). As for male fish, the overall shapes of the two growth curves for female fish were significantly different ($P < 0.0001$; Table 2.22). Therefore, the likelihood ratio tests suggest that a significant change in the growth curves of male and female fish has occurred over the 30 year period. However, it is important to note that the 'shape' of the von Bertalanffy growth curve when the fish are young can be strongly influenced by the presence/absence of young fish in the data set and this can influence the slope of the curve (*i.e.* k value) and the intercept on the X-axis (*i.e.* t_0 value). The absence of any young fish, due to the fishing of areas not frequented by juveniles, or an unreliable estimate of average size-at-age for these young fish, due to gear selectivity resulting in small sample sizes (Gibson, 2005), can result in a growth curve with a more negative t_0 value and a lower k value. The 1974-1977 growth curves for male and female fish do show this pattern compared to the 2004-2005 growth curves (Table 2.21). In Basimi's study, the size of the 0-group fish were based on fish retained by the otter trawl and comprised of fish 14-17 cm TL: 0⁺⁺ ♂ = 16.0 cm TL, ♀ = 15.3 cm TL (Basimi, 1978). The selective retention of the larger fish in this age class may have resulted in an over-estimation of the average size-at-age of 0-group fish in October/November which would produce a growth curve with a more negative t_0 value and a lower k value.

Table 2.22: Comparison of von Bertalanffy growth curves for A = male (M) and B = female (F) plaice of 1= Basimi (1974-1977) and 2= this study (2004-2005) which both caught in the coastal waters off Eastern Anglesey and North West Wales were at different period of times, using the likelihood ratio test (Kimura, 1980).

A	Constraint	$L_{\infty} 1$	$L_{\infty} 2$	k 1	k 2	$t_0 1$	$t_0 2$	Res. SS	LR	df	P
Male (N=15)	None	31.1	34.5	0.791	0.336	-0.147	-1.003	9.55	-	-	-
	$L_{\infty} 1=L_{\infty} 2$	34.6	34.6	0.463	0.331	-0.557	-1.036	16.026	8.28	1	0.004
	k 1=k 2	37.1	34.7	0.325	0.325	-1.025	-1.09	22.456	13.74	1	0.0002
	$t_0 1=t_0 2$	38.5	35.3	0.263	0.282	-1.520	-1.520	28.933	17.73	1	<0.0001
	All above	34.6	34.6	0.325	0.325	-1.520	-1.520	55.17	20.20	3	<0.001
B	Constraint	$L_{\infty} 1$	$L_{\infty} 2$	k 1	k 2	$t_0 1$	$t_0 2$	Res. SS	LR	df	P
Female (N=26)	None	47.6	51.4	0.219	0.282	-0.970	-0.549	26.74	-	-	-
	$L_{\infty} 1=L_{\infty} 2$	49.63	49.63	0.180	0.320	-1.487	-0.419	34.57	5.4	1	0.0201
	k 1=k 2	46.9	53.4	0.240	0.240	-0.722	-0.785	31.60	3.5	1	0.0614
	$t_0 1=t_0 2$	47.5	53.1	0.223	0.238	-0.907	-0.907	32.78	4.30	1	0.0381
	All above	49.63	49.63	0.240	0.240	-0.907	-0.907	202.043	42.5	3	<0.0001

Note: 1 = 1974-1977 (Basimi, 1978) 2 = 2004-2005 (this study)
 LR = $-N * \ln(\text{Res SS}_{\text{no constraints}}/\text{Res SS}_{\text{constrained}})$

In contrast, in the current study, additional 0-group fish collected from Red Wharf Bay/Llanfairfechan at the same time of year were included in the estimates of the average size of male and female 0⁺⁺ plaice added to the growth curves (17 in 2004, 20 in 2005) due to the scarcity of 0⁺⁺ fish recorded in the otter trawl catches (zero in 2004 and 10 in 2005). This resulted in smaller average TL estimates for 0⁺⁺ plaice in the current study ($\sigma = 13.2$ cm, $\text{♀} = 13.3$ cm) compared to those recorded by Basimi (1978).

The maturity curves indicating the length and age at 50% maturity for plaice in the study area for 1974-1977 (using data from Basimi, 1978) and 2004-2005 (this study) are presented for male fish in Figures 2.25 (L_{50}) and 2.27 (A_{50}) and for female

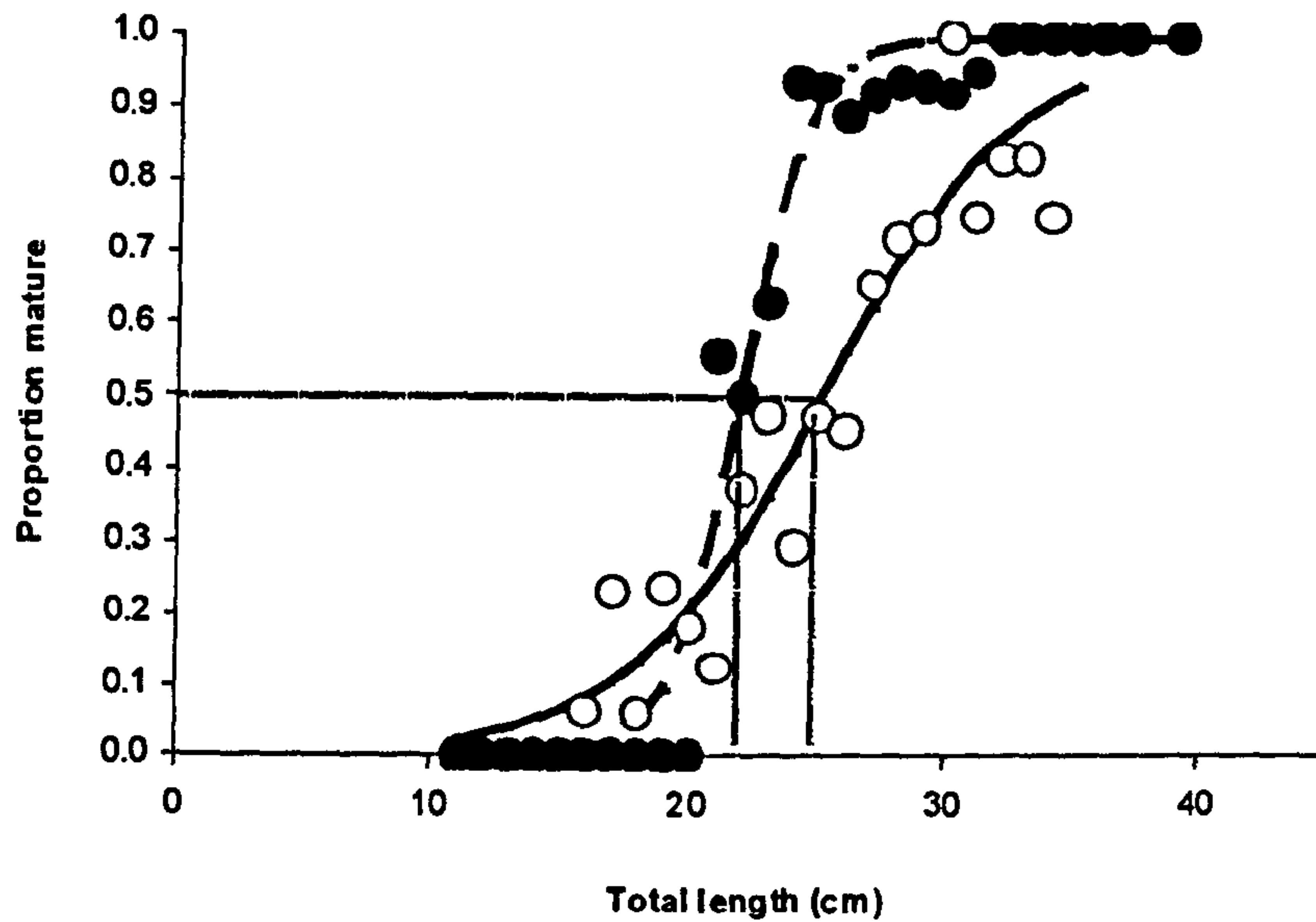


Figure 2.25. The estimated total length at first maturity (L_{50} , cm) for male plaice caught in October/November in the coastal waters of Eastern Anglesey and North West Wales, Irish Sea in 1974 – 1977 (open circles, solid line; Basimi, 1978) and 2004-2005 (solid circles, dashed line; this study). The dotted lines superimposed on the plot indicate the L_{50} values for 1974-1977 ($L_{50} = 25.1$ cm TL) and 2004-2005 ($L_{50} = 21.9$ cm TL).

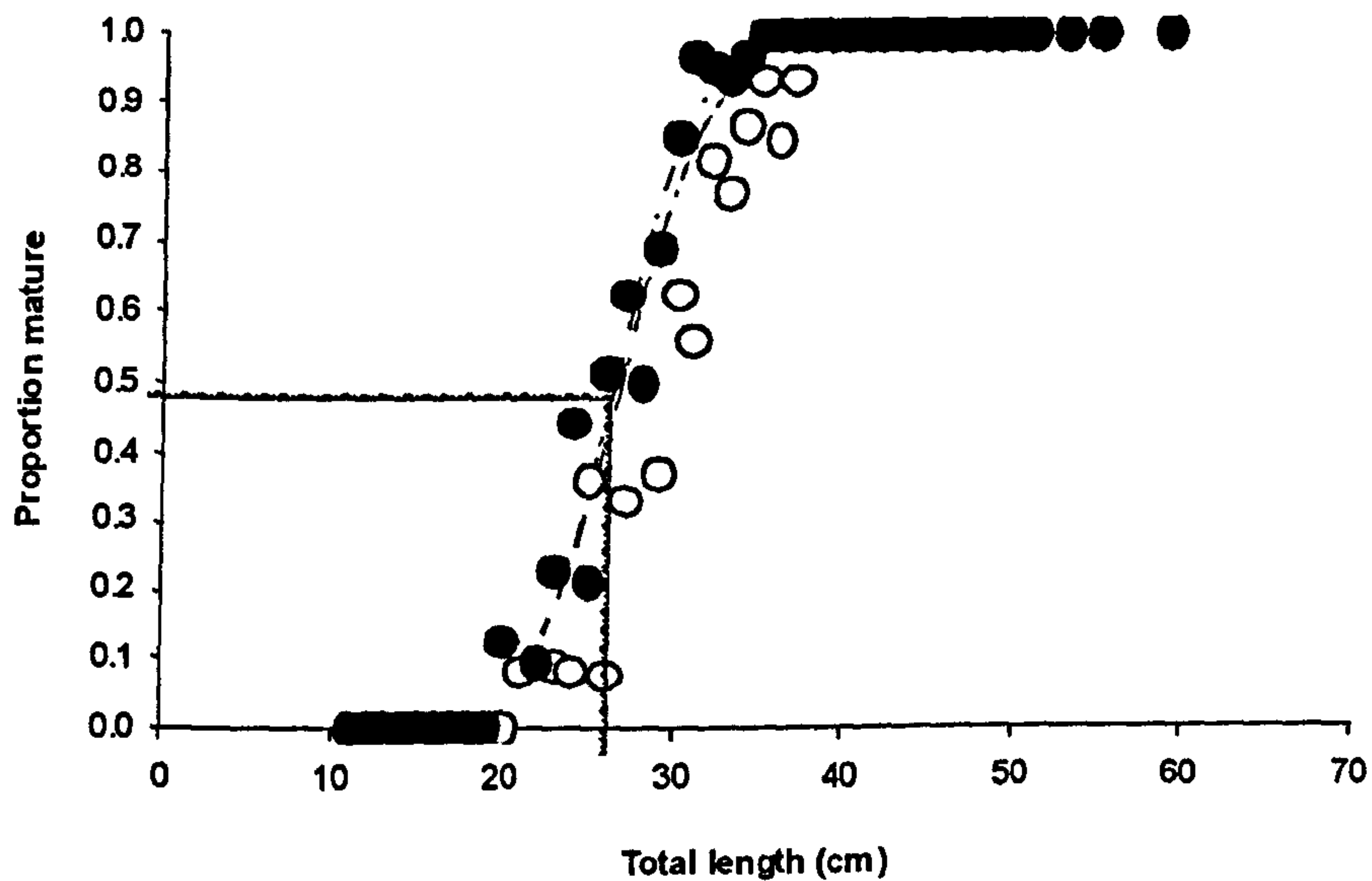


Figure 2.26. The estimated total length at first maturity (L_{50} , cm) for female plaice caught in October/November in the coastal waters of Eastern Anglesey and North West Wales, Irish Sea in 1974 – 1977 (open circles, solid line; Basimi, 1978) and 2004-2005 (solid circles, dashed line; this study). The dotted lines superimposed on the plot indicate the L_{50} values for 1974-1977 ($L_{50} = 26.3$ cm TL) and 2004-2005 ($L_{50} = 26.$ cm TL).

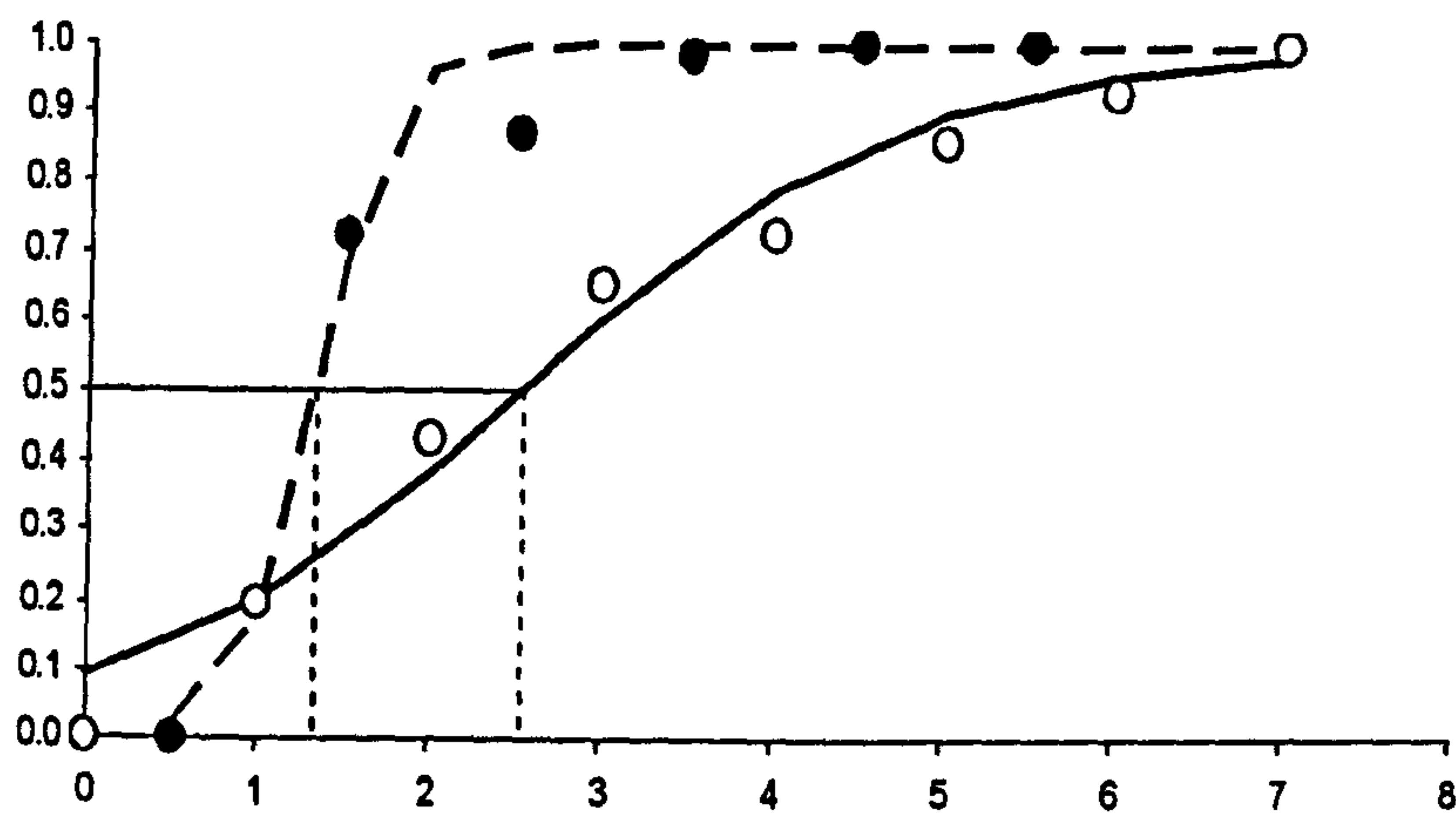


Figure 2.27. The estimated age at first maturity (A_{50} , years) for male plaice caught in October/November in the coastal waters of Eastern Anglesey and North West Wales, Irish Sea in 1974 – 1977 (open circles, solid line; Basimi, 1978) and 2004-2005 (solid circles, dashed line; this study). The dotted lines superimposed on the plot indicate the A_{50} values for 1974-1977 ($A_{50} = 2.5$ years) and 2004-2005 ($A_{50} = 1.3$ years).

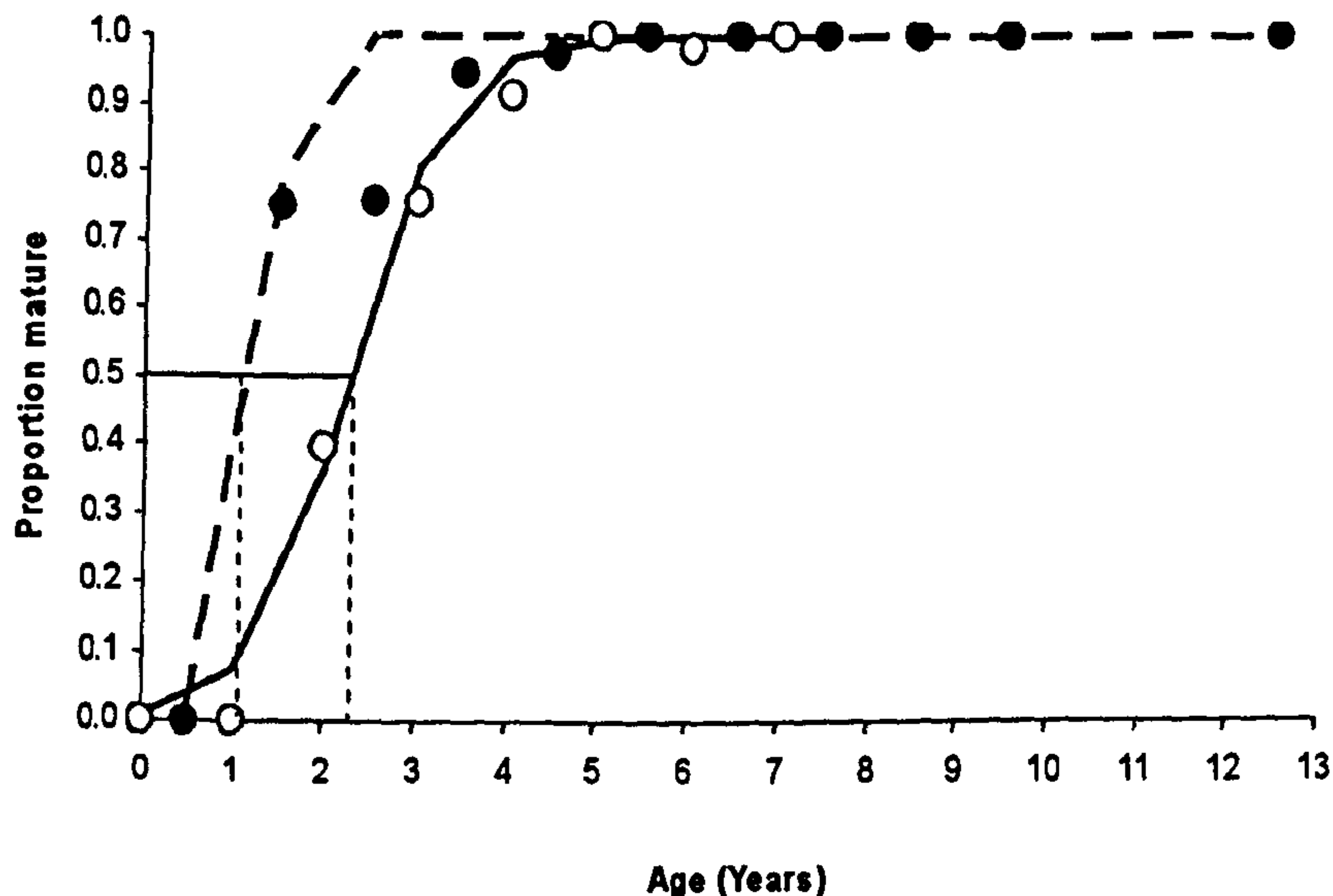


Figure 2.28. The estimated age at first maturity (A_{50} , years) for female plaice caught in October/November in the coastal waters of Eastern Anglesey and North West Wales, Irish Sea in 1974 – 1977 (open circles, solid line; Basimi, 1978) and 2004-2005 (solid circles, dashed line; this study). The dotted lines superimposed on the plot indicate the A_{50} values for 1974-1977 ($A_{50} = 3.02$ years) and 2004-2005 ($A_{50} = 1.30$ years).

fish in Figures 2.26 (L_{50}) and 2.28 (A_{50}) respectively. The logistic equations describing these maturity curves are presented in Tables 2.23 (L_{50}) and 2.24 (A_{50}).

These plots indicate that L_{50} has decreased for male fish by 3 cm between 1974-1977 and 2004-2005 but there has been little change in the L_{50} of female plaice

over the same time period (Table 2.23). In contrast, the A_{50} values for male and female plaice in 2004-2005 are much lower than those reported by Basimi in 1974-1977 (Table 2.24) with a decrease in the average age at maturity of 1.7 years for male fish and 0.9 years for female fish respectively.

Table 2.23: The estimation of length at first maturity (L_{50} , r , R^2 , Residual and P) of male and female plaice caught in the coastal water of Eastern Anglesey and North West Wales, Irish Sea on October 2004, 2005 and combined data.

Year	Fish Sexes	L_{50} (cm)	Slope (r)	R^2	P
1974 – 1977	Male	25.06 ± 0.414	0.269 ± 0.028	0.939	0.008
	Female	26.29 ± 0.320	0.354 ± 0.035	0.965	0.005
2004 and 2005	Male	21.92 ± 0.226	0.772 ± 0.119	0.969	0.007
	Female	26.46 ± 0.192	0.452 ± 0.035	0.986	0.003

Table 2.24: The estimation of age at first maturity (A_{50} , r , R^2 and P) of male and female plaice caught in the coastal water of Eastern Anglesey and North West Wales, Irish Sea on October 2004, 2005 and combined data.

Years	Fish Sexes	A_{50} (yr)	Slope (r)	R^2	P
1974 – 1977	Male	2.52 ± 0.183	0.900 ± 0.137	0.968	0.005
	Female	2.28 ± 0.076	1.984 ± 0.261	0.992	0.002
2004 and 2005	Male	1.30 ± 0.151	3.807 ± 2.244	0.938	0.010
	Female	1.26 ± 0.250	5.692 ± 5.741	0.944	0.006

To summarise, due to the use of the same sampling methodologies in the same locations, it has been possible to investigate changes in the population dynamics of the plaice population in the inshore coastal waters off Eastern Anglesey and North West Wales between 1974-1977 (Basimi, 1978) and 2004-2005 (this study) which correspond to time periods of heavy and low fishing pressure on plaice in the Irish Sea (Table 2.20; ICES, 2008a). The analyses presented here indicate that significant changes have occurred in the size-structure of the population (Figures 2.21 and 2.22), growth, *i.e.* changes in growth rate and maximum size (Figure 2.24, Table 2.21) and in the average length at maturity (Figures 2.25 and 2.26, Table 2.23). In addition, the

age at maturity of male fish has also changed (Figures 2.27 and 2.28, Table 2.24). Since the School of Ocean Sciences has been conducting these fishing surveys since 1972, it is possible to expand this analysis from the comparison of two time periods (*i.e.* 1974-1977 vs. 2004-2005) to the examination of a time-series of data from 1972 to the present and this will be the focus of Chapter 3.

2.4.4 Comparing the population dynamics of plaice in North West Europe.

The distribution of plaice *P. platessa* L. in the North East Atlantic ranges from the Atlantic coast of Andalusia in Southern Spain to the Barents Sea in the North plus the Western Mediterranean Sea, the Kattegat and Southern Baltic and around the coast of Iceland (URL 5). It is one of the most important flatfish species in Europe and has been exploited for centuries (Bolle *et al.* 2004). Commercial fisheries for plaice are to be found in the Barents Sea (Kuznetsova *et al.*, 2004), the Baltic Sea (Nielsen *et al.*, 2004; ICES, 2007c), and the coastal shelf seas of the Northeast Atlantic, such as the North Sea, Irish/Celtic Seas and the English Channel (Cefas 2008; ICES, 2008a, 2008b). Given its commercial importance, regular surveys on the population dynamics and biomass of these populations have been conducted (*e.g.* Basimi and Grove, 1985b; Rijnsdorp, 1989; Rijnsdorp and van Leeuwen, 1996; Bromley, 2000; Kuznetsova *et al.*, 2004; Nielsen *et al.*, 2004; Parker-Humphreys, 2004a, 2004b, 2005). These surveys provide information that is used by ICES to assess the current level of exploitation, the status of these stocks and to provide management advice (*e.g.* ICES 2008a, 2008b, 2008c). Therefore, it is possible to compare the results on the size/age structure, growth and maturity ogives for the SE Irish Sea plaice stock obtained in this current study (summarized in Figure 2.29) with contemporary data for other exploited plaice stocks in the coastal waters of North West Europe (summarized in Table 2.25, Figures 2.30-2.32). The available data for each population, presented separately for male and female plaice where possible, are presented in Table 2.25. Contemporary data on the size/age structure, growth and maturity ogives were available for plaice populations around the British Isles (*i.e.* the UK and Ireland: Celtic Sea, Bristol Channel, Irish Sea, English Channel and North Sea) plus the Kattegat and the Barents Sea. Unfortunately data were not available for any plaice

populations south of the English Channel, e.g. the Atlantic coasts of France, Spain and Portugal and for the Mediterranean.

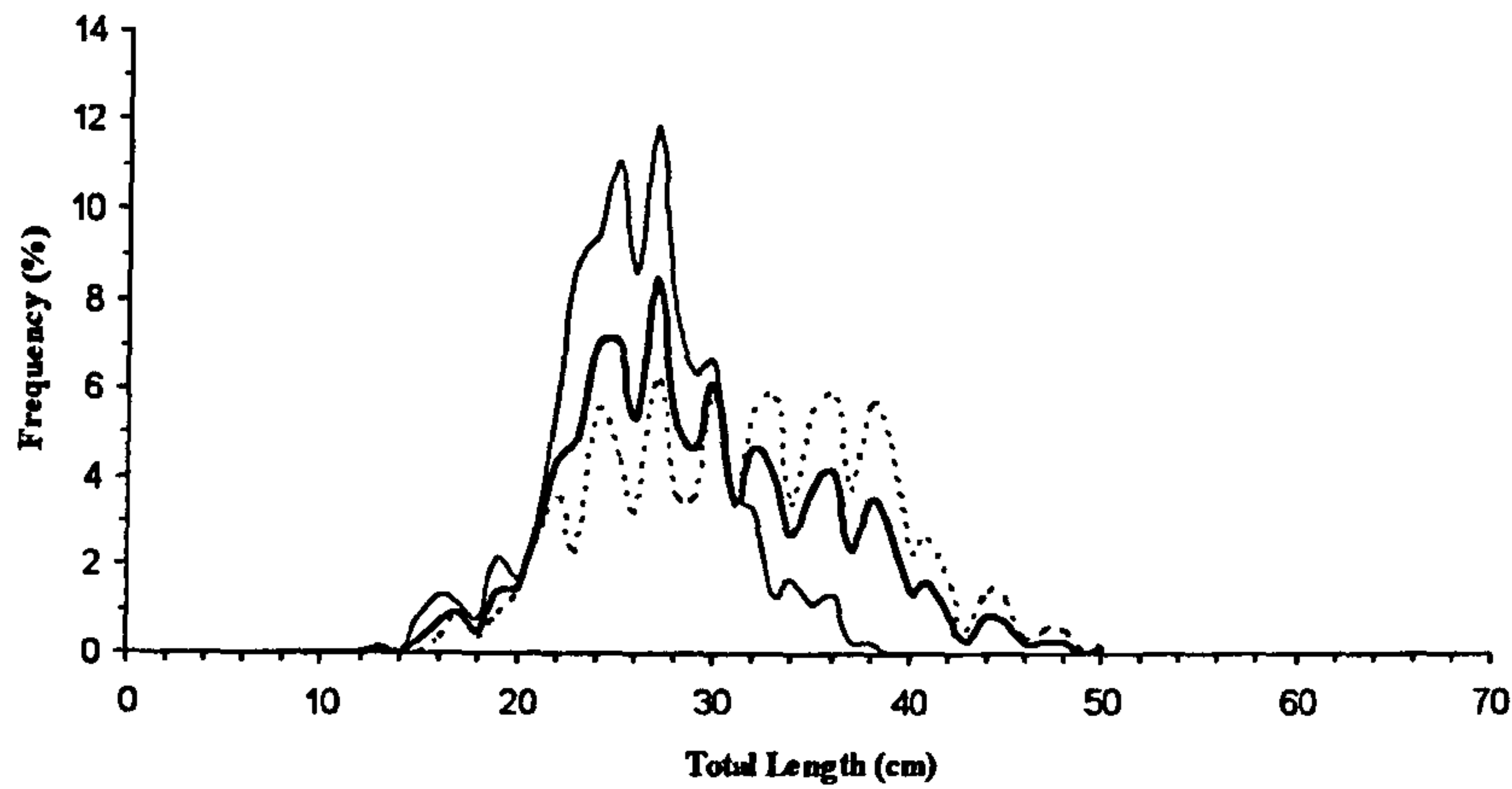
Comparison of the length frequency distributions (standardised as percentage frequency distributions to allow comparison between studies where sample sizes may be different) are presented in Figure 2.29 (South East Irish Sea stock, this study) and Figure 2.30 (other stocks). The percentage length frequency distributions were similar for most populations, with male plaice ranging in size from 6 to 35/40 cm TL and female plaice ranging in size from 6 to 50/60 cm TL and with modal total lengths (*i.e.* the most common size class in the catch and presumably the most common size class in the adult population) for male and female plaice in the mid 20s (Table 2.25). The exception to this pattern was the Barents Sea plaice population where the size range (males, 23-55 cm TL; females 23-84 cm TL) and modal size (males, 36 cm TL; females 41 cm TL) of male and female plaice were larger (Table 2.25). A size structure in the catches from the Barents Sea, comprising much larger fish, is most likely due to a larger mesh size of 120 mm that has been used in this fishery for longer than in UK waters (Kuznetsova *et al.*, 2004; Cefas, 2008) plus lower levels of exploitation compared to other plaice populations (Tables 2.1 and 2.25). However, this is the most northerly of the plaice populations studied and there is evidence that in fish species individuals tend to be slower growing and longer lived in northerly populations compared to more southerly populations of the same species.

As expected, all the plaice populations showed the same pattern of growth with males growing faster (higher k values) and attaining a smaller maximum size (lower L_{\max} values) compared to females (Table 2.25). L_{\max} values for male plaice ranged between 25 and 64 cm TL, with most populations exhibiting L_{\max} values of *ca.* 25-35 cm TL, with the exception being the Barents Sea (64.2 cm TL). In contrast, L_{\max} values for female plaice ranged between 42 and 64 cm TL, with most populations exhibiting L_{\max} values of *ca.* 42-50 cm TL, the exception again being the Barents Sea (88 cm TL). K values for male plaice ranged between 0.13 and 0.93 year⁻¹, with most populations exhibiting k values of *ca.* 0.3-0.7 year⁻¹. The exceptions to the general pattern were the Barents Sea ($K = 0.13$ year⁻¹) and the Bristol Channel ($K = 0.93$ year⁻¹). In contrast, K values for female plaice ranged between 0.07 and 0.31 year⁻¹, with most populations exhibiting K values of *ca.* 0.2-0.3 year⁻¹. The exceptions being low growth rates observed for female plaice in the Barents Sea ($K = 0.07$ year⁻¹) and the Western Irish Sea ($K = 0.11$ year⁻¹). The low K values observed in some

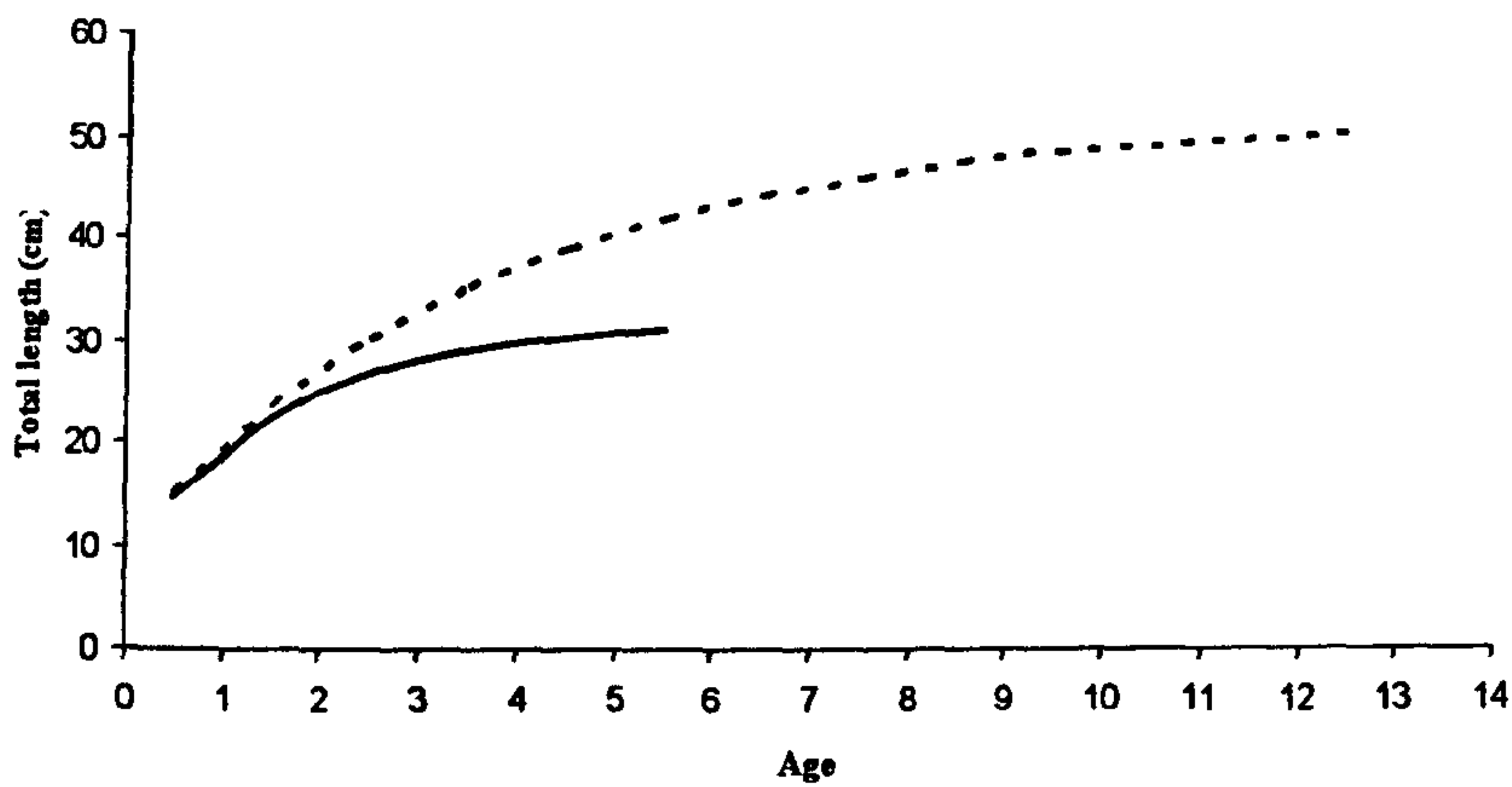
populations (e.g. the Barents Sea) may be true representations of the growth rates of male and female plaice but may also reflect the absence of smaller/younger age classes in the growth curve. In contrast, the L_{max} value of each population will be more accurate as a sufficient number of year classes were available for each study to allow the curve fitting programme in SPSS to determine the asymptote for the growth curve. The ratio of the L_{max} values for female:male plaice for the different populations are presented in Figure 2.33a. The ratios of $\text{♀ } L_{max} : \text{♂ } L_{max}$ for the different populations exhibited little variation and ranged from 1.2 to 2.0 (Figure 2.33a). On average, the L_{max} value for female plaice was 1.6 ± 0.3 times higher than the L_{max} value for male plaice from that population. The ratio of the growth coefficient values for male:female plaice for the different populations are presented in Figure 2.33b. The ratios of $\text{♂ } k : \text{♀ } k$ for the different populations exhibited less variation than the L_{max} values ranging from 1.0 to 3.0 (Figure 2.33b). On average, the k value for female plaice was 2.1 ± 0.7 times higher than the k value for male plaice from that population. The growth patterns of the male and female fish were the most similar in the plaice populations in the North Sea and Kattegat, which are areas where the plaice populations have had the longest histories of exploitation (Bolle *et al.*, 2004).

As expected, all the plaice populations showed the same pattern of maturation with males maturing at a smaller size (lower L_{50} values) and a younger age (lower A_{50} values) compared to females (Table 2.25). L_{50} values for male plaice ranged between 14 and 28 cm TL and for female plaice ranged between 22 and 33 cm TL. The largest L_{50} values (male and female) were found in the North Sea and English Channel plaice populations and the smallest L_{50} values found in the Kattegat and South East Irish Sea populations (Table 2.25). The ratio of the L_{50} values for female:male plaice for the different populations are presented in Figure 2.34a. The ratios of $\text{♀ } L_{50} : \text{♂ } L_{50}$ for the different populations exhibited little variation and ranged from 1.2 to 1.8 (Figure 2.34a). On average, the L_{50} value for female plaice was 1.4 ± 0.3 times higher than the L_{50} value for male plaice from that population. In most populations the age at 50% maturity in male plaice was 1 – 3 years old (average 1.6 ± 0.6 years), however, the A_{50} values for female plaice were more variable ranging from 1.9 (this study) to 4.5 (W. Irish Sea) years old (average 3.2 ± 1.3 years) (Table 2.25). The ratios of $\text{♀ } A_{50} : \text{♂ } A_{50}$ for the different populations ranged from 1.2 to 3.5 (Figure 2.34b) with the A_{50} value for female plaice 2.1 ± 0.8 times higher on average than the A_{50} value for male plaice from that population.

SE Irish Sea Plaice



SE Irish Sea plaice



SE Irish Sea plaice

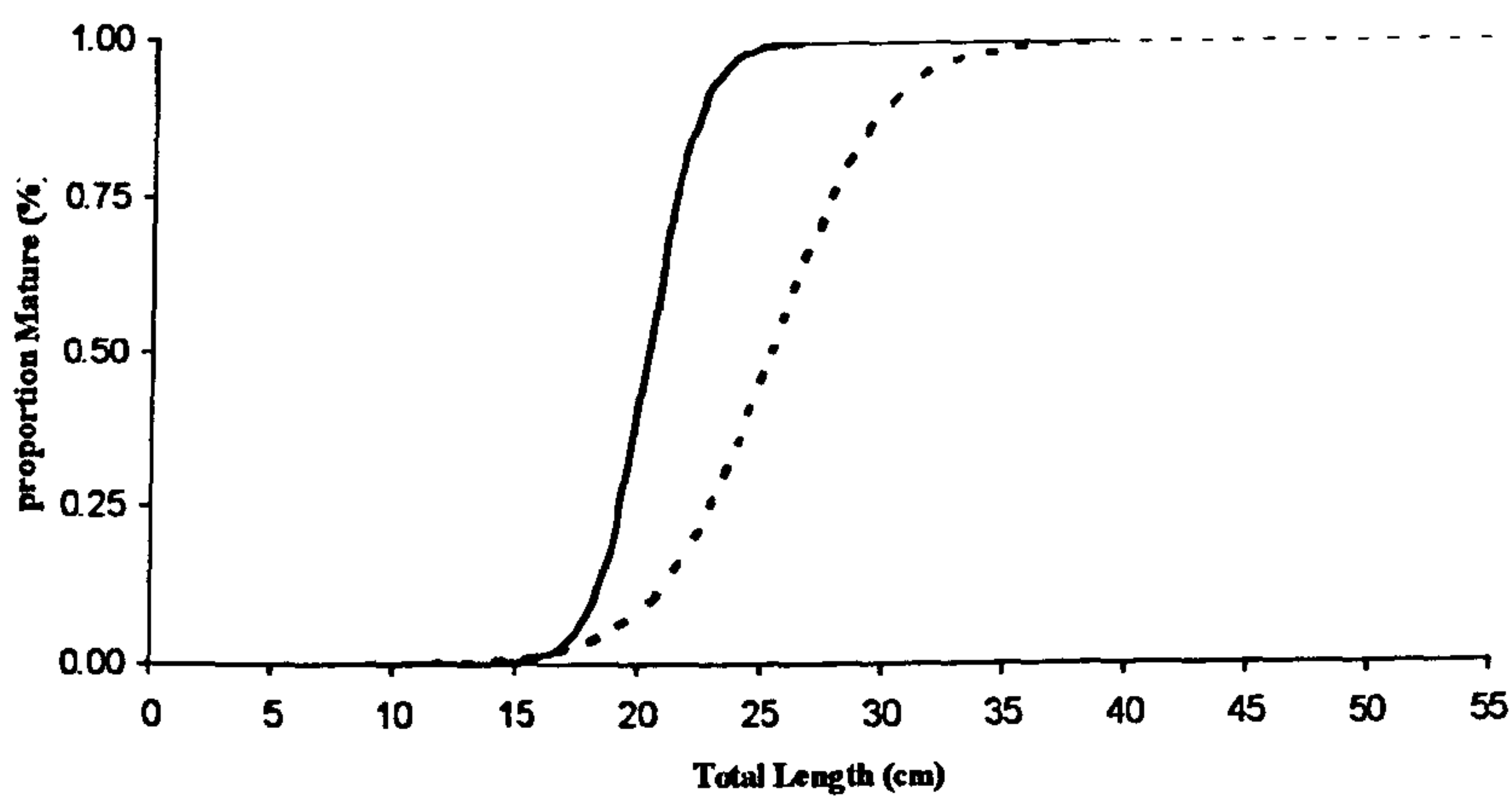


Figure 2.29. Percentage length frequency distributions (male, solid line; female, dotted line; combined data, bold solid line), von Bertalanffy growth curves (male, solid line; female dotted line) and length at 50% maturity (male, solid line; female, dotted line) for plaice *P. platessa* in the coastal waters of Eastern Anglesey and North West Wales (data source: this study).

Table 2.25: A summary of the biological characteristics of plaice *P. platessa* L. from different populations in the inshore coastal waters of North West Europe. Data are presented for von Bertalanffy growth coefficients (K , year⁻¹; L_{max} , cm Total length), maturity ogives [Length/Age at 50% maturity; L_{50} (cm TL)/ A_{50} (years)] and the size/age structure of the populations

Reference	Location	ICES	Date	SEX	K	L_{∞}	L_{50}	A_{50}	Modal TL	TL range	Modal Age	Age range
This Study	SE Irish Sea	VIIa	2004 –	♂	0.66	26.4	18.1	1.3	27	7.7 – 39.2	1	0 – 5
			2005	♀	0.25	43.8	21.8	1.9	27	7.5 – 54.8	2	0 – 12
Parker-Humphreys (2004a)	E Irish Sea	VIIa	1993 –	♂	0.52	29.9	19.0	1.5	23	6.7 – 39.1	1	0 – 16
			2001	♀	0.25	45.3	27.5	3.1	25	5.8 – 62.1	2	0 – 22
Parker-Humphreys (2004a)	W Irish Sea	VIIa	1993 –	♂	0.33	25.6	15.0	1.8	20	7.1 – 34.8	1	0 – 12
			2001	♀	0.11	53.8	26.5	4.7	21	7.3 – 48.6	2	0 – 13
BIM (2007)	Celtic Sea	VIIIh-k	2006	♂	0.21	37.4	-	-	30*	22 – 50*	-	2 – 10
				♀	0.12	64.1	-	-	-	-	-	-
Parker-Humphreys (2004b)	Bristol Channel	VIIIf	1993 –	♂	0.93	29.6	23.0	1.6	24	6.7 – 37.0	1	-
			2001	♀	0.31	44.8	29.5	2.6	25	5.8 – 51.4	1	-
Parker-Humphreys (2005)	English Channel	VIIId	1993 –	♂	0.51	26.2	28.0	2.9	29	7.0 – 45.6	1	-
			2001	♀	0.27	51.6	33.0	3.5	29	6.0 – 58.5	1	-
ICES (2008b)	North Sea	IV	2000 –	♂	0.31	34.0	28.0	1.3**	20*	5.0 – 50.0*	-	0 – 10*
			2003	♀	0.23	42.6	33.0	4.5**	-	-	-	-
Nielsen <i>et al.</i> (2004)	Kattegat	IIIa		♂	0.25	35.6	14.0	-	22*	8.0 – 38.0	-	-
				♀	0.26	42.7	23.8	-	-	4.0 – 55.0	-	-
Kuznetsova <i>et al.</i> (2004)	Barents Sea		1999 –	♂	0.13	64.2	-	-	36	23.0 – 55.0	6	4 – 12
			2001	♀	0.07	87.7	-	-	41	23.0 – 84.0	8	4 – 22

* = male and female data combined ** = calculated using equation $A_{50} = t_0 - (1/k) \ln[1 - (L_{50}/L_{\infty})]$ (Stergiou, 1999)

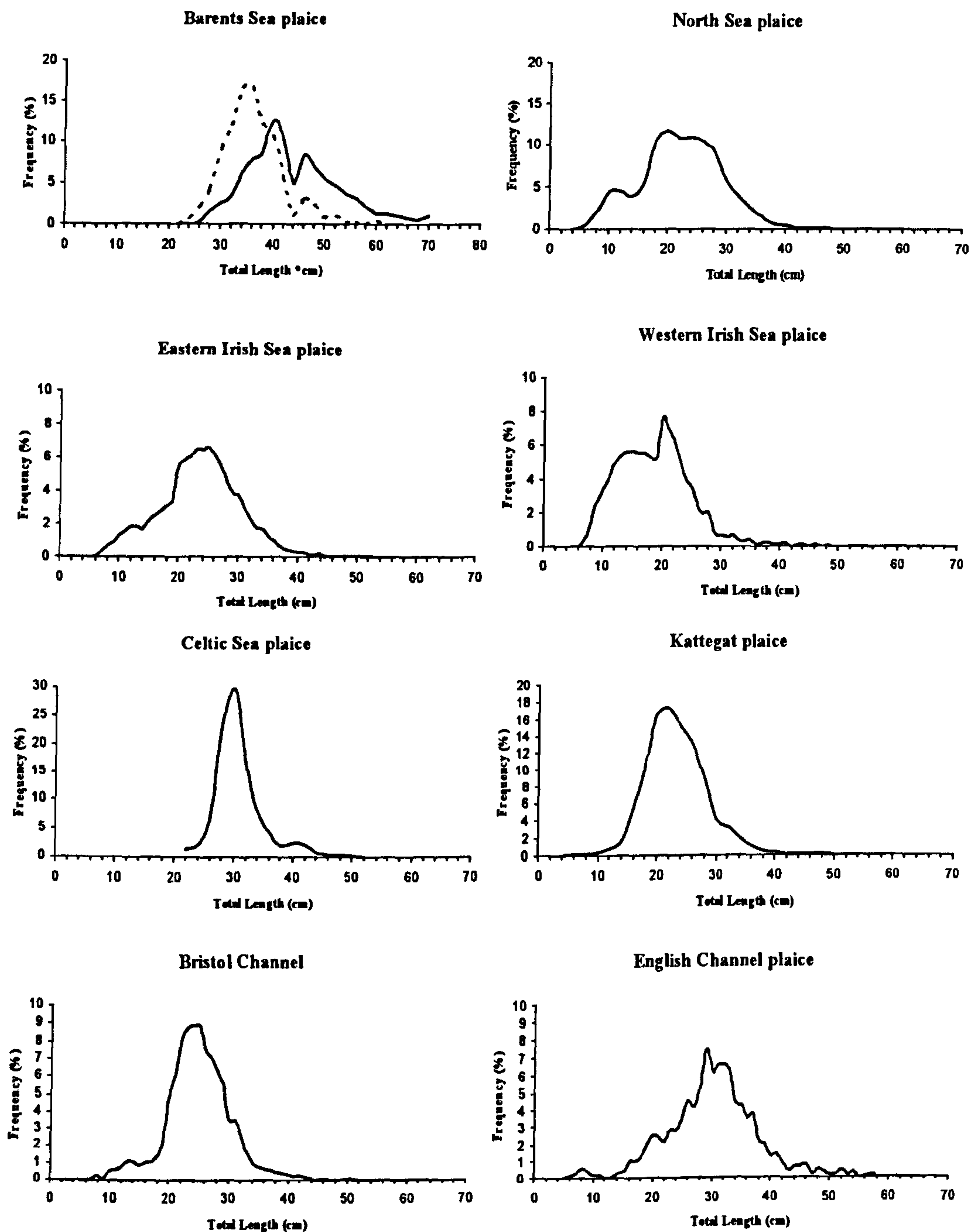


Figure 2.30: Percentage length frequency distributions (male, solid line; female, dotted line) for plaice *P. platessa* in the coastal waters of North West Europe. Data sources: Barents Sea (Kuznetsova *et al.*, 2004), North Sea (ICES, 2008b), Eastern Irish Sea (Parker-Humphreys, 2004a), Western Irish Sea (Parker-Humphreys, 2004a), Celtic Sea (BIM, 2007), Kattegat (Nielsen *et al.*, 2004), Bristol Channel (Parker-Humphreys, 2004b), English Channel (Parker-Humphreys, 2005).

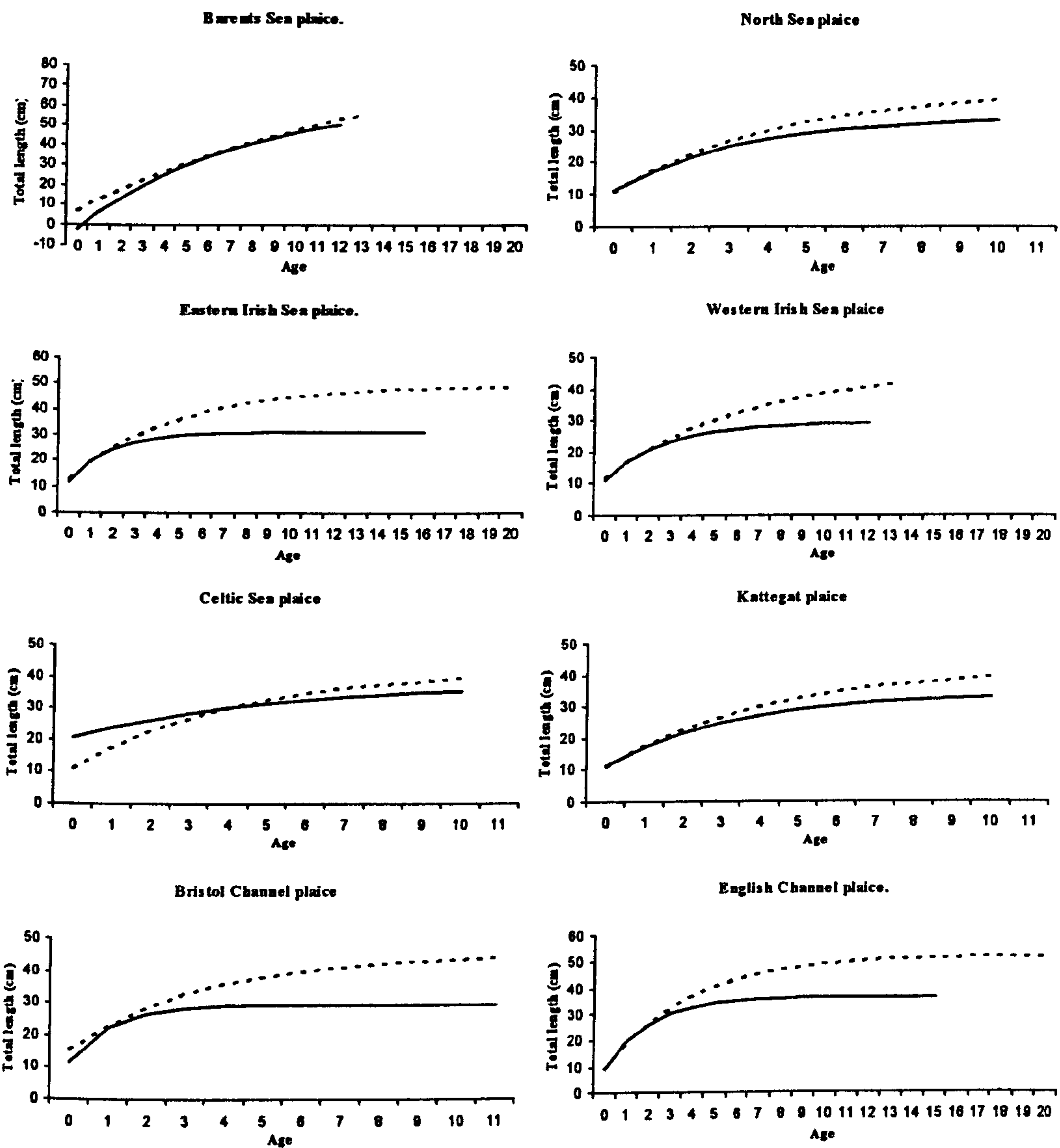


Figure 2.31: Von Bertalanffy growth curves (male, solid line; female, dotted line) for plaice *P. platessa* in the coastal waters of North West Europe. Data sources: Barents Sea (Kuznetsova *et al.*, 2004), North Sea (ICES, 2008b), Eastern Irish Sea (Parker-Humphreys, 2004a), Western Irish Sea (Parker-Humphreys, 2004a), Celtic Sea (BIM, 2007), Kattegat (Nielsen *et al.*, 2004), Bristol Channel (Parker-Humphreys, 2004b), English Channel (Parker-Humphreys, 2005).

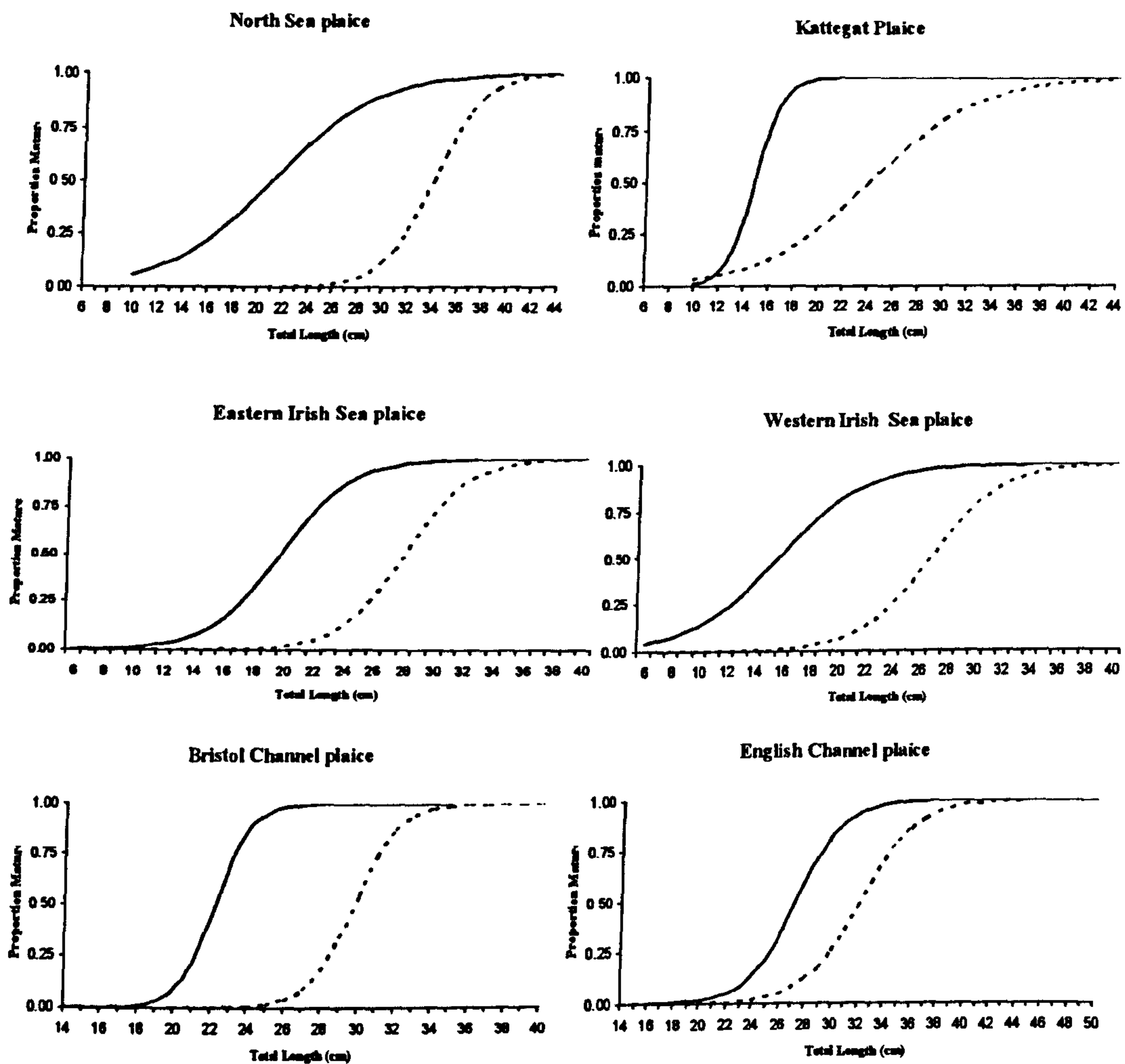
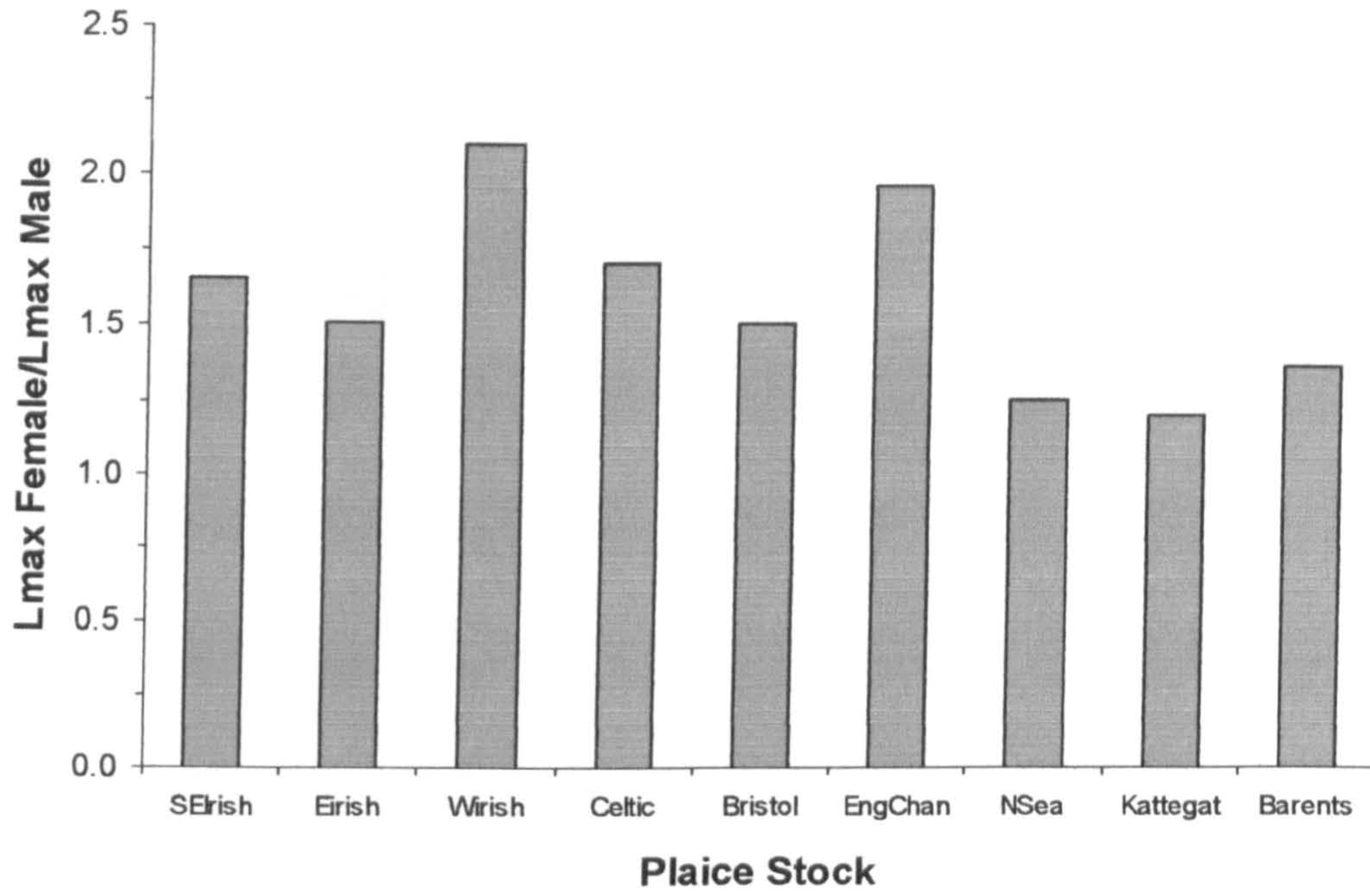


Figure 2.32. Maturity ogives (Length at 50% maturity) for plaice *P. platessa* (male, solid line; female, dotted line) in the coastal waters of North West Europe. Data sources: North Sea (Rijnsdorp, 1985), Kattegat (Nielsen *et al.*, 2004), Eastern Irish Sea (Parker-Humphreys, 2004a), Western Irish Sea (Parker-Humphreys, 2004a), Bristol Channel (Parker-Humphreys, 2004b), English Channel (Parker-Humphreys, 2005).

a)



b)

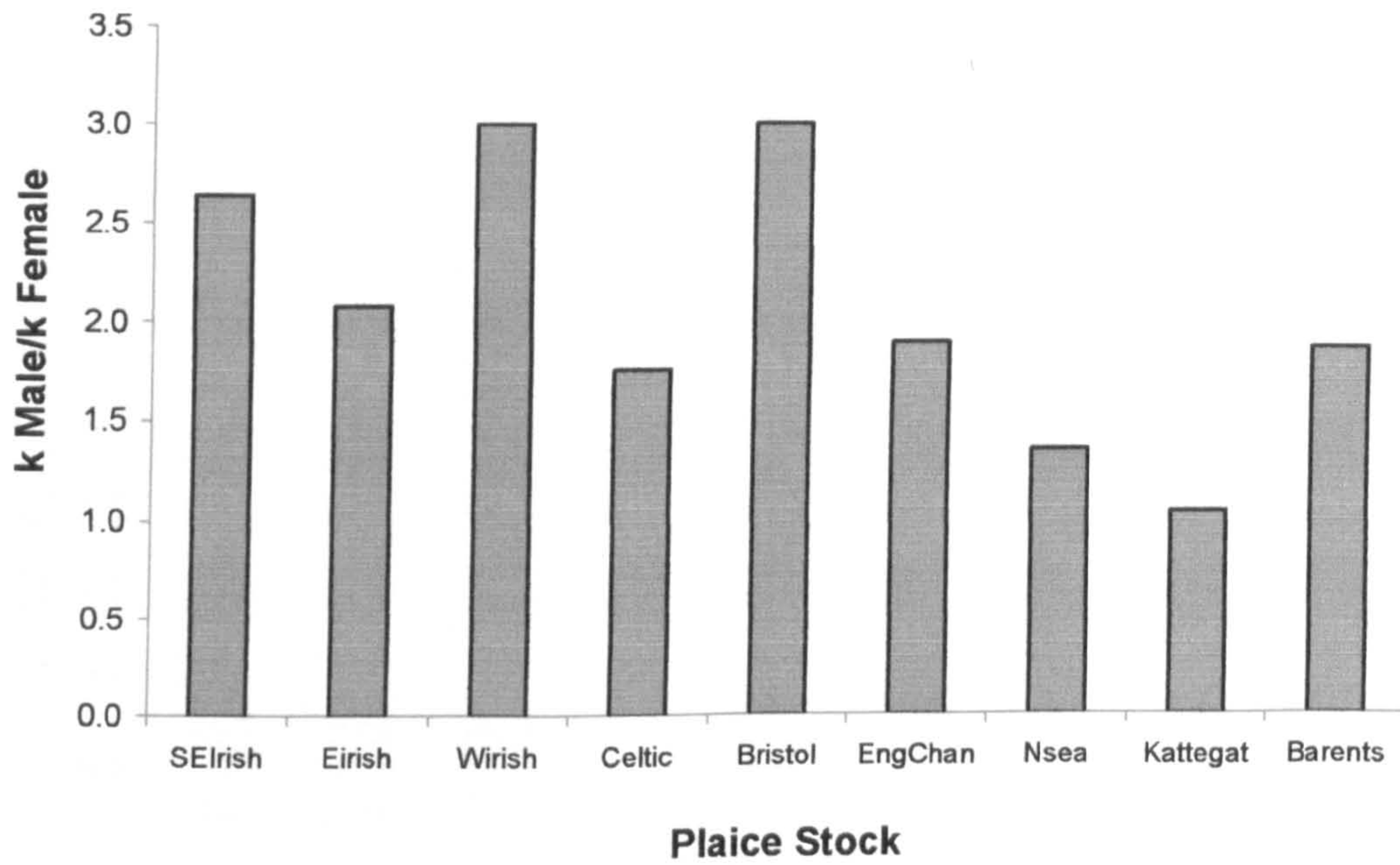
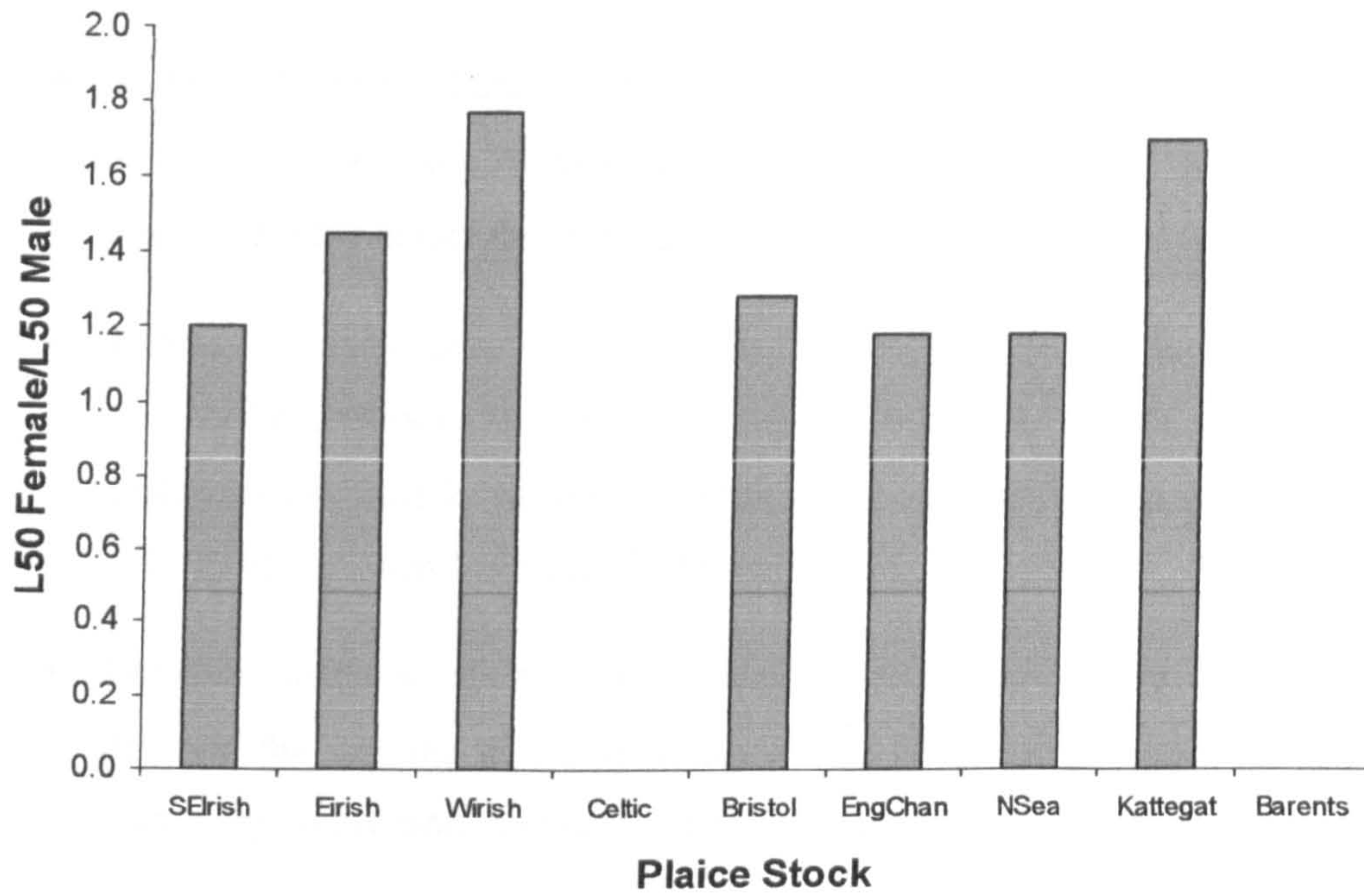


Figure 2.33. Differences between the Von Bertalanffy growth coefficients of male and female plaice from different stocks of plaice *P. platessa* in the coastal waters of North West Europe expressed as the ratio of the female value/male value. Ratios are presented for (a) L_{max} (TL cm) and (b) K ($year^{-1}$) values from data presented in Table 2.25.

a)



b)

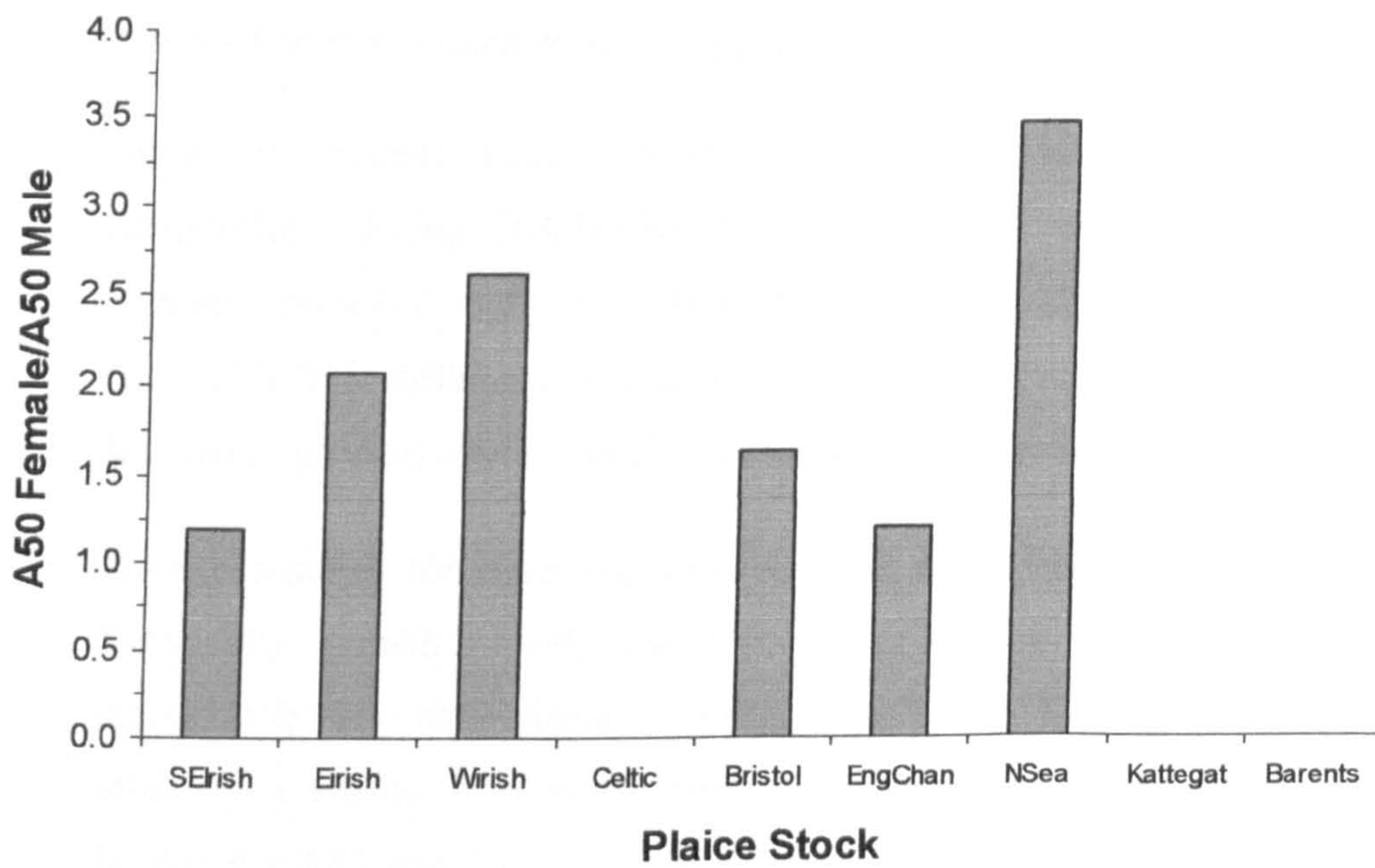


Figure 2.34. Differences between the maturity ogives of male and female plaice from different stocks of plaice *P. platessa* in the coastal waters of North West Europe expressed as the ratio of the female value/male value. Ratios are presented for (a) L_{50} (TL cm) and (b) A_{50} (years) values from data presented in Table 2.25. Missing data in the plot indicates that values are not available for this population.

2.4.5 Summary

- A detailed survey of the population ecology of the European plaice *P. platessa* L. in the inshore coastal waters of North West Wales and Eastern Anglesey was conducted in October/November in 2004 and 2005.
- Catches of plaice were obtained from three inshore (Red Wharf Bay, Conwy Bay, Inshore Colwyn Bay) and two offshore (Offshore Point Lynas, Offshore Colwyn Bay) sites by rockhopper Otter trawl (stretched mesh size of cod end = 76 mm) deployed from the RV *Prince Madog*.
- Detailed analyses of the length-stratified subsample were conducted to describe the size/age structure, length/weight relationship, size-at-age growth curves, mortality rates and length/age at maturity for male and female plaice.
- Examination of the length-stratified sub-sample showed that the size/age structures of male and female plaice were different with the older, larger and heavier fish in the catch comprising predominately of female fish.
- Male and female plaice exhibited differences in their length/weight relationships during October/November 2004/2005 with males exhibiting isometric growth ($b = 3.02$) and females exhibiting positive allometric growth ($b = 3.20$). This difference was attributed to increased reproductive investment (*i.e.* larger gonads) seen in female fish at this time of year.
- Growth patterns for male and female plaice were described using the von Bertalanffy growth model. The growth curves for the two sexes were significantly different with male plaice exhibiting significantly faster growth rates and attaining a smaller theoretical maximum size compared to female plaice (males, $k = 0.66 \text{ year}^{-1}$, $L_{\infty} = 26.4 \text{ cm}$; females, $k = 0.25 \text{ year}^{-1}$, $L_{\infty} = 43.8 \text{ cm}$).
- Although the instantaneous rate of total mortality (Z , year^{-1}) tended to be higher in males ($Z = 1.05 \text{ year}^{-1}$) than females ($Z = 0.64 \text{ year}^{-1}$), no significant difference was found between the two sexes.
- Male and female plaice exhibited differences in their length (L_{50}) and age (A_{50}) at 50% maturity. The results showed that males mature at smaller sizes

and younger ages (male $L_{50} = 18.1\text{cm}$, $A_{50} = 1.3$ years) compared to females (female $L_{50} = 21.8\text{ cm}$, $A_{50} = 1.9$ years).

- The results of the present study (October/November 2004/2005) were compared with an earlier study conducted by Basimi (1978) in October//November 1974-1977. These two studies being conducted during periods of heavy (1974-1977) and low (2004-2005) fishing pressure. The results of the comparative analysis showed that the size structure of the stock had increased in 2004/2005 but there was a decrease in the number of older (*i.e.* $>5^{++}$ years old) fish present in the catch. Significant differences in patterns of growth of both male and female fish were seen between 1974-1977 and 2004-2005. Growth rates increased for both males (K , year^{-1} ; 1974-1977 = 0.34 vs. 2004-2005 = 0.79) and females (K , year^{-1} ; 1974-1977 = 0.0.22 vs. 2004-2005 = 0.28) whilst the theoretical maximum size decreased for males (L_{∞} , cm; 1974-1977 = 34.5 vs. 2004-2005 = 31.1) but increased for females (L_{∞} , cm; 1974-1977 = 47.9 vs. 2004-2005 = 51.4). Examination of the pattern of maturity showed a decrease in L_{50}/A_{50} values for male plaice (1974-1977, $L_{50} = 25.1\text{ cm}/ A_{50} = 2.5$ years; 2004-2005, $L_{50} = 21.9\text{ cm}/ A_{50} = 1.3$ years). In contrast, female plaice showed a change in age at maturity (1974-1977, $A_{50} = 2.3$ years; 2004-2005, $A_{50} = 1.3$ years), but no change in length at maturity (1974-1977, $L_{50} = 26.3\text{ cm}$; 2004-2005, $L_{50} = 26.5\text{ cm}$).
- A meta-analysis of the population biology of exploited populations of plaice from different inshore coastal populations in North West Europe (English Channel, Bristol Channel, Irish Sea, Celtic Sea, North Sea, Kattegat and Barents Sea) was conducted using the available data. This analysis revealed consistent similarities in the size-structure and the patterns of growth and maturation between the populations with the exception being the Barents Sea population. Consistent sex-specific differences were also observed which follow the patterns expected for temperate water marine teleost populations with male fish growing faster and attaining a smaller maximum size than females and reaching maturity at a smaller size and younger age.

Chapter 3:

Changes in the population biology of plaice *Pleuronectes platessa* L. in the coastal waters of Northwest Wales and Eastern Anglesey between 1970 and 2006 compared to other demersal fish species and in relation to fishing pressure and climate change.

3.1 Introduction

Long-term data sets are proving to be a valuable resource in understanding the cyclical nature in the distribution and abundance of marine organisms and the factors responsible for these changes (Southward, 1995). It is self-evident that overfishing can alter distribution and abundance patterns of fishes, however, it is also becoming clear from the study of long-term data sets that various environmental/climatic cycles also influence the distribution and abundance of marine organisms (*e.g.* Attrill and Power, 2002; Chavez *et al.*, 2003; Genner *et al.*, 2004; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008; Frid *et al.*, 2009). Climate change can influence the structure and function of marine ecosystems in two ways: direct effects on the organisms themselves or indirect effects through changes in ocean currents (Southward *et al.*, 1995). Ultimately, spatial and temporal fluctuations in marine species abundance will be the result of physical and biological processes which affect the production and survival of eggs and larvae, growth and mortality during the juvenile and adult phases and other factors such as migration patterns and environmental carrying capacity (Jennings, *et al.*, 2001).

Long-term data sets, of varying lengths of time, are now available for a range of marine organisms from plankton through to fishes (*e.g.* Klyashtorin, 2001; Beaugrand *et al.*, 2002, 2003; Beaugrand and Reid, 2003; Hiscock *et al.*, 2004; Hays *et al.*, 2005; Frid *et al.*, 2009). However, some of the most comprehensive data sets, and those showing the most marked changes in response to climate change, are for rocky shore intertidal habitats (*e.g.* Barry *et al.*, 1995; Sagarin *et al.*, 1999; Southward *et al.*, 2005; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008). The length and nature of these data sets varies. For example, a data set may be based on the direct observation/measurement of organisms as part of an ongoing monitoring programme: these data sets are usually less than 100 years in length (although see for example, Jonsson, 1994; Klyashtorin, 2001; Southward *et al.*, 2005) with time series of 20-50 years being the most common (*e.g.* Greenwood *et al.*, 2002; Collie *et al.*, 2008; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008; Frid *et al.*, 2009). For some study species, such as exploited fish species, the use of archived data (such as records of fishing effort/landings or scale/otolith collections) is proving to be a valuable resource for studying temporal changes in distribution/abundance and population biology over time scales ranging from decades to over one hundred years (*e.g.* Klyashtorin, 2001;

Boylan and Adams, 2006). Finally, continuous data sets of much longer time scales are available for some marine organisms through the use of hard material (e.g. scales, shells) deposited on the sea bed or in surface sediments. The time series for these data sets can range from several hundred years to 2000 years (e.g. Baumgartner *et al.*, 1992; O'Connell & Tunnicliffe, 2001; Richardson, 2001; Finney *et al.*, 2002 Valdes *et al.*, 2008). One characteristic of many of these longer term continuous time series data sets is the use of data collected in the recent past, where the parameter of interest can be correlated to known climatic variables, to 'ground truth' the data set and to allow extrapolation into the past to estimate parameters such as distribution/abundance (e.g. Baumgartner *et al.*, 1992) or growth rate (e.g. Richardson, 2001).

3.1.1 Long-term data sets: < 50 years

Long term data sets have clearly shown changes in the species composition of marine communities and in the distribution/abundance of individual species in relation to climate change. For example, the Plymouth Continuous Plankton Recorder (CPR) has operated since 1931 (Jonas *et al.*, 2004) and has shown clear changes in the distribution/abundance of individual species and in the species composition of the plankton community in the North Atlantic (Colebrook, 1978; Beaugrand *et al.*, 2002, 2003; Brander *et al.*, 2003; Hays *et al.*, 2005). These changes in phytoplankton and zooplankton communities have been correlated with changes in the North Atlantic Oscillation (Beaugrand *et al.*, 2002, 2003). The study of intertidal rocky shore communities in south west England since the 1950s have also shown changes in the distribution/abundance of individual species and in overall species composition (Kendall *et al.* 2004; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008). As annual average sea surface temperature in the Western English Channel has increased by *ca.* 1°C (Hawkins *et al.*, 2003), there have been changes in the geographical distributions of three barnacle species in the study area; *Semibalanus balanoides* (a northern species favouring colder water) and *Chthamalus montagus* and *C. stellatus* (both southern species favouring warmer water). The results of this long term survey have shown a northward movement by all three species with a decline in abundance of *S. balanoides* and an increase in the abundance of the *Chthamalus* species (Kendall *et al.* 2004; Southward *et al.*, 2005;

Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008). The population dynamics of these barnacle species correlate to long term changes in water temperature of inshore coastal waters and provide a model for predicting the future effects of global warming on coastal water communities (*e.g.* Poloczanska *et al.*, 2008). In addition, this long term survey has also shown a decrease in the abundance and productivity of furoid algae with warming which is likely to have a significant effect for waders. Furoid algae shelter a community of small soft-bodied invertebrates from heat and desiccation that are a major food source for some wading seabirds and changes in furoid biomass could present the loss of potentially rich feeding grounds for species such as the ruddy turnstone *Arenaria interpres* (Kendall, *et al.*, 2004).

Data sets also exist showing the effects of climate change on fishes. Greenwood *et al.* (2002) present data on the abundance of benthic and demersal fishes in the lower Forth estuary (East Scotland) collected between 1982 and 2001. The results of this time-series study showed significant decreases in the total annual abundance for 30 species, with the greatest declines observed for whiting *Merlangius merlangus* and eelpout *Zoarces viviparus* and a significant linear increase in fatherlasher *Myoxocephalus scorpius*. Some species were observed to become infrequent or rare in the catches whilst other species were seen to be moving northward. For example, eelpout were considered to be declining in numbers and retreating northwards with regional warming of the North Sea over the study period and are predicted to become extinct in the Forth estuary in 20-40 years time (Greenwood *et al.*, 2002). Fatherlasher increased in abundance over the study period taking over the niche occupied by eelpout and numbers of sea bass *Dicentrarchus labrax L.*, a southerly species, were seen to increase indicating a northward movement of this species. Greenwood *et al.* (2002) suggest that the most likely reasons for the observed changes in catch composition and individual species distribution/abundance over the 20 year study period were due either to the warming of local water over the last two decades and/or overfishing of some species such as whiting. Similarly Genner *et al.* (2004) examined long-term databases to show how regional climate change has affected the community composition and abundance of two fish assemblages in the English Channel (EC, inshore marine assemblage; 1913–2002) and the Bristol Channel (BC, estuarine assemblage; 1981–2001). As annual average, sea surface temperature in both ecosystems had increased by 1 (EC) to 1.5 (BC) °C in the last 100 years, declines and increases in abundance were noted for different fish

species. Each assemblage contained a group of dominant species whose abundances were strongly linked to annual mean sea-surface temperature but interestingly the trends in abundance (increase/decline) by individual species was not mirrored between sites. This suggests that within a region, local environment-specific factors will cause populations of the same species to respond differently to climatic change and that species-level responses to climate change for fish species could be difficult to predict (Genner *et al.*, 2004).

The use of archived fisheries data is proving to be a valuable resource in determining the effects of climate change on the distribution and abundance of exploited fish species. Using data collected by ICES since 1973, Hannesson (2007) has shown that as water temperatures in the Norwegian and Barents Seas have risen as a result of global warming, the productivity of cod stock in this regions and the catches landed by the fishery have also increased. In contrast, he found no correlation between cod catches and temperature in the North Sea, although there was positive correlation between increasing temperature and higher recruitment rates of cod in both seas. Finally, Hannesson (2007) reported a positive correlation between temperature and the catches of Atlantic mackerel *Scomber scombrus* in North and Norwegian seas and between temperature and the catches of sardines *Sardina pilchardus* in the North Sea. Similarly, the relative abundances of Pacific sardine *Sardinops sagax* and Peruvian anchoveta *Engraulis ringens* correlate with changes in the El Niño Southern oscillation (Chavez *et al.*, 2003). Chavez *et al.* (2003) present a model which shows a 50 year oscillation in climate with corresponding ecosystem shifts from a cool “anchovy regime” (where anchoveta are the dominant pelagic species) to a warm “sardine regime” (where Pacific sardine are the dominant pelagic species). The value of long-term fisheries survey data in determining the effect of regional climate change on fish assemblages is also shown in the recent study by Hiddink and Ter Hofstede (2008). In this study, Hiddink and Ter Hofstede (2008) utilised data collected from the ICES-coordinated International Bottom Trawl Survey (IBTS) programme between 1985 and 2006 to show an increase in species richness and latitudinal range shifts in the fish community between 51 and 62° latitude in the North Sea. More than eight times as many fish species displayed increased distribution ranges (mainly small-sized species of southerly origin) compared with those whose range decreased (primarily large and northerly species).

3.1.2 Long-term data sets: *ca.* 100 – 200 years

As a result of the long term exploitation of certain fish species for food or as a recreational angling resource, there are time series in excess of 100 years for species such as the Atlantic salmon *Salmo salar* (Boylan and Adams, 2004) and Pacific herring *Clupea pallasii pallasii* (Klyashtorin, 2001). For example, Boylan and Adams (2006) have examined catches of Atlantic salmon in the Foyle system (*i.e.* estuary and river catches combined) in Ireland between 1875 and 2001. During this time period catches have varied but changes in salmon abundance relate to variations in the North Atlantic Oscillation index (NAOI). A negative relationship between the wNAOI and the abundance of migrant Atlantic salmon returning to the River Foyle in Ireland was found for indices <0.151 . Above 0.151 this relationship breaks down and at higher values there is no significant relationship between wNAOI and catch abundance. Boylan and Adams (2004) conclude that the NAOI may be affecting Atlantic salmon numbers by influencing survival rates during the juvenile freshwater phase, when feeding at sea, or through the number of adults surviving to spawn more than once (multi-sea-winter fish). The 90 year survey of the fish community in the Bristol Channel by Genner *et al.* (2004) provides another clear example of how climatic factors affect fish diversity and abundance.

3.1.3 Long-term data sets: *ca.* 1000 + years

Through the use of sediment deposits, changes in estimated abundance over the last 2000 years have been reported for several fish species (Baumgartner *et al.*, 1992; Finney *et al.*, 2002) and preserved midden deposits have been used to derive records of fish growth and abundance for time periods ranging from 800 years (Bolle *et al.*, 2004) to 4500 years (Maeschner *et al.*, 2008). Baumgartner *et al.* (1992) report changes in the estimated abundances of Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* off the coast of California over the last 2000 years. Scale deposition rates for the two species in the anoxic sediments in the Santa Barbara Basin between 1932 and 1965 were correlated with stock assessment estimates of population size conducted by US government fisheries biologists. This relationship between scale deposition rate and stock size was then used to ‘hind-cast’ and estimate population size over the last 2000 years from scale deposits in sediment cores. The

results have shown dramatic fluctuations in population size for both species over time with estimated stock sizes varying from 2-18 million individuals, these fluctuations occurring in the absence of any fishing pressure and alternate shifts in dominance between Pacific sardine and northern anchovy on a 50-100 year cycle. This work was extended by Chavez *et al.* (2003) who also showed a correlation between the estimated abundances of the two species, with one species tending to be numerically predominant at any point in time and producing a model confirming a 50 year cycle in dominance-shift between the two species. This alternating dominance between sardines and anchovies in a coastal upwelling zone has also been reported for the Peruvian upwelling (Jennings *et al.*, 2001); in Peru the anchoveta *Engraulis ringens* is the dominant species whilst in California it is the Pacific sardine (Jennings *et al.*, 2001). Although, Baumgartner *et al.* (1992) did not correlate their estimated abundance data with any climatic variables, Chavez *et al.* (2003) confirmed that the cycles of abundance for the two species are driven by climatic factors associated with the El Niño Southern Oscillation (ENSO). In fact, climatic cycles have been proposed as the driver determining the cyclical patterns of abundance and ecosystem dominance between anchovies and sardines worldwide (Schwartzlose *et al.*, 1999).

Similar long-term fluctuations driven by climatic variation have also been reported for Pacific salmonids in Alaska. Finney *et al.* (2002) have estimated the number of sockeye salmon *Oncorhynchus nerka* returning to spawn in Karluk Lake over the last 2000 years from the abundance and species composition of diatoms and the $\delta^{15}\text{N}$ isotopic signature of organic matter from sediment cores taken from the lake. Within Boreal freshwater lakes, the species composition of the diatom community varies depending on the concentration of dissolved nutrient such as nitrates and phosphates, with some species predominating in oligotrophic (*i.e.* nutrient poor) and other species predominating in eutrophic (*i.e.* nutrient rich) conditions (Finney *et al.*, 2002). Pacific salmon are semelparous (*i.e.* spawn once and then die) and therefore the annual spawning run of salmon into the lake will result in the mass transfer of nutrients from the marine environment into the lake ecosystem. As a result, any temporal change in the size of the salmon stock will result in changes in the nutrient input into the lake, and therefore changes in the abundance and composition of the diatom community over time. In addition, the $\delta^{15}\text{N}$ isotopic signature of organic matter is significantly higher in the marine environment compared to the freshwater environment (McCarthy and Waldron, 2000) and so temporal changes in the $\delta^{15}\text{N}$

signal of organic matter in the sediment core over time will also reflect changes in the number of returning adult salmon. Finney *et al.* (2002) examined the abundance of the tests of different diatom species (*i.e.* oligotrophic and eutrophic species) and the $\delta^{15}\text{N}$ signal of organic matter in sediment cores taken from Karluk Lake and the results showed regular periodic fluctuations between oligotrophic and eutrophic conditions in the lake over the last 2000 years. Test deposition rates and species composition correlated with the $\delta^{15}\text{N}$ signal in the sediment core suggesting large fluctuations in the abundance of sockeye salmon over time. Taken together, the results of Baumgartner *et al.* (1992) and Finney *et al.* (2002) provide clear evidence of dramatic fluctuations in the abundance of fishes (in the case of the sockeye salmon lasting centuries) in the absence of fisheries or other anthropogenic impacts.

3.1.4 Long-term data sets: Fisheries Induced Evolution

Clearly, there is great value in the acquisition of long-term data sets, either through ongoing research surveys or from archived data material. The correlation of these data with climatic variables have allowed us to ‘hind-cast’ to understand climatic variation and fluctuations in species abundance and community composition in the past and also allow us to ‘fore-cast’ the potential impacts of climate change in the future. However, overlying changes in the distribution and abundance for many fish species in the marine environment as a result of climate change is the impact of overfishing on the population biology of the target species. It has become evident that sustained fishing pressure on many fish stocks has resulted in evolutionary changes in the population biology of these stocks, a phenomenon that has been termed ‘*Fisheries-Induced Evolution*’ (Kuparinen and Merila, 2007; Law, 2007; Hutchings and Fraser, 2008). Fisheries-induced evolution has been reported for a range of freshwater and marine fish species subjected to commercial or recreational fishing pressure (see review by Hutchings and Fraser, 2007); for example European and Pacific salmonid species (*S. salar* and *Oncorhynchus* spp.), lake whitefish (*Coregonus clupeaformis*), Atlantic cod (*Gadus morhua*) and plaice (*P. platessa*). Since fishing usually targets the largest individuals, the most common evolutionary response observed is a decrease in the size and/or age at maturity, although slower growth and smaller body size can also be selected for (Kuparinen and Merila, 2007; Hutchings and Fraser, 2008). Fisheries-induced evolution has been reported for a number of commercially

important demersal fish species in the North Atlantic such as cod (*e.g.* Barot *et al.*, 2004; Olsen *et al.*, 2004, 2005; Hutchings, 2005) and flatfish species including American plaice *Hippoglossoides platessoides* (Barot *et al.*, 2005), sole *Solea solea* (Mollet *et al.*, 2007) and plaice (Grift *et al.*, 2003, 2005; Rijnsdorp *et al.*, 2005). Sustained heavy fishing pressure for 50 years (ICES, 2008b) has resulted in a decrease in age at maturity (Grift *et al.*, 2003, 2005) and an increase in reproductive investment (Rijnsdorp *et al.*, 2005) in North Sea plaice. However, no comparative analysis has been conducted for plaice in the Irish Sea to examine whether fishing pressure has caused any responses in life history.

3.1.5 The School of Ocean Sciences Autumnal Fishing Survey

Since 1970, the School of Ocean Sciences at Bangor University has conducted fishing surveys each year during October/November in the coastal inshore waters off eastern Anglesey and Northwest Wales. Although the primary aims of these trips are for teaching purposes, the data collected from these surveys has been archived and provides a valuable and ongoing research resource to examine changes in the local demersal fish communities over time. Data collected within the School between 1970 and 2001 was archived by Dr David Grove (now retired) and data collected since 2002 has been archived by Dr Ian McCarthy. The autumnal fishing trips record data on the abundance and population biology (size, age, growth, maturity and feeding data) of six demersal fish species in the inshore waters of eastern Anglesey (Red Wharf Bay, Point Lynas) and northwest Wales (Conwy Bay, Colwyn Bay). Since 1970, data has been collected for plaice *Pleuronectes platessa*, dab *Limanda limanda* and whiting *Merlangius merlangus*. Since 1999, data has also been collected for three gurnard species; red gurnard *Aspitrigla cuculus*, grey gurnard *Eutrigla gurnardus*, and tub gurnard *Trigla lucerna*. Changes in the abundance and population biology for two of these target species have been examined recently. Historical data for the local dab population over 34 years was analysed by Seisay (2001). This is a species that is not commercially exploited and the results have shown that the local dab population has remained relatively stable over time (Seisay, 2001) although the data were not correlated with any climate change variables. In contrast, Preston (2007) has shown significant declines in abundance and significant changes in the population biology of whiting since 1980. Whiting have been heavily overexploited in the Irish Sea (ICES

2008a) and Preston (2007) attributed the observed changes to overfishing although the data were not directly correlated with any parameters related to fishing pressure or to any climatic variables. Although data on the catches of plaice and various population biology parameters (*e.g.* size/age composition, growth rate, size/age at first maturity) have been collected by School of Ocean Sciences since 1970, this long term data series has not been analysed in relation to changes in fishing pressure or any environmental variables such as temperature and NAOI.

The exploitation of plaice in the Irish Sea has been intermediate between that of dab (unexploited, Seisay 2001) and whiting (sustained overexploitation, ICES 2008a) and it will be interesting to examine whether any changes in the abundance and population biology of plaice in the Irish Sea have occurred, and the magnitude of those changes since 1970, compared to these other species. Also, the survey data set covers a time period during which the plaice fishery has gone through periods of increasing and sustained exploitation (1970-1989) and followed by decreasing exploitation (1990 to date) and it will be interesting to compare any changes in the abundance and population biology of plaice, and the magnitude of those changes, during these two periods of differing exploitation. Finally, plaice in the Irish Sea have not been as intensively exploited as in the North Sea (ICES 2008b) and it will be interesting to compare any changes in the population biology of plaice in the Irish Sea with changes in the North Sea and to determine whether there is any evidence of fisheries-induced evolution in either the North Sea or the Irish Sea.

3.1.6 The aims of chapter 3:

- 1) To investigate whether there have been any long-term changes in the abundance and population biology of the plaice caught in the inshore waters of eastern Anglesey and northwest Wales during the autumnal fishing surveys between 1970 and 2006.
- 2) To examine whether any changes in the abundance or population biology between 1970 and 2006 are a result of sex-specific changes in either males or females.

- 3) To examine whether any changes in the population biology of plaice caught in the inshore waters of eastern Anglesey and northwest Wales during the autumnal fishing surveys between 1970 and 2006 correlate with changes in either fishing pressure for plaice in the Irish Sea (*e.g.* fishing mortality rates or spawning stock biomass) or environmental variables (*e.g.* sea surface temperature and the North Atlantic Oscillation).

- 4) To compare any changes in the population biology of plaice caught in the inshore waters of eastern Anglesey and northwest Wales during the autumnal fishing surveys between 1970 and 2006 with the population dynamics of dab and whiting from the same survey reported by Seisay (2001) and Preston (2007).

3.2 Methods

3.2.1 Data collation

Annual fishing surveys have been conducted in October/November by undergraduate and MSc students from the School of Ocean Sciences, Bangor University using the R.V. *Prince Madog* since 1970. The data collected from these 39 years of cruises has been archived in the School of Ocean Sciences by Dr David Grove (1970-2001) and then Dr Ian McCarthy (2002 to date) in a variety of formats, *e.g.* electronic data storage, paper copies of cruise data (trawling details, length-frequency sheets for the total catch) and otolith envelopes from length-stratified subsamples (containing length/weight/age/sex/maturity data). Some data were archived and available in an unanalysed format (*i.e.* 'raw' data; length, weight, age etc) whilst other data were available in a processed form (*i.e.* von Bertalanffy growth coefficients, L_{50} values, mortality rates etc) either from Dr David Grove, Dr Ian McCarthy, various unpublished MSc fisheries reports (Source: Dr Ian McCarthy) or from two MSc thesis (Chuenpagdee, 1990; Seyhan, 1990). In this chapter, data has been sourced for the time period 1970-2006 from the various sources listed above, except data for 2004-2005 which has been sourced from the results presented in Chapter 2. Where possible, 'raw data' was used to derive the parameters investigated in this chapter.

Since these surveys have all been conducted using the same sampling gear (Rockhopper otter trawl, 76 mm stretched mesh size in the cod end) and sampling protocol (towed at 2-4 knots for one hour) in the same locations (see Figure 3.2) at the same time of year (October/November), the results obtained for each year are considered directly comparable and form the basis in this chapter for a 36 year time-series study (1970-2006) on the population dynamics of plaice in the inshore waters of Eastern Anglesey and North west Wales. A summary of the trawl data are presented in Table 3.1. Although in some years, data were available from fishing trips conducted at other times of the year (*i.e.* spring and summer), these were not included in the analyses conducted in this chapter. In most years, at least three, and up to seven locations in the coastal waters of Eastern Anglesey and North West Wales were fished in October/November (Table 3.1). These sites were a combination of inshore (*i.e.* in Red Wharf Bay, Conwy Bay or south of the Constable Banks in Colwyn Bay) and offshore (*i.e.* off Point Lynas and north of the Constable Banks in Colwyn Bay).

Table 3.1 lists each of the specific location fished and these are indicated on Figure 3.2. Between 1970 and 2006, an average of 7 (\pm 3 SD, range 3-13) days of fishing were conducted each year (Table 3.1). On each fishing trip, several tows were usually conducted and on average, 13 (\pm 8 SD, range 4-41) tows were conducted each year (Table 3.1). The mean total number of plaice caught per year was (1581 \pm 1222 SD) comprised of 679 (\pm 482 SD) females and 874 (\pm 770 SD) males (Table 3.1). In total, the 37 year time-series (1970-2006) was comprised of data collected from 24262 male plaice and 18873 female plaice. In general, between 2-6% of the total number of male or female fish were caught in any given year (Figure 3.1), although high numbers of males were caught in 1975 and 1983 and high numbers of female fish in 1983 (Figure 3.1). In some years, data on the total catch were missing and only data from the length-stratified subsample were available – these years were 1970, 1982, 1992, 1993 and 1997 respectively (Table 3.1). Data were available for both sexes in most years, however, in some particular years, only data for females (1970 and 1978) or male (1982) were available (Table 3.1). For most years, it was possible to use raw data to directly determine in this study the percentage length and age frequency distributions, the von Bertalanffy growth function coefficients (k , L_{∞}), and length and age at first maturity (L_{50} , A_{50}). The statistical software SPSS (v. 12), was used to calculate these values using the equations presented in Chapter 2. However, in some years where the raw data were not available and it was not possible to directly determine certain parameters, some values analysed by other students [*e.g.* Chuenpagdee (1990), Seyhan (1990), or unpublished MSc fisheries reports] had to be used.

3.2.2 Data analysis

3.2.2.1 Fishing effort and abundance data

Annual fishing effort was expressed as the number of days fished and the number of trawls conducted each year. To examine whether any changes in fishing effort had occurred during the 37 year survey, the fishing effort data were collated into 5 year intervals (*i.e.* 1970-1974, 1975-1979 etc) and compared using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 below for more details). The average trawl times (in minutes) were also collated into 5 year intervals (*i.e.* 1970-1974, 1975-1979 etc) and compared using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 below for more details). In order to examine

any changes in plaice abundance in the survey area in October/November over time, the catch was expressed as the number of plaice caught per hour of trawling: this measure of catch per unit effort is routinely used in fisheries surveys (e.g. Pawson, 1995; Svedang, 2003; Parker-Humphreys 2004a, b; Casini et al., 2005; Daan *et al.*, 2005). It may be more informative to express abundance in terms of the number of fish per unit area trawled in order to account for differences in the distance covered during each tow (e.g. Seisay, 2001). Unfortunately, longitude/latitude data were not available for the trawl data pre-1989, and it was not possible to calculate the distance of the trawl and the area of seabed fished in order to calculate abundance data in terms of number of fish per hectare (see Seisay, 2001). Therefore, catch data were expressed as number of fish caught per hour as an estimate of abundance. To examine whether any changes in abundance had occurred during the 37 years survey, the data were collated into 5 year intervals (*i.e.* 1970-1974, 1975-1979 etc) for comparison using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details).

3.2.2.2 Length and age distributions

Since the number of fish in each yearly sample varied (Table 3.1), the length and age frequency distributions were expressed on a percentage basis to allow direct comparison between years. The length data for male and female plaice were divided up into 1 cm total length (TL, cm) intervals (*e.g.* fish between 15.5 and 16.4 cm TL were classified in the 16 cm TL class) and the number of fish in each 1 cm TL class expressed as a percentage of the total number of male or female fish in the total catch for that year. In order to examine whether there were any changes in the size distributions of the plaice caught over time, the relationships between a number of parameters and year were examined using Spearman Rank Correlation analysis since the time was a discrete variable. These parameters were average total length, modal total length (*i.e.* the most common length class) maximum and minimum total length and the ratio between maximum/minimum length. Since the average and modal total length values recorded may be dependent on the degree of fishing effort in any year, and also subject to random biological variation, annual values for these parameters were also calculated as a three year moving average (average for any given year calculated from the value for that year plus the year before and the year after) in order to reduce the inter-annual variability and 'smooth out' any long term trends in the data

set. Correlation analysis will only examine whether there has been any significant upward or downward trend in size over time, but will not pick up any variations in size over time within the 37 year time period. Therefore, the actual size data and the 'smoothed' average total length and modal total length values were collated into 5 year intervals and compared using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details). As well as examining any changes in the size range and central tendency in the plaice catch over time, changes in the size composition were examined by dividing the data into 5 year intervals and calculating the percentage of fish in the following total length classes: <14, 15-19, 20-24, 25-29, 30-34, 35-39 and > 40 cm TL.

In order to examine whether any changes in the age structure of the plaice catch had occurred during the 37 year survey, similar analyses to those conducted with the length data. The age data for male and female plaice were divided up into year classes and the number of fish in each age class expressed as a percentage of the total number of male or female fish in the total catch for that year. To examine any changes in age structure over time, the average age, and maximum and minimum ages (both raw data and three year 'smoothed' values), were correlated against year using Spearman Rank Correlation analysis (since age and year are discrete data). Smoothed data (*i.e.* three year moving averages) for average, maximum and minimum ages were collated into 5 year intervals and compared using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details). In addition to examining any changes in range and central tendency in the age data over time, changes in the age composition of the plaice catch were examined by dividing the data into 5 year intervals and calculating the percentage of fish in the following total age classes: 0-1, 2, 3, ≥ 4 years old.

3.2.2.3 Sex ratio

Sex ratio was calculated as the proportion of males in the catch in any given year (*i.e.* number of males/total number of fish). Since the number of male and female plaice in the annual catch varied from year to year, an examination of sex ratios over time was considered to be the most appropriate method of analysis. To examine any changes in sex ratio over time, both the raw data and the three year 'smoothed' sex ratio values were correlated against year using Spearman Rank Correlation analysis (since time

was a discrete variable). The actual and the 'smoothed' sex ratio data were collated into 5 year intervals and any changes in sex ratio over time examined using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details).

3.2.2.4 Growth and maturity parameters

Population biology parameters, *i.e.* coefficients for the von Bertalanffy growth curve (K , year⁻¹; L_{∞} , cm) and maturity ogives [size/age at first maturity; TL_{50} (cm), A_{50} (years)], for male and female plaice were calculated from raw data (where possible) or previously calculated values collated from the archived dataset (1970-2003, 2006) and from data collected during this thesis (2004-2005). In order to examine whether any changes in growth or maturity had occurred for male or female plaice during the 37 year survey, the data were examined using the same set of analyses as conducted for the size/age data. To examine any changes in L_{∞} , K , L_{50} or A_{50} over time, both the actual raw and the three year 'smoothed' average values were correlated against year using Spearman Rank Correlation analysis (since time was a discrete variable). The actual and the 'smoothed' growth and maturity data were also collated into 5 year intervals to examine whether there were any differences between the time intervals using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details).

In addition to comparing the von Bertalanffy growth parameters derived for each year, the size/age data were collated into 5 year time periods (1970-1974, 1975-1979 etc), average size at age values calculated and von Bertalanffy growth curves derived for each 5 year time period (see section 2.2.3 for more details). The 7 growth curves were then compared with each other using the likelihood ratio test of Kimura (1980) to see whether there were any significant differences in the pattern of growth between the different time periods (see section 2.2.3 for more details). Finally, all the size/age data were collated into one data set and a single von Bertalanffy growth curve for the 37 year time series was calculated. The seven 5 year-interval growth curves were then compared with this overall 37-year growth curve using the likelihood ratio test of Kimura (1980) to see whether there were any significant differences in the pattern of growth between each time period and the long-term average growth curve (see section 2.2.3 for more details).

3.2.2.5 Length at age data

To examine whether there has been any change in the average size of male and female plaice over time, the data were divided up by sex and age class and the average TL plotted against year for each age class and examined for significance using Spearman's Rank Correlation test (since year was a discrete variable). Since correlation analysis will only examine whether there has been any significant upward or downward trend in size over time, but will not pick up any variations in size over time within the 37 year time period, the actual and the 'smoothed' average total length data for each age class were collated into 5 or 10 year intervals (as appropriate depending on the range of data available for that age class) and compared using a one way ANOVA or a Kruskal Wallis test as appropriate (see section 3.2.2.6 for more details).

3.2.2.6 Statistical analyses of the time series data

To examine trends in the overall data set over time, Spearman's Rank correlation coefficient was used to relate each parameter to year since the time was a discrete variable. Comparisons between male and female plaice were performed using a 2 sample *t*-test since these data were normally distributed and the test is robust to use with equal or unequal variance. To examine differences between time periods, all data were tested for normality (Kolmogorov-Smirnov test) and equality of variance (Levene's test) in order to determine the appropriate choice of test statistic. For comparisons between the seven time intervals in the time series data which had equal variances, a one way ANOVA was used. If the ANOVA indicated a significant difference, pairwise comparisons of the mean values were performed using Scheffe's test (since sample sizes were unequal) to determine which time intervals were different from each other. Where data did not exhibit equal variances, a Kruskal Wallis test was used to compare between the 5-year time intervals. Where a significant difference was found, pairwise comparisons between time periods was conducted using a Wilcoxon Signed Rank test. Statistical tests were conducted using SPSS v14 and Minitab v15. For all statistical tests, differences present at the 5% level were considered significant.

Table 3.1: A summary of the available data on the autumnal fishing surveys conducted in the coastal waters of Eastern Anglesey and North West Wales in October/November. Data are presented for the coastal area fished, fishing effort (number of days fished, number of trawls), the number of male and female fish in the length-stratified subsample and caught in total (subtotal) and the total catch.

Year	Area	in/off	Female		Male		Grand total	Trawls	Days
			Sub-sample	Subtotal	Subsample	Subtotal			
1970	RWB, CON	In	23	23	n/a	n/a	n/a	41	13
1972	OCB	Off	n/a	267	n/a	648	928	7	3
1973	CNB, CON, RWB OCB, LPL, PL	In Off	n/a	699	n/a	1033	1899	23	10
1974	CON, RWB COL	In Off	n/a	951	n/a	1242	2193	15	8
1975	COL OCB	In Off	n/a	1275	n/a	2731	4028	26	12
1976	CON, RWB COL	In Off	n/a	1062	n/a	1400	1462	14	5
1977	CON, RWB	In	n/a	900	n/a	1090	2004	12	6
1978	CON, RWB	In	n/a	670	n/a	n/a	1580	11	5
1979	CON, RWB OCB	In Off	n/a	1337	n/a	2229	3165	14	10
1981	CON, RWB	In	n/a	290	n/a	488	1133	4	4
1982	RWB	In	n/a	n/a	n/a	141	n/a	4	3
1983	CON, RWB	In	n/a	2295	n/a	2799	5079	6	7
1984	CON, RWB OCB	In Off	n/a	904	n/a	1651	2535	5	3
1985	CON, RWB OCB	In Off	n/a	1306	n/a	1781	3149	14	6
1986	CON, RWB OCB	In Off	n/a	815	n/a	1500	2338	12	7
1987	ORM, RWB OCB	In Off	n/a	331	n/a	704	1059	12	7
1988	CON, ICB, ORM, RWB OCB	In Off	n/a	245	n/a	345	590	10	8
1989	CON, ORM, RWB OCB, PL	In Off	n/a	211	n/a	133	360	11	5
1990	CON, PUF, RWB	In	125	264	87	264	525	16	6
1991	CON, PUF, RWB OCB, PL	In Off	139	450	98	473	928	15	8
1992	CON, PUF, RWB OCB, PL	in off	62	62 *	122	No	n/a	17	10

Table 3.1: Continued

Year	Area	In/Off	Female		Male		Grand total	Hauls	Days
			Sub-sample	Sub-total	Sub-sample	Sub-total			
1993	PUF, RWB	IN	88	88 *	72	72 *	n/a	n/a	4
1997	CON, ICB, MOE, RWB PL	In Off	238	400	189	358	758	15	9
1998	CON, ICB PL	In Off	93	308	103	586	894	9	5
1999	CON, RWB OCB, PL	In Off	222	538	114	348	888	13	9
2000	CON, ORM, RWB OCB	In Off	265	962	178	1327	2289	13	9
2001	CON, RWB OCB, PL	In Off	145	628	125	557	1191	15	6
2002	CON, ICB, RWB OCB	In Off	235	775	181	1167	1969	7	7
2003	CON, MOE, RWB OCB	In Off	223	688	136	718	1414	8	6
2004	CON, ICB, RWB OCB	In Off	250	739	169	525	1274	9	7
2005	CON, ICB, MOE, RWB OCB, PL	In Off	277	996	141	322	1374	15	8
2006	CON, MOE, PUF, RWB OCB, PL	In Off	191	728	111	497	1225	13	9

Note:

1 - Inshore sites:

CNB = Caernarfon Bay

CON = Conwy Bay

ICB = Inshore Colwyn Bay

MOE = Moelfre (Part of Red Wharf Bay)

ORM = North Great Orme (Part of Colwyn Bay)

PUF = Off Puffin Island (Part of Red Wharf Bay)

RWB = Red Wharf Bay

2 - Offshore sites

LPL = Liverpool Bay

OCB = Offshore Colwyn Bay

PL = Offshore Point Lynas

3 - Any number with (*) represents subsample with no data about the total catch.

4 - Total catch includes fish which could not be sexed.

5 - n/a = Data not available

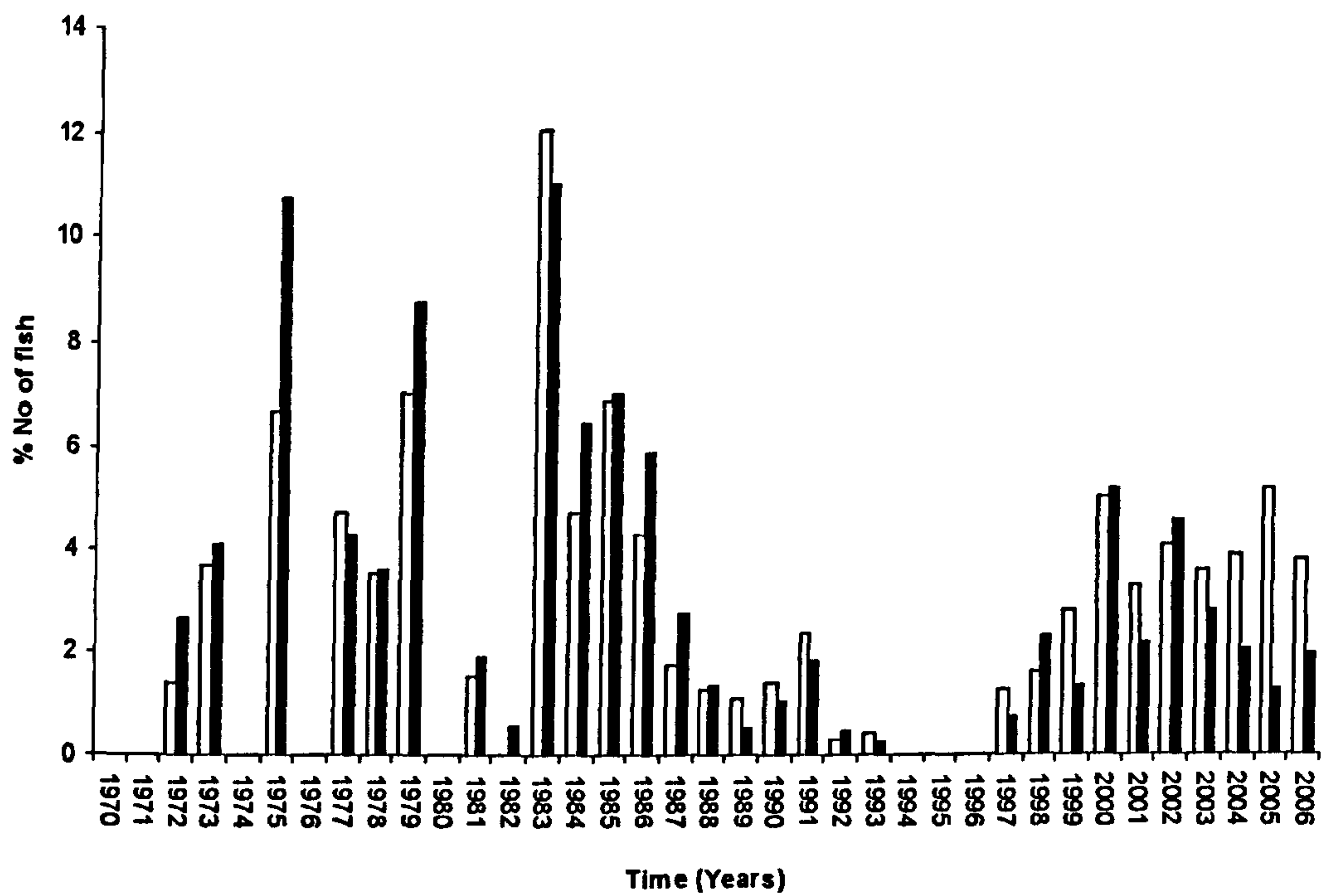


Figure 3.1: The number of male (solid bar) and female (open bar) fish caught each year, expressed as a percentage of the total catch (male, n = 24262; female, n = 18873), for plaice caught in the inshore coastal waters of Eastern Anglesey and North West Wales during the October/November fishing surveys for the period 1970 – 2006.

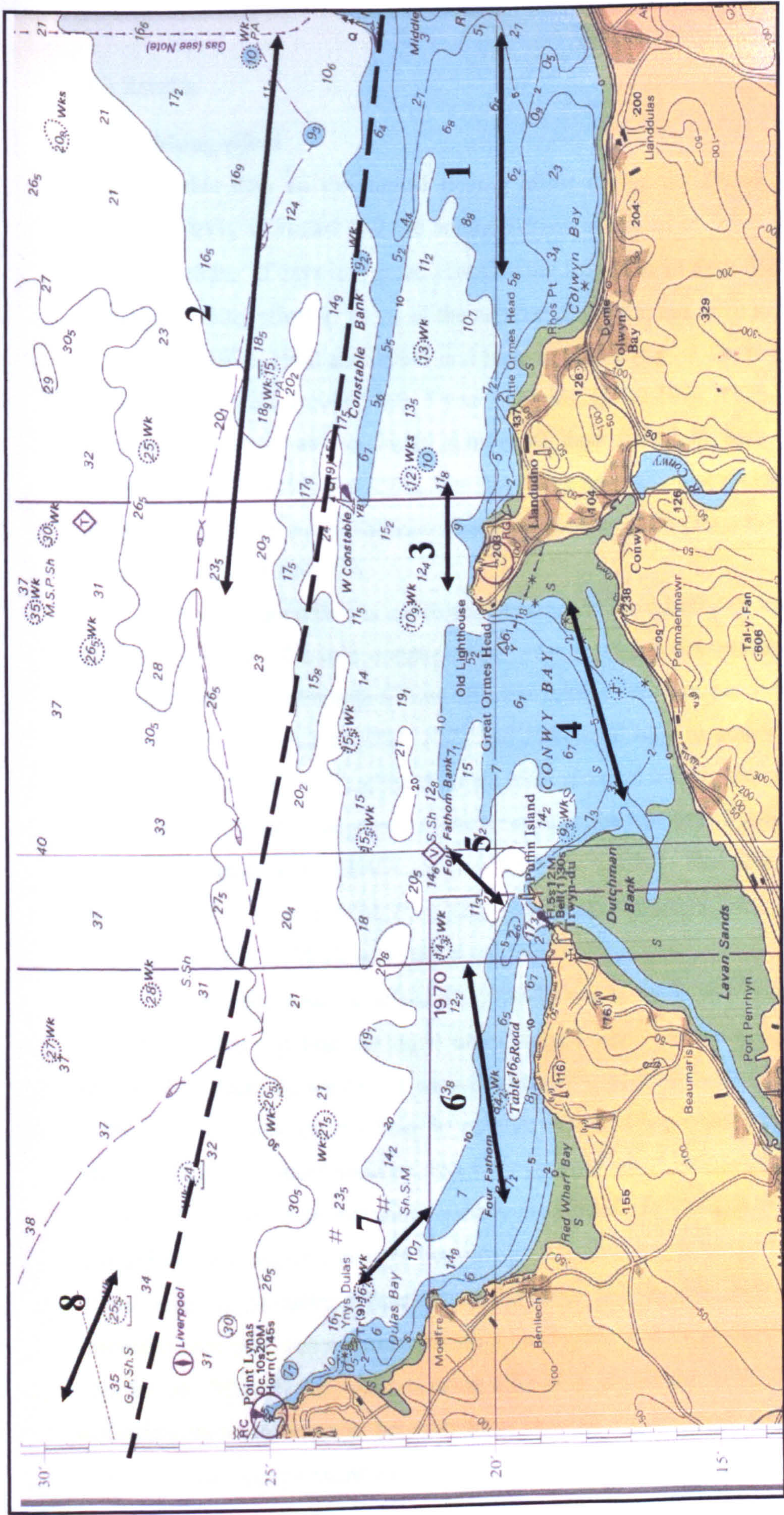


Figure 3.2: A general map of the survey areas where trawls were carried out during the October/November fishing surveys between 1970 and 2006. 1 = Inshore Colwyn Bay; 2 = Offshore Colwyn Bay; 3 = North Great Orme; 4 = Inshore Conwy Bay; 5 = Puffin Island; 6 = Red Wharf Bay; 7 = Moelfre; 8 = Offshore Point Lynas. The dashed line indicates the general separation between inshore (below dashed line) and offshore (above dashed line) survey areas.

3.3 Results

3.3.1 Fishing effort

The available data on the annual fishing effort during the *Prince Madog* autumn fisheries survey indicated that the annual survey consisted of 6.9 ± 2.2 days fishing with the number of days in a given year ranging from 3 to 13 days fishing (Table 3.1). Although fishing effort in terms of the number of days at sea were low in some years (*e.g.* $n = 3$, 1972, 1982 and 1984) and high in others (*e.g.* > 10 in 1970 and 1975), when the data were grouped into 5 year intervals, (1970-1974, 1975-1979 etc), there were no differences in the mean number of days fished in each 5 year interval (ANOVA, $F_{6,23} = 0.55$, $p = 0.76$). The data were normally distributed ($Z = 0.14$, $n = 30$, $P = 0.14$) with equal variances between time periods ($W_{6,23} = 1.24$, $P = 0.32$) allowing the use of ANOVA.

When fishing effort is expressed in terms of the number of trawls conducted, the mean number of trawls conducted per year is 13.2 ± 6.8 trawls (range 5 to 41 trawls) (Table 3.1). Although fishing effort in terms of the number of trawls were low in some years (*e.g.* < 7 in 1972, 1982 and 1984) and high in others (*e.g.* $n = 41$ in 1970 and $n = 27$ in 1975), when the data were grouped into 5 year intervals, (1970-1974, 1975-1979 etc), there were no differences in the number of trawls conducted in each 5 year interval (ANOVA, $F_{6,23} = 0.80$, $P = 0.58$). The data were normally distributed ($Z = 0.12$, $n = 30$, $P > 0.20$) with equal variances between time periods ($W_{6,23} = 1.56$, $P = 0.20$) allowing the use of ANOVA.

The average trawl time for the 1970-2006 was 59 ± 14 minutes, however, it must be pointed out that the trawl times ranged from 19 minutes to 110 minutes (Figure 3.3). Most trawls (80%) were between 40 and 70 minutes duration although 6.7% of trawls were shorter than 40 minutes and 12.4% greater than 70 minutes in duration. When the trawl duration data were grouped into 5 year intervals, (1970-1974, 1975-1979 etc), the data were not normally distributed ($Z = 0.12$, $n = 343$, $P < 0.001$) and did not have equal variances between groups ($W_{6,336} = 2.66$, $P = 0.02$). The lack of normality is probably a function of the large sample size since the percentage frequency plot indicates a normal distribution (Figure 3.3). Analysis of the trawl time data for the different time periods using a Kruskal Wallis test indicated a significant difference in trawl duration between time intervals ($\chi^2 = 26.68$, 6 df, $P < 0.001$). When pairwise comparisons of the time periods were conducted using a Wilcoxon

Signed Rank test, the overall pattern was for the median trawl times in 1985-1989 and 1990-1994 to be significantly lower compared to the other 5 year time periods (Table 3.2). This is most likely due to the percentage of trawls of less than 40 minutes duration conducted during these two time periods and the percentage of trawls of more than 70 minutes duration conducted during the other time periods (Table 3.2). Therefore, in order to allow data to be compared over time, abundance data for each trawl in the 1970-2006 fishing survey were expressed as numbers of fish per hour to standardise for the differences in trawl time.

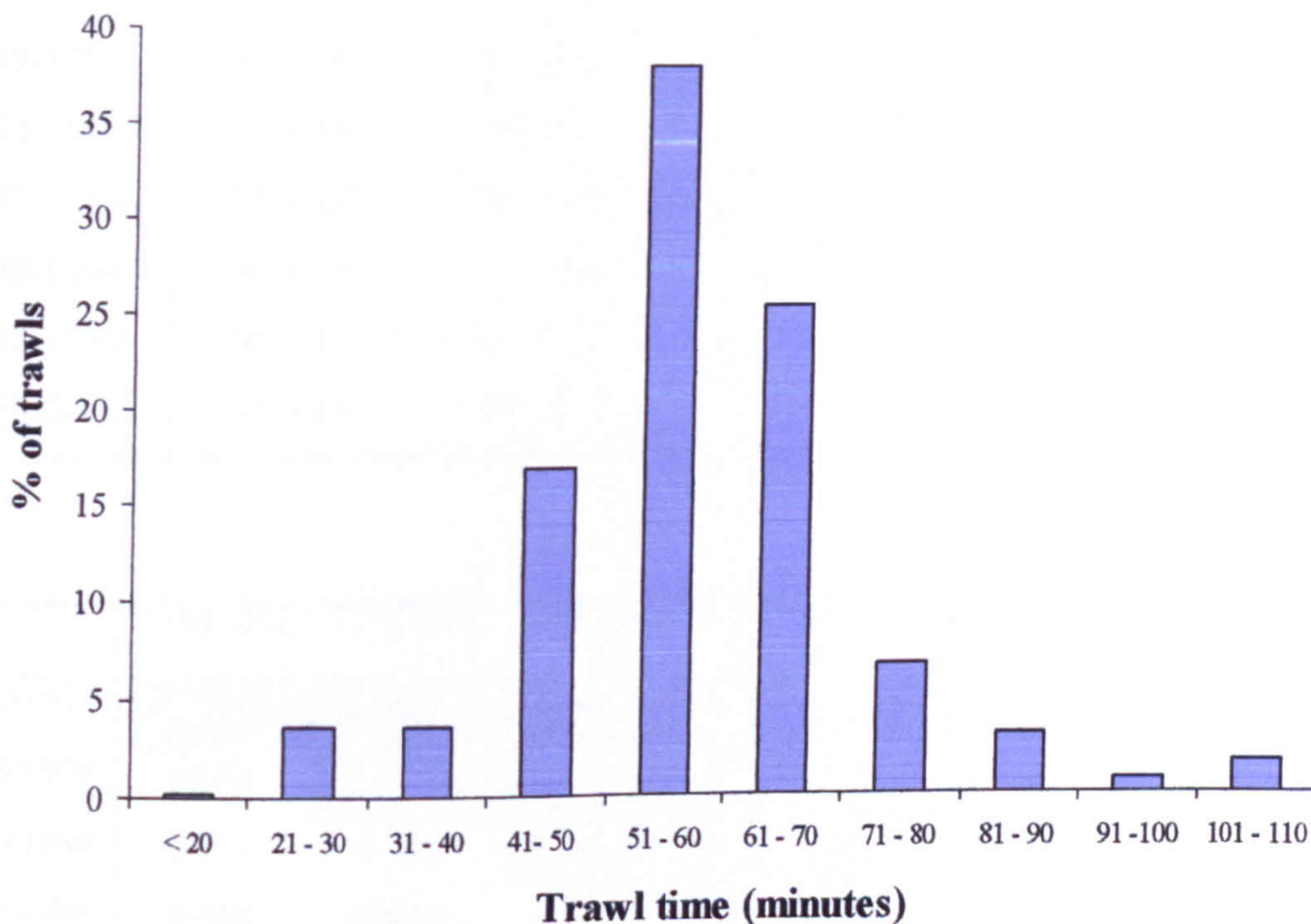


Figure 3.3. The percentage-frequency distribution of trawl times in the 1970-2006 RV *Prince Madog* autumn fishing survey data. Trawls times have been grouped in 10 minute intervals (n=381).

3.3.2 Abundance

The average number of plaice caught per hour of trawling for the years 1970-2006 are shown in Figure 3.4a. The average catch over the 1970-2006 time period was 124.5 plaice hour⁻¹, however, there was considerable inter-annual variation in relative

Table 3.2. (a) Data on the duration (minutes) of trawls in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Trawl durations are expressed as Median \pm Interquartile range. (b) Significance values for the *post-hoc* comparisons of trawl duration using the Wilcoxon Signed Rank test (significant differences at the 5% level are highlighted in bold and trends $0.10 < P < 0.05$ are underlined).

a)

<i>Time period</i> (years)	<i>Trawl time</i> (minutes)	<i>Range</i> (minutes)	<i>n</i>	<i>n < 40</i> minutes	<i>n > 70</i> minutes
1970-1974	70 \pm 15	20 - 85	39	2	7
1975-1979	60 \pm 5	38 - 110	70	1	8
1980-1984	60 \pm 15	49 - 87	29	0	1
1985-1989	57 \pm 12	20 - 105	63	8	1
1990-1994	46 \pm 15	24 - 82	59	6	4
1995-1999	60 \pm 15	19 - 110	37	3	12
2000-2006	62 \pm 13	28 - 89	84	4	10

b)

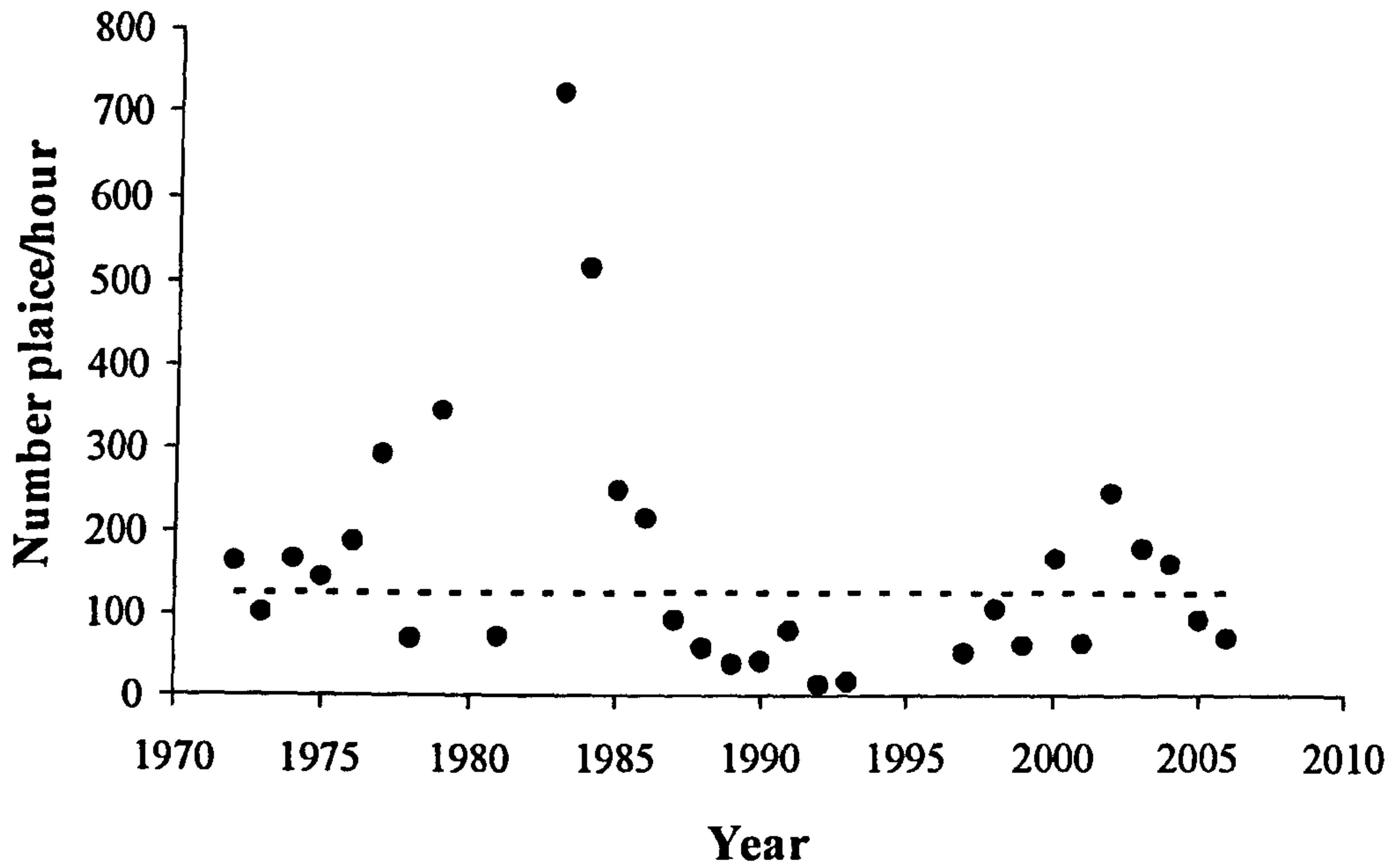
	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.664					
1980-1984	0.717	0.733				
1985-1989	0.025	0.001	0.007			
1990-1994	0.005	0.041	0.002	0.732		
1995-1999	0.005	0.981	0.443	0.012	0.019	
2000-2006	<u>0.059</u>	0.201	0.587	0.187	0.282	0.132

abundance ranging from 722 plaice hour⁻¹ in 1983 to 12.8 plaice hour⁻¹ in 1992 (Figure 3.4a). These data were not normally distributed ($Z = 0.20$, $n = 30$, $P = 0.005$) and did not have equal variances between groups ($W_{6,23} = 6.92$, $P < 0.001$). Analysis of the abundance data for the different time periods using a Kruskal Wallis test indicated no significant differences between time intervals although a trend was evident ($\chi^2 = 12.09$, 6 df, $P = 0.06$). In order to normalise the data, a Log₁₀ transformation was applied to the data ($Z = 0.04$, $n = 31$, $P > 0.20$) and the Log₁₀ relative abundance data are shown in Figure 3.4b. There was a trend for Log₁₀ relative abundance to decline over time, but this was not significant at the 5% level ($r_s = -0.321$, $n = 30$, $P = 0.08$). However, a cyclical trend in abundance was apparent with peaks in abundance occurring in the mid 1980s and mid 2000s and corresponding low levels of abundance in the mid 1970s and mid 1990s (Figure 3.4b, Table 3.3). In order to illustrate this, a 6th order polynomial curve has been superimposed on the data in Figure 3.4b. The data for the 5 year time periods are shown in Table 3.3 and Figure 3.5.

Table 3.3. Relative abundance data [plaice caught hour⁻¹ and Log₁₀(plaice caught hour⁻¹)], grouped in 5 year intervals, for the trawls during the autumn fisheries surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as median values \pm interquartile range for number of plaice caught hour⁻¹ and mean values \pm SD for the log-transformed data.

<i>Time period</i> (years)	<i>Plaice hour⁻¹</i>	<i>Range</i>	<i>Log₁₀(plaice hour⁻¹)</i>	<i>Range</i>
1970-1974	161.5 \pm 65	97.9 – 163.3	2.14 \pm 0.13	1.99 – 2.21
1975-1979	184.9 \pm 213	66.9 – 343.2	2.25 \pm 0.28	1.83 – 2.54
1980-1984	514.4 \pm 651.2	70.5 – 721.7	2.47 \pm 0.55	1.85 – 2.86
1985-1989	91.0 \pm 183.5	38.7 – 247.3	2.00 \pm 0.35	1.59 – 2.39
1990-1994	28.1 \pm 53.7	12.8 – 76.1	1.45 \pm 0.36	1.11 – 1.88
1995-1999	60.2 \pm 52	49.0 – 101.0	1.82 \pm 0.16	1.69 – 2.00
2000-2006	157.7 \pm 106.9	63.1 – 244.8	2.09 \pm 0.23	1.80 – 2.39

a)



b

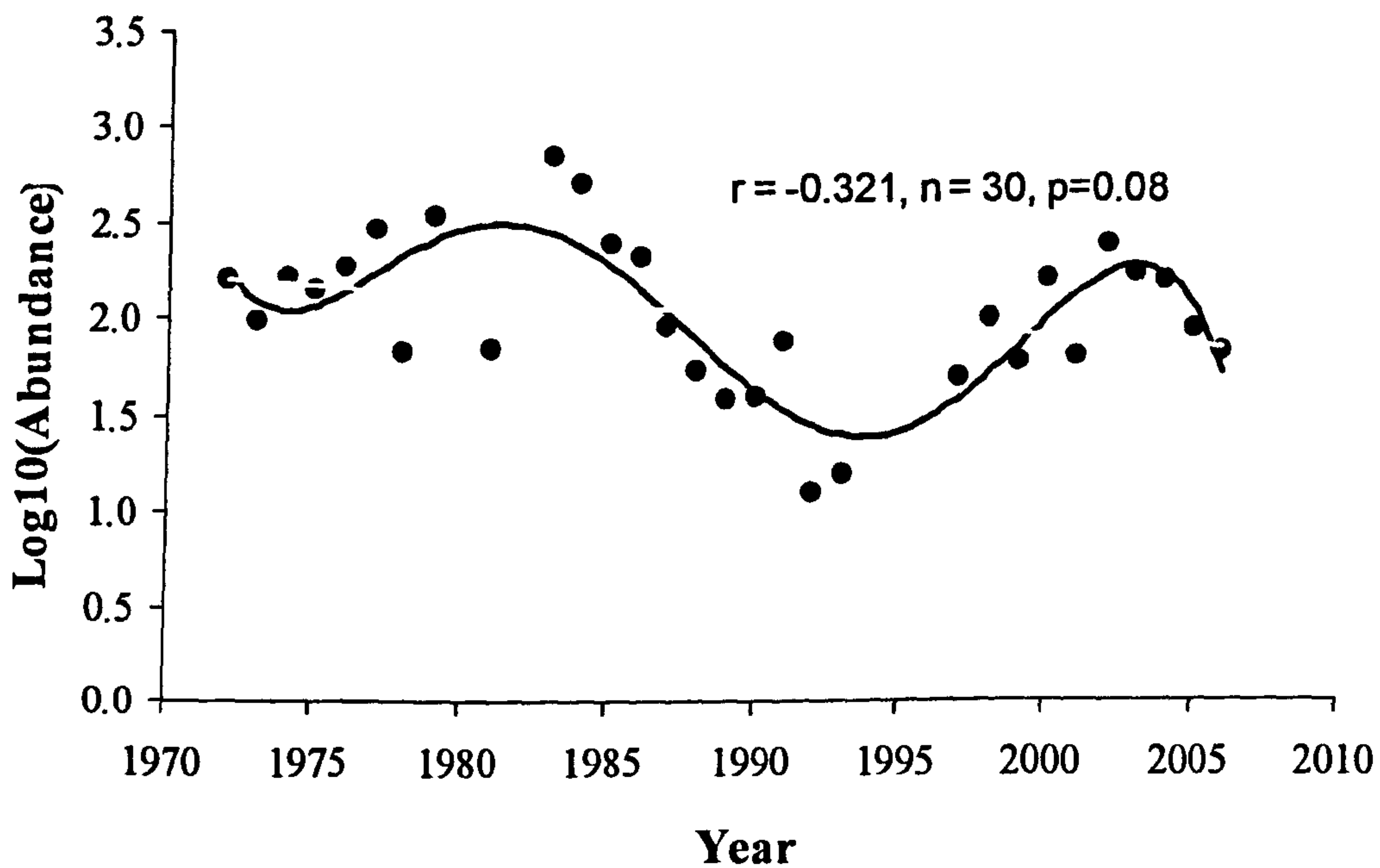
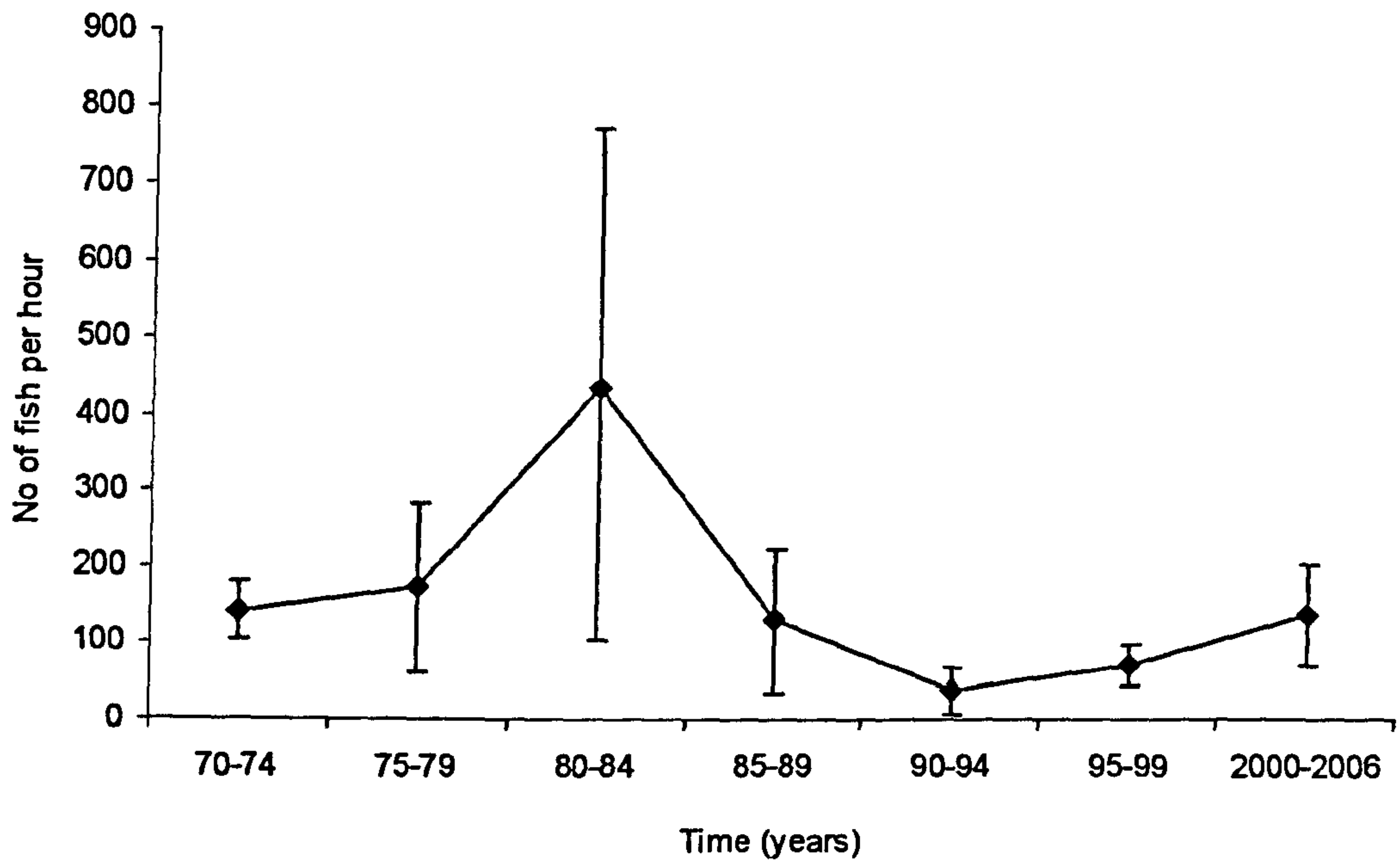


Figure 3.4. (a) Relative abundance of plaice caught during the RV *Prince Madog* autumn fisheries surveys between 1970 and 2006. (a) The annual average number caught hour⁻¹ for the period 1972-2006. The overall average for 1972-2006 (125 fish hour⁻¹, excluding the data for 1983 & 1984) is indicated by the dotted line. (b) Log₁₀ (average number caught hour⁻¹) for the period 1972-2006. A 6th order polynomial curve is shown for illustrative purposes to highlight the apparent decadal cycle in abundance.

a)



b)

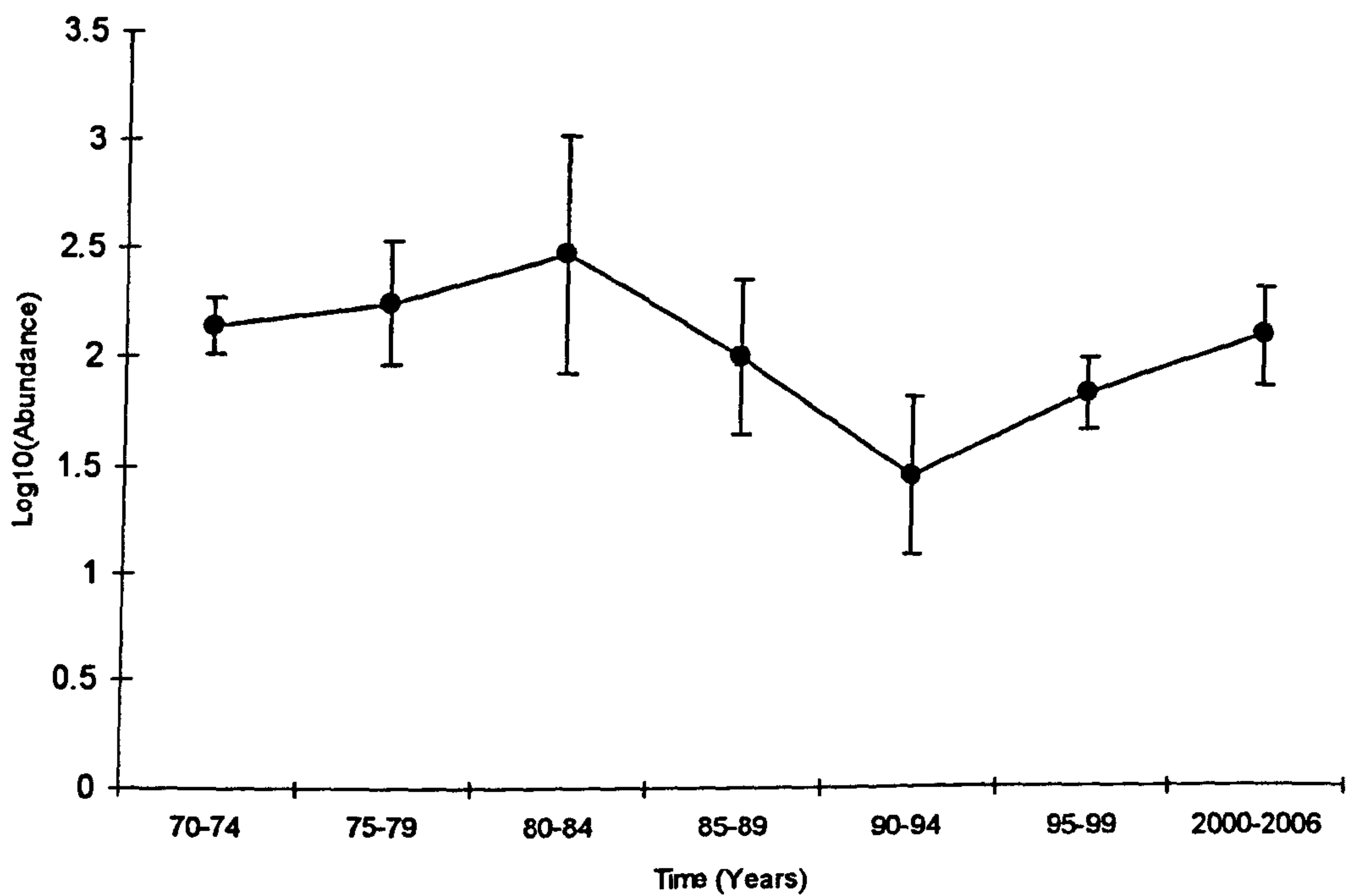


Figure 3.5. (a) Relative abundance of plaice caught during the RV *Prince Madog* autumn fisheries surveys between 1970 and 2006. (a) The annual average number caught hour⁻¹ per 5 year time period (1970-1974, 1975-1979 etc). (b) Log₁₀ (average number caught hour⁻¹) per 5 year time period (1970-1974, 1975-1979 etc). Data are presented as mean values ± SD.

3.3.2 Size and Age structure 1970-2006

The results presented in Chapter 2 (Stock assessment chapter) have shown that the current size range of plaice caught in the inshore waters of Eastern Anglesey and Northwest Wales in October 2004/2005 using a rockhopper otter trawl (76 mm cod end mesh size) ranged between 7.7 and 37.1 cm TL for male fish and 7.5 and 54.8 cm TL for female fish respectively. The average size for male and female fish during the current survey were 24.0 and 29.1 cm TL respectively. The age range for male and female fish were 0.5 to 5.5 years old and 0.5 to 12.5 years old respectively with an average age of 2.6 years for male fish and 3.1 years for female fish. In this section, the size/age structure of the stock over the period 1970-2006 is examined to determine whether there have been any significant changes in the size/age structure of plaice in the inshore waters of Eastern Anglesey and Northwest Wales in the autumnal fishing surveys during this time period.

The length-frequency distributions for male and female plaice for the time period 1970-2006 are presented in Figure 3.6. This figure summarises the available data. For some years, *e.g.* 1970, 1978 and 1982, size data are only available for one sex (Table 3.1, Figure 3.6). For some years, *e.g.* 1970, 1992 and 1993, data are only available for the length-stratified subsamples (Table 3.1, Figure 3.6). Finally, data were missing for some years, *e.g.* 1971, 1980 and 1994-1996 (Table 3.1, Figure 3.6). However, sufficient data are available between 1970 and 2006 to examine trends in the data set to see if there have been any changes in the size/age structure during this time period. The length-frequency distributions for male and female plaice in a given year are expressed as a percentage of the number of male or female plaice caught in the autumn surveys in that year in order to standardise for differences in sample size between years. A number of consistent trends are evident in the data set. Firstly, in most years (19/30, 63.3%) there is a unimodal skewed size distribution for both male and female plaice with the majority of fish being found in the smaller size classes and a 'tail' of a small number of larger-sized individuals (Figure 3.6). However in some years the size distributions of male or female fish appear unimodal/normally distributed (*e.g.* 1973, 1981, 1989, 1991, 1993; 16.7% occurrence) or bimodal (*e.g.* 1985, 1988, 1990, 2001, 2005; 20% occurrence). There was considerable inter-annual variation in the number of fish caught between years (Table 3.1) and the size range of fish also between years. Figure 3.7 shows the minimum and maximum size (Total Length, cm) of male and female plaice caught for the years that data are available between 1970 and 2006. The minimum size caught varied between 5 and 20 cm TL for male plaice with a mean minimum size of 12.6 ± 3.2 cm TL.

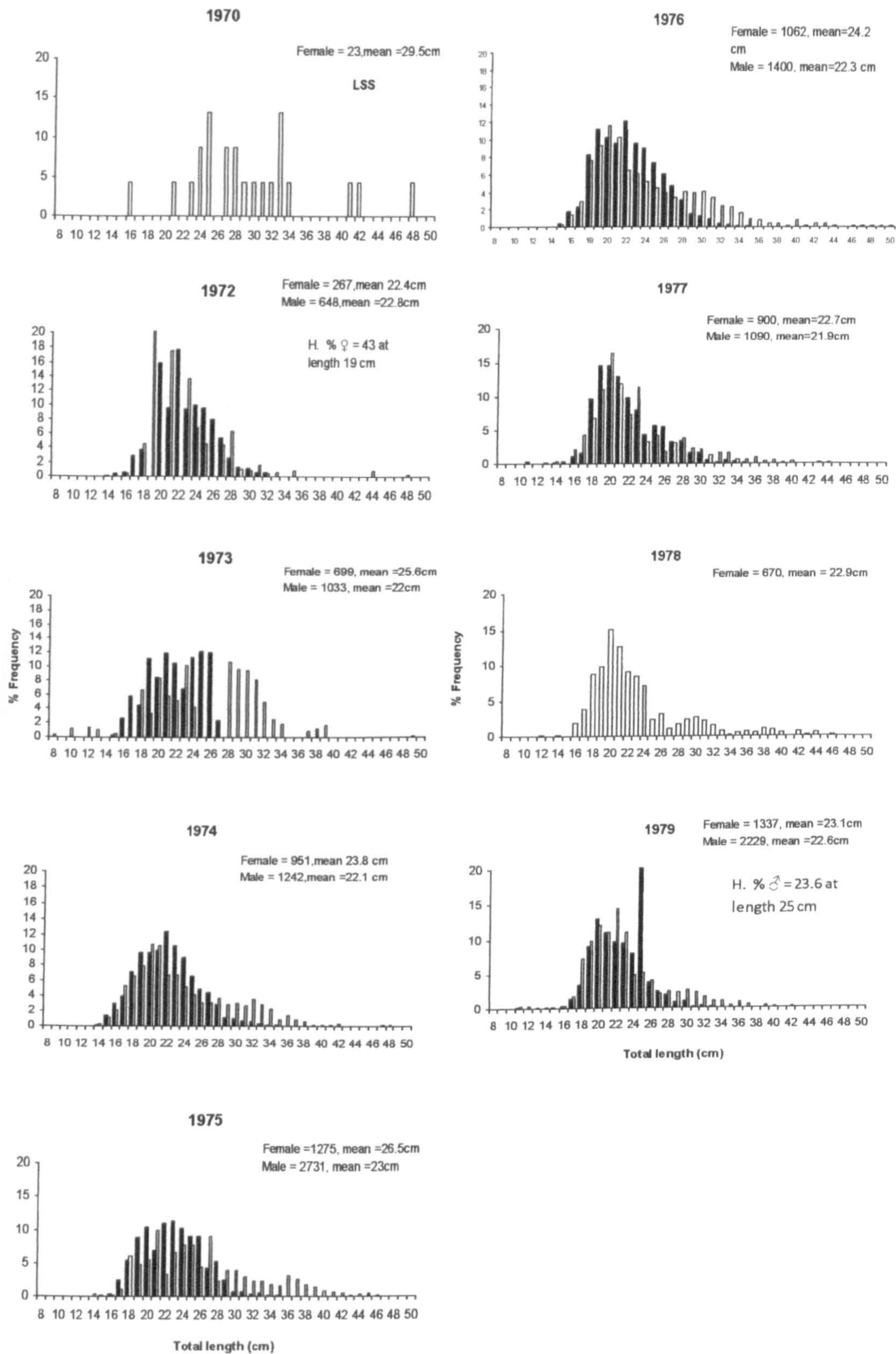


Figure 3.6 (a): 1970-1979

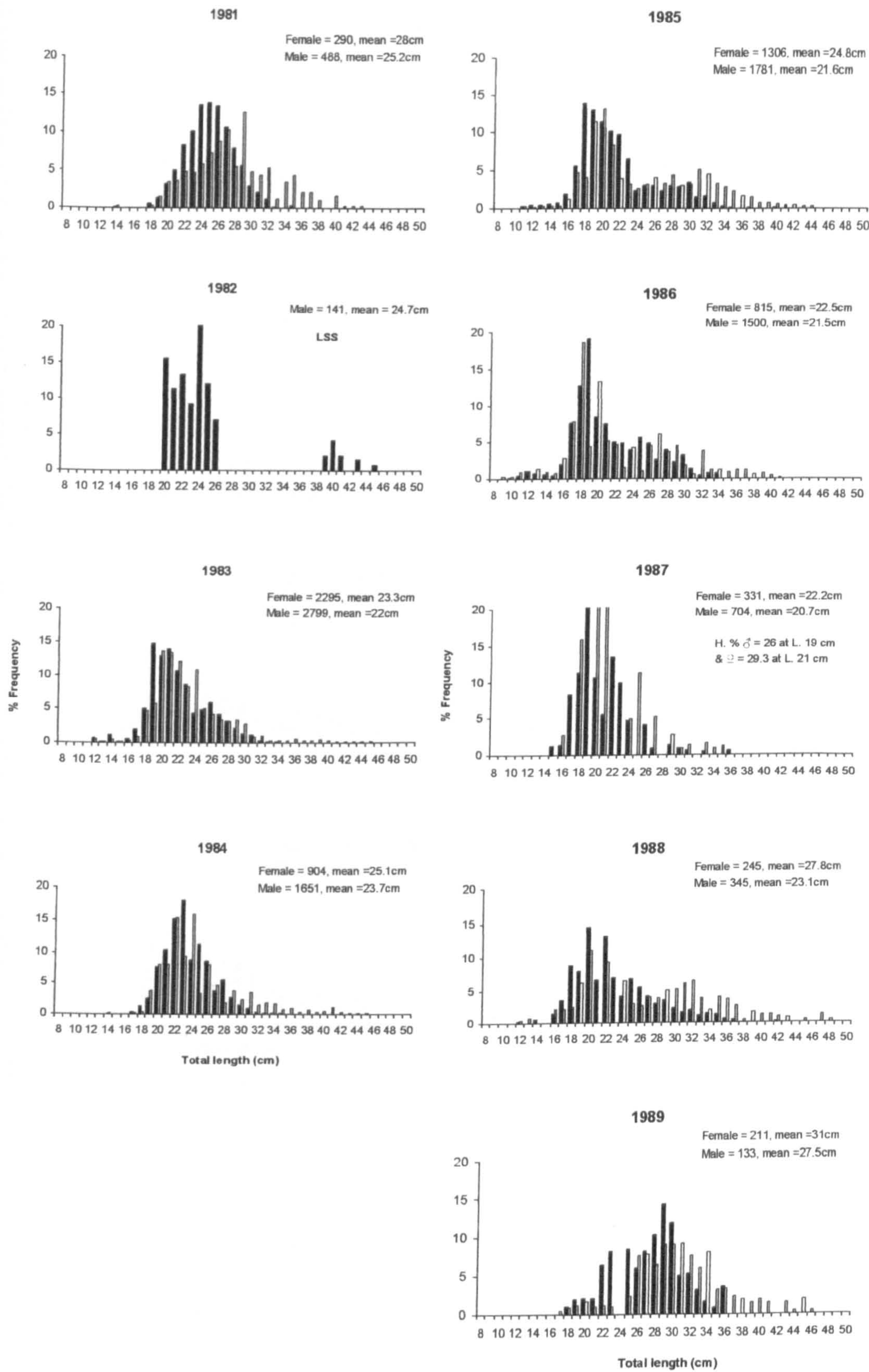


Figure 3.6 (b): 1980-1989

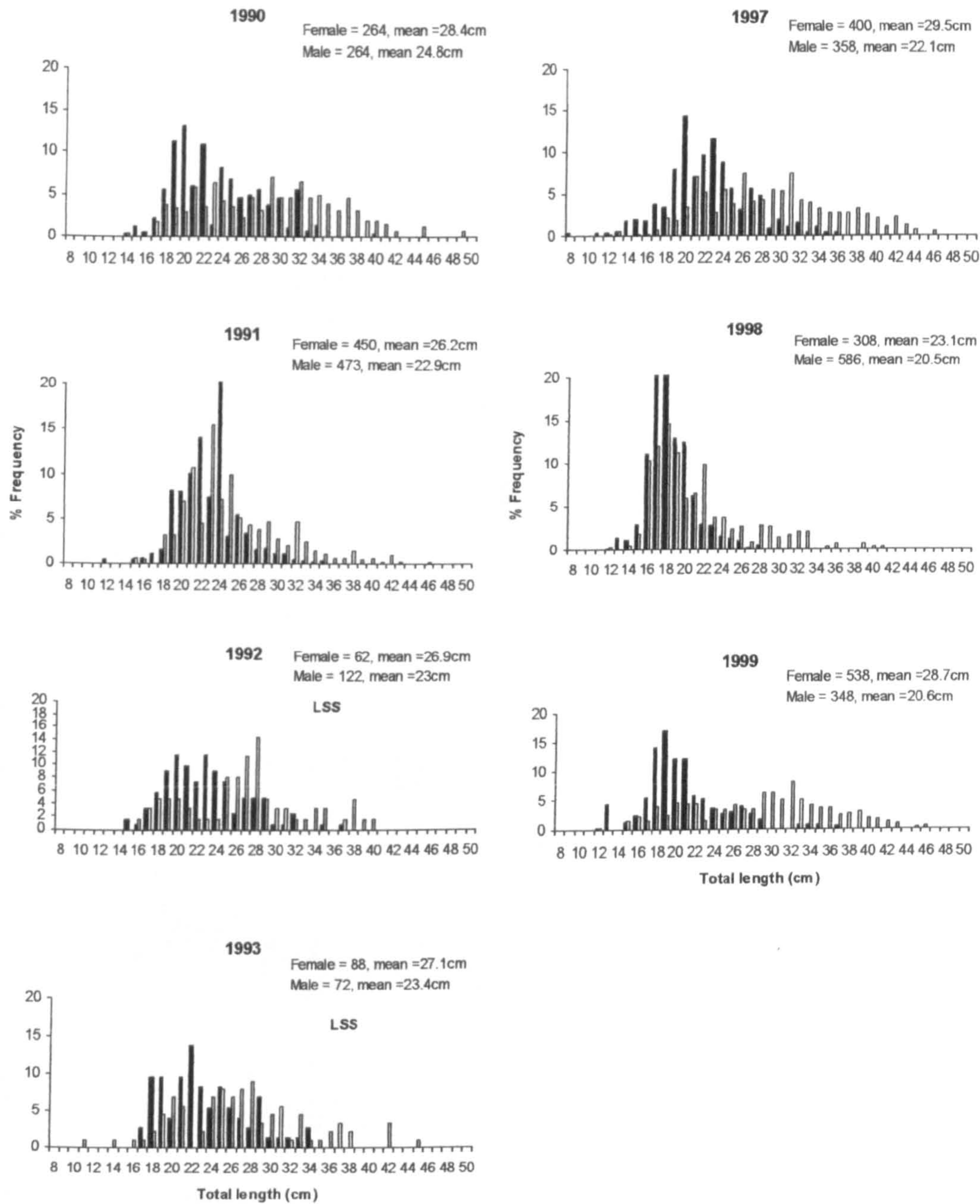


Figure 3.6 (c): 1990-1999

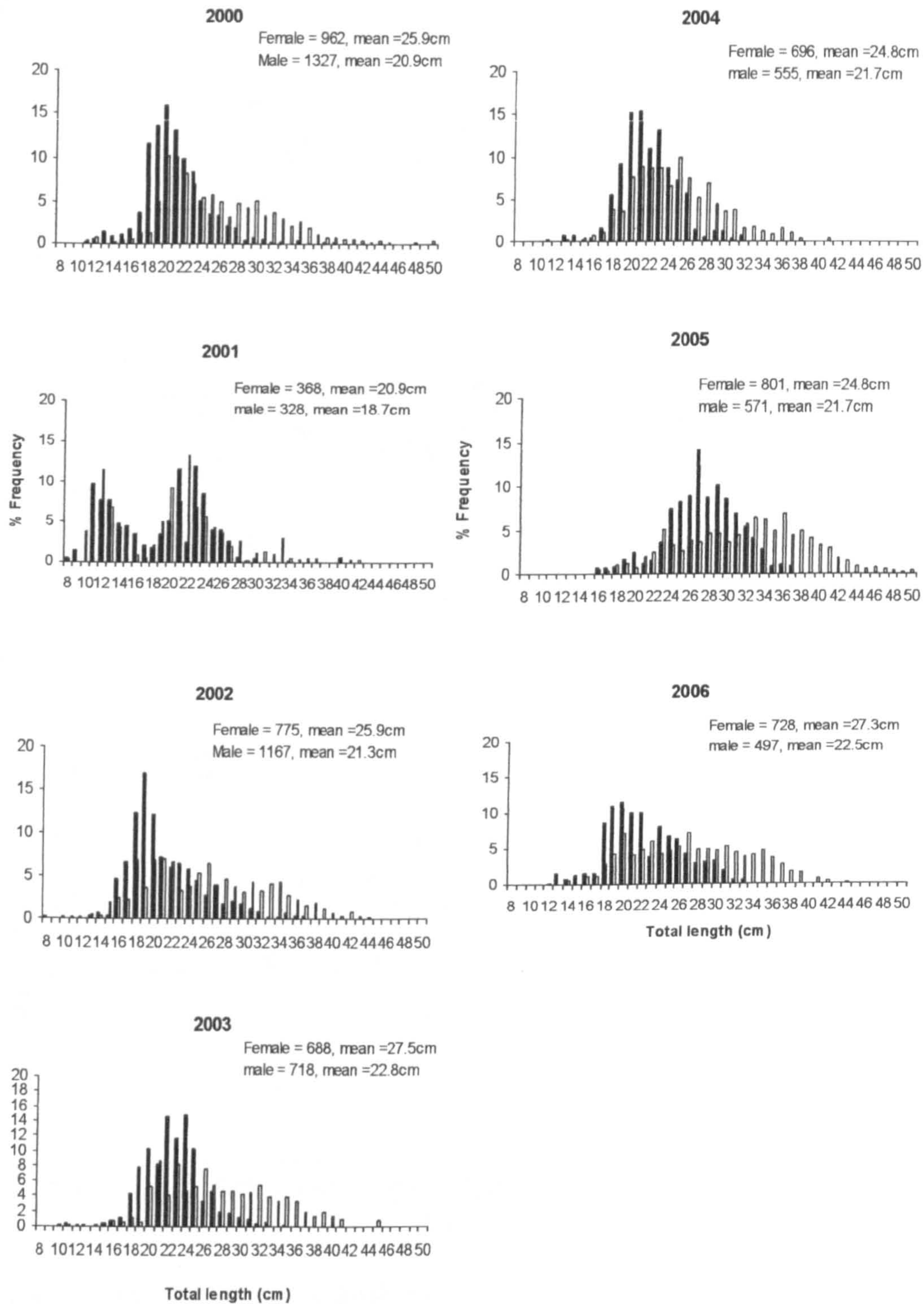
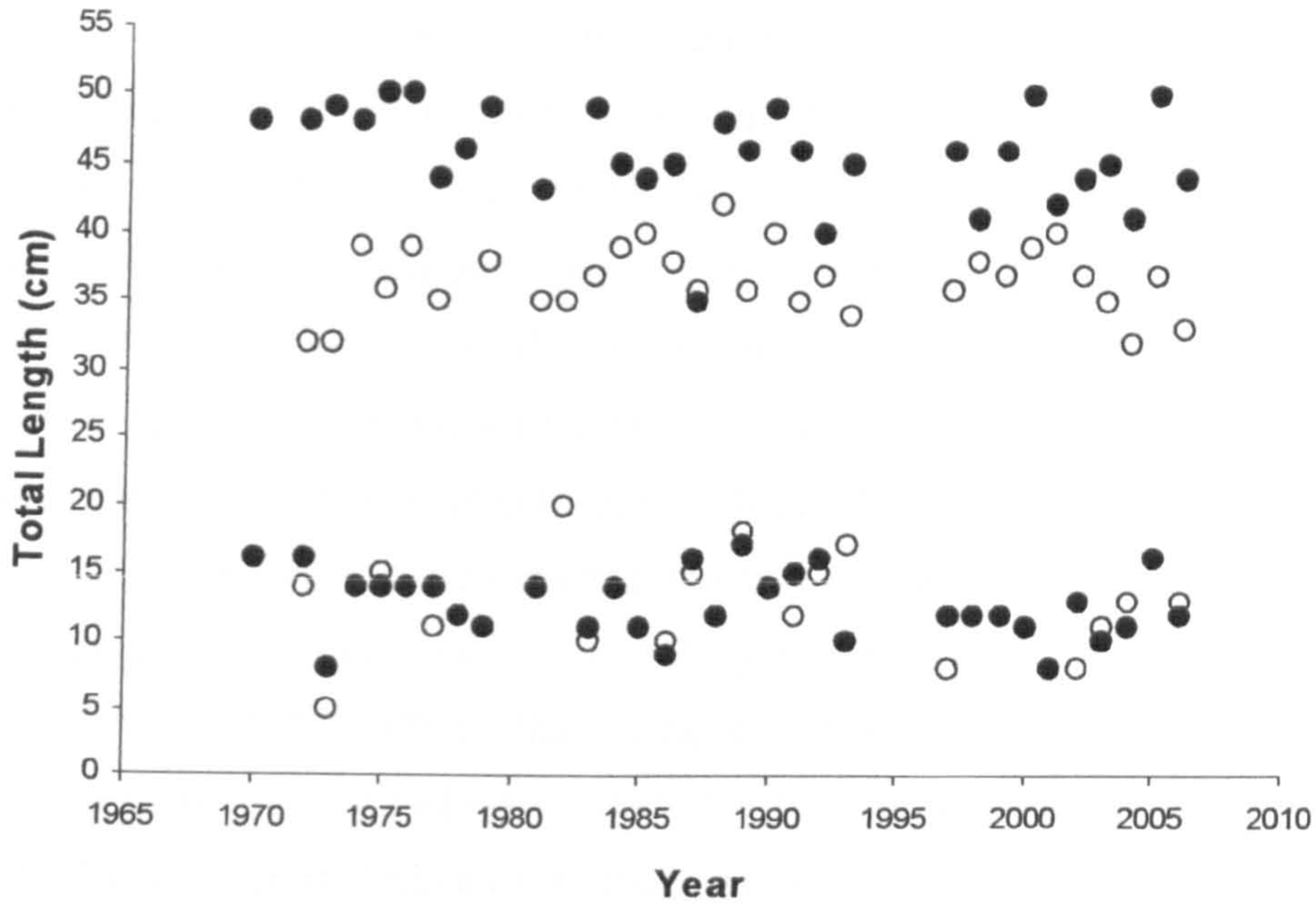


Figure 3.6 (d): 2000-2006

Figure 3.6: Length-frequency distributions of male (soled bar) and female (open bar) plaice caught in coastal water of E. Anglesey and N. W. Wales, Irish Sea of the period (1970 – 2006), with indication of the abundance percentage is highest (H) than 20% and at which length (L). LSS means samples based on length stratified sub-sample.

a)



b)

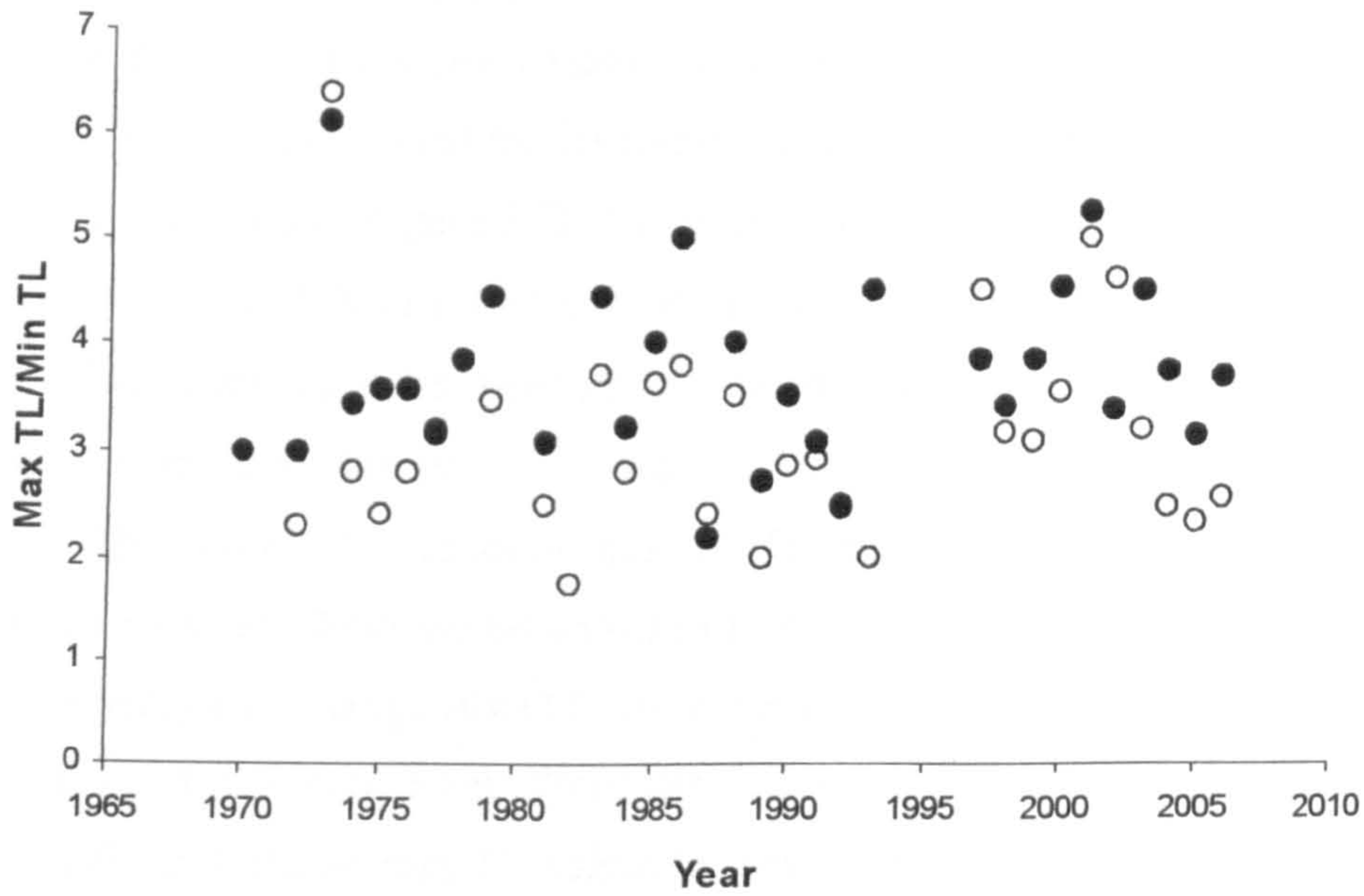
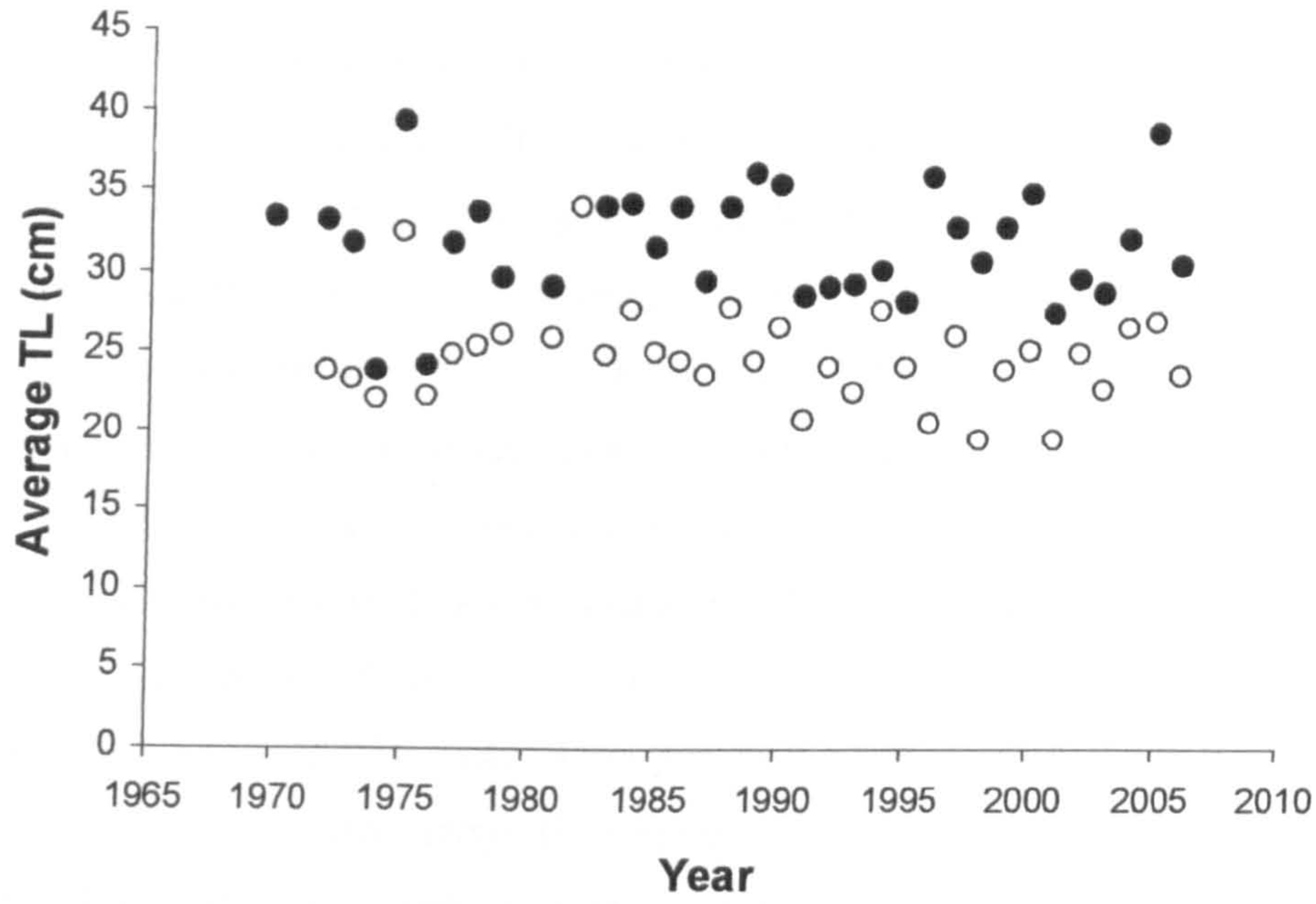


Figure 3.7: (a) Maximum and minimum Total Lengths (cm) of female (solid circles) and male (open circles) plaice caught in the October fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. (b) The size range, expressed as the ratio of maximum TL/Minimum TL for female (solid circles) and male (open circles) plaice caught in the October fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006.

For female plaice, the minimum size caught varied between 8 and 17 cm TL with a mean minimum size of 12.7 ± 2.4 cm TL. Overall, there was no difference in the average minimum size (TL) of male and female plaice caught during the 1970-2006 survey ($t = 0.05$, 58 df, $P = 0.96$). There was no correlation between time (survey year) and minimum size (TL) for either male ($r_s = -0.11$, $P = 0.56$) or female fish ($r_s = -0.24$, $P = 0.19$). Thus, there has been no overall change in the minimum size of male or female fish caught during the 1970-2006 survey. The maximum size of male plaice caught during the 1970-2006 survey varied between 32 and 42 cm TL with a mean maximum size of 36.6 ± 3.6 cm TL. For female plaice, the maximum size caught varied between 36 and 54.8 cm TL with a mean maximum size of 45.8 ± 3.8 cm TL. As expected, the average maximum size (TL) of female plaice was significantly larger than that of the male plaice caught during the 1970-2006 survey ($t = 11.08$, 59 df, $P < 0.0001$). There was no correlation between time (survey year) and maximum size (TL) for male ($r_s = -0.01$, $P = 0.66$). There was a trend for the maximum size (TL) of female fish to decline over time (Figure 3.7a), however, this was not significant at the 5% level ($r_s = -0.35$, $P = 0.053$). Thus, there has been no significant change in the maximum size of male or female plaice caught during the 1970-2006 survey. In order to examine whether there has been any change in the size range of plaice caught in the survey, the maximum size was divided by the minimum size for the catch data for each year and these data are presented in Figure 3.7b. There was no correlation between time (survey year) and size range (Max TL/Min TL) for both male ($r_s = 0.08$, $P = 0.69$) and female plaice ($r_s = -0.18$, $P = 0.34$). Thus, there has been no significant change in the size range of male or female plaice caught during the 1970-2006 survey.

The average TL values of male and female plaice for the years that data are available between 1970 and 2006 are presented in Figure 3.8. There was no correlation between time (survey year) and average size (TL) for either male ($r_s = -0.10$, $p = 0.56$) or female fish ($r_s = -0.05$, $p = 0.80$) (Figure 3.8a). When the data were grouped in 5 year intervals (1970-1974, 1975-1979 etc), the average TL values for both sexes were normally distributed (♂ , $Z = 0.10$, $n = 34$, $P > 0.20$; ♀ , $Z = 0.08$, $n = 34$, $P > 0.20$) with both data sets having equal variances between time periods (♂ , $W_{6,27} = 0.98$, $P = 0.46$; ♀ , $W_{6,27} = 0.60$, $P = 0.73$). There were no differences over time in the average size of male fish (ANOVA, $F_{(6,27)} = 1.71$, $P = 0.16$) or female fish (ANOVA, $F_{(6,27)} = 0.29$, $P = 0.94$). Since, the annual average TL values recorded may be dependent on the degree of fishing effort in any year and also subject to random biological variation, average annual TL was also calculated as a three year moving average (average for any given year calculated from the value for that year plus the year before and

a)



b)

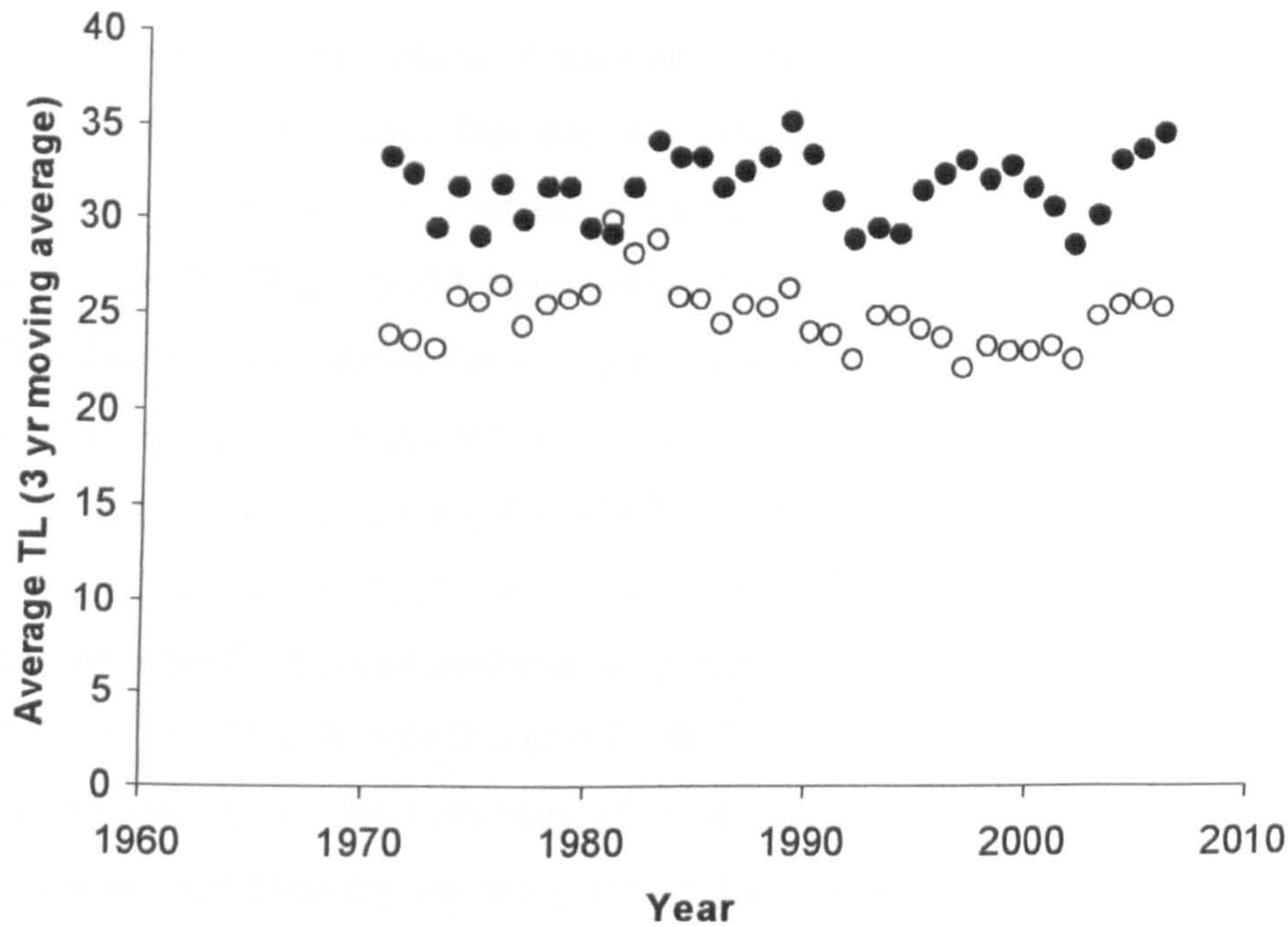


Figure 3.8: Average Total Lengths (cm) of female (solid circles) and male (open circles) plaice caught in the October fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the TL values for any given year plus the values for the year before and the year after.

the year after) in order to reduce the inter-annual variability and to ‘smooth out’ any long-term trends in the data set. Analysis of this ‘smoothed’ data set also indicated that there was no correlation between time (survey year) and average size (TL) female fish ($r_s = 0.13$, $n = 36$, $P = 0.45$), however, average TL showed a significant decrease over time for male plaice ($r_s = -0.37$, $n = 36$, $P = 0.03$) (Figure 3.8a). When the smoothed average TL data were grouped together into 5 year intervals (1970-1974, 1975-1979 etc), the data for both sexes were normally distributed (σ , $Z = 0.13$, $n = 36$, $P = 0.11$; ϕ , $Z = 0.12$, $n = 36$, $P > 0.20$) with both data sets having equal variances between time periods (σ , $W_{6,29} = 1.59$, $P = 0.18$; ϕ , $W_{6,29} = 1.67$, $P = 0.16$). There was a significant difference in the smoothed average TL between the time intervals for male plaice (ANOVA, $F_{(6,29)} = 8.31$, $P < 0.001$) but not for female plaice (ANOVA, $F_{(6,29)} = 1.49$, $P = 0.22$) (Table 3.4). Pairwise comparisons of the smoothed average TL for male plaice for each time interval (Table 3.4) showed that male plaice in 1980-1984 were larger than those caught in the early 1970s or from 1990 onwards (Table 3.4). Thus, the results indicate that although there has been no change in the average TL of female plaice between 1970-2006, there has been a significant decline in the average TL of male plaice during the same time period.

The modal TL values of male and female plaice, *i.e.* the most abundant length class (Figure 3.6), for the years that data are available between 1970 and 2006 are presented in Figure 3.9. There was no correlation between time (survey year) and modal size (TL) for female ($r_s = 0.174$, $p = 0.35$), but a negative trend was reported for male fish ($r_s = -0.309$, $P = 0.10$) (Figure 3.9a). When the data were grouped in 5 year intervals (1970-1974, 1975-1979 etc), the modal TL values for both sexes were not normally distributed (σ , $Z = 0.17$, $n = 30$, $P = 0.03$; ϕ , $Z = 0.22$, $n = 31$, $P = 0.001$) but both data sets had equal variances between time periods (σ , $W_{6,23} = 1.15$, $P = 0.37$; ϕ , $W_{6,24} = 1.85$, $P = 0.13$) allowing the use of ANOVA. There were no differences over time in the average modal sizes of male fish (ANOVA, $F_{(6,23)} = 1.44$, $P = 0.24$) or female fish (ANOVA, $F_{(6,24)} = 1.40$, $P = 0.26$) in each of the 5 year time intervals. Because of the ‘noisiness’ of the annual modal TL values (Figure 3.9a), a three year moving average (average for any given year calculated from the value for that year plus the year before and the year after) was calculated for modal size in order to reduce the inter-annual variability and to ‘smooth out’ any long-term trends in the data set. Analysis of this ‘smoothed’ data set also indicated that there was no correlation between time (survey year) and modal size (TL) for female fish ($r_s = 0.22$, $P = 0.19$), however, modal size (TL) decreased over time for male plaice ($r_s = -0.47$, $P = 0.005$) (Figure 3.9b). When the smoothed average modal TL data were grouped together into 5 year intervals (1970-1974, 1975-1979 etc),

Table 3.4. (a) smoothed average TL (cm) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. Smoothed average values calculated as a three year running average. (b) Significance values for the *post-hoc* comparisons of smoothed average TL using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold).

a)

<i>Time period</i> (years)	<i>Male</i> <i>Smoothed</i> <i>average TL</i>	Female Smoothed average TL
1970-1974	24.1 \pm 1.3	31.7 \pm 1.6
1975-1979	25.5 \pm 0.8	30.8 \pm 1.2
1980-1984	27.7 \pm 1.8	31.5 \pm 2.2
1985-1989	25.4 \pm 0.7	33.1 \pm 1.3
1990-1994	24.0 \pm 0.9	30.4 \pm 1.8
1995-1999	23.2 \pm 0.8	32.3 \pm 0.7
2000-2006	24.2 \pm 1.3	31.8 \pm 2.1

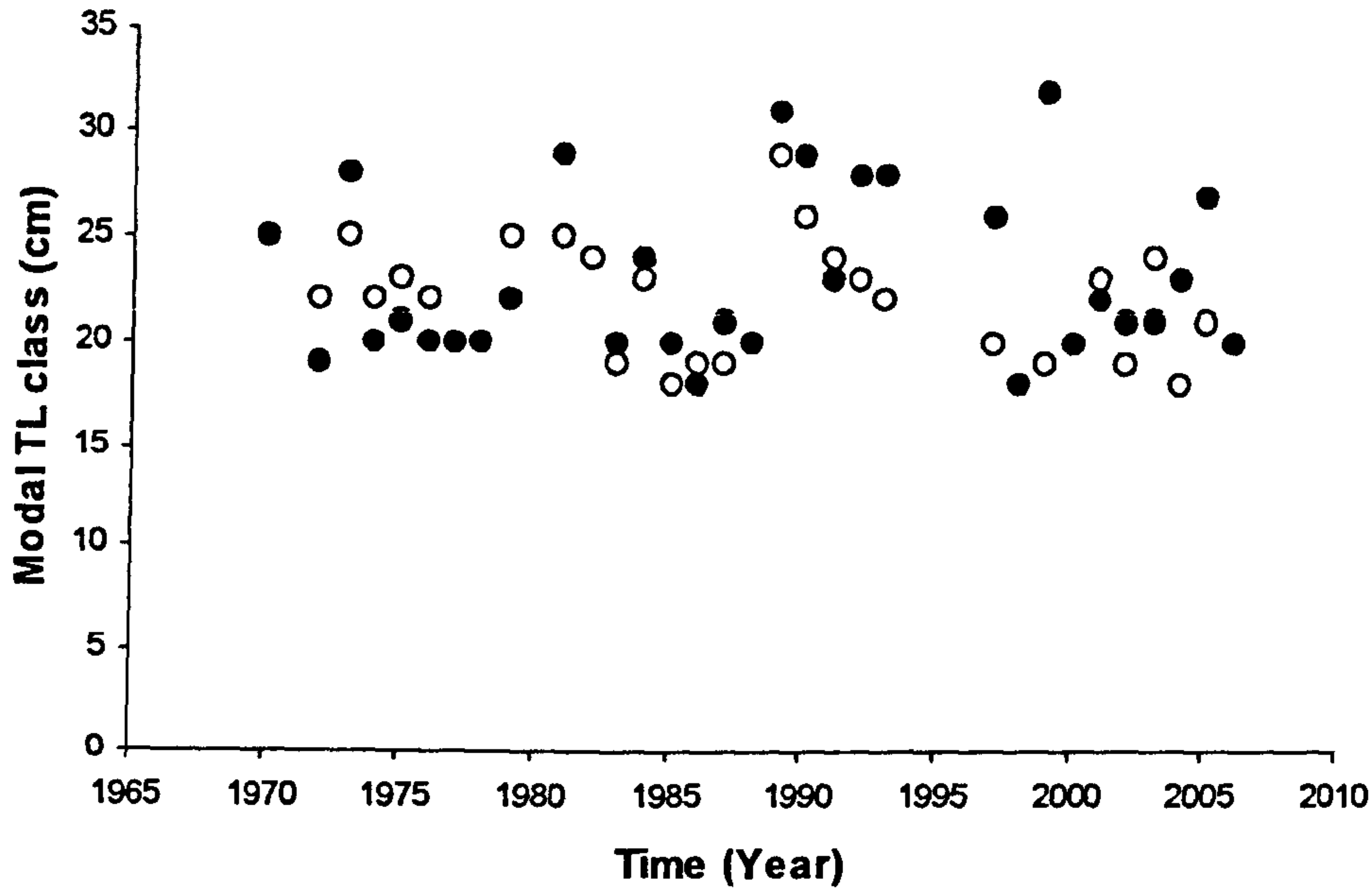
b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.77					
1980-1984	0.008	0.19				
1985-1989	0.81	1.00	0.17			
1990-1994	1.00	0.67	0.03	0.71		
1995-1999	0.97	0.18	0.0001	0.21	0.98	
2000-2006	1.00	0.78	0.003	0.82	1.00	0.87

the data for both sexes were normally distributed (σ , $Z = 0.09$, $n = 36$, $P > 0.20$; ϕ , $Z = 0.13$, $n = 36$, $P = 0.17$) but with unequal variances between time periods (σ , $W_{6,28} = 3.41$, $P = 0.012$; ϕ , $W_{6,29} = 4.36$, $P = 0.003$) precluding the use of ANOVA. Analysis of the smoothed modal size data for the different time periods using a Kruskal Wallis test indicated a significant difference between time periods intervals for both male plaice ($\chi^2 = 17.53$, 6 df, $P = 0.008$) and female plaice ($\chi^2 = 19.71$, 6 df, $P = 0.003$). When pairwise comparisons of the time periods were conducted using a Wilcoxon Signed Rank test, the overall pattern was for the smoothed modal sizes of the male fish in 1995-1999 to be smaller compared to the other 5 year time periods and for female fish in 1990-1994 to be larger compared to the other 5 year time periods (Table 3.5). Thus, the results indicate that although there have been no consistent changes in the modal TL of male plaice between 1970-2006, there has been a trend for the modal TL of male plaice to decrease during the same time period (Figure 3.10).

The preceding data analyses has examined whether there have been any changes in size over time in terms of maximum/minimum TL and in average/modal TL but have not examined whether there has been any change in the size composition of the catch over time. Therefore, the data were grouped into 5 year intervals as before, and the percentage of fish in the following size classes determined: <14, 15-19, 20-24, 25-29, 30-34, 35-39 and >40 cm TL. The percentage frequencies in each of the 6 size classes for each 5 year interval were calculated for male, female and combined data and are presented in Figure 3.11. For male plaice, the most abundant size class was the 20 – 24 cm TL class with an average of 47% (range 33-54%) found in this size class. For most 5 year time periods this was the most abundant size class, except 1995-1999 where the 15-19 cm size class was most abundant (53%) (Figure 3.11). In all 5 year time periods, the majority of male plaice (average 94%, range 91-98%) comprised of plaice between 15 and 29 cm in size with fish >30 cm TL rarely being caught. For female plaice, the most abundant size class was also the 24 – 29 cm TL class with an average of 36% (range 21-55%) found in this size class. However, the second most abundant size class was the 25-29 cm TL size class with an average of 21% (range 18-25%). In all 5 year time periods, the majority of female plaice (average 84%, range 72-91%) comprised of plaice between 15 and 29 cm in size, however, a greater proportion of fish >30 cm TL (average 14%, range 8-23%) were caught compared to male plaice (Figure 3.11).

(a)



b)

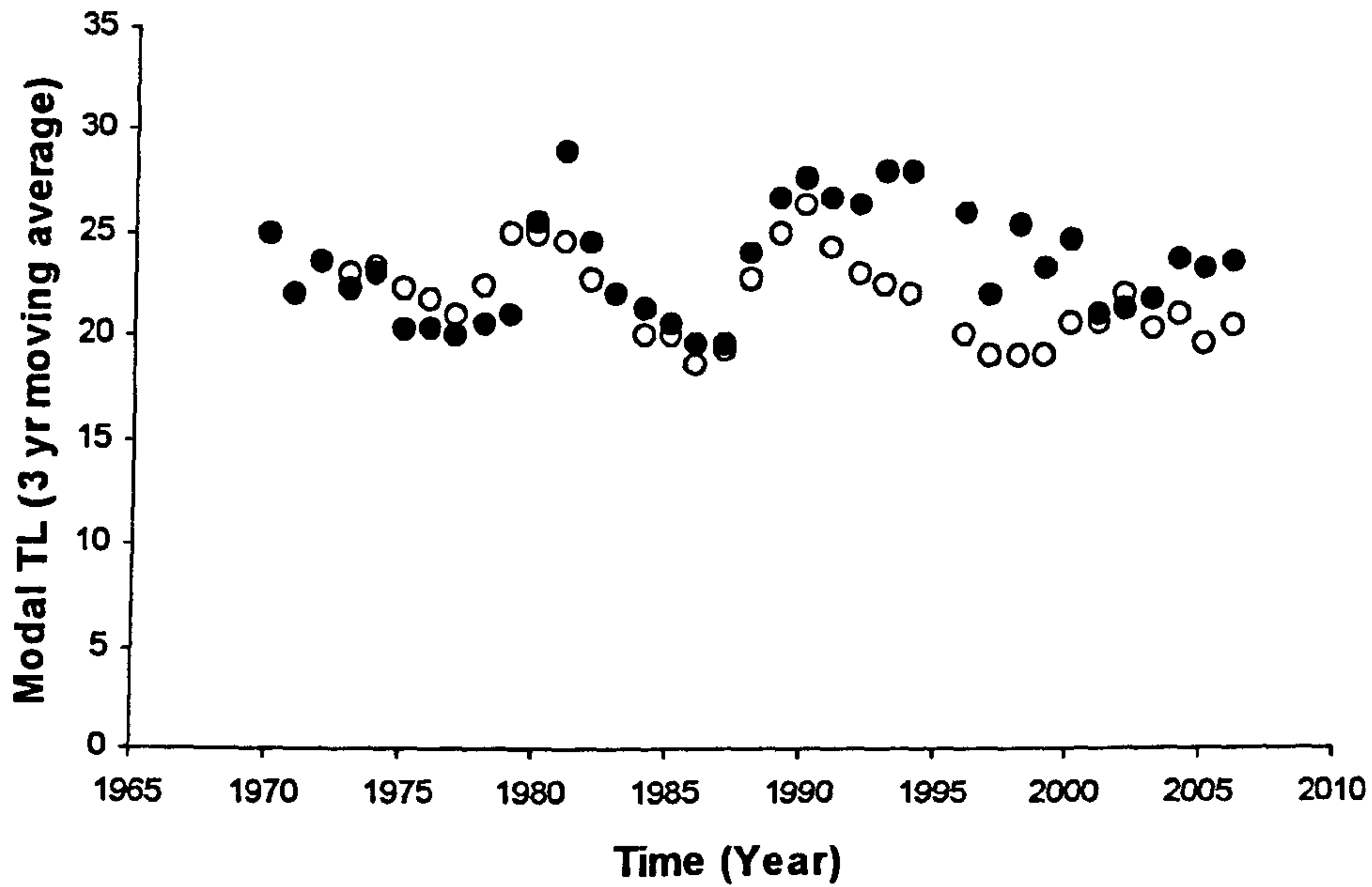


Figure 3.9: Modal Total Lengths (cm) of female (solid circles) and male (open circles) plaice caught in the October fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the TL values for any given year plus the values for the year before and the year after.

Table 3.5: (a) Smoothed modal TL (cm) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as median values \pm interquartile. Smoothed values calculated as a three year running average. (b) & (c) Significance values for the *post-hoc* comparisons of smoothed modal TL for (b) male and (c) female plaice using the Wilcoxon Signed Rank test (significant differences at the 5% level are highlighted in bold and trends, $0.10 < p < 0.05$, are underlined).

a)

<i>Time period</i> (years)	<i>Male</i> <i>Smoothed</i> <i>modal TL</i>	<i>Female</i> <i>Smoothed</i> <i>modal TL</i>
1970-1974	23.0 \pm 0.7	23.2 \pm 1.2
1975-1979	22.5 \pm 1.5	20.5 \pm 0.4
1980-1984	22.8 \pm 2.0	24.5 \pm 3.1
1985-1989	21.1 \pm 2.6	22.1 \pm 3.1
1990-1994	23.6 \pm 1.7	27.3 \pm 0.8
1995-1999	19.3 \pm 0.5	24.2 \pm 1.8
2000-2006	20.7 \pm 0.7	22.7 \pm 1.4

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.144					
1980-1984	0.715	0.686				
1985-1989	<u>0.068</u>	0.144	0.416			
1990-1994	0.285	0.465	<u>0.080</u>	0.225		
1995-1999	<u>0.068</u>	<u>0.068</u>	<u>0.068</u>	0.414	<u>0.068</u>	
2000-2006	<u>0.068</u>	0.104	0.138	0.893	0.042	<u>0.068</u>

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.043					
1980-1984	0.500	0.043				
1985-1989	0.345	0.345	0.498			
1990-1994	0.043	0.043	0.225	0.042		
1995-1999	0.102	<u>0.068</u>	0.715	0.144	<u>0.066</u>	
2000-2006	0.225	0.043	0.225	0.893	0.043	<u>0.068</u>

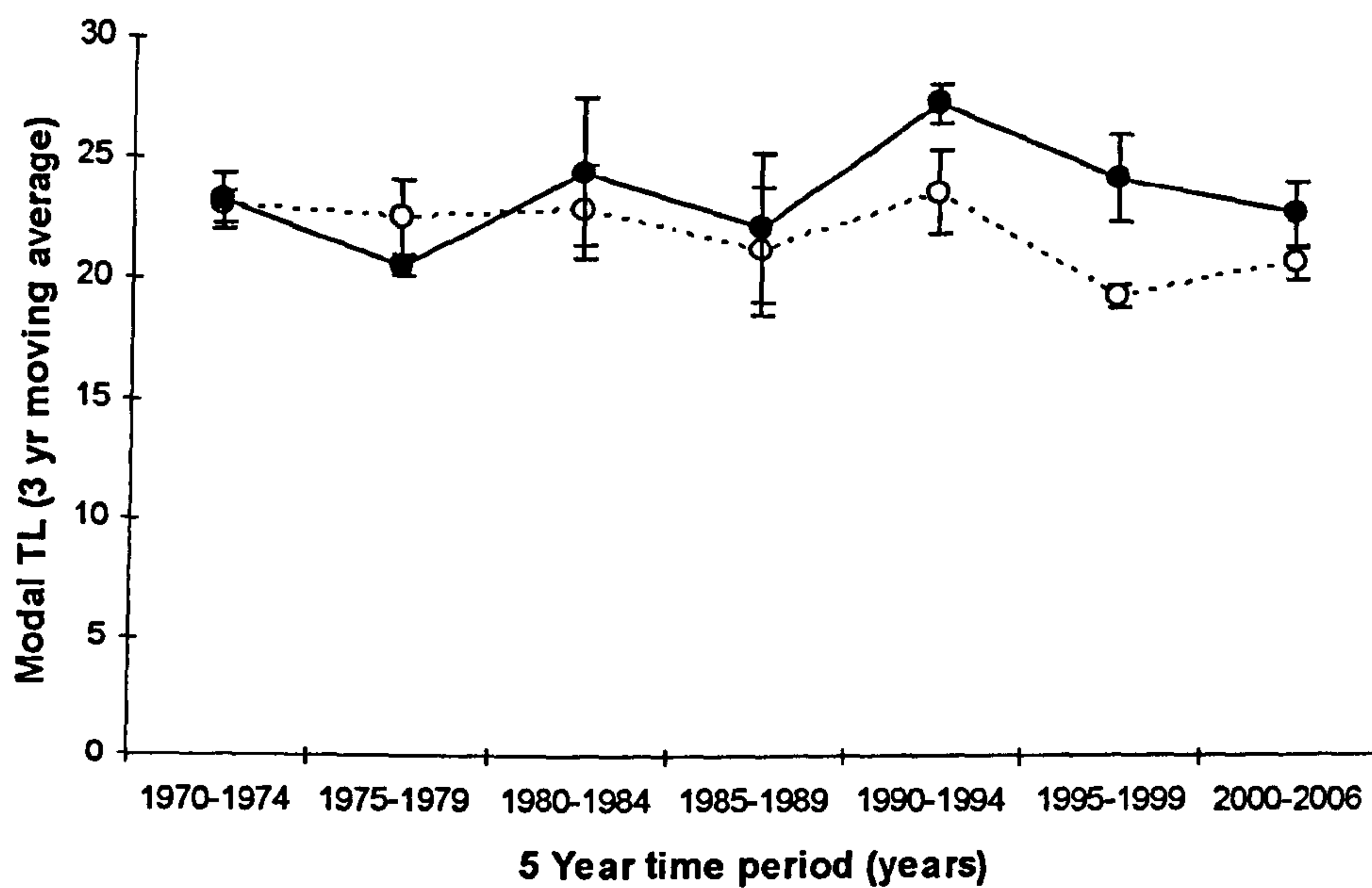


Figure 3.10: Modal Total Lengths (cm), calculated as a three year moving average) of female (solid circles) and male (open circles) plaice caught in the October fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as median \pm interquartile values for 5 year time periods (1970-1974, 1975-1979 etc).

The temporal changes in the proportion of fish in each size class are presented for male, female and male/female plaice combined in Figure 3.12. This plot illustrates whether the same patterns in the size composition of the catch are observed between the seven time periods. For male plaice, most 5 year time periods show the same pattern of size distribution, with a peak in the 20-24 cm TL size class, although the actual peak value in this size class varies between time periods. The exceptions are 1985-1989 and 1995-1999 where the peak abundance is observed in the 15-19 cm size class (Figure 3.12a). For female plaice, the same pattern of size distribution is observed in each time period with peak abundance seen in the 20-24 cm TL size class (Figure 3.12b). However, a greater proportion of female fish can be consistently found in the larger size classes (> 30 cm TL) compared to male plaice. When the data are combined, the patterns observed mirror those observed in the male and female plaice, *i.e.* the influence of the large numbers of 15-19 cm TL male plaice caught in 1985-1989 and 1994-1995, and the larger numbers of large female plaice can be seen in the size-distribution plots (Figure 3.12c).

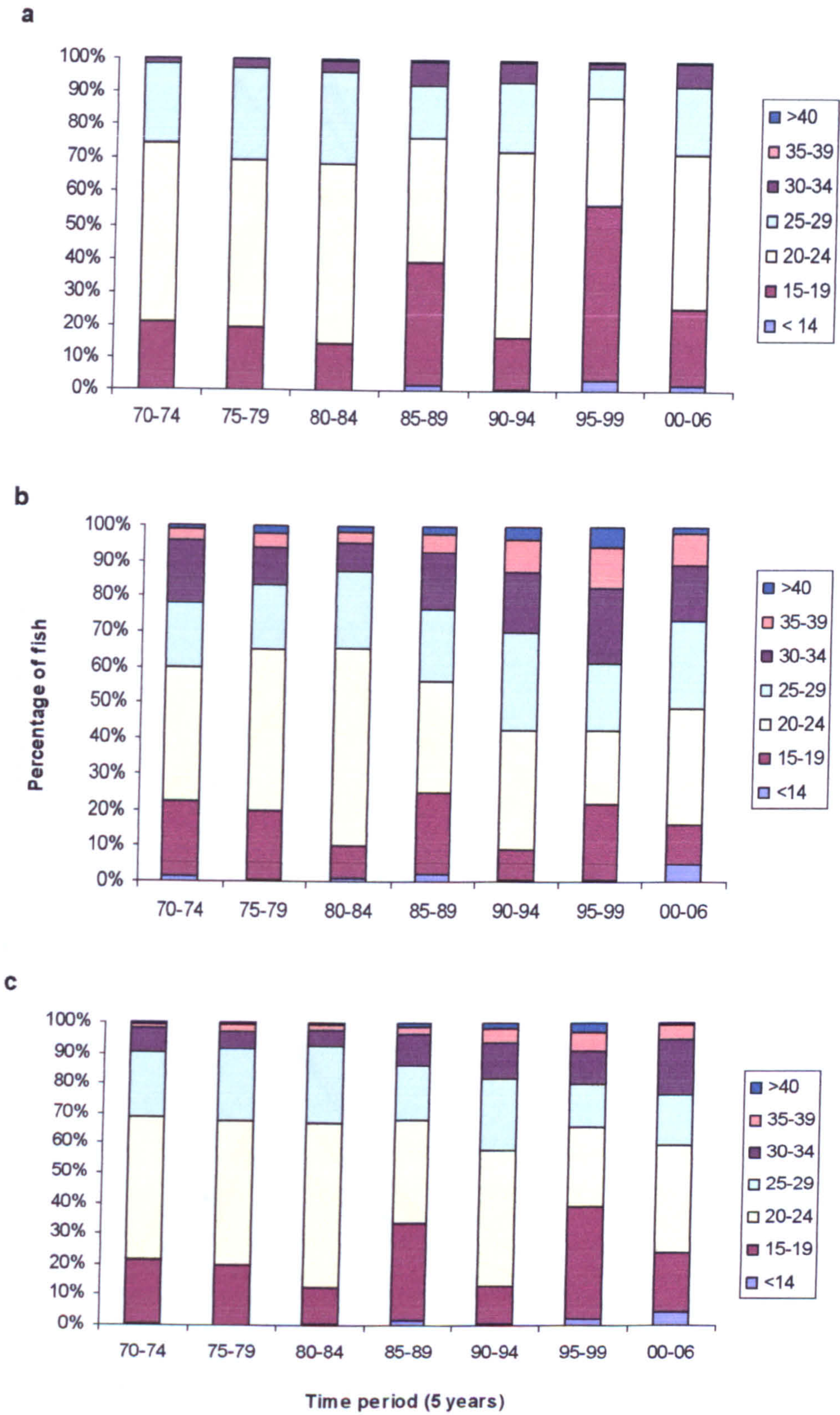


Figure 3.11: Percentage frequencies of plaice in different size classes (TL, cm) caught in the autumn fisheries surveys conducted in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented for (a) male, (b) female and (c) male and female combined for 5 year time intervals.

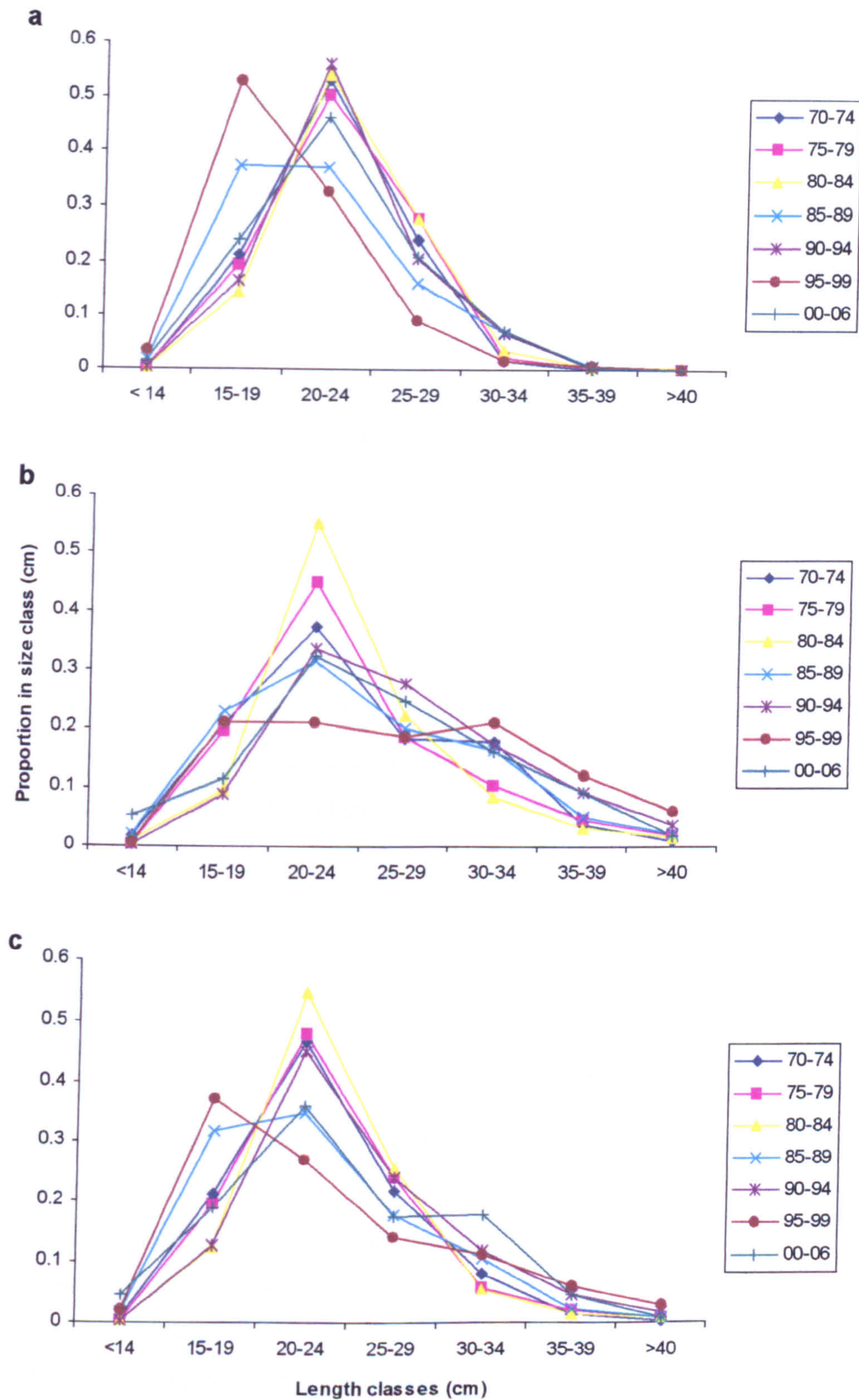


Figure 3.12: Proportion of plaice in different size classes (TL, cm) for 5 year time intervals (1970-1974, 1975-1979, etc) caught in the autumn fisheries surveys conducted in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented for (a) male, (b) female and (c) male and female combined for the different size classes.

The age-frequency distributions of male and female plaice for the 36 year time period, 1970-2006, are shown in Figure 3.13. Data were available for both male and female plaice in most years except 1971, 1980 and 1992, when no data are available for either sex of plaice, 1970 and 1978 when only female data were available and 1982 when only male data were available (Table 3.1, Figure 3.13). Due to sample sizes varying from year to year, age-frequency distributions of male and female plaice have been standardised by expressing them as the percentage of the total number of male or female plaice in a given year (Figure 3.13). The majority of the age-frequency distributions appear negatively skewed with a high percentage of 1.5 to 3.5 year old fish, although the age distributions in 2005 and 2006 appears to be normally distributed. Most of the age-frequency distributions for male plaice between 1970-2006 are biased towards the younger age classes (Figure 3.13). The age-frequency distributions of female plaice between 1970-2006 also show a predominance of younger age classes but also exhibit more of a skew to the right with the presence of smaller numbers of older fish in the age distribution (Figure 3.13). Overall, the age range in the data set is between 0.5 to 14.5 years old, although as previously mentioned, the greatest number of plaice are concentrated in the 1.5 to 3.5 age classes. Figure 3.13 clearly illustrates differences in the age ranges between male and female plaice in most years. For both sexes, the minimum age caught in the net varies between 0.5 and 1.5 years old. For male plaice, the minimum age caught in October was 0.5 years old on 18 occasions and 1.5 years old on 13 occasions. The minimum male age recorded in 1991, 3.5 years old (Figure 3.13), is probably erroneous due to mistakes in ageing. For female plaice, the minimum age caught in October was 0.5 years old on 20 occasions, 1.5 years old on 9 occasions and 2.5 years old on 4 occasions (Figure 3.13). The minimum age data were not normally distributed for either sex (♂ , $Z = 0.34$, $n = 31$, $P < 0.001$; ♀ , $Z = 0.39$, $n = 31$, $P < 0.001$). The median minimum ages for male and female plaice were both dominated by the 0.5 year old age class. Median minimum ages for male and female plaice were similar (Mann Whitney $U = 524.5$, $P = 0.96$) with a median value of 1 ± 0.5 (interquartile range) for both sexes. However, there was a significant negative correlation between minimum age and time over 36 years for both male and female plaice (male, $r_s = -0.427$, $P = 0.015$; female, $r_s = -0.516$, $P = 0.002$) indicating that the minimum age of plaice caught in the autumn surveys had decreased between 1970 and 2006 (Figure 3.14). The maximum age of male plaice varied from year to year and ranged between

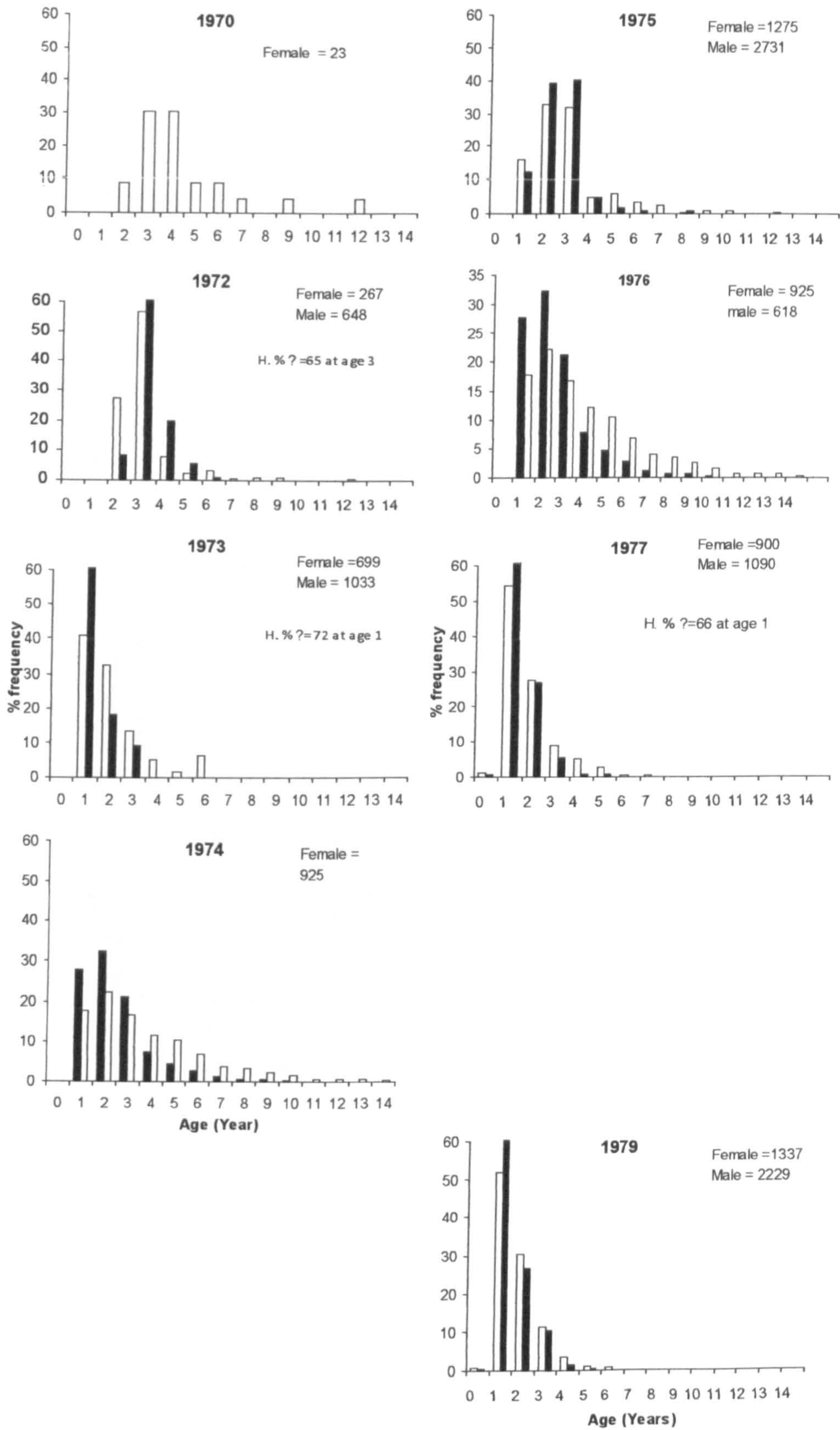


Figure 3.13 (a): 1970-1979

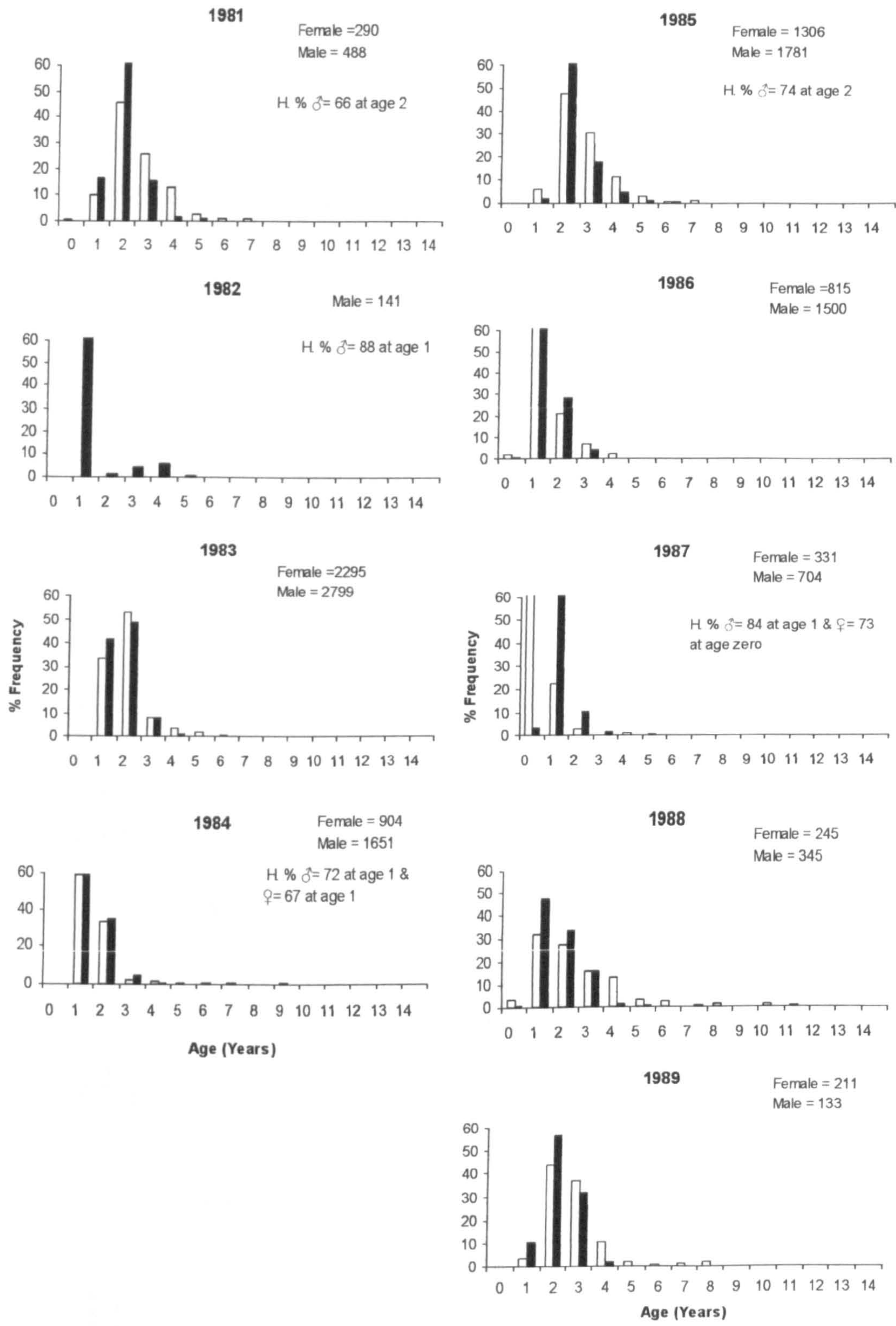


Figure 3.13 (b): 1980-1989

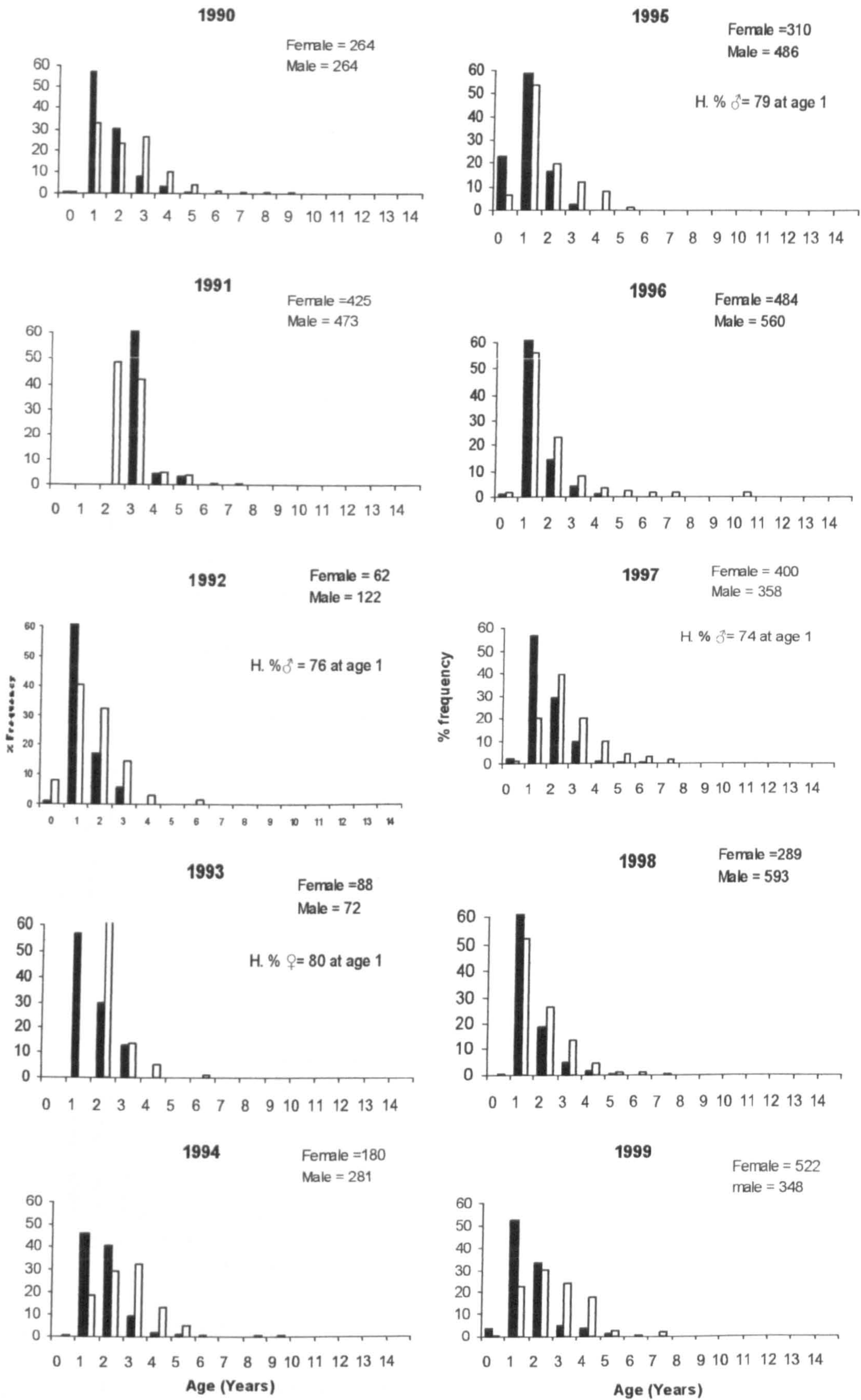


Figure 3.13 (c): 1990-1999

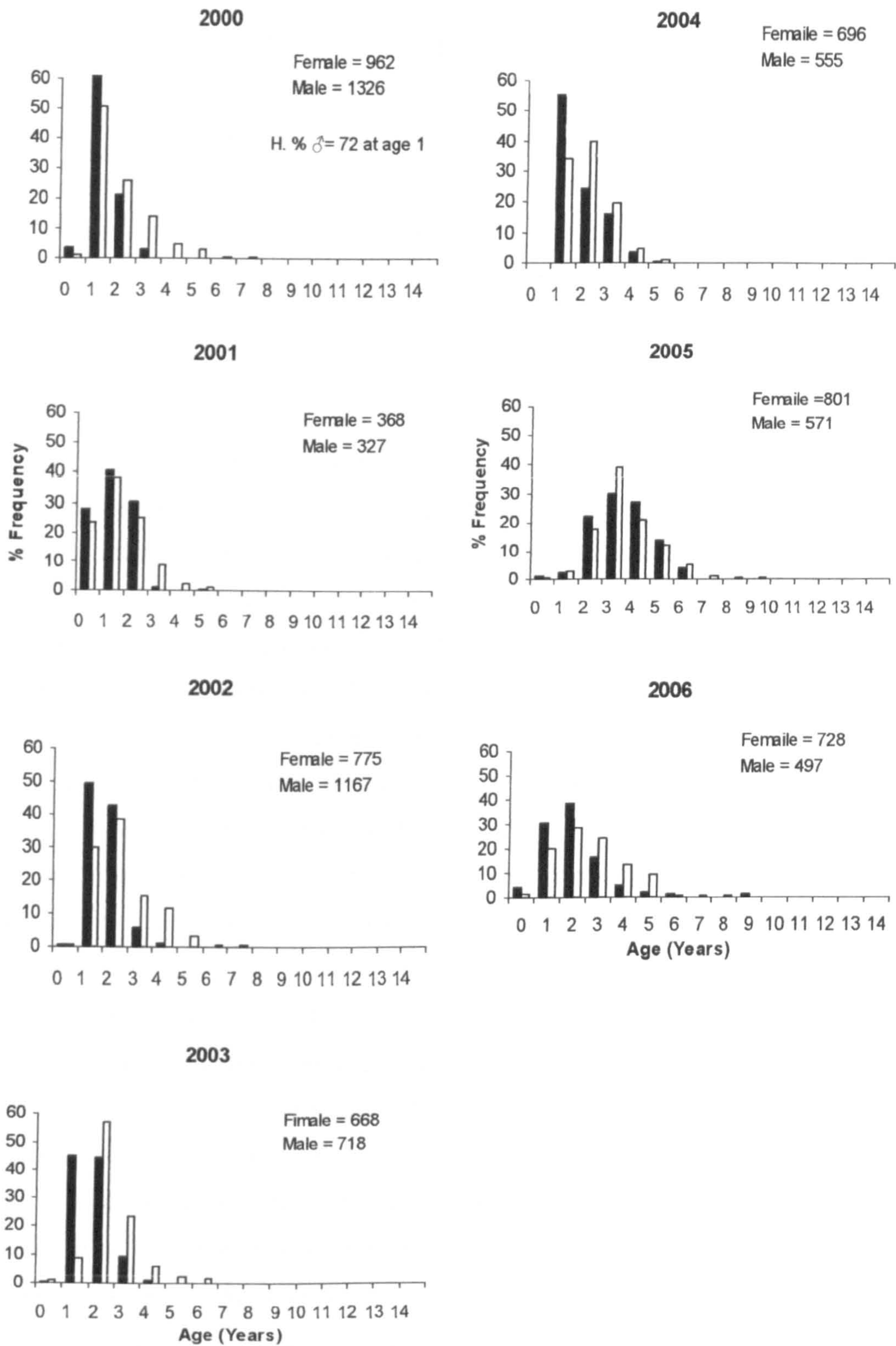


Figure 3.13 (d): 2000-2006

Figure 3.13: Percentage age-frequency distributions of male (solid bar) and female (open bar) plaice caught in the coastal inshore waters of E. Anglesey and N. W. Wales in October/November between 1970 and 2006.

3.5 and 10.5 years old (Figure 3.14) with a median maximum age of 5.5 (Interquartile range = 2.75) years old. The maximum age of female plaice varied from year to year and ranged between 5.5 and 15.5 years old (Figure 3.14) with a median maximum age of 8.5 (IQ = 4.00) years old. The maximum age data were not normally distributed for either sex (σ , $Z = 0.19$, $n = 31$, $P = 0.008$; φ , $Z = 0.16$, $n = 31$, $P = 0.032$). The median maximum ages of male and female fish were significantly different (Mann Whitney $U = 163.5$, $P < 0.001$).

There was a significant negative correlation between maximum age (years old) and time (survey year) for female plaice ($r_s = -0.393$, $P = 0.02$) indicating that the maximum age of female plaice caught in the autumn surveys had decreased between 1970 and 2006, however, no such correlation was found for male plaice ($r_s = -0.228$, $P = 0.21$) (Figure 3.14a). Since, the age data obtained may be dependent on the degree of fishing effort in any year and also subject to random biological variation, average annual minimum/maximum ages were also calculated as a three year moving average (average age for any given year calculated from the value for that year plus the year before and the year after) in order to reduce the inter-annual variability and to 'smooth out' any long-term trends in the data set. Although this analysis produces annual age values that are not 'X.5/X'' years old, *i.e.* continuous rather than interval data, it allows some of the 'noise' in the data set to be 'smoothed out'. Analysis of this 'smoothed' data set indicated that there were significant negative correlations between time (calendar year) and age (years old) for male fish and female fish for both minimum age (σ , $r_s = -0.431$, $P = 0.010$; φ , $r_s = -0.594$, $P < 0.001$) and maximum age (σ male, $r_s = -0.390$, $P = 0.021$; φ , $r_s = -0.608$, $P < 0.001$) (Figure 3.14b). When the smoothed minimum age data were grouped together into 5 year intervals (1970-1974, 1975-1979 etc) for male and female plaice, data were not normally distributed (σ , $Z = 0.24$, $n = 36$, $P < 0.001$; φ , $Z = 0.21$, $n = 36$, $P < 0.001$) and had unequal variances between time periods (σ , $W_{6,28} = 3.32$, $P = 0.013$; φ , $W_{6,30} = 3.68$, $P = 0.007$) precluding the use of ANOVA. Analysis of the smoothed minimum age data for the different time periods using a Kruskal Wallis test indicated a significant difference between time intervals for both males ($\chi^2 = 21.77$, 6 df, $P = 0.001$) and females ($\chi^2 = 28.91$, 6 df, $P < 0.001$). For male, when pairwise comparisons of the time periods were conducted using a Wilcoxon Signed Rank test, the overall pattern was for the smoothed minimum ages in 1990-1994 to be significantly older compared to the other 6 year time periods (Table 3.6). For female,

the overall pattern of causing significance that the 1970-1974 was older in minimum ages and 1995-1999 was smaller compared to the other time periods. When the smoothed maximum age data were grouped in 5 year intervals (1970-1974, 1975-1979 etc) for male and female plaice, the data for both sexes were not normally distributed (σ^2 , $Z = 0.26$, $n = 36$, $P < 0.001$; σ^2 , $Z = 0.15$, $n = 36$, $P = 0.04$) but exhibited equal variances between time periods (σ^2 , $W_{6,28} = 2.37$, $P = 0.06$; σ^2 , $W_{6,30} = 2.36$, $P = 0.06$). However, since the Levene's tests for male and female plaice were both almost significant it was decided that the nonparametric Kruskal Wallis test was a more appropriate test to compare between time periods. There were significant differences between the smoothed maximum age values for each time interval for both male ($\chi^2 = 20.27$, 6 df, $P < 0.001$) and female plaice ($\chi^2 = 17.98$, 6 df, $P = 0.006$) (Table 3.7). Pairwise comparisons of the smoothed maximum age values for male and female plaice for each time interval are presented in Table 3.7. This analysis showed that the maximum ages of male plaice in 1975-1979 were significantly older compared to the 5 year time periods from 1980-1984 to 2000-2006. For female plaice, the maximum ages in the 1970s were generally older than the time periods from 1985-1989 onwards. In addition, the smoothed maximum age of female plaice in 2000-2006 tended to be younger than female fish in the other time periods (Table 3.7).

The average ages of male and female plaice caught during the autumn fisheries surveys between 1970-2006 are shown in Figure 3.15. There was a significant negative correlation between average age and time for female plaice ($r_s = -0.379$, $P = 0.03$) indicating that the average age of female plaice caught in the autumn surveys had decreased between 1970 and 2006, however, no such correlation was found for male plaice ($r_s = -0.158$, $P = 0.39$) (Figure 3.15a). After grouping the data into 5 year intervals (1970-1974, 1975-1979, etc) (Figure 3.16), the data were normally distributed for female (σ^2 , $Z = 0.10$, $n = 34$, $P > 0.20$) but not for male plaice (σ^2 , $Z = 0.26$, $n = 32$, $P < 0.001$) and with equal variance for both sexes (σ^2 , $W_{6,25} = 1.15$, $P = 0.36$; σ^2 , $W_{6,27} = 2.10$, $P = 0.09$). Thus, ANOVA was used for both data sets to compare the average age in each time period (Table 3.8). ANOVA analysis indicated no differences in the average age over time for male plaice ($F_{(6,25)} = 1.05$, $P = 0.42$) but there were significant change in the average age of female plaice over time ($F_{(6,27)} = 3.40$, $P = 0.012$). Pairwise comparisons of the average age values using Scheffe's test indicated few differences between time periods, with the average age of

female age in 1970-1974 significantly older than 1985-1989 and tending to be older than 1995-1999 and 2000-2006 (Table 3.8b).

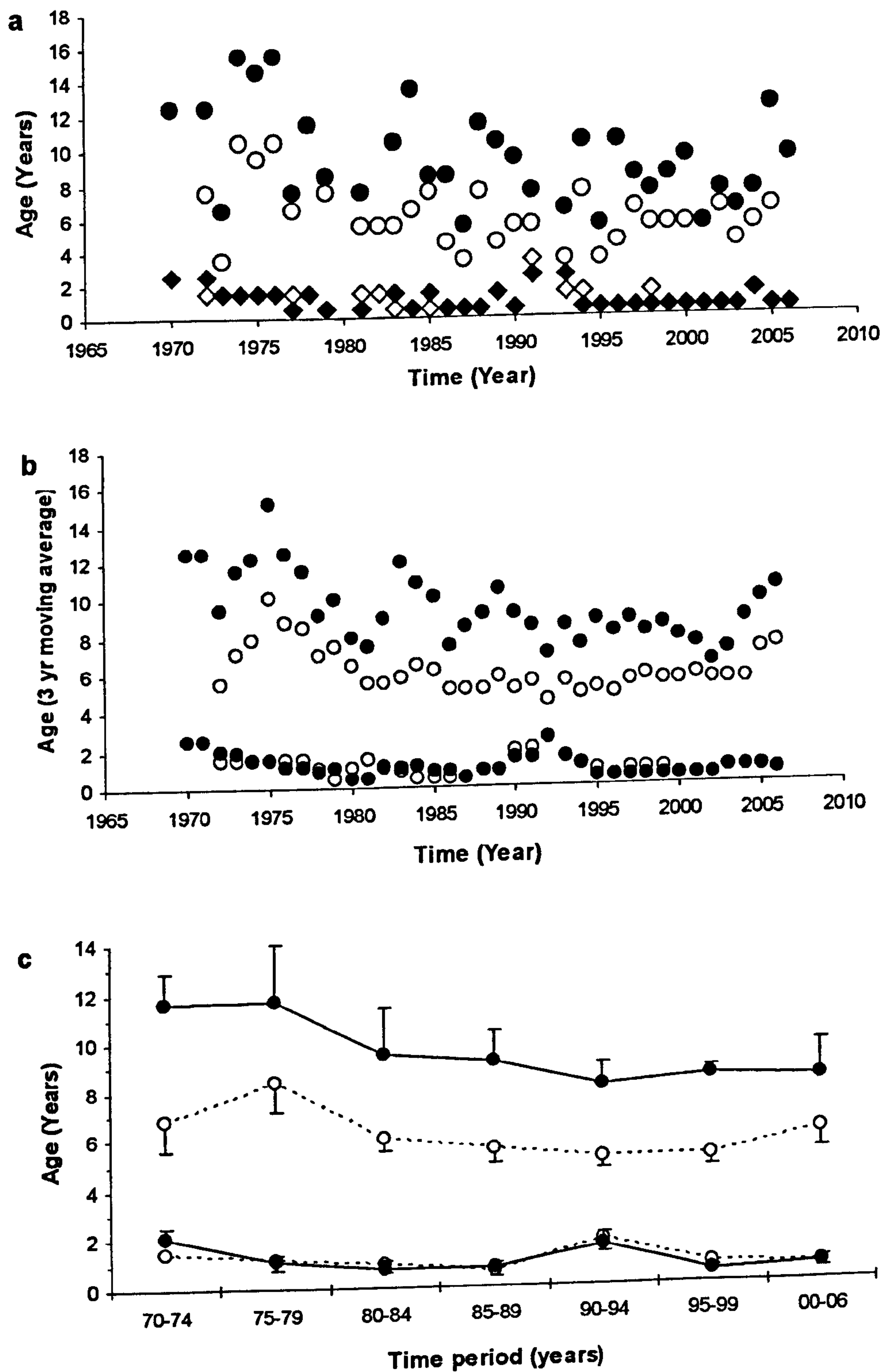


Figure 3.14: Maximum and minimum ages (year) of female (solid circle) and male (open circle) plaice caught in autumn fisheries surveys in the inshore waters of Eastern Anglesey and northwest Wales between 1970 and 2006. (a) raw data, (b) 3 year moving averages, (c) median value (\pm interquartile range) for 5 year time periods.

Table 3.6: (a) Smoothed minimum age (years) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as median values \pm interquartile range. Smoothed values are calculated as a three year running average. Significance values for the *post-hoc* comparisons of smoothed median age values for (b) male and (c) female plaice using Wilcoxon's Signed Rank test (significant differences at the 5% level are highlighted in bold and trends, *i.e.* $0.05 < P < 0.10$, are underlined).

a)

<i>Time period</i> (years)	<i>Male</i> <i>Smoothed minimum age</i>	<i>Female</i> <i>Smoothed minimum age</i>
1970-1974	1.5 \pm 0	2.0 \pm 0.85
1975-1979	1.5 \pm 0.75	1.2 \pm 0.45
1980-1984	1.0 \pm 0.7	1.0 \pm 0.6
1985-1989	0.5 \pm 0.3	0.8 \pm 0.15
1990-1994	1.8 \pm 0.9	1.5 \pm 0.65
1995-1999	0.8 \pm 0.15	0.5 \pm 0
2000-2006	0.7 \pm 0.3	0.7 \pm 0.3

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	1.000					
1980-1984	0.180	0.109				
1985-1989	<u>0.083</u>	0.131	0.144			
1990-1994	0.109	0.042	0.042	0.043		
1995-1999	0.102	0.136	0.273	0.157	0.043	
2000-2006	<u>0.083</u>	0.131	0.144	1.000	0.043	0.157

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.042					
1980-1984	0.042	0.336				
1985-1989	0.042	<u>0.066</u>	0.498			
1990-1994	0.221	<u>0.068</u>	<u>0.066</u>	0.039		
1995-1999	0.042	0.042	0.102	0.046	0.039	
2000-2006	0.042	<u>0.066</u>	0.109	0.157	0.042	0.157

Table 3.7: (a) Smoothed maximum age (years) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as median values \pm interquartile range. Smoothed values are calculated as a three year running average. Significance values for the *post-hoc* comparisons of smoothed median age values for (b) male and (c) female plaice using Wilcoxon's Signed Rank test (significant differences at the 5% level are highlighted in bold and trends, *i.e.* $0.05 < P < 0.10$, are underlined).

a)

<i>Time period</i> (years)	<i>Male</i> <i>Smoothed maximum age</i>	<i>Female</i> <i>Smoothed maximum age</i>
1970-1974	7.2 \pm 2.3	12.2 \pm 2.0
1975-1979	8.5 \pm 2.25	11.5 \pm 4.25
1980-1984	5.8 \pm 1.0	9.0 \pm 3.65
1985-1989	5.2 \pm 0.8	9.2 \pm 2.35
1990-1994	5.2 \pm 0.85	8.5 \pm 1.6
1995-1999	5.5 \pm 0.65	8.5 \pm 0.6
2000-2006	5.5 \pm 1.7	7.8 \pm 2.6

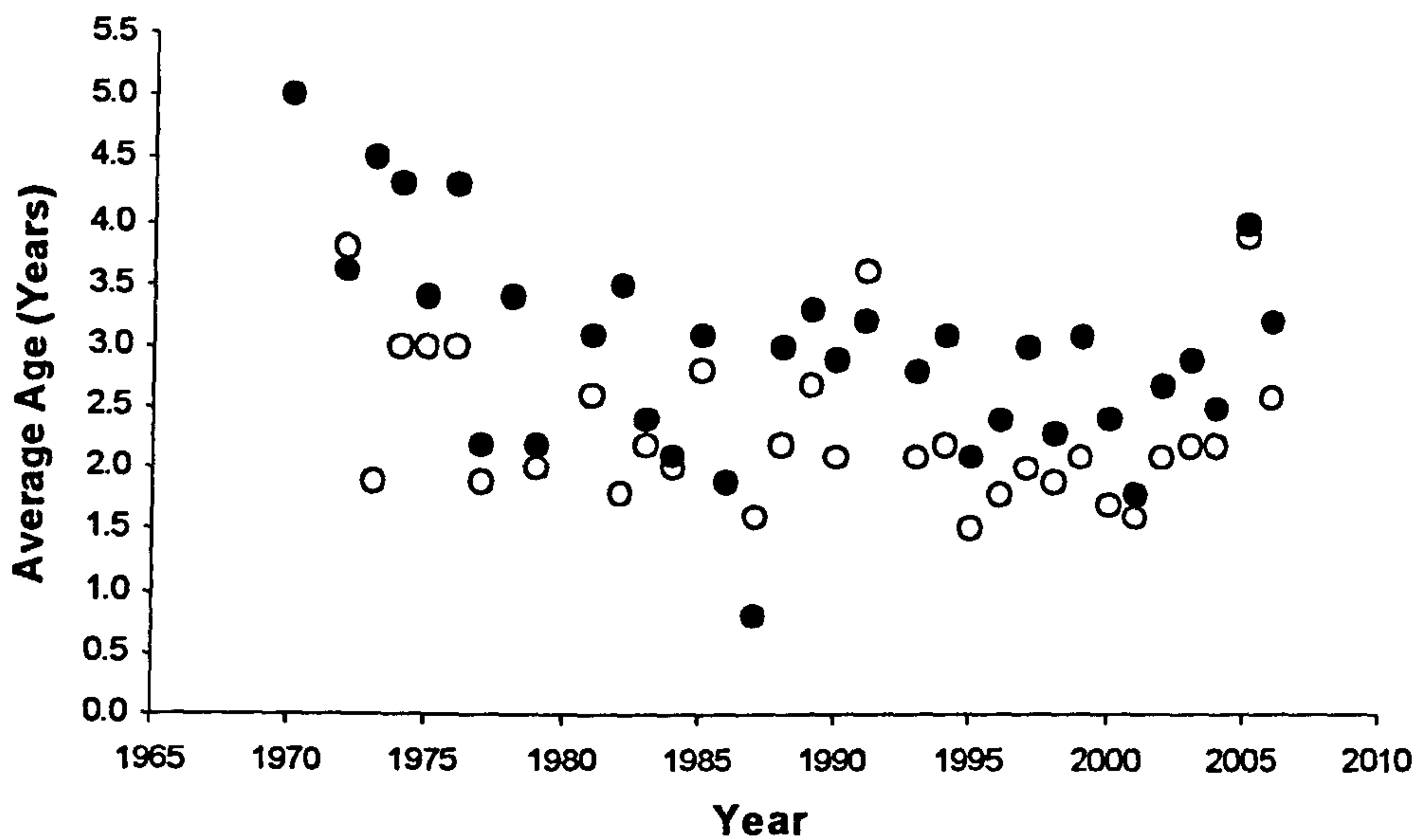
b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.109					
1980-1984	0.285	0.043				
1985-1989	0.285	0.043	0.039			
1990-1994	0.109	0.043	<u>0.068</u>	0.221		
1995-1999	0.109	0.043	0.109	0.588	0.357	
2000-2006	0.180	0.042	0.194	0.891	<u>0.066</u>	0.414

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	1.000					
1980-1984	0.104	0.345				
1985-1989	0.042	0.141	0.465			
1990-1994	0.043	0.043	0.225	0.176		
1995-1999	0.042	0.043	0.500	0.225	0.684	
2000-2006	0.043	0.042	<u>0.068</u>	<u>0.066</u>	0.279	<u>0.078</u>

a)



b)

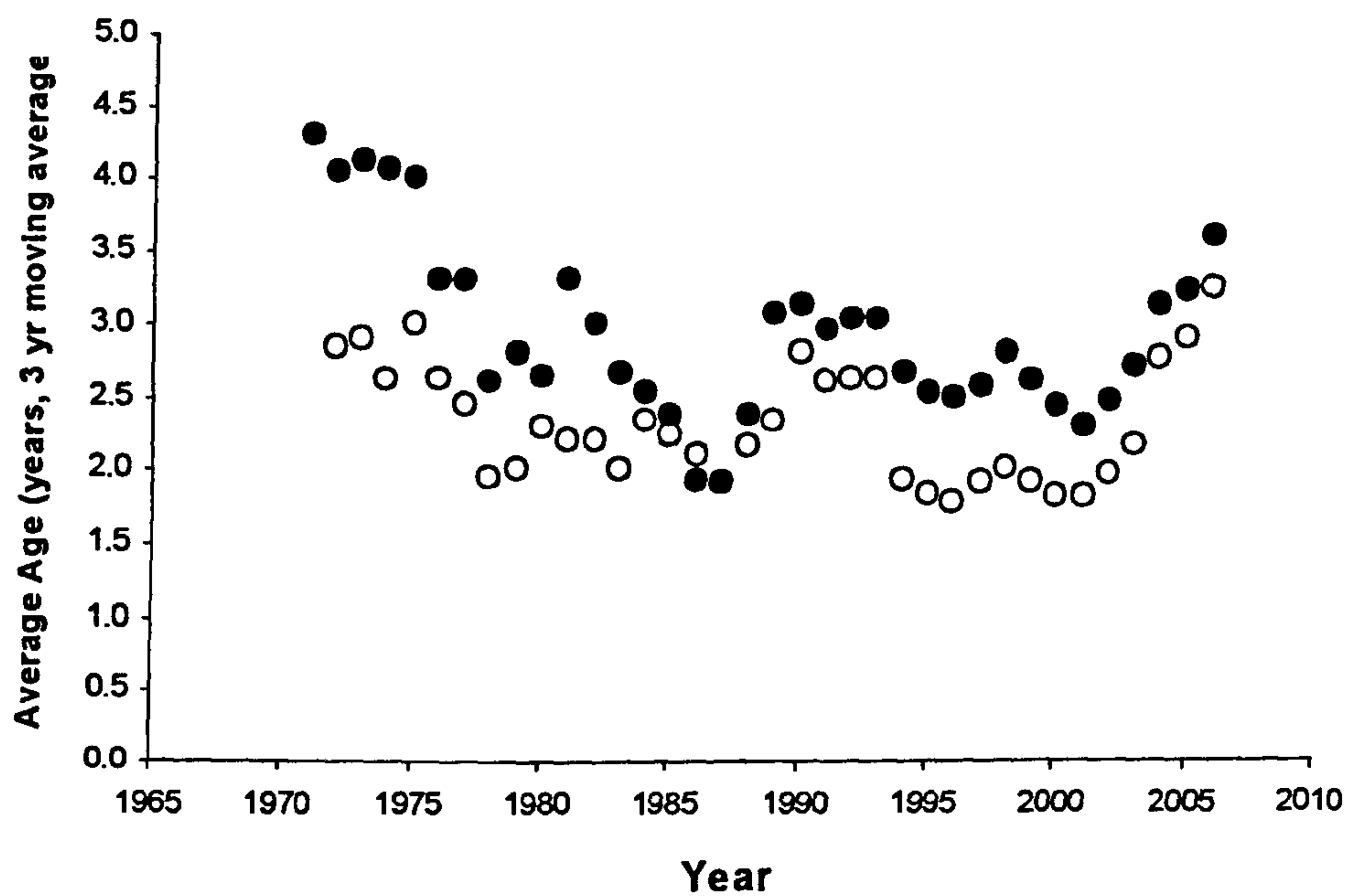


Figure 3.15: Average age (years) of female (solid circle) and male (open circle) plaice caught in autumn fisheries surveys in the inshore waters of Eastern Anglesey and northwest Wales between 1970 and 2006. (a) Raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the age values for any given year plus the values for the year before and the year after.

Table 3.8: (a) Average age (years) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the *post-hoc* comparisons of average age values for female plaice using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold and trends, *i.e.* $0.05 < P < 0.10$, are underlined).

a)

<i>Time period</i> (years)	<i>Male</i> <i>Average age</i>	<i>Female</i> <i>Average age</i>
1970-1974	2.9 \pm 1.0	4.4 \pm 0.6
1975-1979	2.6 \pm 0.6	3.1 \pm 0.9
1980-1984	2.2 \pm 0.3	2.8 \pm 0.6
1985-1989	2.2 \pm 0.5	2.4 \pm 1.1
1990-1994	2.5 \pm 0.7	3.0 \pm 0.2
1995-1999	1.9 \pm 0.2	2.6 \pm 0.4
2000-2006	2.3 \pm 0.8	2.8 \pm 0.7

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.37					
1980-1984	0.18	1.00				
1985-1989	0.03	0.89	1.00			
1990-1994	0.34	1.00	1.00	0.96		
1995-1999	<u>0.07</u>	0.97	1.00	1.00	0.99	
2000-2006	<u>0.09</u>	1.00	1.00	0.99	1.00	1.00

Since, the age data obtained may be dependent on the degree of fishing effort in any year and also subject to random biological variation, average ages for each year were also calculated as a three year moving average (average age for any given year calculated from the value for that year plus the year before and the year after) in order to reduce the inter-annual variability and to 'smooth out' any long-term trends in the data set. After smoothing, there was a significant negative correlation between average age and time for female plaice ($r_s = -0.400$, $P = 0.016$) and a trend in the data for male plaice ($r_s = -0.287$, $P = 0.095$). Thus, the results indicated that the average age of male and female plaice caught in the autumn surveys has tended to decrease between 1970 and 2006 (Figure 3.15b). In order to determine where the significant differences in average age occurred, the data set were grouped into 5 year intervals (1970-1974, 1975-1979, etc) (Figure 3.17) for male and female plaice. For both sexes, the data were normally distributed (σ , $Z = 0.15$, $n = 35$, $P = 0.052$; ϕ , $Z = 0.13$, $n = 36$, $P = 0.13$) but exhibited unequal variances between time periods (σ , $W_{6,28} = 6.41$, $P < 0.001$; ϕ , $W_{6,29} = 2.92$, $P = 0.024$) precluding the use of ANOVA. Analysis of the smoothed average age data for the different time periods using a Kruskal Wallis test indicated significant differences for both male and female plaice between time intervals (σ , $\chi^2 = 13.21$, 6 df, $P = 0.04$; ϕ , $\chi^2 = 19.00$, 6 df, $P = 0.004$). When pairwise comparisons of the time periods were conducted using a Wilcoxon Signed Rank test, the average age of the male plaice in 1990-1994 was significantly older than in 1995-1999 and male plaice in 1985-1989 tended to be older than those in the 1990s (Table 3.9b). For female plaice, the *post-hoc* comparisons indicated that the average age of female plaice in 1970-1974 tended to be older than the other 5 year time periods, the average age in 1985-1989 was significantly greater than 2000-2006, and the average age in 1990-1994 tended to be greater than 1985-1989 and 1995-1999 (Table 3.9c).

The percentage data analyses have examined whether there have been any changes in age over time in terms of maximum/minimum/average age but have not examined whether there has been any change in the age structure of the catch over time. Therefore, the data were grouped into 5 year intervals as before, and the percentage of fish in the following age classes determined: 0-1, 2, 3 and ≥ 4 years old. The percentage frequencies in each of the 4 age classes for each 5 year interval were calculated for male, female and combined data and are presented in Figure 3.18.

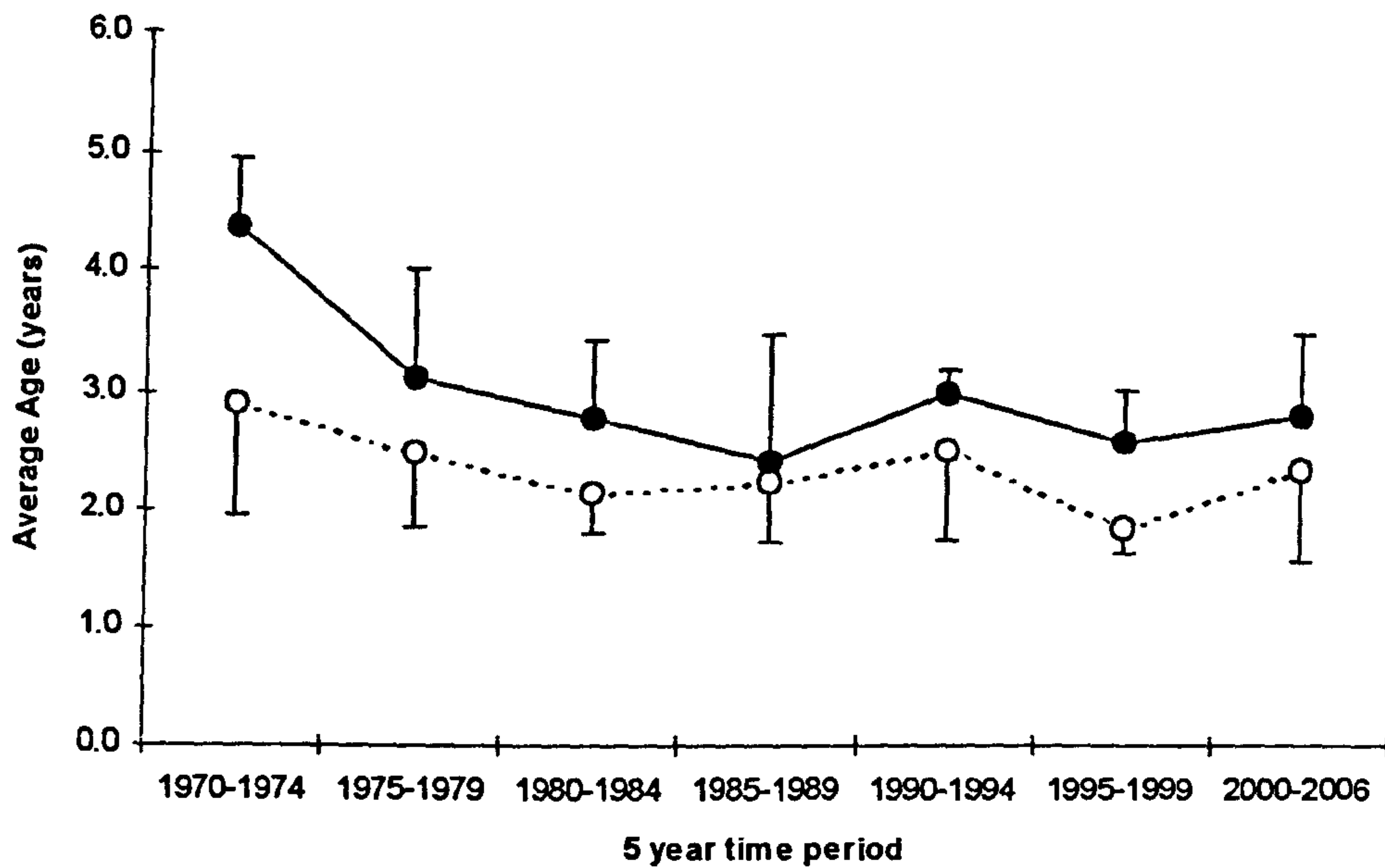


Figure 3.16: Average age (years) for female (solid circle) and male (open circle) plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as mean values \pm SD. for 5 year time periods (1970-1974, 1975-1979 etc).

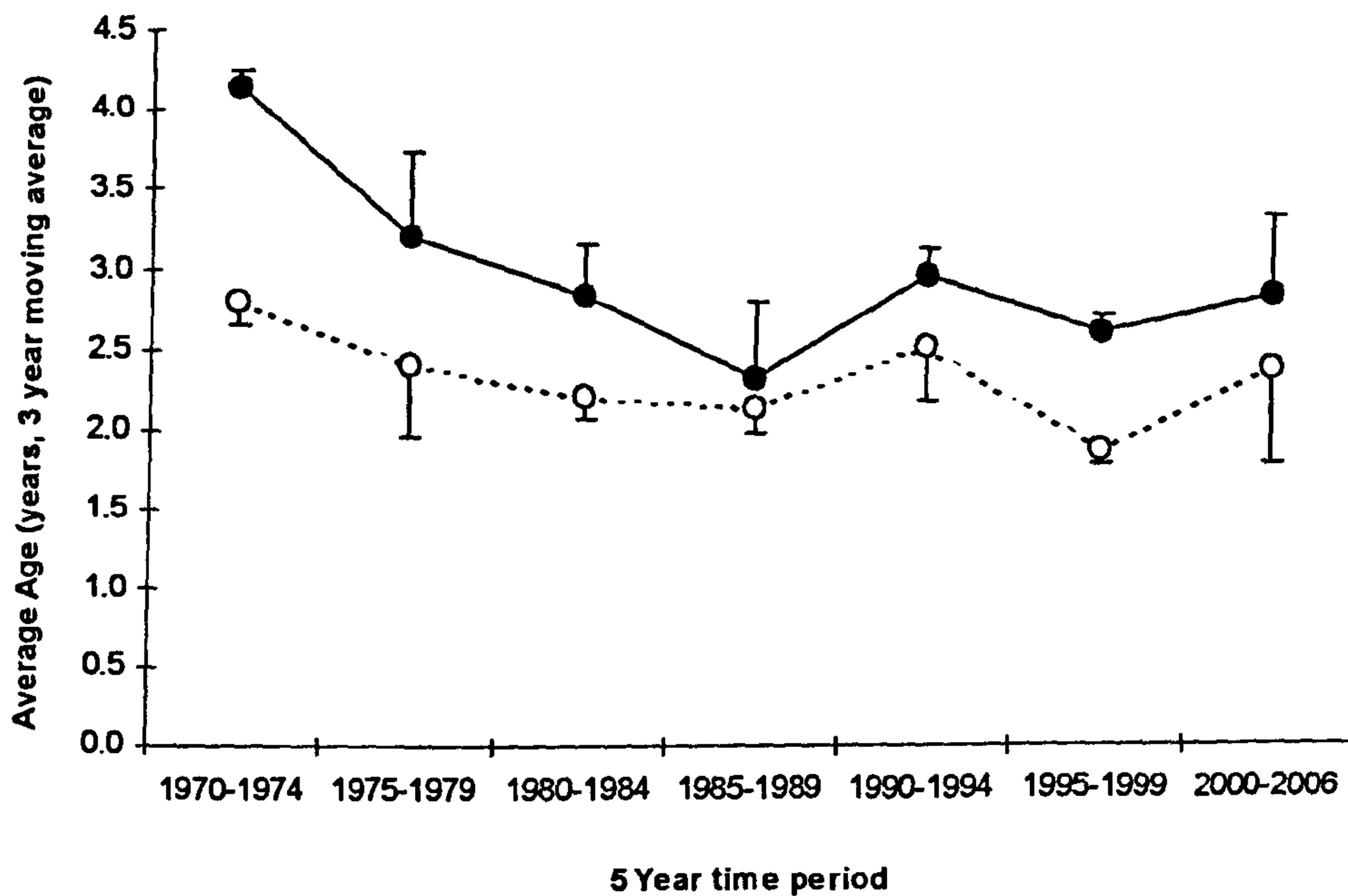


Figure 3.17: Average age (years) for female (solid circle) and male (open circle) plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as mean values \pm SD. Smoothed age values for each year were calculated as a three year running average and mean values are for 5 year time periods (1970-1974, 1975-1979 etc).

Table 3.9. (a) Smoothed average age (years) for male and female plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. Smoothed values calculated as a three year running average. Significance values for the *post-hoc* comparisons of smoothed average TL for (b) male and (c) female plaice using Dunnett's multiple comparison test (significant differences at the 5% level are highlighted in bold and trends, *i.e.* $0.05 < p < 0.10$, are underlined).

a)

<i>Time period</i> (years)	<i>Male</i> Smoothed average age	<i>Female</i> Smoothed average age
1970-1974	2.9 \pm 0.3	4.1 \pm 0.2
1975-1979	2.5 \pm 0.8	3.3 \pm 1.0
1980-1984	2.2 \pm 0.2	2.7 \pm 0.6
1985-1989	2.2 \pm 0.3	2.4 \pm 0.8
1990-1994	2.6 \pm 0.5	3.0 \pm 0.3
1995-1999	1.9 \pm 0.2	2.6 \pm 0.2
2000-2006	2.2 \pm 1.1	2.7 \pm 0.8

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.29					
1980-1984	0.11	0.35				
1985-1989	0.11	0.23	0.47			
1990-1994	0.18	0.89	0.10	<u>0.08</u>		
1995-1999	0.11	<u>0.08</u>	<u>0.07</u>	<u>0.07</u>	0.043	
2000-2006	0.11	0.35	0.50	1.00	0.35	0.104

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	<u>0.068</u>					
1980-1984	<u>0.068</u>	0.14				
1985-1989	<u>0.068</u>	0.14	0.23			
1990-1994	<u>0.068</u>	0.35	0.23	<u>0.08</u>		
1995-1999	<u>0.068</u>	0.10	0.35	0.23	0.04	
2000-2006	<u>0.068</u>	0.23	0.50	0.04	0.14	0.49

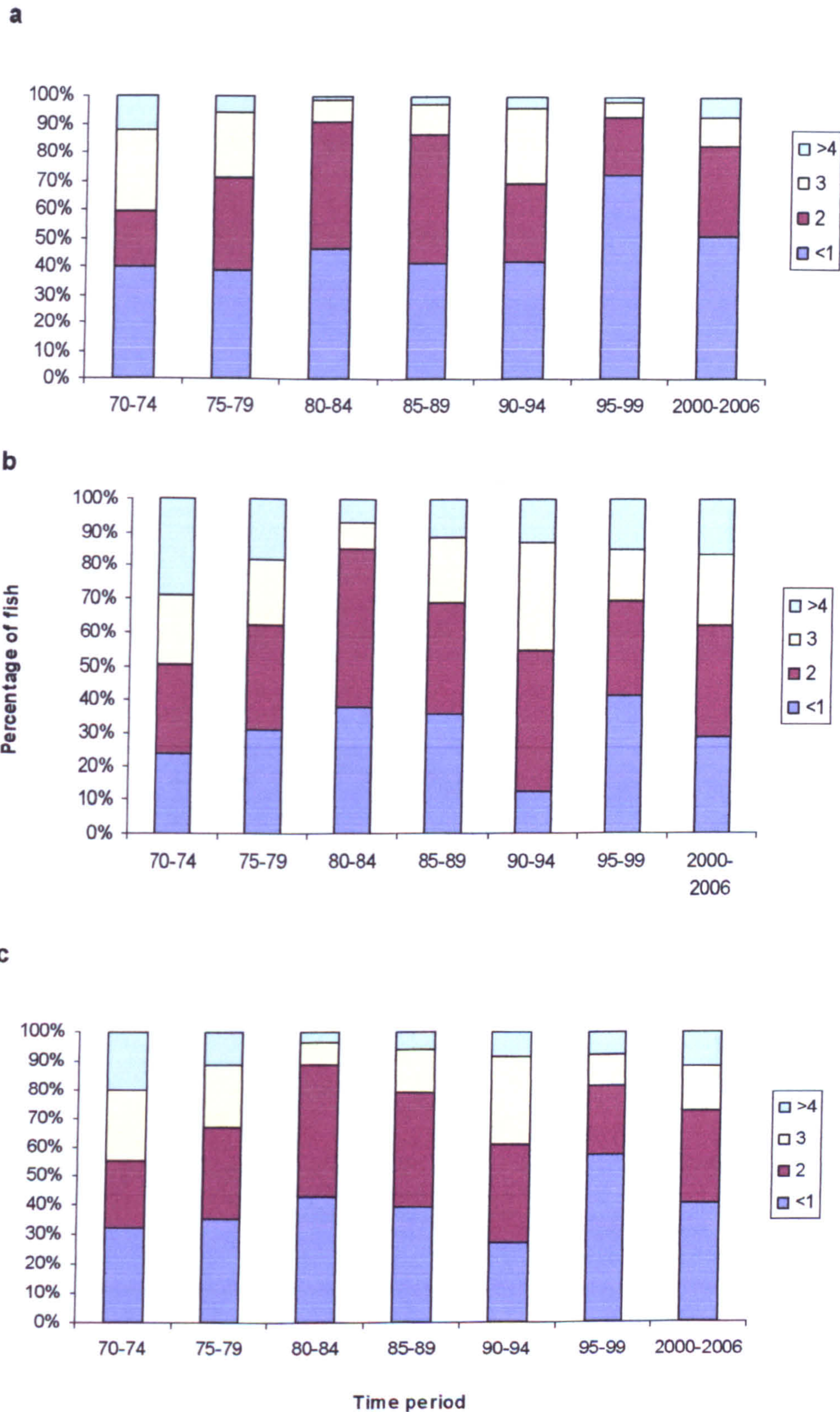


Figure 3.18: Percentage frequencies of plaice in different age classes (years) caught in the autumn fisheries surveys conducted in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented for (a) male, (b) female and (c) male and female combined for 5 year time intervals.

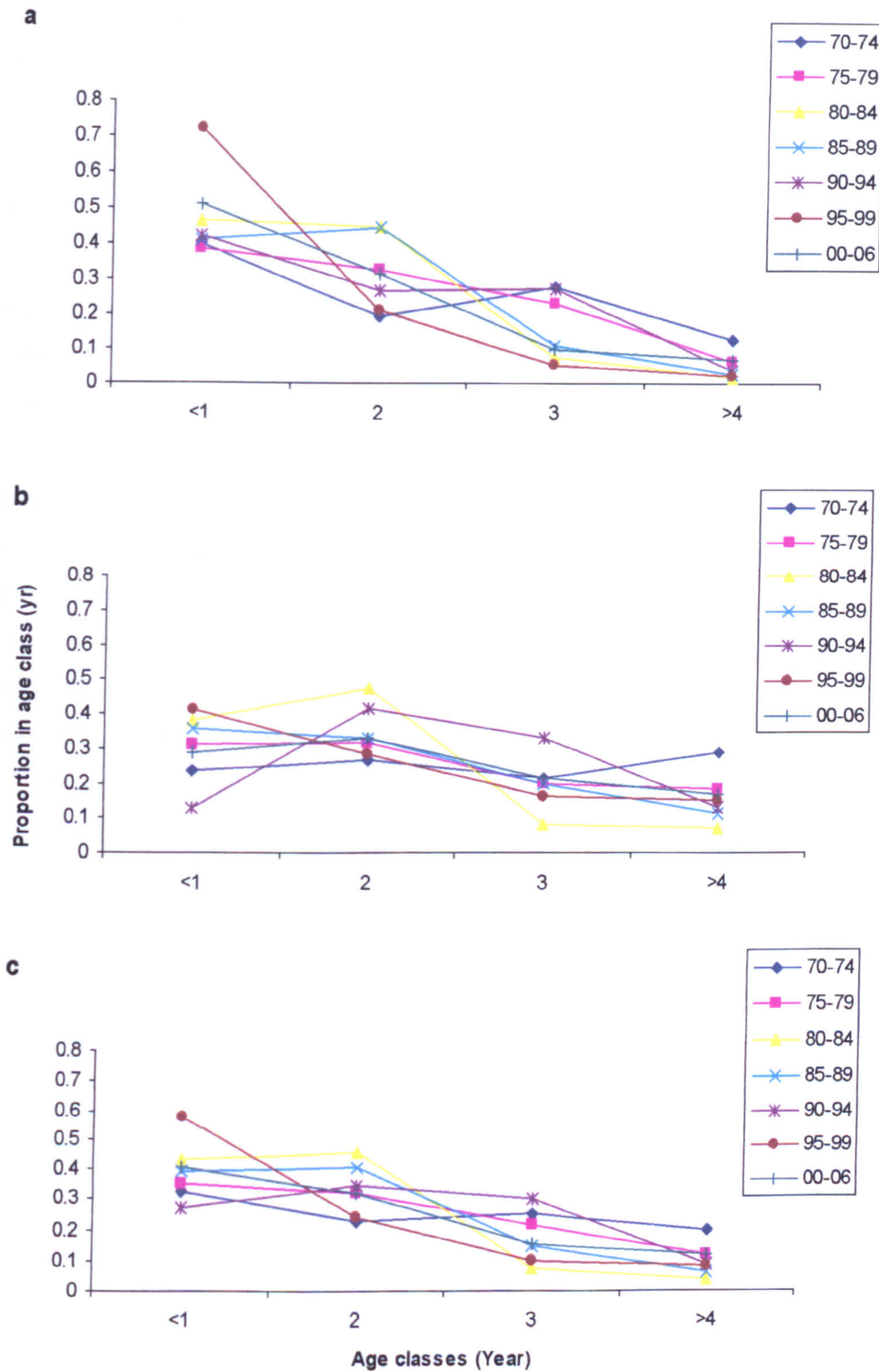


Figure 3.19: Proportion of plaice in different age classes (years) for 5 year time intervals (1970-1974, 1975-1979 etc) caught in the autumn fisheries surveys conducted in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented for (a) male, (b) female and (c) male and female combined for the different size classes.

For male plaice, the most abundant age class was the 0-1 year old class with an average of 47% (range 39-72%) found in this age class. For most 5 year time periods this was the most abundant age class, except 1980-1980 and 1985-1989 where the 2 year old age class was equally as abundant as the 0-1 year old age class (Figure 3.18). In all 5 year time periods, the majority of male plaice (average 79%, range 59-93%) comprised of plaice between 0 and 2 years old with fish ≥ 4 years old rarely being caught (average 5%, range 2-12%). For female plaice, the most abundant age class was the 2 year old age group with an average of 34% (range 26-47%) found in this age class. However, the second most abundant age class, the 0-1 year old age class, which comprised an average of 30% (range 13-41%). In all 5 year time periods, the majority of female plaice (average 84%, range 71-93%) comprised of plaice ≤ 3 years old. However, a greater proportion of female plaice 4 years or older (average 16%, range 7-29%) were caught compared to male plaice (Figure 3.18).

The temporal changes in the proportion of fish in each age class are presented for male, female and male/female plaice combined in Figure 3.19. This plot illustrates that the same patterns in the age composition of the catch are observed between the seven time periods for male (Figure 3.19a) and female (Figure 3.19b) plaice and when the data for the two sexes are combined (Figure 3.19c).

3.3.4 Sex ratio

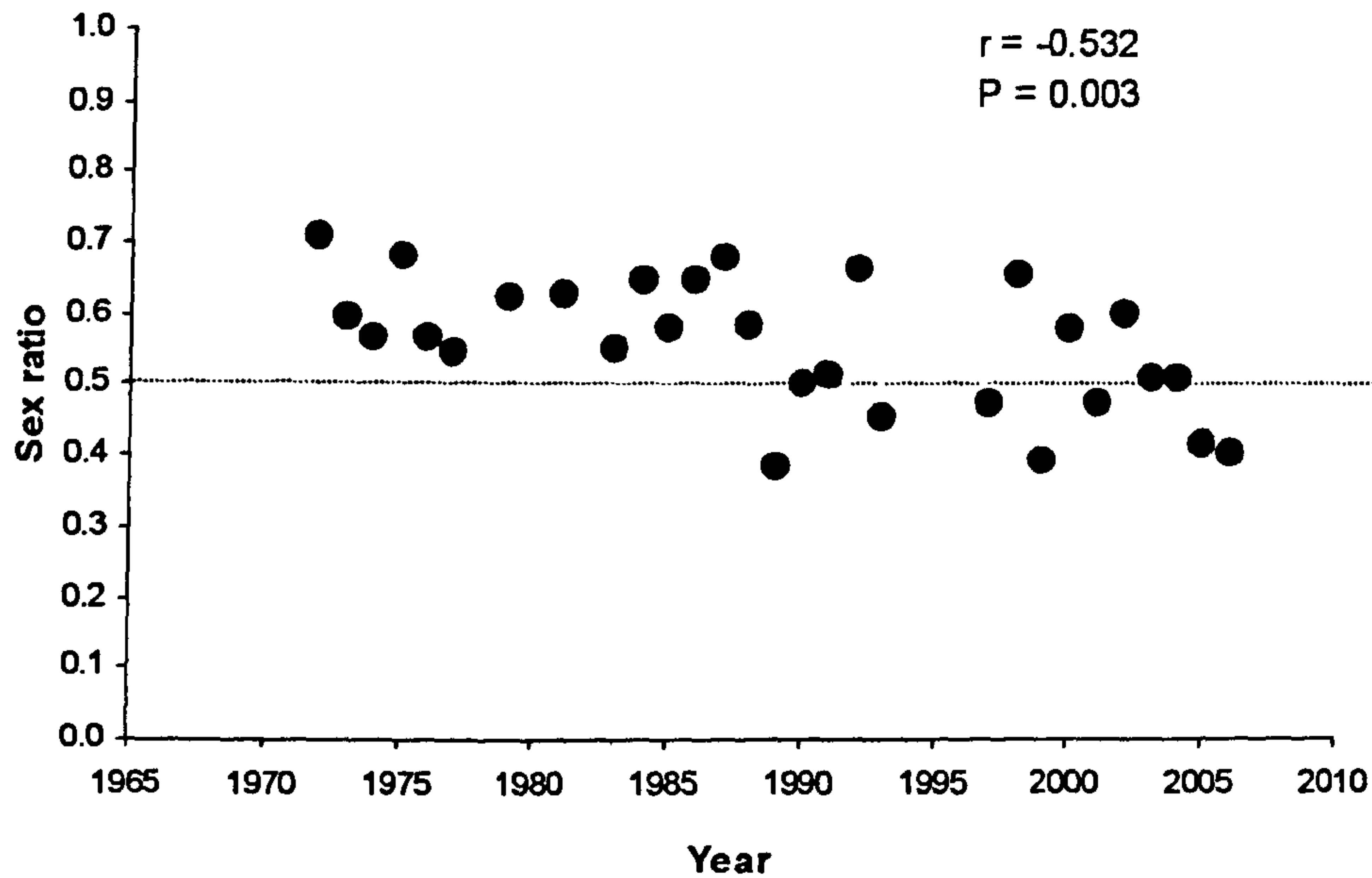
The number of male and female fish caught each year in the autumnal fishing surveys and the sex ratios, expressed as the proportion of males in the population, are shown in Table 3.10. The number of male and female fish varied from year to year due to variable fishing effort and total catch, therefore, temporal changes in the sex ratio provides a more informative and comparative parameter to analyse.

Table 3.10: The number of males and females, and the calculated sex ratio (expressed as the proportion of males in the sample) for male and female plaice caught in autumn survey conducted by RV *Prince Madog* in the coastal waters of eastern Anglesey and northwest Wales between 1972 and 2006.

Year	Number of Females	Number of Males	Total catch	Sex ratio
1972	267	678	945	0.72
1973	699	1033	1732	0.60
1975	1275	2731	4006	0.68
1977	900	1090	1990	0.55
1978	670	910	1580	0.58
1979	1337	2229	3566	0.63
1981	290	488	778	0.63
1982		141		
1983	2295	2799	5094	0.55
1984	904	1651	2555	0.65
1985	1306	1781	3087	0.58
1986	816	1500	2316	0.65
1987	331	704	1035	0.68
1988	245	345	590	0.58
1989	211	133	344	0.39
1990	264	264	528	0.50
1991	450	473	923	0.51
1992	62	122	184	0.66
1993	87	72	159	0.45
1997	238	189	427	0.44
1998	308	586	894	0.66
1999	538	348	886	0.39
2000	962	1327	2289	0.58
2001	628	557	1185	0.47
2002	775	1167	1942	0.60
2003	688	718	1406	0.51
2004	739	525	1264	0.42
2005	996	322	1318	0.24
2006	728	497	1225	0.41

The sex ratio in the annual fishing surveys varied between 0.24 and 0.72 (Table 3.10) with an average value of 0.55 ± 0.09 for the time period 1972-2006. Figure 3.20a indicates that there is a significant negative correlation between sex ratio and time

a)



b)

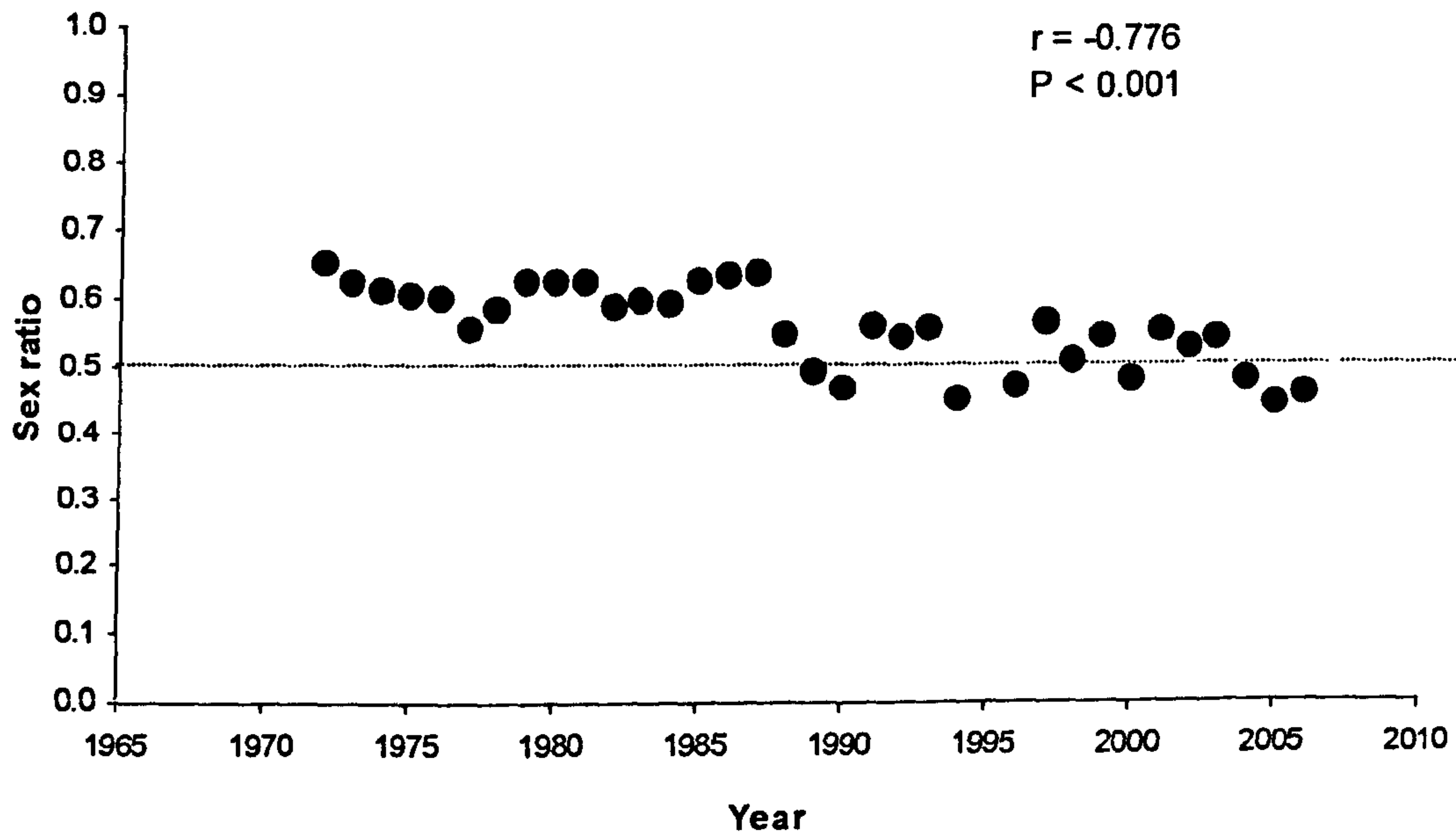
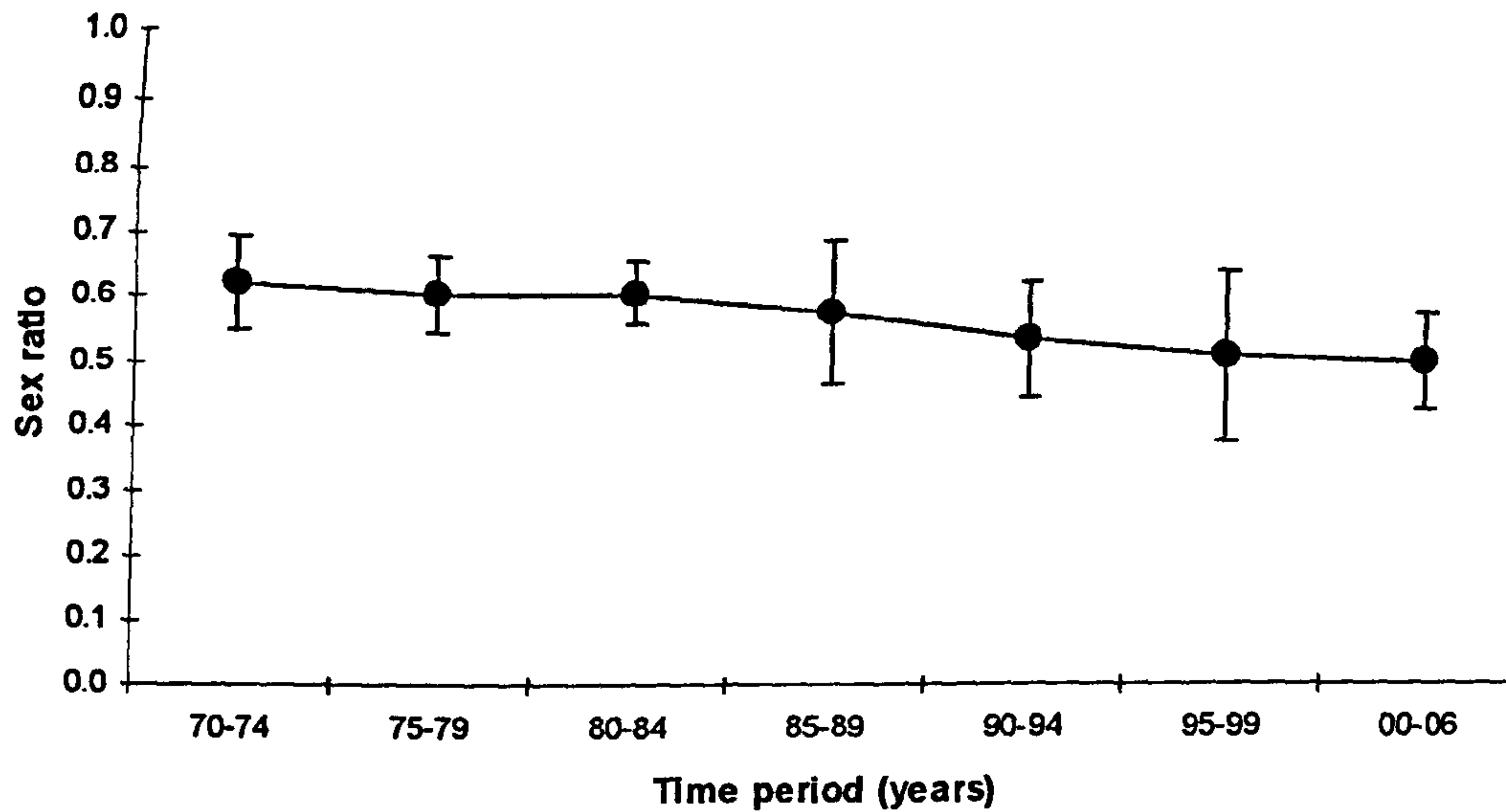


Figure 3.20: Sex ratios, expressed as the proportion of males in a sample, for the time period 1972-2006 for plaiice caught in coastal waters of eastern Anglesey and northwest Wales. Sex ratio data are presented as (a) raw data and (b) 3 year smoothed averages. The horizontal dotted line on each plot represents a 50:50 sex ratio for males:females.

($r_s = -0.552$, $n = 29$, $P = 0.003$) indicating that there has been a decrease in the proportion of male plaice caught in the inshore waters of eastern Anglesey and northwest Wales in autumn over time. Figure 3.20b presents the sex ratio data calculated as a three year moving average (average for any given year calculated from the value for that year plus the year before and the year after) which reduces the inter-annual variability and ‘smooths out’ any long-term trends in the data set. Following smoothing, the correlation between sex ratio and time was stronger ($r_s = -0.776$, $n = 29$, $P < 0.001$). In order to examine where the differences in sex ratio occurred in the time series data set, the data were grouped into 5 year intervals (1970-1974, 1975-1979 etc) and the data arcsine transformed to normalise the data, since proportional data between 0 and 1 are not normally distributed. The arcsine transformed sex ratio data were normally distributed (raw data, $Z = 0.08$, $n = 29$, $P > 0.20$; smoothed data, $Z = 0.11$, $n = 34$, $P > 0.20$) and with equal variance (raw data, $W_{6,22} = 0.51$, $P = 0.80$; smoothed data, $W_{6,27} = 0.43$, $P = 0.65$). Given, the inter-annual variability in the raw data (Figure 3.21a, Table 3.11a), there were no differences in the sex ratios for the different time periods when the raw data is analysed ($F_{(6,28)} = 1.38$, $P = 0.27$). However, when the smoothed data is analysed (Figure 3.21b, Table 3.11a), a significant difference in sex ratio between the seven 5-year time periods was found ($F_{(6,33)} = 7.56$, $P < 0.001$). Pairwise comparisons of the smoothed sex ratio values for each 5-year time interval are presented in Table 3.11b. This analysis showed that the average sex ratio for 1970-74 tended to be larger (*i.e.* there were a greater proportion of males in the catches) than the sex ratios in the 1990s and was significantly greater than the average sex ratio for the time period 2000-2006. The average sex ratio for 2000-2006 was significantly lower (*i.e.* there were fewer males in the catches) than the sex ratios in the 1970s and early 1980s (Table 3.11b). Thus the results of the sex ratio analysis have shown that during the time period 1972-2006, there has been a decline in the number of males caught during the autumnal fishing surveys and there has been a switch from more males present in the catches (*i.e.* sex ratios *ca.* 0.6) to an equal sex ratio (*i.e.* *ca.* 0.5).

a)



b)

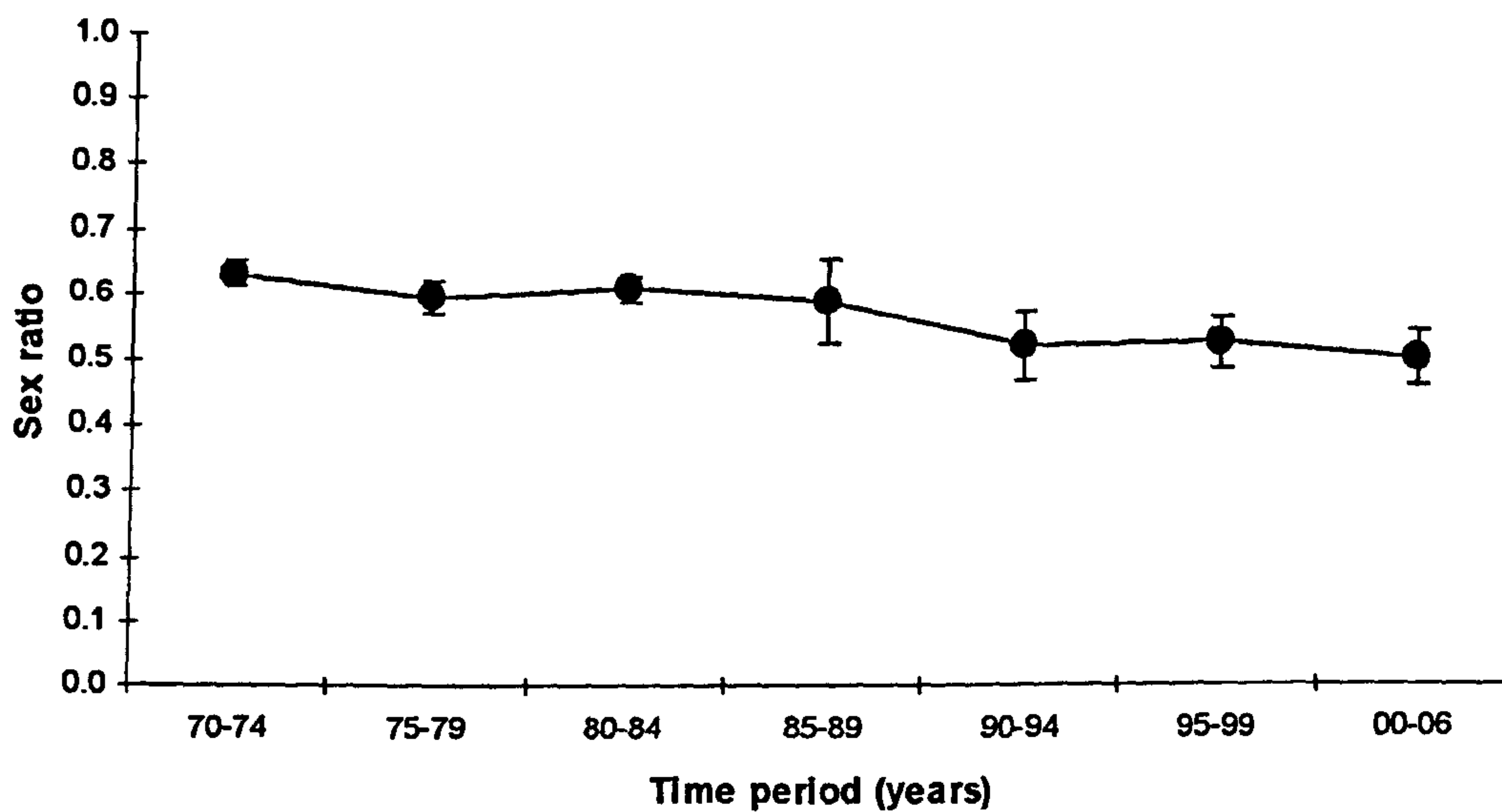


Figure 3.21: Mean (\pm SD) sex ratios, expressed as the proportion of males in a sample, for 5 year time periods for plaice caught in coastal waters of E. Anglesey and N. W. Wales. The five year average sex ratio values are presented for (a) raw data and (b) annual data calculated as 3 year smoothed averages.

Table 3.11: (a) Sex ratio data (expressed as the proportion of male fish) for plaice caught in the autumn fisheries surveys conducted by the RV *Prince Madog* in 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD for the 5 year time periods calculated from the raw data and from the smoothed average values calculated as a three year running average. (b) Significance values for the *post-hoc* comparisons of smoothed average sex ratio values using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold and trends, *i.e.* $0.05 < P < 0.10$, are underlined).

a)

<i>Time period</i> <i>(years)</i>	<i>Sex ratio</i> <i>(raw data)</i>	<i>Sex ratio</i> <i>(Smoothed data)</i>
1970-1974	0.62 \pm 0.07	0.63 \pm 0.02
1975-1979	0.61 \pm 0.06	0.59 \pm 0.02
1980-1984	0.61 \pm 0.05	0.61 \pm 0.02
1985-1989	0.58 \pm 0.11	0.59 \pm 0.06
1990-1994	0.53 \pm 0.09	0.52 \pm 0.05
1995-1999	0.51 \pm 0.13	0.52 \pm 0.05
2000-2006	0.50 \pm 0.07	0.50 \pm 0.04

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1985-1989	1995-1999
1970-1974						
1975-1979	0.96					
1980-1984	0.99	1.00				
1985-1989	0.91	1.00	1.00			
1990-1994	<u>0.053</u>	0.22	0.11	0.31		
1995-1999	<u>0.098</u>	0.36	0.20	0.47	1.00	
2000-2006	0.009	0.04	0.02	<u>0.07</u>	1.00	0.99

3.3.5 Length at age and Growth parameters

In this section the Von Bertalanffy growth (VBG) parameters – theoretical maximum length, L_{∞} (cm), and growth rate (k , year⁻¹) – for male and female plaice have been collated from the autumn fisheries surveys (1970 – 2006) (Table 3.12). Data were obtained from 4 sources – the raw data appendices in Seyhan (1990) and Chuenpagdee (1990), unpublished data from the autumn fisheries surveys archived by Dr David Grove (1990-2000) and Dr Ian McCarthy (2001-2004) and from the results presented in Chapter 2 (2005-2006). Where possible, the VBG coefficients were recalculated by utilising the raw size-at-age data to fit the VBG model using the non-linear regression function in SPSS (Ver. 12.0). For the time-series analyses, data were not available for male plaice for 1971 and 1980 and for female plaice for 1971, 1980 and 1982 (Table 3.12).

The L_{∞} (total length) values for male and female plaice for the time period 1970-2006 are presented in Figure 3.22a. Male plaice L_{∞} values ranged between 27.2 and 50.8 cm with an overall average of 35.3 ± 6.1 cm TL while female L_{∞} values ranged between 35.9 and 51.7 cm and attained an average of 44.9 ± 3.8 cm. The L_{∞} data were both normally distributed for males and females (σ^2 , $Z = 0.12$, $n = 35$, $P = 0.20$; σ^2 , $Z = 0.14$, $n = 34$, $P = 0.08$) but had unequal variance (σ^2 , $W = 0.12$, $n = 35$, $P = 0.20$; σ^2 , $W = 6.09$, $P = 0.02$) The average L_{∞} values of male and female plaice for the time period 1970-2006 were significantly different (t -test assuming unequal variance; $t = 7.98$, 59.5 df, $P < 0.001$). Both male and female plaice showed significant, but contrasting, correlations between L_{∞} and time (survey year): for female plaice the correlation between L_{∞} and time was positive ($r_s = 0.372$, $P = 0.03$) whilst for male plaice it was negative ($r_s = -0.480$, $P = 0.003$). When the data were grouped in 5 year intervals (1970-1974, 1975-1979 etc), the L_{∞} values for both sexes were normally distributed (σ^2 , $Z = 0.12$, $n = 35$, $P = 0.20$; σ^2 , $Z = 0.14$, $n = 34$, $P = 0.08$) with both data sets having equal variances between time periods (σ^2 , $W_{6,28} = 1.64$, $P = 0.18$; σ^2 , $W_{6,27} = 0.51$, $P = 0.79$). There were no significant differences between the average L_{∞} values of female plaice (ANOVA, $F_{(6,27)} = 0.78$, $P = 0.59$) for each time interval but significant differences between the average L_{∞} values of male plaice (ANOVA, $F_{(6,28)} = 7.06$, $P < 0.001$) (Table 3.13). Pairwise comparisons of the average L_{∞} values for male plaice for each time interval (Table 3.13) showed that the

Table 3.12: Coefficients for the von Bertalanffy curves for male and female plaice caught in the autumn fisheries surveys in the inshore waters of eastern Anglesey and North West Wales between 1970 and 2006. Data are presented for the theoretical maximum total length (L_{∞} , cm), growth rate (k , year⁻¹) and theoretical age at zero length (t_0 , year).

Year	Male			Female		
	L_{∞}	k	t_0	L_{∞}	k	t_0
1970	37.8	0.277	-0.057	43.6	0.264	-0.228
1972	33.1	0.361	-0.462	43.0	0.223	-0.568
1973	29.7	0.517	-1.133	46.2	0.279	-1.237
1974	36.3	0.27	-1.97	46.0	0.25	-1.2
1975	35.9	0.171	-1.638	45.0	0.281	-0.897
1976	36.3	0.27	-1.97	46.0	0.25	-1.2
1977	31.3	0.609	-0.224	36.2	0.460	-0.753
1978	35.4	0.322	-0.447	44.4	0.290	0.012
1979	41.7	0.17	-2.085	44.5	0.262	-1.312
1981	34.9	0.22	-2.466	40.4	0.338	-1.170
1982	50.8	0.273	-0.773			
1983	38.8	0.301	-1.301	45.2	0.316	-0.641
1984	46.9	0.152	-2.283	42.9	0.371	-1.049
1985	45.8	0.171	-1.638	46.7	0.282	-0.415
1986	37.4	0.414	-1.008	43.3	0.429	-0.622
1987	44.3	0.231	-2	35.9	0.536	-0.028
1988	42.3	0.304	-0.813	46.6	0.317	-0.968
1989	43.0	0.219	-2.049	47.1	0.314	-0.769
1990	33.7	0.717	-0.353	51.7	0.234	-1.224
1991	33.5	0.436	-1.339	43.0	0.363	-1.215
1992	34.7	0.595	-0.630	39.5	0.361	-1.634
1993	28.2	0.49	-1.33	46.9	0.353	-0.548
1994	33.3	0.728	0.408	46.1	0.19	-1.36
1995	27.5	0.62	-1.21	49.1	0.21	-1.26
1996	31.3	0.63	-0.13	39.0	0.51	0.09
1997	35.8	0.357	-1.174	46.2	0.25	-0.998
1998	27.2	0.53	-0.14	46.0	0.17	-1.64
1999	30.8	0.6	-0.1	47.20	0.3	-0.45
2000	31.2	0.42	-1.49	51.4	0.2	-1.67
2001	27.8	0.57	-1.107	50.4	0.199	-1.44
2002	40.8	0.337	-1.11	47.7	0.253	-1.19
2003	33.7	0.429	-0.54	49.0	0.254	-0.621
2004	30.1	0.903	-0.013	43.2	0.392	-0.315
2005	28.5	0.51	-0.488	47.0	0.28	-0.416
2006	27.6	0.47	-1.87	41.0	0.27	-1.72

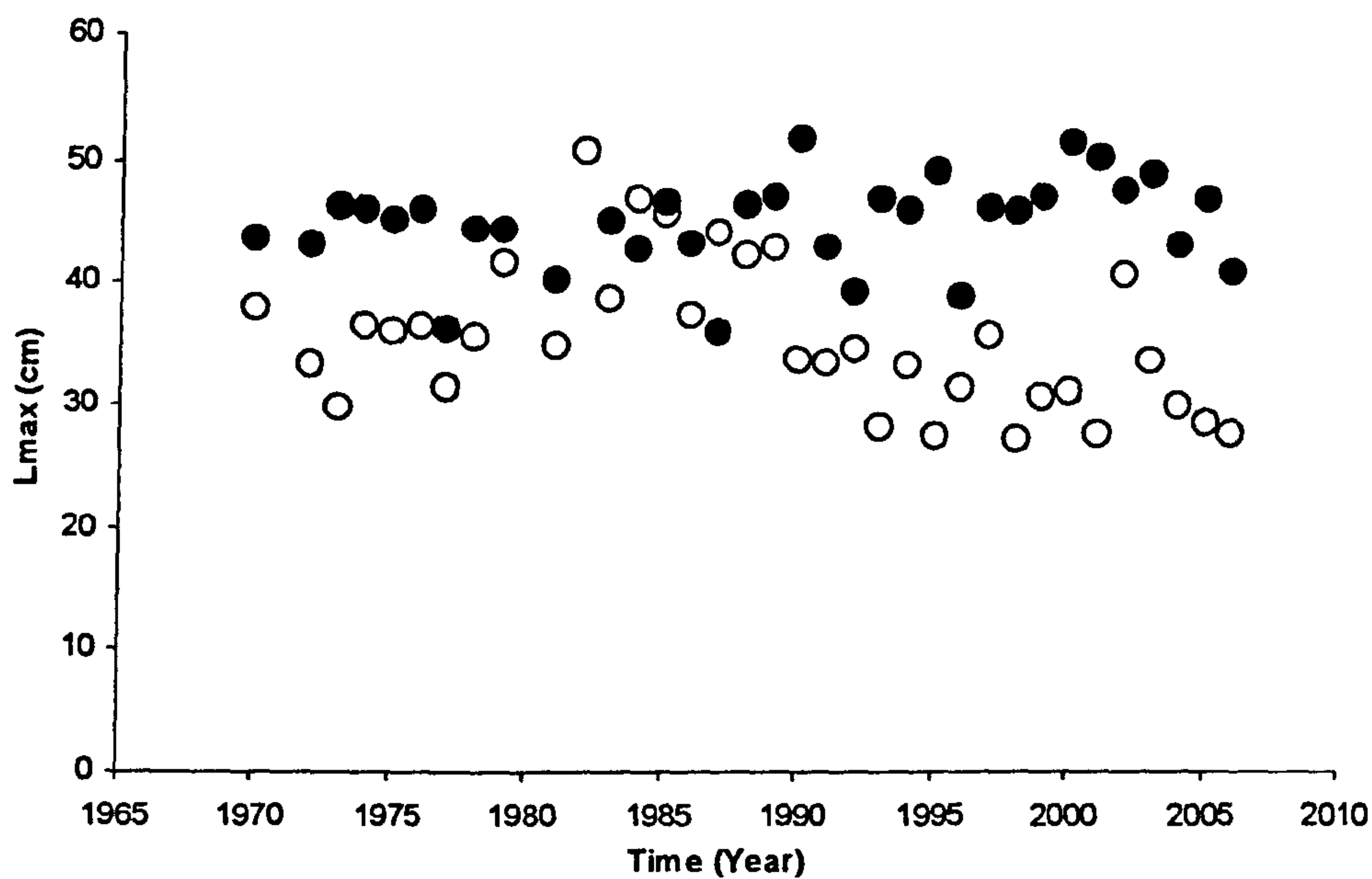
values recorded during the 1980s (*i.e.* 1980-1984 and 1985-1989) were higher than those recorded post-1990 (*i.e.* 1990-1994, 1995-1999 and 2000-2006).

As in the previous analysis of length and age data, it is important to reduce the inter-annual variations by smoothing the curve by calculating 3 year moving average. Analysis of this smoothed data also indicated that there were highly significant correlations between L_{∞} values and time for both sexes, with L_{∞} decreasing over time for males ($r_s = -0.521$, $n = 36$, $P = 0.001$) and increased for females ($r_s = 0.452$, $n = 36$, $P = 0.006$) (Figure 3.22b). When the data were grouped in 5 year intervals (1970-1974, 1975-1979 etc) (Figure 3.23b), the L_{∞} values for both sexes were normally distributed (σ , $Z = 0.134$, $n = 36$, $P = 0.10$; φ , $Z = 0.127$, $n = 36$, $P = 0.15$) with both data sets having equal variances between time periods (σ , $W_{6,29} = 1.44$, $P = 0.23$; φ , $W_{6,29} = 1.01$, $P = 0.44$). In contrast to the raw data, there was a significant effect of time interval on the 'smoothed' average L_{∞} values of female plaice (ANOVA, $F_{(6,29)} = 3.00$, $P = 0.02$) for each time interval. The male 'smoothed' average L_{∞} values of male plaice also showed significant differences between time periods. (ANOVA, $F_{(6,29)} = 28.03$, $P < 0.001$), table 3.14. Pairwise comparisons of the average L_{∞} values for female plaice for each time interval showed that the only difference was between 1980-1984 and 2000-2006 with a P-value of 0.09. Therefore, it is likely that the ANOVA for the smoothed L_{∞} values for female plaice is a Type I error and there are no differences between time periods. Pairwise comparisons of the average L_{∞} values for male plaice for each time interval (Table 3.14) showed that the values recorded during the 1980s (*i.e.* 1980-1984 and 1985-1989) were higher than those recorded during the 1970s, 1990s and 2000-2006. Thus, the results of this analysis have shown that the L_{∞} values for female plaice have tended to increase over the time period 1970-2006, this increase has not been significant and the long-term L_{∞} value for female plaice is *ca.* 45 cm TL. In contrast, the L_{∞} values for male plaice have shown a significant increase during the 1980s, but have since declined and the long-term L_{∞} value for male plaice is *ca.* 35 cm TL.

The von Bertalanffy growth rate (k , year^{-1}) values for male and female plaice for the time period 1970-2006 are presented in Figure 3.24a. Male plaice k values ranged between 0.152 and 0.903 year^{-1} with an overall average of $0.417 \pm 0.186 \text{ year}^{-1}$ while female k values ranged between 0.170 and 0.536 year^{-1} and attained average of $0.302 \pm 0.088 \text{ year}^{-1}$. The average k values of male and female plaice for the time period 1970-2006 were significantly different (t -test assuming unequal variance; $t =$

3.20, 51.2 df, $P = 0.002$). Male plaice showed significant positive correlation between k and time ($r_s = 0.531$, $P = 0.001$) whilst female plaice showed no correlation ($r_s = -0.126$, $P = 0.48$).

a)



b)

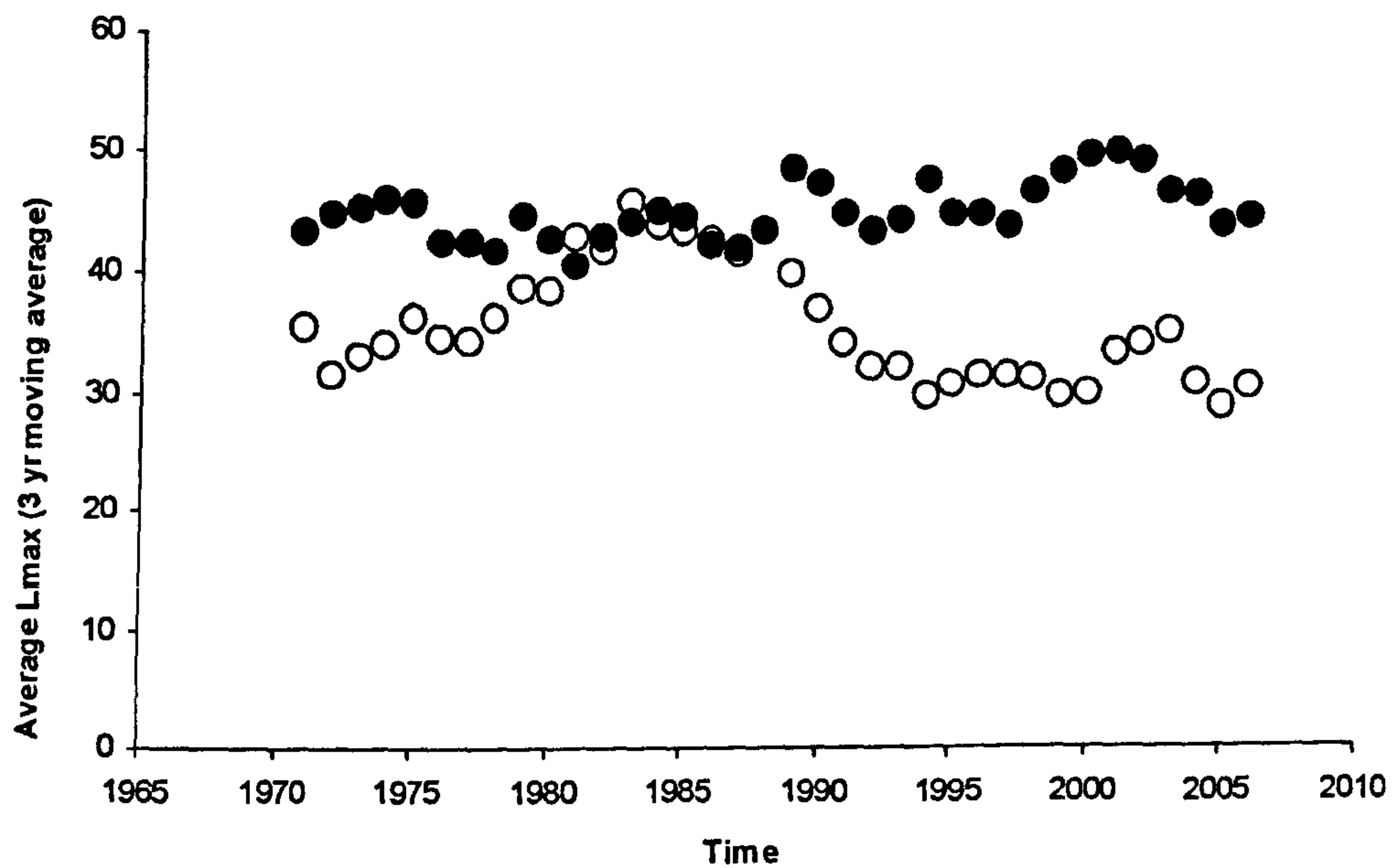


Figure 3.22: The theoretical maximum length L_{∞} (cm) values for female (solid circles) and male (open circles) plaice caught in the autumn fisheries surveys in the inshore waters of eastern Anglesey and north west Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the L_{∞} values for any given year plus the values for the year before and the year after.

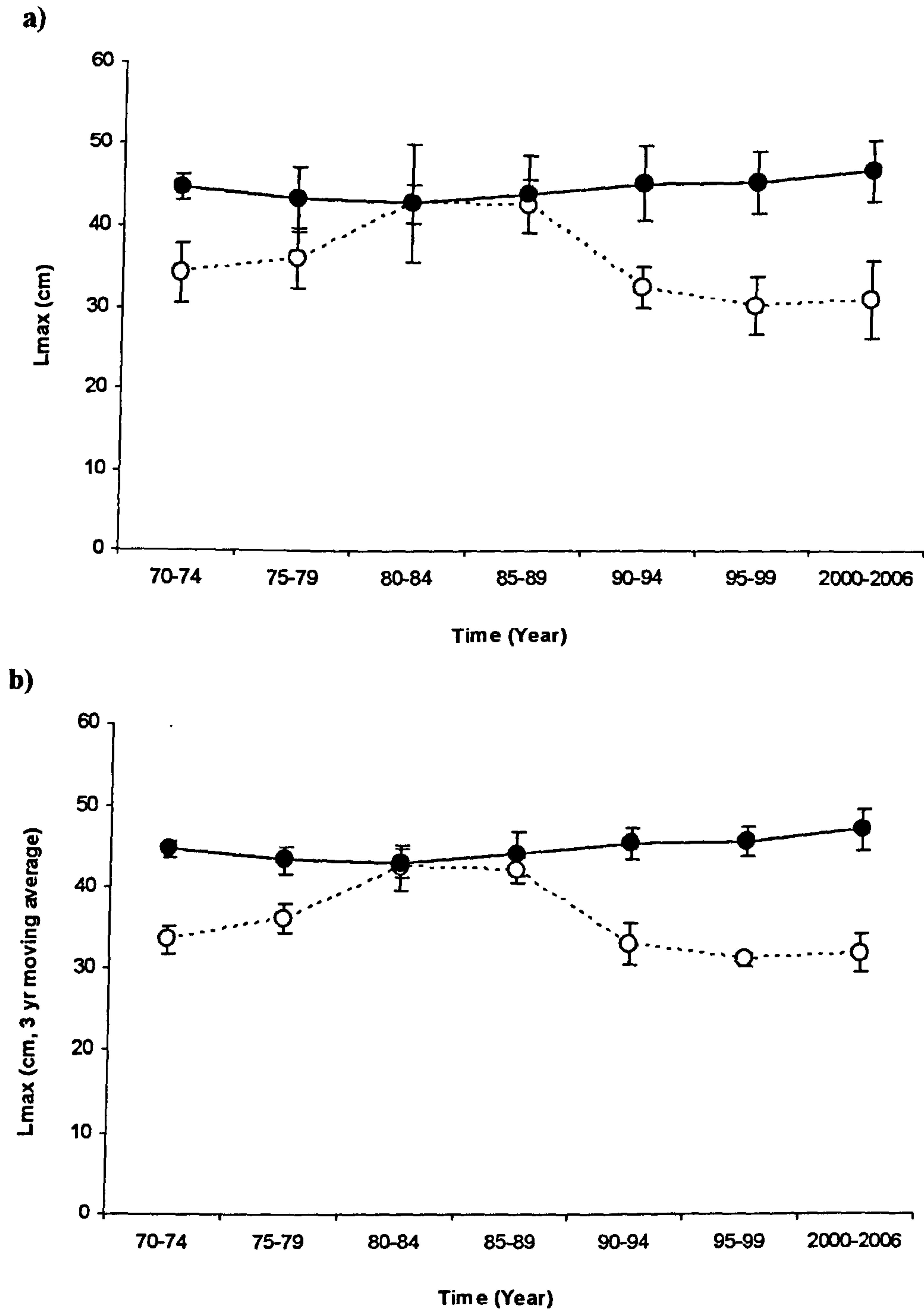


Figure 3.23: The theoretical maximum length L_{∞} (cm) values for female (solid circles) and male (open circles) plaice caught in the autumn fisheries surveys in the inshore waters of eastern Anglesey and north west Wales between 1970 and 2006. Data are presented as mean \pm SD values for 5 year time periods (1970-1974, 1975-1979 etc). (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the L_{∞} values for any given year plus the values for the year before and the year after.

Table 3.13. (a) Average theoretical maximum length values (L_{∞} , cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the *post-hoc* comparisons of average male L_{∞} values using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold).

a)

	Male L_{∞}	Female L_{∞}
1970-1974	34.2 \pm 3.6	44.7 \pm 1.6
1975-1979	36.1 \pm 3.7	43.2 \pm 4.0
1980-1984	42.8 \pm 7.3	42.8 \pm 2.4
1985-1989	42.5 \pm 3.2	43.9 \pm 4.7
1990-1994	32.7 \pm 2.6	45.4 \pm 4.6
1995-1999	30.5 \pm 3.5	45.5 \pm 3.9
2000-2006	31.4 \pm 4.7	47.1 \pm 3.8

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.998					
1980-1984	0.254	0.485				
1985-1989	0.235	0.467	1.000			
1990-1994	0.999	0.942	<u>0.079</u>	<u>0.065</u>		
1995-1999	0.938	0.623	0.017	0.012	0.995	
2000-2006	0.976	0.716	0.018	0.012	1.000	1.000

Table 3.14. (a) Average theoretical maximum length values (L_{∞} , cm), calculated as a three year moving average, for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the *post-hoc* comparisons of average male L_{∞} values using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold).

a)

	Male smoothed L_{∞}	Female smoothed L_{∞}
1970-1974	33.5 \pm 1.7	44.7 \pm 1.0
1975-1979	35.9 \pm 1.7	43.3 \pm 1.7
1980-1984	42.4 \pm 2.7	42.9 \pm 1.7
1985-1989	42.0 \pm 1.5	44.0 \pm 2.7
1990-1994	32.9 \pm 2.6	45.3 \pm 1.9
1995-1999	30.9 \pm 0.7	45.6 \pm 1.8
2000-2006	31.7 \pm 2.3	47.1 \pm 2.5

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.767					
1980-1984	0.001	0.004				
1985-1989	0.001	0.008	1.000			
1990-1994	1.000	0.497	0.001	0.001		
1995-1999	0.750	0.044	0.001	0.001	0.876	
2000-2006	0.930	<u>0.088</u>	0.001	0.001	0.985	0.998

When the growth rate data were grouped in 5 year intervals (Figure 3.25b), the k values for both sexes were normally distributed (σ , $Z = 0.10$, $n = 35$, $P > 0.20$; φ , $Z = 0.145$, $n = 34$, $P = 0.07$) with both data sets having equal variances between time periods (σ , $W_{6,28} = 0.79$, $P = 0.52$; φ , $W_{6,27} = 0.172$, $P = 0.15$). There were no significant differences between the average k values of female plaice (ANOVA, $F_{(6,28)} = 1.18$, $P = 0.35$) for each time interval but significant differences between the average k values of male plaice (ANOVA, $F_{(6,28)} = 5.42$, $P < 0.001$) (Table 3.15). However, when pairwise comparisons of the average k values for male plaice for each time interval were conducted using Scheffe's multiple comparison test, no significant differences were detected although the k values during the 1980s tended to be lower than those recorded during 1990-1994 (Table 3.15b).

When the data were 'smoothed, using a 3 year moving average (Figure 3.24b), female plaice still exhibited no correlation between growth rate and time ($r_s = -0.186$, $P = 0.28$) whilst the correlation for male plaice was highly significant ($r_s = 0.698$, $P < 0.001$). The smoothed k values for both sexes were normally distributed (σ , $Z = 0.122$, $n = 36$, $P = 0.19$; φ , $Z = 0.091$, $n = 36$, $P > 0.20$) with equal variances between time periods observed for the male plaice ($W_{6,29} = 1.08$, $P = 0.40$) but not for female plaice ($W_{6,29} = 2.62$, $P = 0.04$). The male 'smoothed' average k values of male plaice also showed significant differences between time periods (ANOVA, $F_{(6,29)} = 21.06$, $P < 0.001$) (Table 3.16). Pairwise comparisons of the average growth rate values for male plaice for each time interval showed that the k values separated into two clear groups (Table 3.16): the growth rates recorded during the 1970s and 1980s were similar to each other and significantly lower than those recorded post-1990, with the growth rates post-1990 also being similar to each other (Table 3.16). In contrast to the raw data, there was a significant effect of time interval on the 'smoothed' average k values of female plaice (Kruskal Wallis, $\chi^2 = 16.96$, 6df. $P = 0.009$). Pairwise comparisons of the average k values for female plaice for each time interval using Wilcoxon's signed rank test showed that higher growth rates were observed in the 1980s (*i.e.* 1980-1984 and 1985-1989) compared to the other time periods (Table 3.16). Thus, the results of this analysis have shown that the k values for both male and female plaice have shown changes over the time period 1970-2006. The k values for male plaice were similar between 1970-1989 with an average k value of *ca.* 0.292 year^{-1} before increasing post-1990 to an average k value of *ca.* 0.550 year^{-1} . Changes in the k value for female plaice have been more variable increasing from *ca.* 0.291 year^{-1} in the 1970s to *ca.*

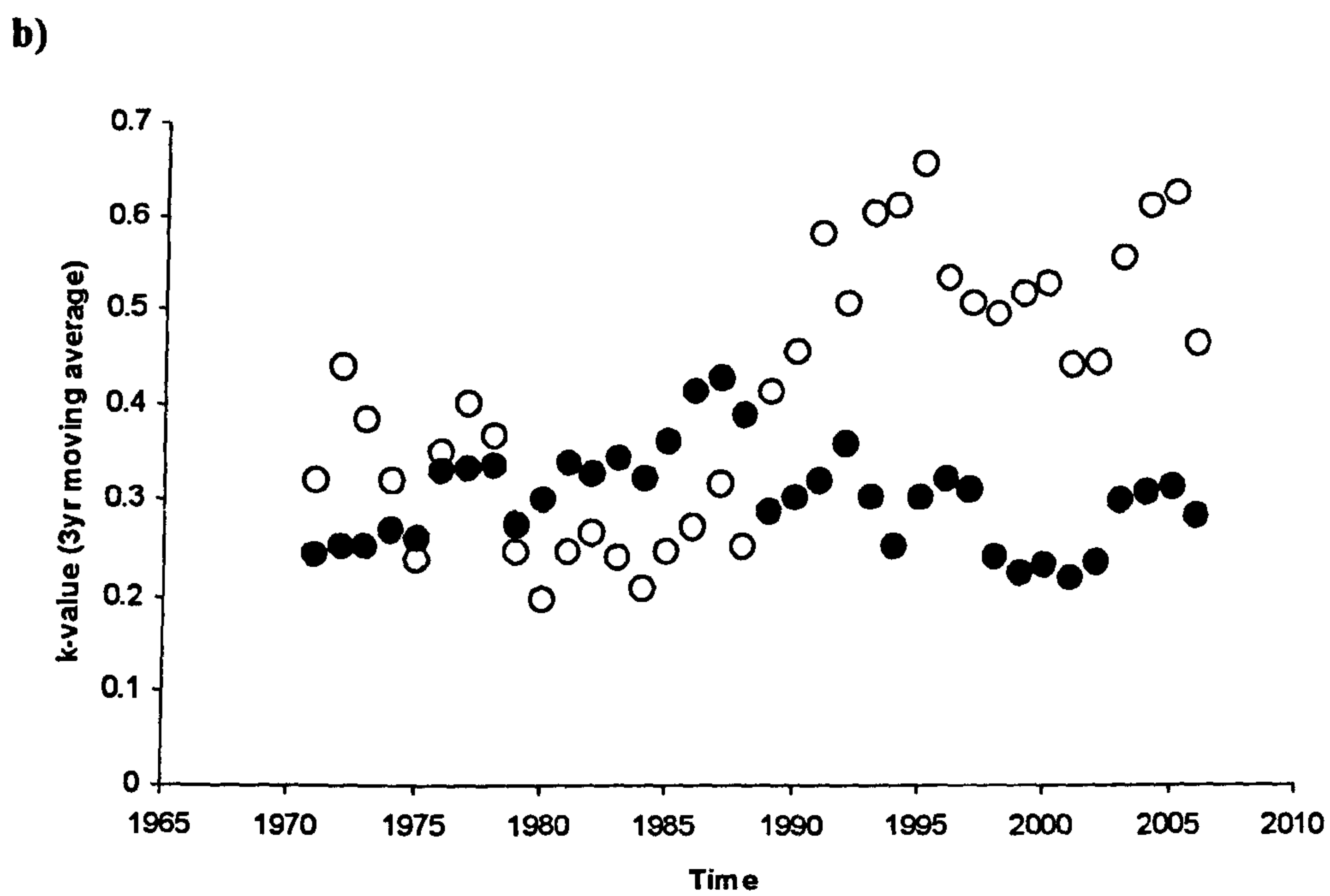
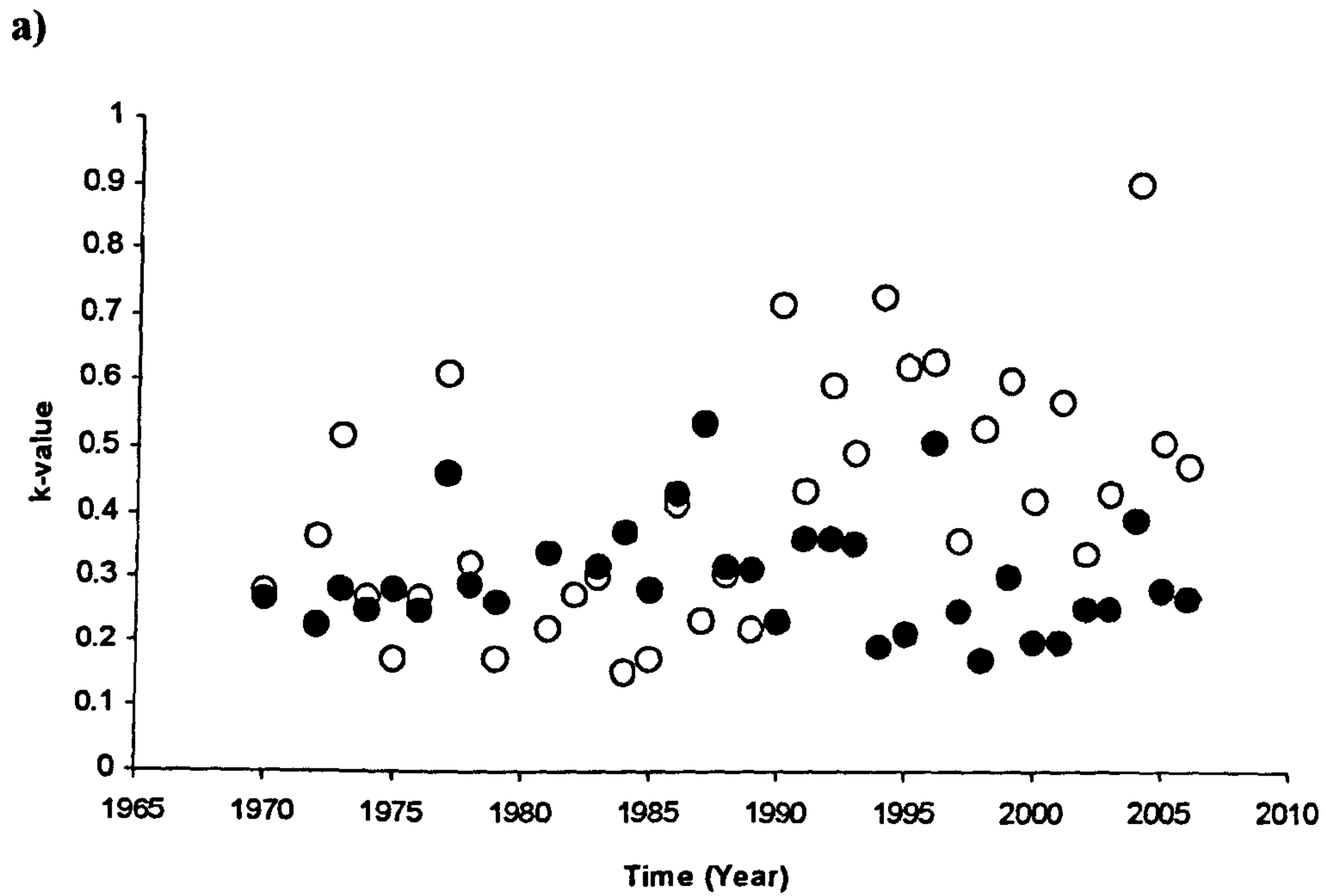


Figure 3.24: The von Bertalanffy growth coefficients, k (year^{-1}) for female (solid circles) and male (open circles) plaice caught in the autumn fisheries surveys in the inshore waters of eastern Anglesey and north west Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the k values for any given year plus the values for the year before and the year after.

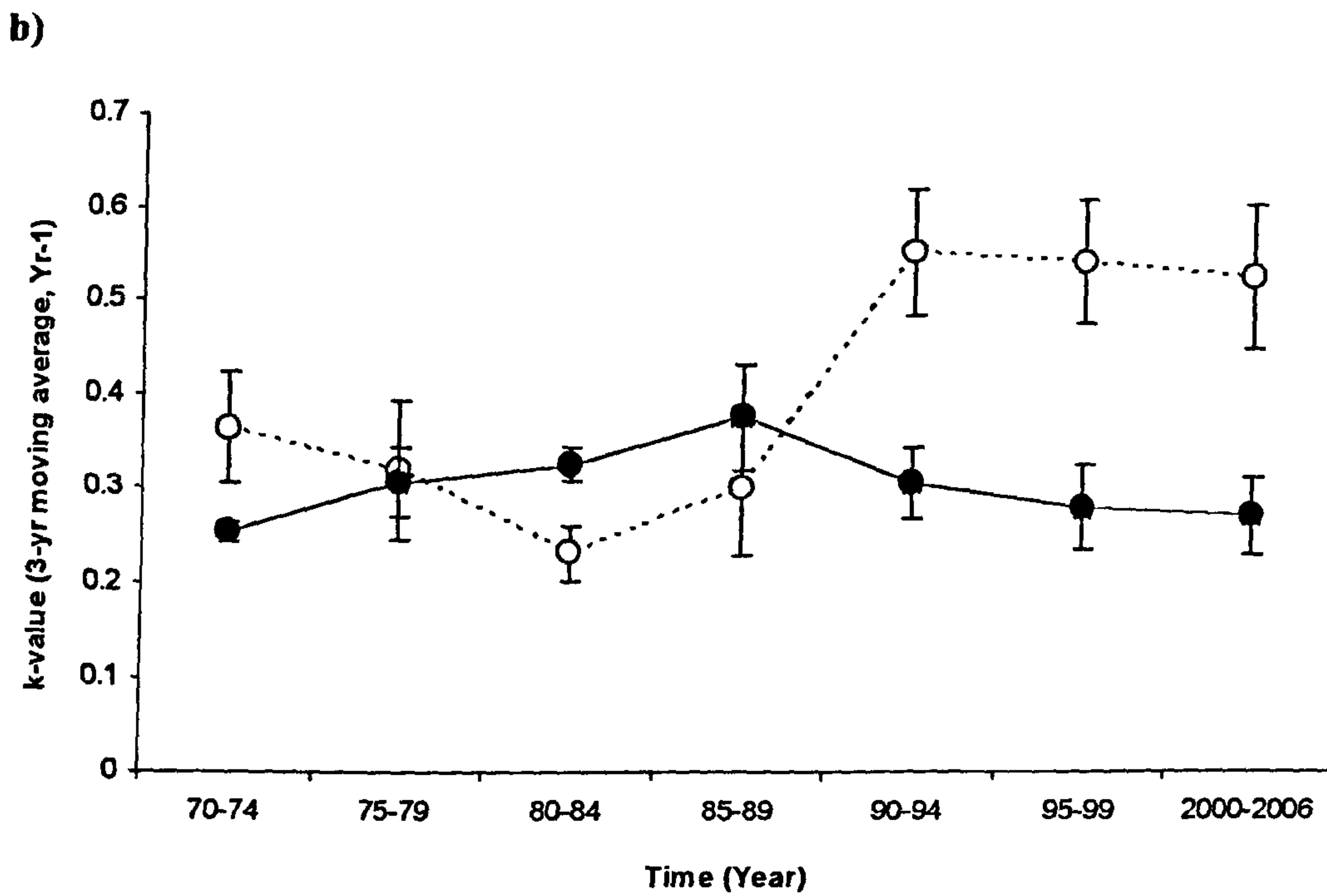
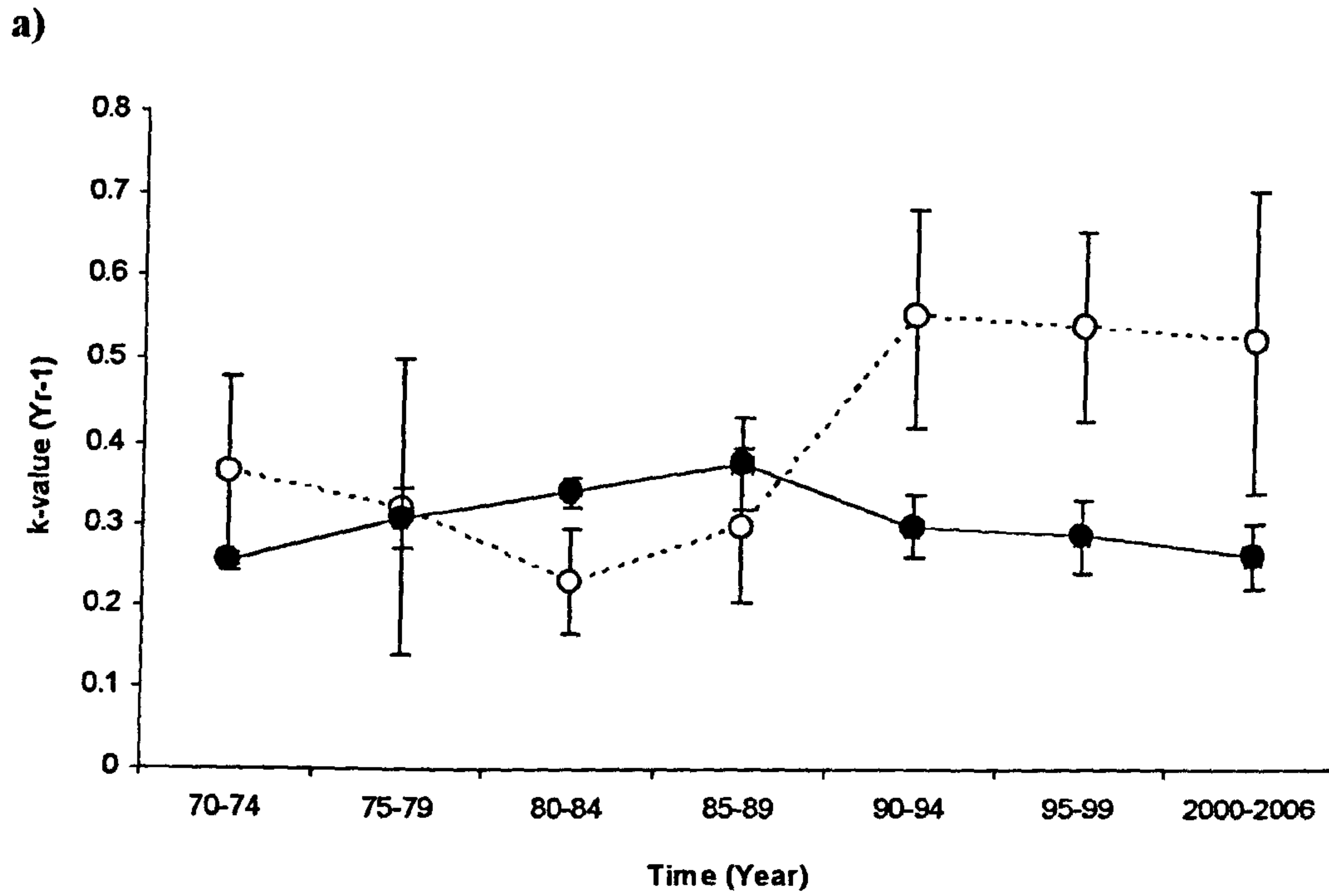


Figure 3.25: The von Bertalanffy growth coefficients, k (year^{-1}) for female (solid circles) and male (open circles) plaice caught in the autumn fisheries surveys in the inshore waters of eastern Anglesey and north west Wales between 1970 and 2006. Data are presented as mean \pm SD values for 5 year time periods (1970-1974, 1975-1979 etc). (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the k values for any given year plus the values for the year before and the year after.

Table 3.15. (a) Average von Bertalanffy growth coefficients, k (year⁻¹) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the *post-hoc* comparisons of average male k values using Scheffe's multiple comparison test (significant differences at the 5% level are highlighted in bold).

a)

	Male k	Female k
1970-1974	0.356 \pm 0.115	0.254 \pm 0.024
1975-1979	0.308 \pm 0.180	0.308 \pm 0.086
1980-1984	0.236 \pm 0.066	0.342 \pm 0.028
1985-1989	0.268 \pm 0.095	0.376 \pm 0.105
1990-1994	0.593 \pm 0.131	0.300 \pm 0.082
1995-1999	0.547 \pm 0.113	0.288 \pm 0.133
2000-2006	0.520 \pm 0.184	0.264 \pm 0.065

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	1.000					
1980-1984	0.956	0.996				
1985-1989	0.988	1.000	1.000			
1990-1994	0.401	0.147	<u>0.051</u>	<u>0.065</u>		
1995-1999	0.653	0.322	0.125	0.162	1.000	
2000-2006	0.738	0.375	0.144	0.186	0.991	1.000

Table 3.16. (a) ‘Smoothed’ average von Bertalanffy growth coefficients, k (year⁻¹) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD for male and female plus median values \pm interquartile range for females. Significance values for the *post-hoc* comparisons of (b) mean male k values using Scheffe’s multiple comparison test and (c) median female k values using Wilcoxon’s Signed Rank test. Significant differences at the 5% level are highlighted in bold.

a)

	Male smoothed k -value	Female smoothed Mean k -value	Female smoothed Median k -value
1970-1974	0.365 \pm 0.058	0.254 \pm 0.011	0.251 \pm 0.020
1975-1979	0.320 \pm 0.074	0.307 \pm 0.036	0.350 \pm 0.142
1980-1984	0.231 \pm 0.029	0.327 \pm 0.017	0.327 \pm 0.029
1985-1989	0.300 \pm 0.069	0.376 \pm 0.055	0.389 \pm 0.097
1990-1994	0.553 \pm 0.068	0.307 \pm 0.039	0.304 \pm 0.063
1995-1999	0.543 \pm 0.067	0.280 \pm 0.045	0.303 \pm 0.085
2000-2006	0.526 \pm 0.078	0.270 \pm 0.041	0.284 \pm 0.076

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.983					
1980-1984	0.208	0.613				
1985-1989	0.898	1.000	0.841			
1990-1994	0.021	0.001	0.001	0.001		
1995-1999	0.035	0.002	0.001	0.001	1.000	
2000-2006	0.044	0.002	0.001	0.001	0.998	1.000

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	0.144					
1980-1984	<u>0.068</u>	0.893				
1985-1989	<u>0.068</u>	0.043	<u>0.080</u>			
1990-1994	<u>0.068</u>	0.686	0.345	0.043		
1995-1999	0.144	0.255	<u>0.080</u>	0.043	0.138	
2000-2006	0.465	0.138	0.043	<u>0.080</u>	0.136	0.500

ca. 0.351 year⁻¹ in the 1980s before decreasing to *ca.* 0.284 year⁻¹ post 1990.

Changes in length at age and in the pattern of growth were examined for male and female plaice between 1970 and 2006. The annual changes in average length at age for each age class of male and female plaice are presented in Figure 3.26. For male plaice, 9 age classes, 0⁺⁺ to 8⁺⁺, have been caught during the 37 year survey with between 4 and 8 age classes recorded in the catch in any given year (Figure 3.26). The 1⁺⁺ to 4⁺⁺ age classes were recorded in the catch in most years (24/31 years, 77%). The most common number of age classes present in the catch for male plaice was 5 to 7 age classes (21/31 years, 68%) with on average 6 age classes present in the catch in any given year (Figure 3.26). Fish older than 7⁺⁺ were rarely caught and were only present in 6 years (1972, 1975, 1978, 1982, 1985, and 1988). For female plaice, 14 age classes, 0⁺⁺ to 13⁺⁺, have been caught during the 37 year survey with between 5 and 13 age classes recorded in the catch in any given year (Figure 3.26). The 1⁺⁺ to 6⁺⁺ age classes were recorded in the catch in most years (25/32 years, 78%). The most common number of age classes present in the catch for female plaice was 6 to 9 age classes (23/32 years, 72%) with on average 8 age classes present in the catch in any given year (Figure 3.26). Fish older than 9⁺⁺ were rarely caught and were only present in 6 years (1970, 1972, 1975, 1978, 1994, and 2005).

To examine whether there have been any changes in the average size of each age class over time, the relationship between total length and year was examined for each age class using Spearman's Rank Correlation test. There were no significant correlations between average size at age and time for any age class for either male or female plaice (Table 3.17) indicating that over time there had been no overall trend for an increase or decrease in the average size of each age class during the 37 year survey.

To examine whether there have been any changes in the pattern of growth over time, the size at age data for male and female plaice were grouped into 5 year time periods (1970-1974, 1975-1979 etc) and the average size for each age class present in that time period was calculated. Von Bertalanffy growth curves were derived for male and female fish for each 5 year time period and are presented in Figure 3.27 with the von Bertalanffy growth coefficients presented in Table 3.18. For each 5 year time period, the same sex-dependent differences in growth as reported in Chapter 2 were observed (Figure 3.27) with male plaice have lower L_{∞} values

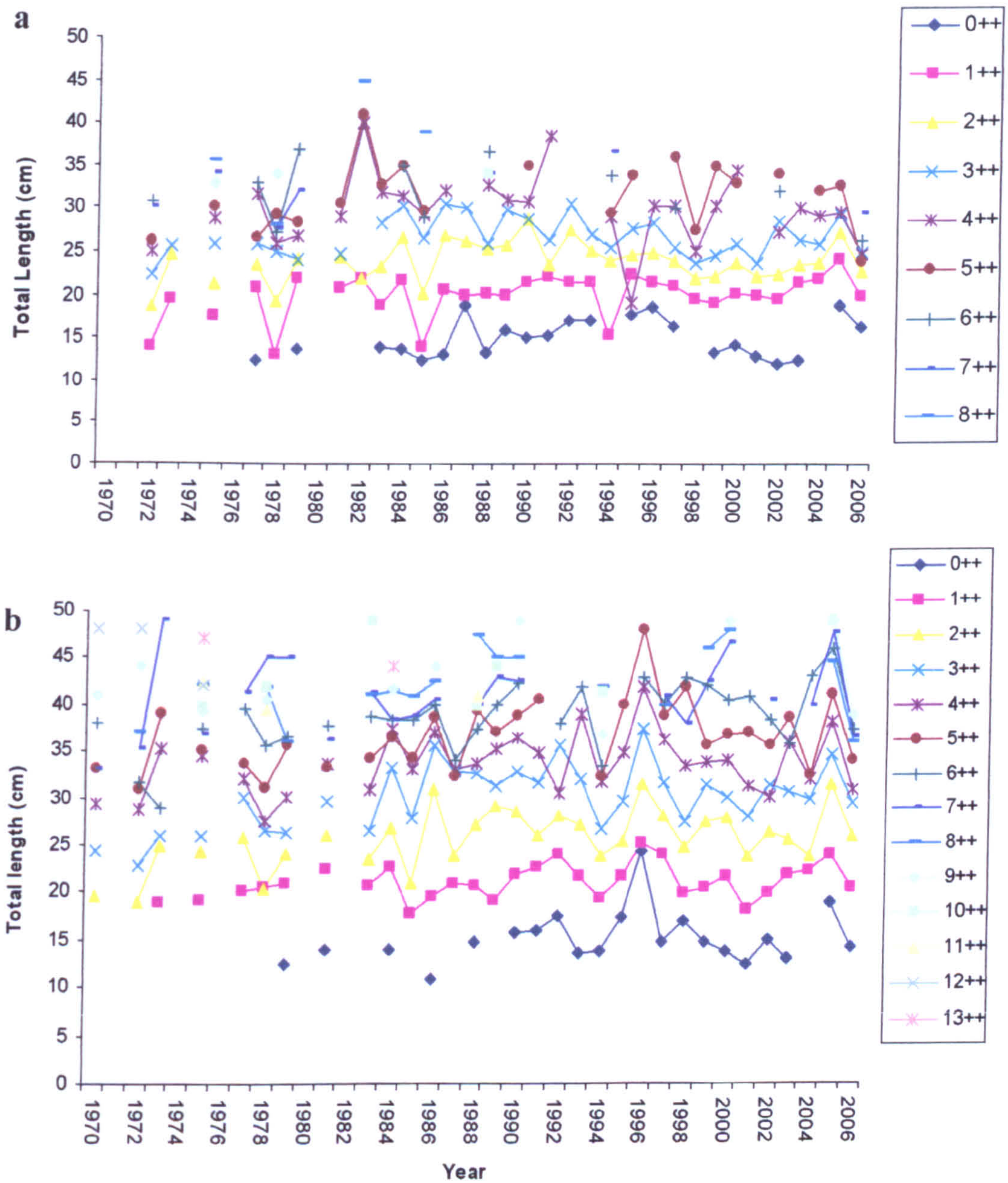


Figure 3.26: Annual changes in length at age (0^{++} , 1^{++} , ..., 13^{++}) for (a) male and (b) female plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and North West Wales between 1970 and 2006.

Table 3.17: Spearman Rank correlation coefficients (r_s) and associated significance values for the relationships between average total length (cm) and year for different age classes (0^{++} , 1^{++} , ..., 13^{++}) of male and female plaice caught in the October/November fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006.

Age Class	Male			Female		
	n	r_s	P	n	r_s	P
0^{++}	24	-0.077	0.72	19	0.044	0.89
1^{++}	31	-0.078	0.68	30	0.182	0.34
2^{++}	32	-0.112	0.54	32	0.100	0.59
3^{++}	31	-0.246	0.18	32	0.106	0.56
4^{++}	27	-0.282	0.16	32	-0.089	0.63
5^{++}	21	0.083	0.72	30	0.114	0.55
6^{++}	12	-0.261	0.41	30	0.203	0.28
7^{++}	7	0.072	0.88	21	0.036	0.88
8^{++}	5	0.600	0.29	15	-0.007	0.98
9^{++}	2	-	-	11	-0.255	0.45
10^{++}	1	-	-	3	-	-
11^{++}				2	-	-
12^{++}				4	-	-
13^{++}				1	-	-

and higher k values compared to female plaice in the same 5 year time period (Table 3.18). Figure 3.28 presents the size at age plots for male and female plaice and for both sexes combined with the plots for each time period superimposed on top of each other. To examine whether there were significant differences in the pattern of growth for male or female plaice over time, the von Bertalanffy growth curves for each of the 7 time periods were compared with each other (Table 3.19) and with the long term average growth curve derived from the 37 year data set (Table 3.20) using the likelihood ratio test (Kimura, 1980). A summary of these analyses, indicating the time intervals where significant differences between L_∞ and k values were recorded, is presented in Table 3.21. For male plaice, the overall pattern in the results was for the growth curves in 1975-1979, 1980-1984 and 2000-2006 to exhibit significant differences when compared to the other time periods. For female plaice, the overall pattern in the results was for the growth curves in 1970-1974 and 2000-2006 to exhibit significant differences when compared to the other time periods. When the growth curve for each 5 year time period was compared to the long-term average growth curve (1970-2006), the male and female growth curves for 2000-2006 were both significantly different from the long term average.

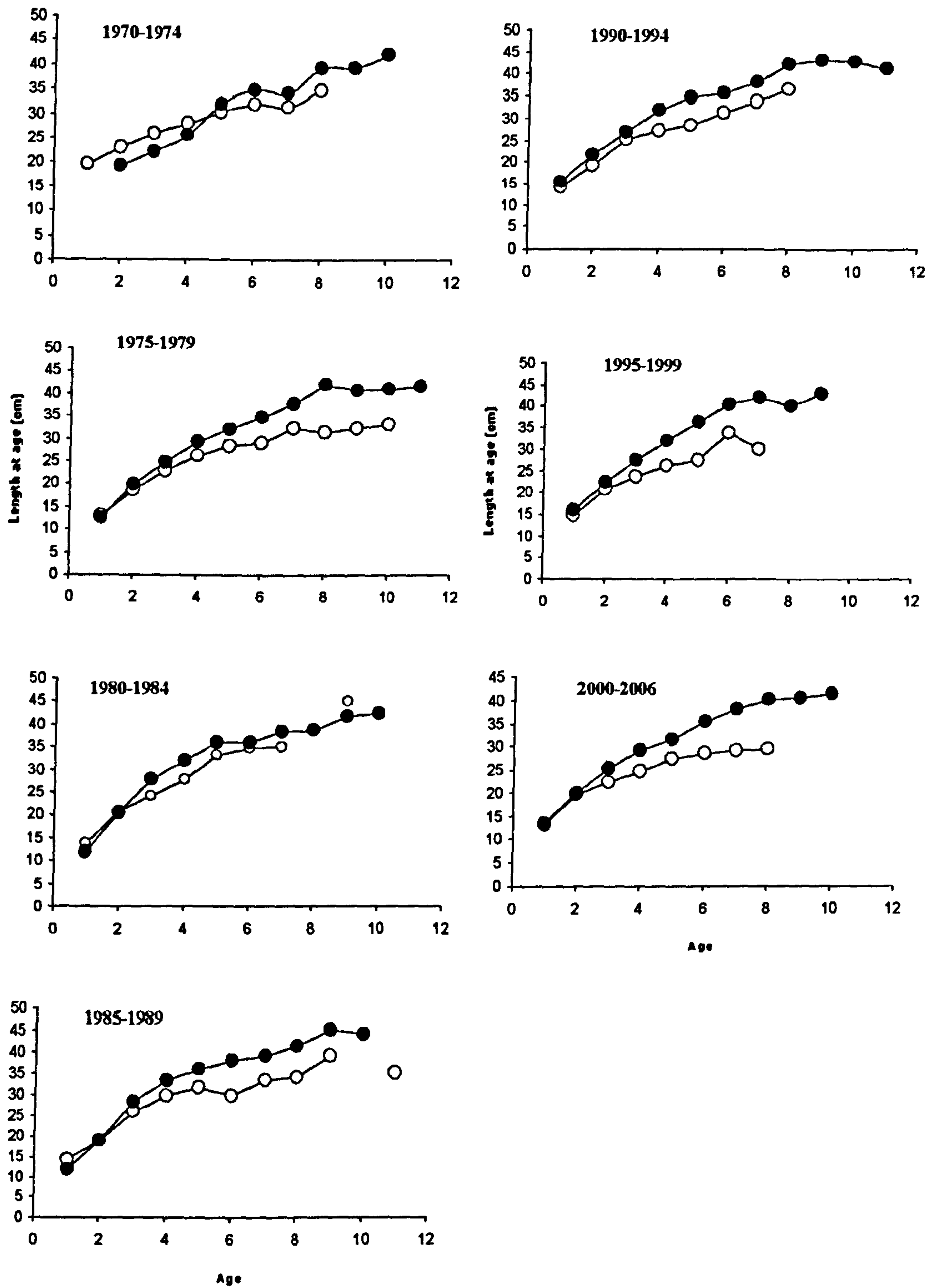


Figure 3.27: Scatter plots of size at age for plaice caught in the October/November fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as mean values for male (open circles) and female (closed circles) plaice for 5 year time periods (1970-1974, 1975-1979 etc) within the 37 year survey.

Table 3.18: Coefficients for the Von Bertalanffy growth curves for plaice caught in the October/November fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as mean values \pm SD for males, females and for male and females combined for 5 year time periods (1970-1974, 1975-1979 etc) between 1970 and 2006 and for the 37 year time period combined.

	1970 - 1974	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994	1995 - 1999	2000 - 2006	1970 - 2006
Male								
L_{∞}	36.3 \pm 7.5	34.5 \pm 1.1	42.6 \pm 4.6	35.3 \pm 1.3	38.4 \pm 3.7	35.4 \pm 6.3	30.9 \pm 0.64	35.5 \pm 0.5
K	0.223 \pm 0.176	0.297 \pm 0.042	0.244 \pm 0.075	0.384 \pm 0.073	0.256 \pm 0.076	0.280 \pm 0.177	0.376 \pm 0.038	0.302 \pm 0.019
t_0	-2.36 \pm 1.92	-1.59 \pm 0.26	-1.61 \pm 0.40	-1.30 \pm 0.31	-1.79 \pm 0.44	-1.94 \pm 1.03	-1.51 \pm 0.16	-1.64 \pm 0.12
R^2	0.924	0.987	0.986	0.971	0.985	0.956	0.995	0.997
Female								
L_{∞}	56.5 \pm 18.1	45.4 \pm 2.0	43.0 \pm 1.0	46.4 \pm 1.6	45.7 \pm 1.7	47.3 \pm 2.7	46.4 \pm 1.5	46.8 \pm 0.7
K	0.117 \pm 0.085	0.238 \pm 0.038	0.338 \pm 0.033	0.298 \pm 0.040	0.255 \pm 0.038	0.259 \pm 0.051	0.216 \pm 0.022	0.233 \pm 0.010
t_0	-2.30 \pm 1.44	-1.35 \pm 0.27	-0.98 \pm 0.14	-0.97 \pm 0.19	-1.55 \pm 0.29	-1.51 \pm 0.32	-1.58 \pm 0.17	-1.46 \pm 0.07
R^2	0.95	0.984	0.992	0.988	0.984	0.985	0.996	0.999
Combined data								
L_{∞}	46.5 \pm 3.2	43.9 \pm 2.2	46.4 \pm 1.7	42.0 \pm 2.4	47.2 \pm 2.4	55.7 \pm 7.7	51.9 \pm 3.2	44.6 \pm 1.4
K	0.183 \pm 0.041	0.203 \pm 0.034	0.237 \pm 0.030	0.335 \pm 0.093	0.211 \pm 0.036	0.148 \pm 0.048	0.148 \pm 0.022	0.233 \pm 0.027
t_0	-1.62 \pm 0.52	-1.74 \pm 0.33	-1.43 \pm 0.21	-1.10 \pm 0.45	-1.66 \pm 0.33	-2.16 \pm 0.52	-2.07 \pm 0.26	-1.54 \pm 0.22
R^2	0.984	0.986	0.992	0.928	0.984	0.984	0.995	0.992

L_{∞} = Theoretical maximum Total length (cm), K = growth rate (year^{-1}), t_0 = theoretical length at the age zero (years)

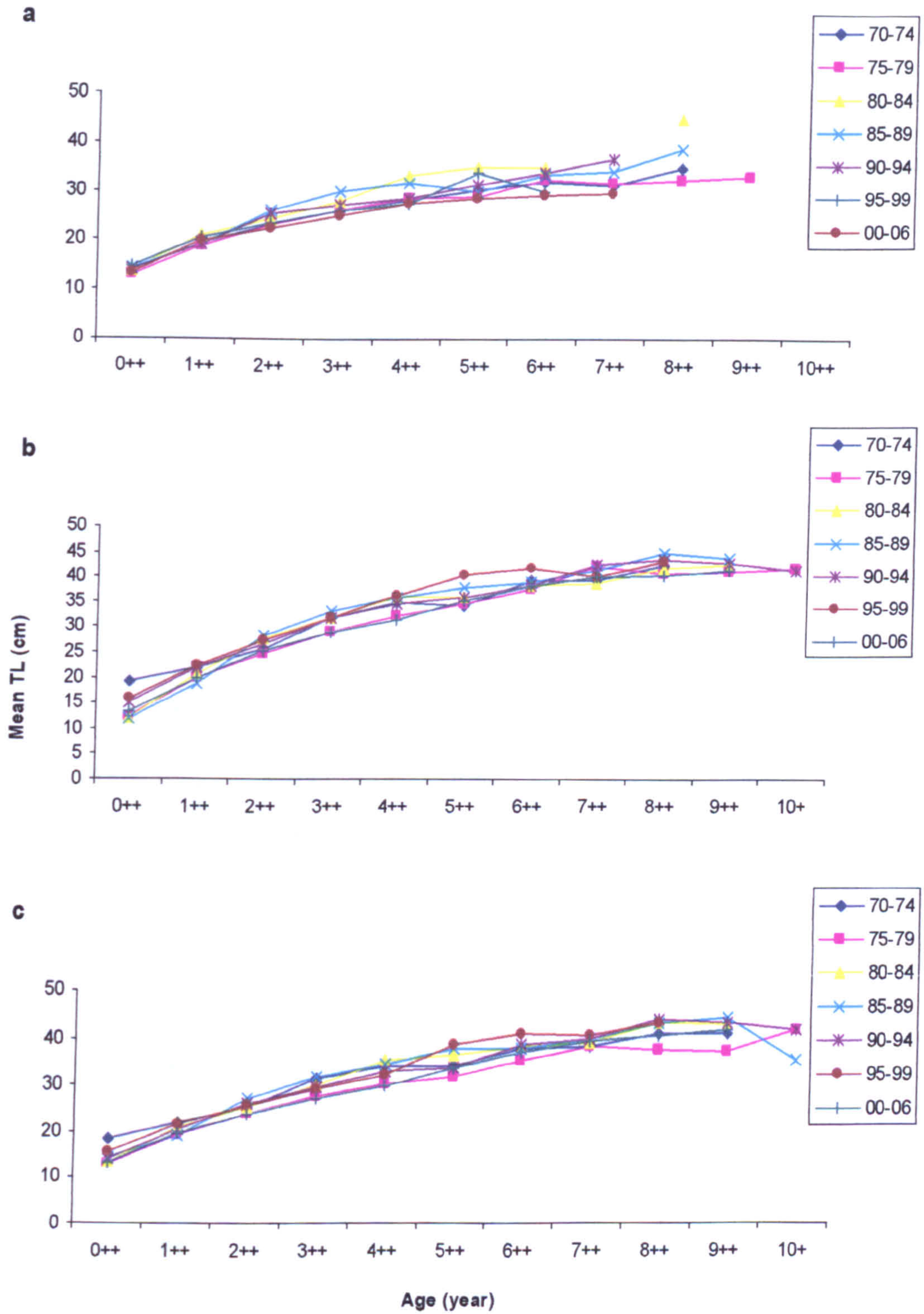


Figure 3.28: Scatter plots of size at age for plaice caught in the October/November fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented (a) male, (b) female and (c) male and females combined divided up into 5 year time periods (1970-1974, 1975-1979 etc) within the 37 year survey.

Table 3.19: Comparisons of von Bertalanffy growth coefficients for the growth curves of male and female plaice caught in the coastal waters of Eastern Anglesey and North West Wales in October/November between 1970 and 2006. Size at age data were grouped into 5 year intervals (1970-1974, 1975-1979, etc) for calculation of the von Bertalanffy growth coefficients. Comparisons were made using the likelihood ratio test (Kimura, 1980). Significant differences ($P < 0.05$) are highlighted in bold with trends ($0.05 < P < 0.10$) underlined.

Time groups	Male			Female		
	L_{∞}	K	t_0	L_{∞}	K	t_0
70-74 vs 75-79	0.396	0.343	0.001	<u>0.069</u>	0.101	0.383
vs 80-84	0.403	0.327	0.340	0.026	0.020	0.144
vs 85-89	0.396	0.348	0.313	0.108	0.015	<u>0.082</u>
vs 90-94	0.498	0.252	0.165	0.013	0.003	<u>0.055</u>
vs 95-99	0.791	0.863	0.603	0.286	<u>0.083</u>	0.152
vs 00-06	0.109	0.029	<u>0.097</u>	0.462	0.689	0.922
75-79 vs 80-84	0.003	0.164	0.475	0.522	0.301	0.740
vs 85-89	0.024	0.212	0.330	0.354	0.527	0.538
vs 90-94	0.014	0.351	0.294	0.543	0.194	0.920
vs 95-99	0.522	0.498	0.009	0.045	0.320	0.346
vs 00-06	0.007	0.016	0.185	0.014	0.271	0.393
80-84 vs 85-89	<0.0001	0.001	0.011	0.313	0.752	0.235
vs 90-94	0.718	0.740	0.292	0.532	0.338	0.689
vs 95-99	<0.0001	0.0005	0.262	0.129	0.399	0.396
vs 00-06	<0.0001	0.003	0.117	0.0001	0.001	0.016
85-89 vs 90-94	0.308	0.410	0.410	0.134	0.277	0.310
vs 95-99	0.532	0.338	0.237	0.671	0.752	0.121
vs 00-06	0.022	<u>0.082</u>	0.235	0.027	0.031	0.021
90-94 vs 95-99	0.269	0.671	0.276	0.029	0.102	0.203
vs 00-06	0.0002	0.013	<u>0.091</u>	<0.0001	<0.0001	0.005
95-99 vs 00-06	<u>0.071</u>	<u>0.071</u>	<u>0.072</u>	<0.0001	0.0001	0.003

Table 3.20: Comparisons of von Bertalanffy growth coefficients for the growth curves of male and female plaice caught in the coastal waters of Eastern Anglesey and North West Wales in October/November between 1970 and 2006. Size at age data were grouped into 5 year intervals (1970-1974, 1975-1979, etc) for calculation of the von Bertalanffy growth coefficients. Comparisons were made using the likelihood ratio test (Kimura, 1980) between the growth curve for each 5 year time period and the overall growth curve, derived from the 37 year data set. Significant differences ($P < 0.05$) are highlighted in bold with trends ($0.05 < P < 0.10$) underlined.

Time groups	Male			Female		
	L_{∞}	K	t_0	L_{∞}	K	t_0
70-74 vs 70-06	0.816	0.317	0.337	0.021	0.011	0.187
75-79 vs 70-06	0.390	0.888	0.708	0.777	0.671	0.842
80-84 vs 70-06	0.351	0.740	0.663	0.423	0.532	0.729
85-89 vs 70-06	0.680	0.480	0.532	0.179	0.554	0.286
90-94 vs 70-06	0.221	0.655	0.708	0.427	0.279	0.284
95-99 vs 70-06	0.842	0.522	0.338	<u>0.072</u>	0.446	0.256
00-06 vs 70-06	0.001	0.037	0.306	<0.0001	0.005	0.128

Table 3.21: A summary of the results (presented in Table 3.19 & 3.20) of the likelihood ratio tests comparing the von Bertalanffy growth curves between different 5 year time periods and between each 5 year time period and the overall growth curve for (a) male and (b) female plaice. The presence of ' L_{∞} ' or 'k' in a cell indicates that this parameter is different between the two time periods being compared.

a) Male

	70-74	75-79	80-84	85-89	90-94	95-99	2000-06
70-74							
75-79	-						
80-84	-	L_{∞}					
85-89	-	L_{∞}	L_{∞}, k				
90-94	-	L_{∞}, k	-	-			
95-99	-	-	L_{∞}, k	-	-		
2000-06	k	L_{∞}, k	L_{∞}, k	L_{∞}	L_{∞}, k	-	
1970-2006	-	-	-	-	-	-	L_{∞}, k

b) Female

	70-74	75-79	80-84	85-89	90-94	95-99	2000-06
70-74							
75-79	-						
80-84	L_{∞}, k	-					
85-89	k	-	-				
90-94	L_{∞}, k	-	-	-			
95-99	-	L_{∞}	-	-	L_{∞}		
2000-06	-	L_{∞}	L_{∞}, k	L_{∞}, k	L_{∞}, k	L_{∞}, k	
1970-2006	L_{∞}, k	-	-	-	-	-	L_{∞}, k

3.3.6 Size and age maturity

The available data for the length and age at 50 % maturity (L_{50} , cm; A_{50} , years) from the 37 year fisheries survey were not as extensive as for the other parameters (size, age and growth). Data for both maturity ogives were missing for both sexes from the early 1990s (1990-1994), which is one of the 5 year time periods considered in the time series analyses. In addition, there were limited L_{50}/A_{50} data for female plaice in the early 1970s as well. Therefore, some comparisons were conducted between decades instead of between 5 year intervals in order to ensure sufficient samples sizes for robust statistical analyses.

During the 37 year survey both male and female plaice showed inter-annual variation in total length at first maturity (L_{50}). For male plaice, L_{50} values ranged from 14.8 to 34 cm TL with an overall median length at first maturity of 23.3 ± 4.4 cm whilst for female plaice L_{50} values ranged from 19.3 to 34.0 cm TL with an overall median total length at first maturity of 24.8 ± 2.8 cm (Figure 3.29a). The L_{50} data for male and female plaice were both normally distributed ($\hat{\sigma}$, $Z = 0.12$, $n = 27$, $P > 0.20$; $\hat{\sigma}$, $Z = 0.08$, $n = 27$, $P > 0.20$) and variances were unequal between sexes (Levene's test, $F = 6.03$, $P = 0.017$). There was no difference in the mean total lengths at 50% maturity (L_{50}) between male and female plaice caught during the 1970-2006 survey (t test, $t = -1.46$, 43.6 df, $P = 0.15$).

A scatter plot of L_{50} values for male and female plaice between 1970 and 2006 are shown in Figure 3.29. For both sexes, L_{50} appears to decline over time although there is no significant correlation for male plaice ($r_s = -0.276$, $P = 0.16$) and a marginally significant correlation for female plaice ($r_s = -0.410$, $P = 0.034$) (Figure 3.29a). However, L_{50} for male and female plaice in 2003 and 2006 appear to be outliers which may be affecting the correlation analysis. When the L_{50} data were grouped by decade, the data for both sexes were normally distributed ($\hat{\sigma}$, $Z = 0.12$, $n = 27$, $P > 0.20$; $\hat{\sigma}$, $Z = 0.08$, $n = 27$, $P > 0.20$) with males exhibiting equal variances between time periods ($W_{3,23} = 0.67$, $P = 0.58$) but females showing unequal variances ($W_{3,23} = 6.04$, $P = 0.003$). There were no differences over time in L_{50} for male fish (ANOVA, $F_{(3,23)} = 0.77$, $P = 0.52$; 1970s = 25.3 ± 4.2 cm, 1980s = 22.0 ± 3.9 cm, 1990s = 23.4 ± 4.6 cm, 2000s = 22.5 ± 5.2 cm) but a significant difference for female fish (Kruskal Wallis, $\chi^2 = 8.10$, 3 df, $P = 0.044$). Pairwise comparisons between the decadal L_{50} values for female plaice using Wilcoxon's signed rank test showed that

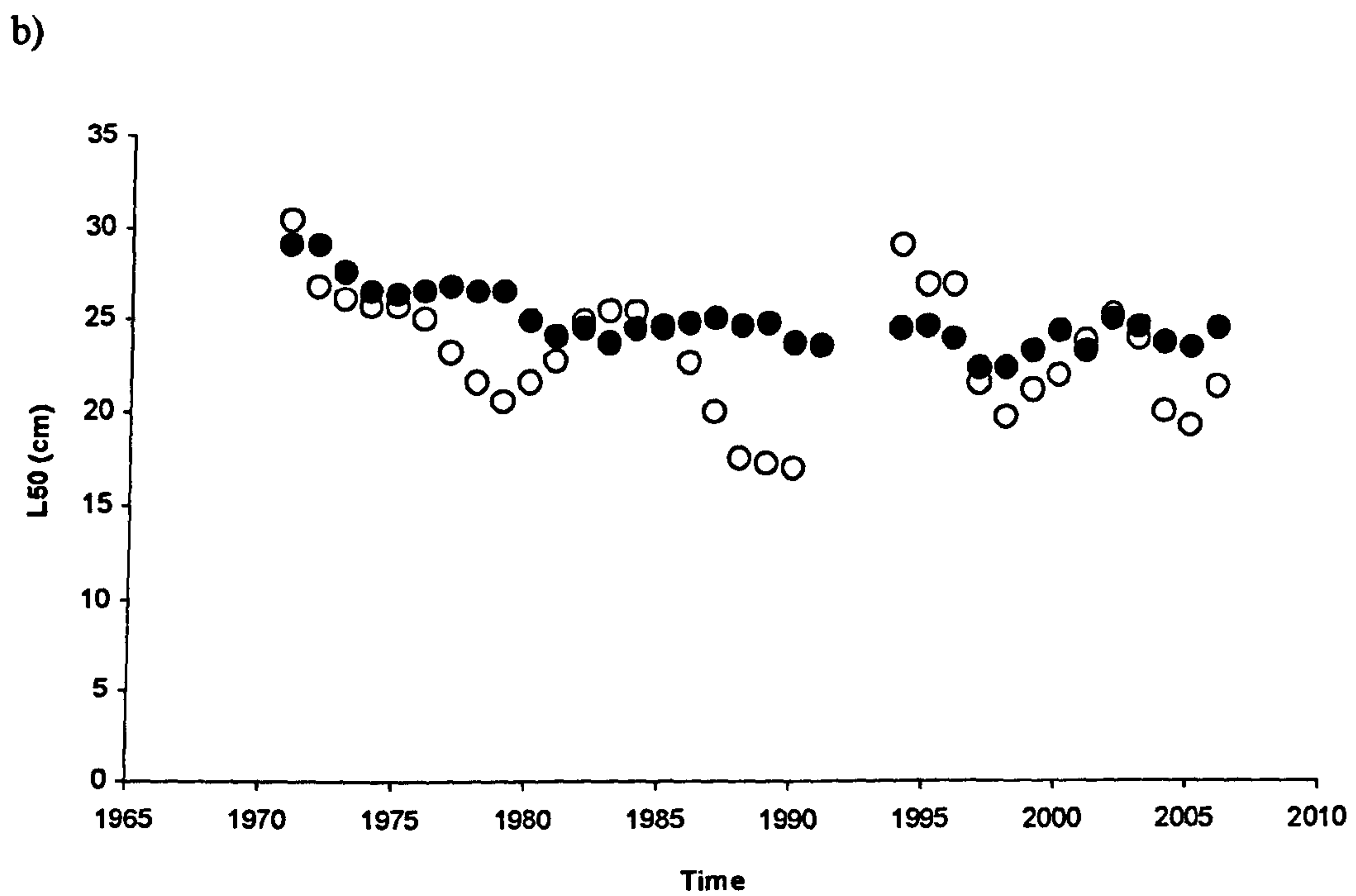
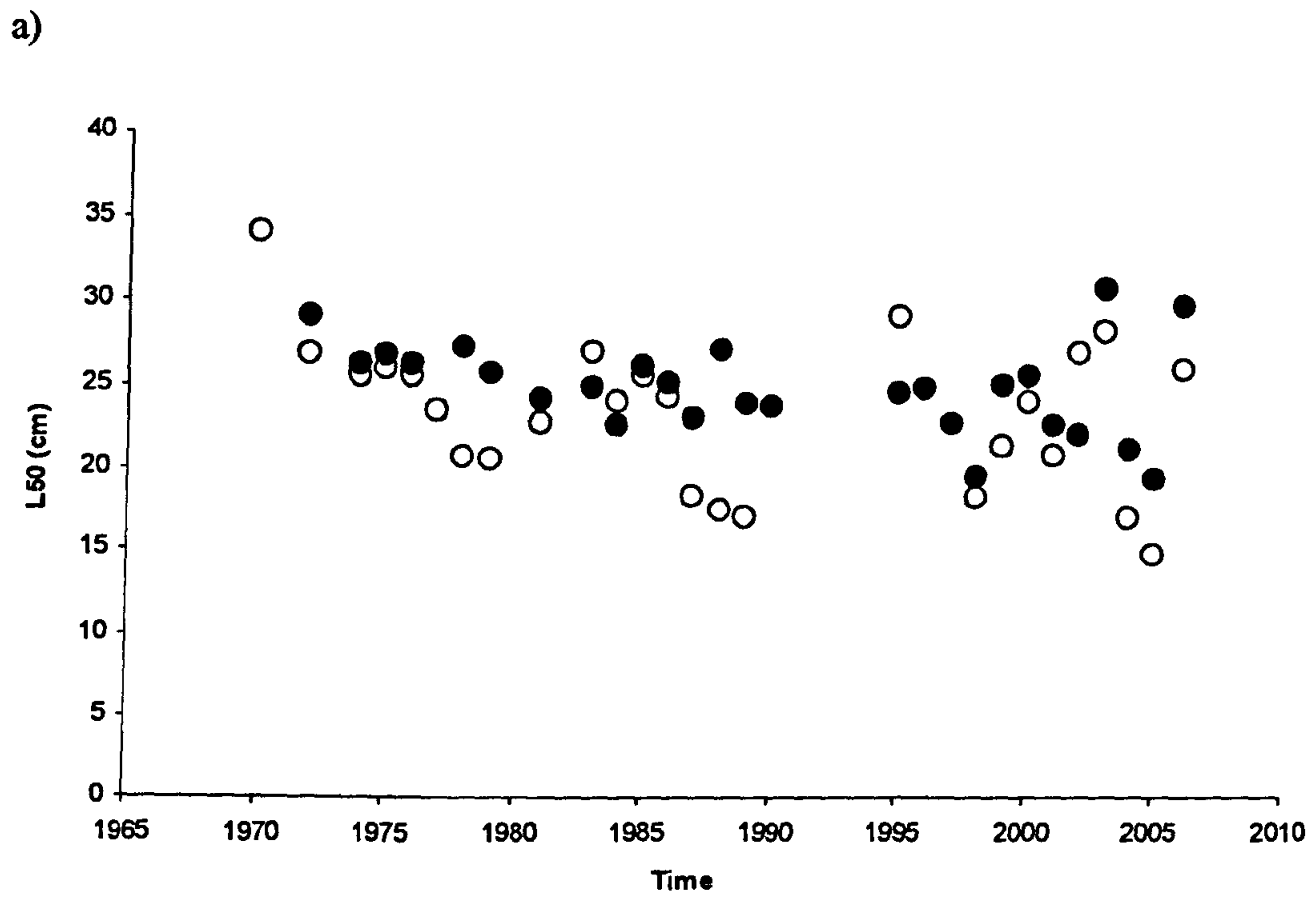


Figure 3.29: Total length at first maturity (L_{50} , cm) for male (open circle) and female (solid circle) plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the L_{50} values for any given year plus the values for the year before and the year after.

length at first maturity was significantly larger in the 1970s (26.9 ± 1.2 cm) comparisons compared to the 1980s (24.6 ± 1.5 cm, $P = 0.046$) and 1990s (23.4 ± 2.1 cm, $P = 0.028$) with no differences between all other pairwise comparisons ($P = 0.12$ to 1.00 ; L_{50} for 2000s = 24.4 ± 4.4 cm).

In order to reduce the influence of inter-annual variability and the presence of outlying points on the analysis of time series data, the male and female L_{50} data were 'smoothed' using a 3 year running average. A scatter plot of the smoothed L_{50} values for male and female plaice between 1970 and 2006 are shown in Figure 3.29b. For both sexes, L_{50} was significantly negatively correlated with time (♂ , $r_s = -0.425$, $P = 0.014$; ♀ , $r_s = -0.704$, $P = 0.001$) indicating a significant decrease in smoothed L_{50} over time. When the smoothed data were grouped together into 5 year intervals (1970-1974, 1975-1979 etc, but excluding 1990-1994 where $n=2$), the data for male plaice was normally distributed ($Z = 0.10$, $n = 31$, $P > 0.20$) and with equal variances between time periods ($W_{5,25} = 1.60$, $P = 0.20$) allowing the use of ANOVA. When the female smoothed L_{50} data were grouped together into 5 year intervals (1970-1974, 1975-1979 etc), the data were not normally distributed ($Z = 0.20$, $n = 34$, $P = 0.001$) and with unequal variances between time periods ($W_{6,27} = 5.90$, $P < 0.001$) precluding the use of ANOVA. There were significant differences in smoothed L_{50} values between time intervals for both male (ANOVA, $F_{(5,25)} = 3.56$, $P = 0.014$) and female (Kruskal Wallis, $\chi^2 = 24.37$, 6 df, $P < 0.001$) plaice (Figure 3.29b; Table 3.22). When the smoothed L_{50} values for males in each time period were compared using Scheffe's multiple comparison test, the only significant difference observed was between 1970-74 and 1985-1989 (Table 3.22). When the smoothed L_{50} values for females in each time period were compared using Wilcoxon's Signed Rank test, the lengths at first maturity in the 1970s (*i.e.* 1970-74 and 1975-1979) tended to be larger than in subsequent time periods and the L_{50} value for 1995-1999 was significantly smaller than in the 1970s and 1980s (Table 3.22). Thus, the analyses of the smoothed L_{50} values have shown there has been a greater change in the length at first maturity for female compared to male plaice between 1970 and 2006.

Table 3.22 (a) Smoothed total length at first maturity L_{50} (cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as mean values \pm SD for males and median values \pm interquartile range for females. Smoothed average values calculated as a three years running average. Significant values for the post-hoc comparisons of smoothed average age using (b) Scheffe's multiple comparison test for male and (c) Wilcoxon's Signed Rank test for females. Significant differences at the 5% level are highlighted in bold and trends ($0.10 < P < 0.05$) are underlined.

a)

	Male smoothed L_{50}	Female smoothed L_{50}
1970-1974	25.8 \pm 2.1	28.3 \pm 2.3
1975-1979	20.6 \pm 2.2	26.5 \pm 0.2
1980-1984	24.1 \pm 1.7	24.5 \pm 0.8
1985-1989	20.4 \pm 3.2	24.7 \pm 0.8
1990-1994	-	24.5 \pm 1.0
1995-1999	23.3 \pm 3.4	23.3 \pm 2.0
2000-2006	22.3 \pm 2.3	24.4 \pm 1.2

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1995-1999
1970-1974					
1975-1979	0.372				
1980-1984	0.627	0.998			
1985-1989	0.022	0.691	0.417		
1995-1999	0.387	1.000	0.998	0.674	
2000-2006	0.120	0.995	0.914	0.993	0.993

c)

	1970-1974	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1970-1974						
1975-1979	<u>0.068</u>					
1980-1984	<u>0.068</u>	0.043				
1985-1989	<u>0.068</u>	0.043	0.500			
1990-1994	0.109	0.109	1.000	0.285		
1995-1999	<u>0.068</u>	0.043	0.043	0.043	0.593	
2000-2006	<u>0.068</u>	0.043	0.686	0.500	1.000	0.345

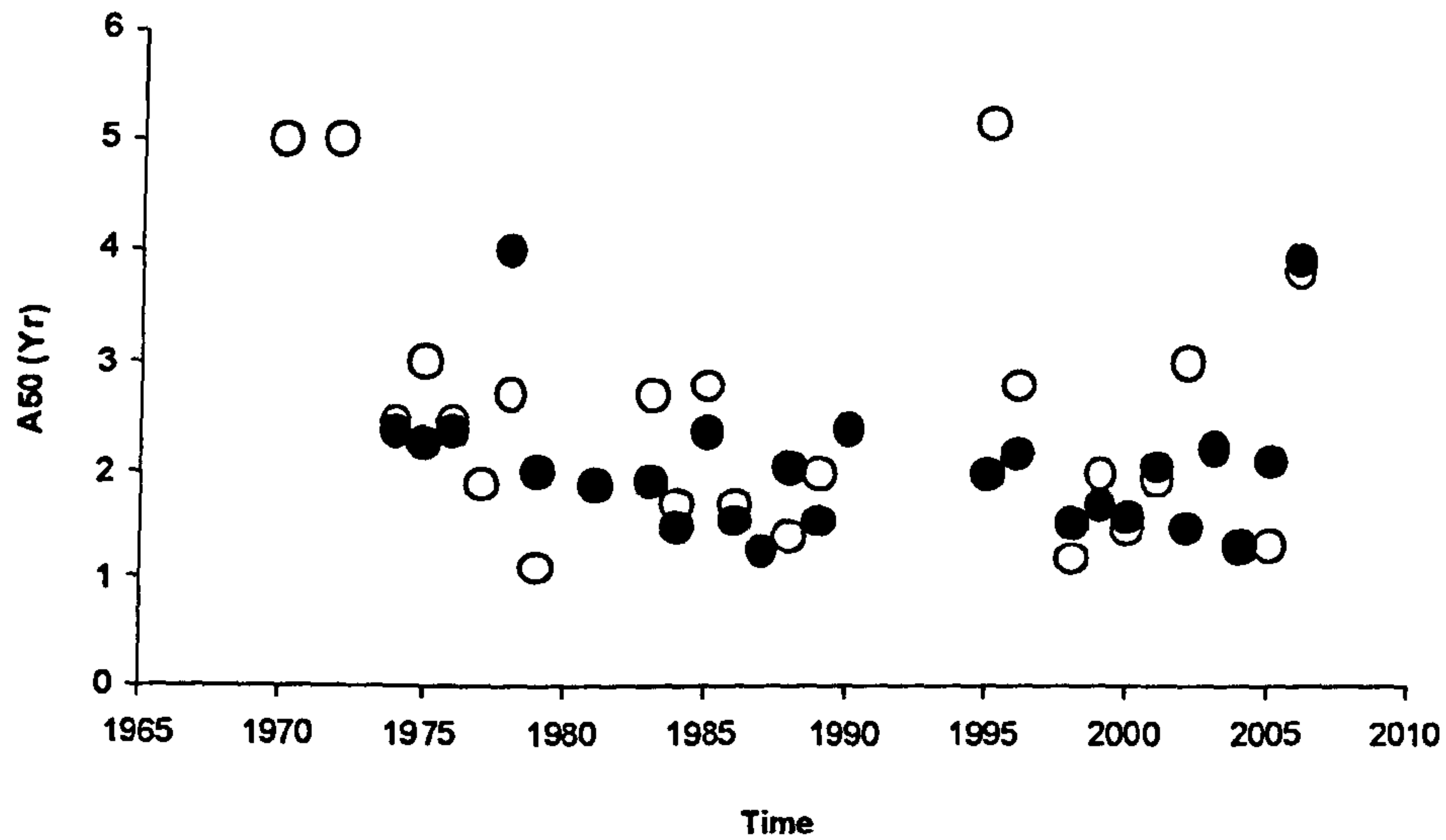
During the 37 year survey, both male and female plaice showed inter-annual variation in age at first maturity (A_{50}). For male plaice, A_{50} values ranged from 1.2 to 5.0 years old with an overall median age at first maturity of 2.1 ± 1.2 (IQ range) years whilst for female plaice A_{50} values ranged from 1.3 to 4.0 years old with an overall median age at first maturity of 2.0 ± 0.8 years (Figure 3.30). The A_{50} data for male plaice was just normally distributed ($Z = 0.17$, $n = 26$, $P = 0.051$) whilst the data for females was not normally distributed ($Z = 0.23$, $n = 23$, $P < 0.003$) and both sexes exhibited equal variances (Levene's test, $F = 5.71$, $P = 0.021$). There was no difference in the median age at 50% maturity (A_{50}) of male and female plaice caught during the 1970-2006 survey (Mann Whitney test, $U = 271.5$, $n = 51$, $P = 0.31$).

A scatter plot of the A_{50} values for male and female plaice between 1970 and 2006 are shown in Figure 3.30a. For both sexes, there was no correlation between time (year) and A_{50} for either male plaice ($r_s = -0.271$, $P = 0.18$) or female plaice ($r_s = -0.218$, $P = 0.30$). When the A_{50} data were grouped into 5 year time periods (excluding 1990-1994 for males and excluding 1970-1974 and 1990-1994 for females, due to small sample sizes or missing data), the data for males were normally distributed ($Z = 0.17$, $n = 26$, $P = 0.051$) and not normally distributed for females ($Z = 0.23$, $n = 23$, $P < 0.003$) but both sexes exhibited equal variances between time periods (σ , $W_{5,20} = 1.37$, $P = 0.28$; σ , $W_{4,18} = 0.93$, $P = 0.47$) allowing the use of ANOVA.

Table 3.23. Age at first maturity (A_{50} , years) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for 5 year intervals within the period 1970-2006. Data are presented as mean values \pm SD.

	Male A_{50}	Female A_{50}
1970-1974	4.2 ± 1.5	---
1975-1979	2.2 ± 0.8	2.7 ± 0.9
1980-1984	2.1 ± 0.5	1.8 ± 0.2
1985-1989	2.0 ± 0.6	1.8 ± 0.4
1995-1999	2.8 ± 1.7	1.9 ± 0.3
2000-2006	2.2 ± 1.0	2.1 ± 0.9

a)



b)

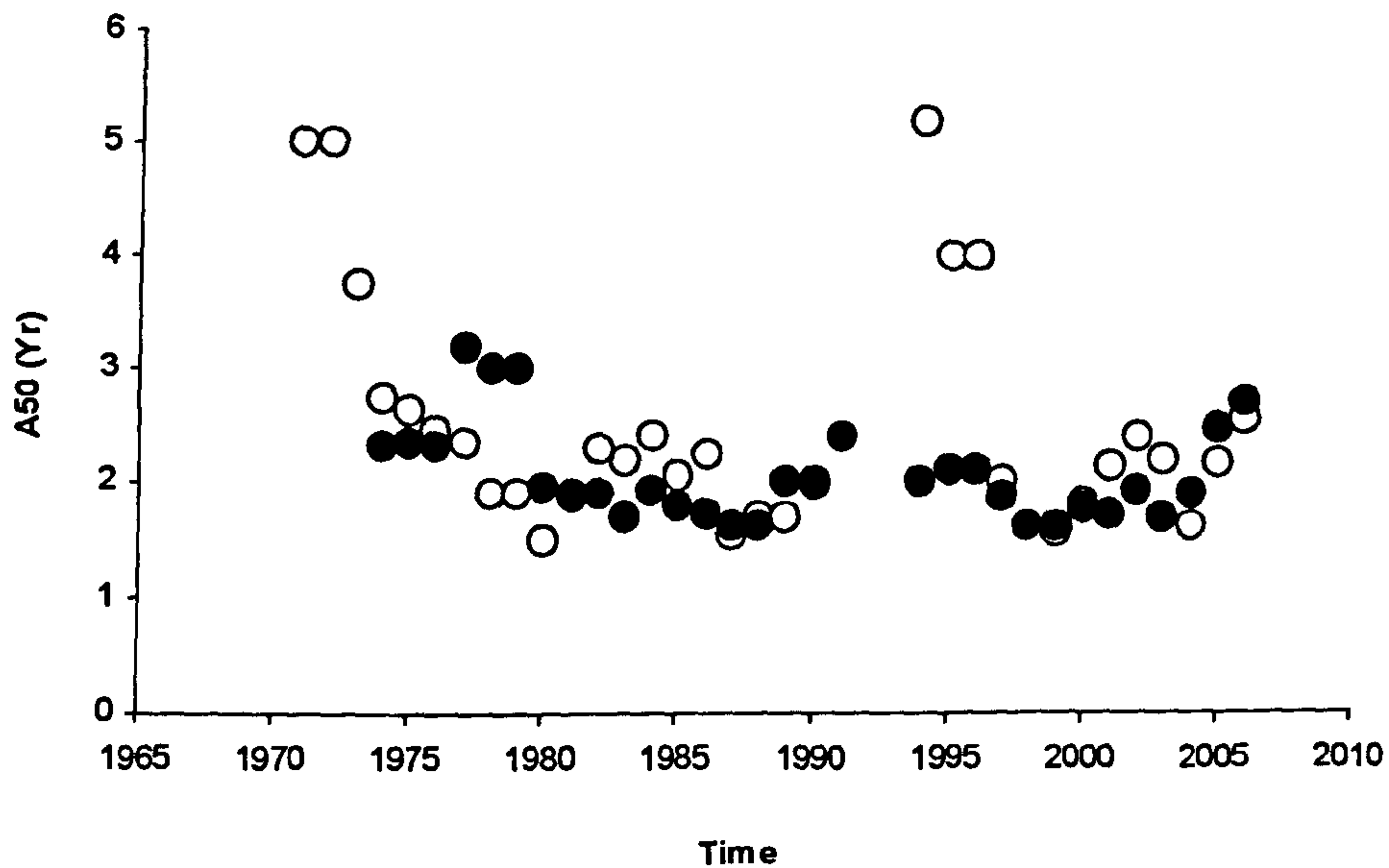


Figure 3.30: Age at first maturity (A_{50} , years) for male (open circle) and female (solid circle) plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. (a) raw data for each year. (b) Three year moving average where the annual average value for a given year is calculated as the average of the A_{50} value for any given year plus the values for the year before and the year after.

There were no differences over time in A_{50} for either male fish (ANOVA, $F_{(5,20)} = 2.00$, $P = 0.12$) or female fish (ANOVA, $F_{(4,18)} = 1.28$, $P = 0.32$) (Table 3.23).

In order to reduce the influence of inter-annual variability and the presence of outlying points on the analysis of time series data, the male and female A_{50} data were 'smoothed' using a 3 year running average. A scatterplot of the smoothed A_{50} values for male and female plaice between 1970 and 2006 are shown in Figure 3.30b. For both sexes, there was no significant correlation with time although a downward trend in A_{50} was evident for both sexes (σ , $r_s = -0.311$, $P = 0.079$; φ , $r_s = -0.310$, $P = 0.089$). When the smoothed data were grouped together into 5 year intervals (excluding 1990-1994 for males and 1970-1974 for female plaice), the data for both sexes were not normally distributed (σ , $Z = 0.25$, $n = 33$, $P < 0.001$; φ , $Z = 0.21$, $n = 31$, $P = 0.002$) and both exhibited unequal variances between time periods (σ , $W_{5,25} = 13.78$, $P < 0.001$; φ , $W_{5,24} = 4.07$, $P = 0.002$) necessitating the use of the Kruskal Wallis test. There were significant differences in smoothed A_{50} values between time intervals for both male ($\chi^2 = 11.00$, 5 df, $P = 0.051$) and female ($\chi^2 = 13.62$, 5 df, $P = 0.02$) plaice (Figure 3.31; Table 3.24a). When the smoothed A_{50} values for males in each time period were compared using Wilcoxon's Signed Rank test, the only significant difference observed was between 1975-79 and 1985-1989 but the A_{50} values for 1970-1974 tended to be different from subsequent time periods (Table 3.24b). When the smoothed A_{50} values for females in each time period were compared using Wilcoxon's Signed Rank test, the A_{50} values for 1975-1979 tended to be significantly older than subsequent time periods (Table 3.24c).

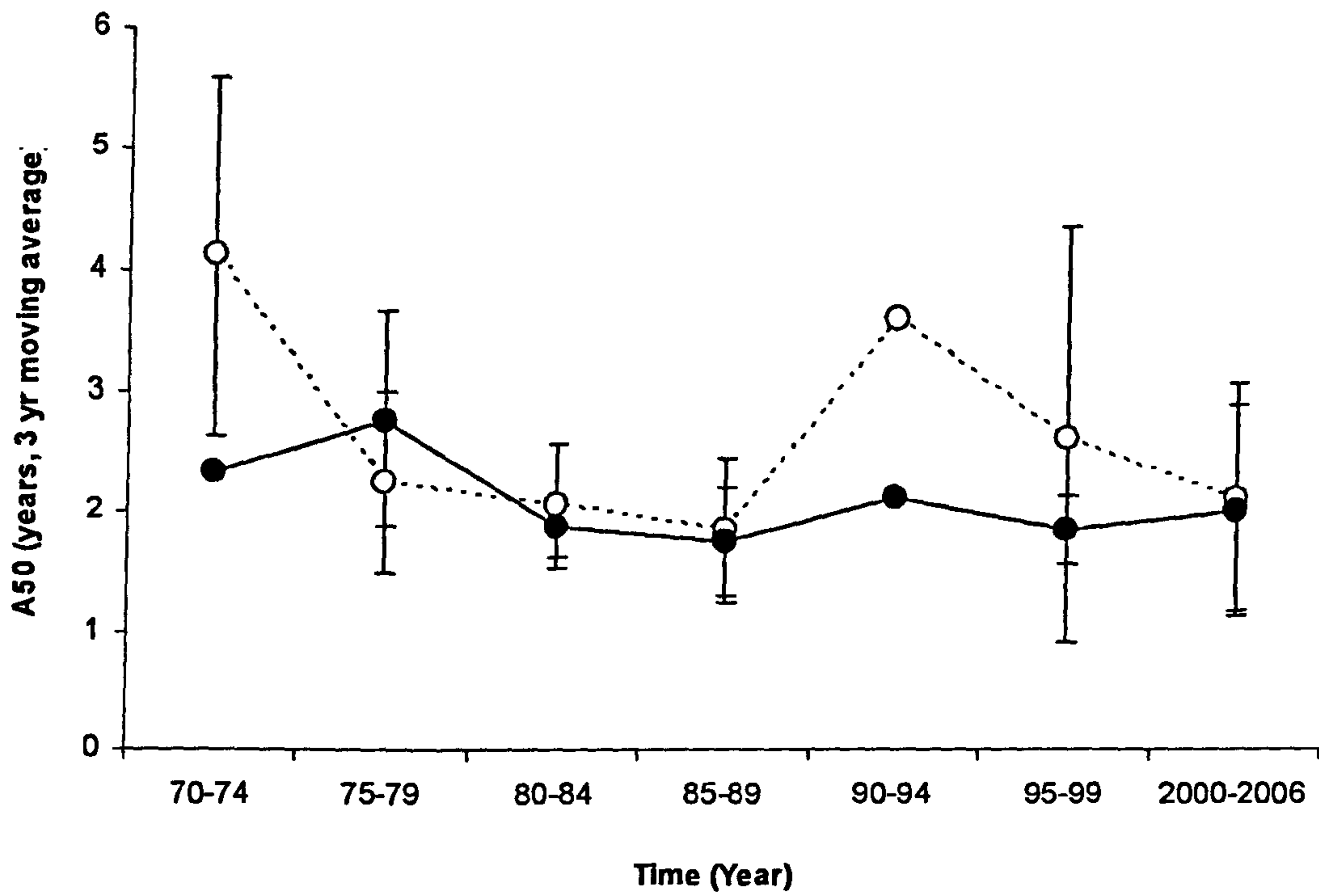


Fig 3.31: Smoothed average age at first maturity (A_{50} , years) for male (solid circle) and female (open circle) plaice caught in the autumn fisheries surveys in the inshore waters of Eastern Anglesey and Northwest Wales between 1970 and 2006. Data are presented as median values \pm interquartile range except for male 1970-1974 and male and female 1990-1994 where single data points are presented. Smoothed A_{50} values for each year were calculated as a three year running average and mean values are for 5 year time periods (1970-1974, 1975-1979 etc).

Table 3.24 (a) Smoothed age at first maturity (A_{50} , years) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* in the 5 year intervals for the period 1970-2006. Data are presented as median values \pm interquartile ranges. Smoothed average values calculated as a three years running average. Significant values for the post-hoc comparisons of smoothed median age using Wilcoxon's Signed Rank test for (b) males and (c) females. Significant differences at the 5% level are highlighted in bold and trends ($0.10 < P < 0.05$) are underlined.

a)

	Male smoothed A_{50}	Female smoothed A_{50}
1970-1974	4.4 \pm 2.0	---
1975-1979	2.4 \pm 0.6	3.0 \pm 0.8
1980-1984	2.2 \pm 0.7	1.9 \pm 0.2
1985-1989	1.7 \pm 0.5	1.7 \pm 0.3
1990-1994	---	2.0 \pm 0.4
1995-1999	2.0 \pm 2.4	1.9 \pm 0.5
2000-2006	2.2 \pm 0.6	1.9 \pm 0.8

b)

	1970-1974	1975-1979	1980-1984	1985-1989	1995-1999
1970-1974					
1975-1979	<u>0.068</u>				
1980-1984	<u>0.068</u>	0.500			
1985-1989	<u>0.068</u>	0.042	0.345		
1995-1999	<u>0.066</u>	0.686	0.686	0.225	
2000-2006	<u>0.068</u>	0.345	0.686	0.686	0.686

c)

	1975-1979	1980-1984	1985-1989	1990-1994	1995-1999
1975-1979					
1980-1984	0.043				
1985-1989	0.043	0.138			
1990-1994	0.285	0.109	0.285		
1995-1999	0.043	0.893	0.686	0.285	
2000-2006	0.043	0.138	0.893	0.109	0.686

3.4 Discussion

3.4.1 Comparing the long-term population dynamics of plaice, dab and whiting in the coastal waters of NW Wales and E Anglesey.

As stated earlier, the RV *Prince Madog* fisheries surveys have been conducted by the School of Ocean Sciences since the early 1970s and the population biology of a range of fish species have been studied including plaice (Basimi, 1978; Basimi and Grove 1985b and c; Chuenpagdee, 1990; Seyhan, 1990), dab (Bakhsh, 1982; Seisay, 2001), flounder *Platichthys flesus* (Nitibhon, 1991), red gumard (Marriott *et al.*, 2009) and whiting (Seyhan, 1994; Preston, 2007). Detailed, long-term survey data are available for three demersal fish species – dab, plaice and whiting – that vary in the degree to which they have been exploited by commercial demersal fisheries in the Irish Sea. Dab are not commercially exploited, although they do feature as significant bycatch in the Irish Sea demersal fisheries (Enever *et al.*, 2007). The population biology of dab in the inshore waters of NW Wales and E Anglesey has been studied in detail (Bakhsh, 1982; Seisay, 2001). Analysis of the long-term survey database for dab by Seisay (2001) has shown that the local dab population has remained relatively stable over time since the 1970s. In contrast, whiting have been overexploited in the Irish Sea with catches declining since the 1990s (ICES, 2008a). Whiting in the Irish Sea have been targeted by semi-pelagic trawlers and otter trawlers but also comprise a substantial component of the bycatch taken in the *Nephrops* fishery (ICES, 2008a). Discard estimates for fleets targeting *Nephrops* are incomplete and imprecise, but are considered substantial (estimated at between 2-4000 t per year in the 1990s). ICES are continuing to try to reduce bycatch in this fishery through gear modifications (*e.g.* increased codend and square-mesh panel mesh sizes, separator panels, and fixed grids) with the aim of substantially reducing bycatch and discarding of whiting in the *Nephrops* fishery (ICES, 2008a). Although stock status reports following the standard ICES format were presented for whiting in ICES division VIIa until 2003 (Figure 3.32), more recently ICES have concluded that there are insufficient data to present a reliable stock assessment and have concluded “on the basis of the stock status, ICES advises that catches of whiting [...] should be the lowest possible” (ICES, 2008a). The ICES whiting stock status report in 2003 indicated that official “landings” (as reported to ICES) had declined dramatically between 1980 and 2002 (Figure 3.32a). Fishing

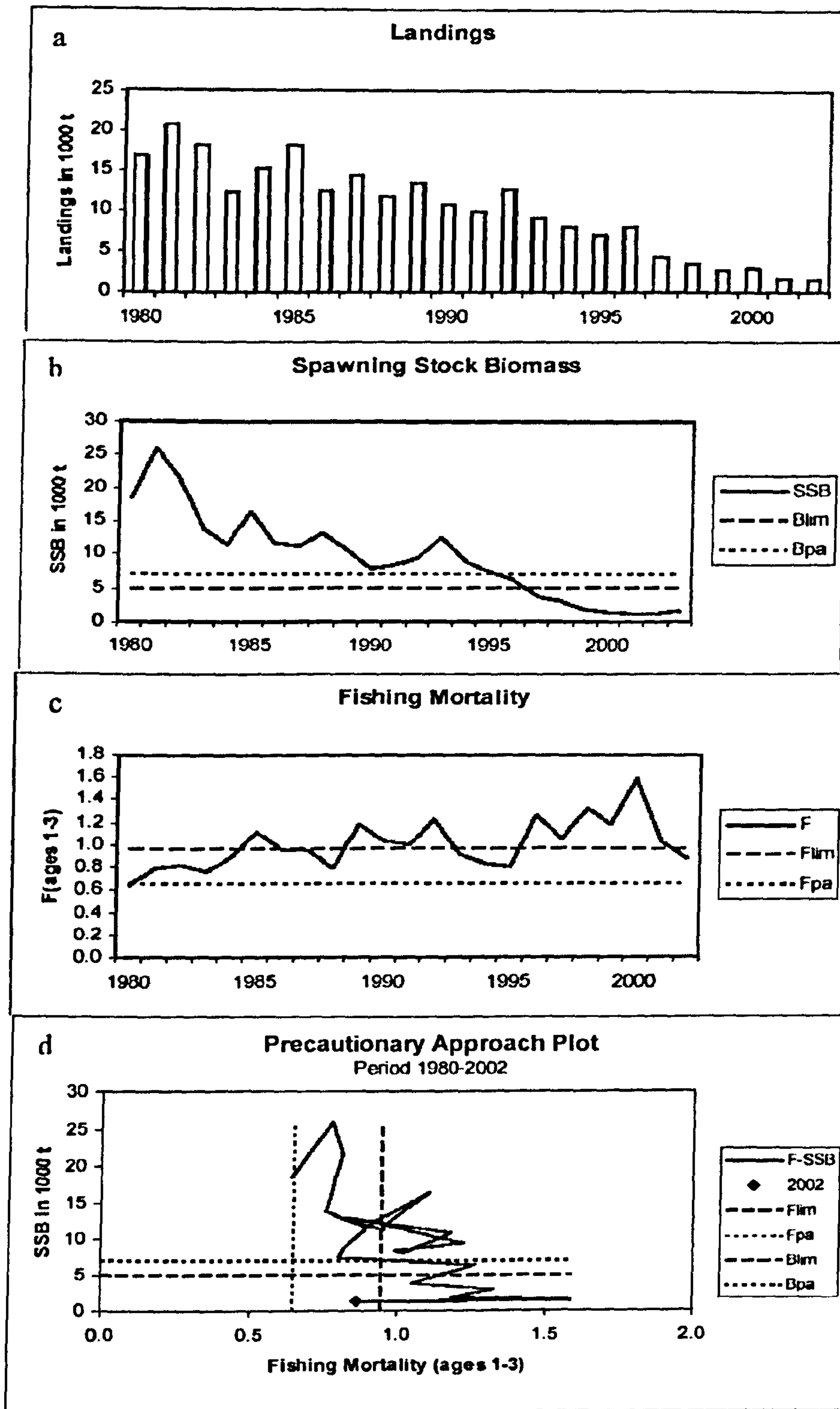


Figure 3.32: ICES stock status summary for whiting *M. merlangus* in ICES division VIIa (Irish Sea) in 2003. Data are presented for landings (tonnes), Spawning Stock Biomass (tonnes), Fishing mortality (year^{-1}) and the precautionary approach plot for the time period 1980-2002. B_{pa} and F_{pa} values are 7000t and 0.65 y^{-1} and B_{lim} and F_{lim} values are 5000t and 0.95 y^{-1} respectively. Data copied from ICES, 2008a.

pressure was at, or had exceeded, the maximum fishing pressure (F_{lim}) since 1985 (Figure 3.32b) resulting in a 10 fold decline in estimated spawning stock biomass (Figure 3.32c). The precautionary approach plot (Beddington *et al.*, 2007) for Irish Sea whiting for the period 1980-2002, presented in Figure 3.32d, shows that the fishery had entered the “overfishing quadrant” by 1985 and the overfished/overfishing quadrant (the worst possible state for a fishery to be in according to Beddington *et al.*, 2007) in 1996. However, ICES recognises that stock assessment of the Irish Sea whiting is hampered by several problems; a lack of knowledge of the basic biology of the stock, misreporting of landings and a lack of accurate quantification of whiting taken as bycatch in other demersal fisheries, especially the *Nephrops* fishery (ICES, 2008a). As a result, it has not produced detailed stock status summaries for Irish Sea whiting since 2002. The current recommendation by ICES (since 2007) is for there to be no catch and discard of whiting in region VIIa (ICES, 2008a). Since 2000, landings of whiting have been minimal (< 1000t per year), however, accurate discard data from the *Nephrops* are not available and so the current stock status is still unknown.

The status of the plaice stocks in the Irish Sea have been discussed in detail in Chapter 2 but are briefly summarised here. Plaice are targeted by beam and otter trawlers as part of a mixed fishery in the Irish Sea which is mainly focussed in the eastern Irish Sea (Dunn and Pawson, 2002; ICES, 2008a). Fishing pressure was highest in the 1970s and 1980s when it was at, or exceeded the F_{lim} value predicted by ICES (Figure 3.33) and correspondingly, the spawning stock biomass remained low during this period (Figure 3.33). During this time period, the fishery was located in the overfishing quadrant (Beddington *et al.*, 2007) in the precautionary approach plot (see Figure 3.34). However, fishing pressure has declined since the early 1990s and the spawning stock biomass has increased since the late 1990s and the stock is now considered to be harvested sustainably and at full reproductive capacity (ICES, 2008a).

Thus, the three demersal species offer three contrasting fishing histories of continued overexploitation (whiting), heavy fishing followed by underexploitation (plaice) and non-exploitation (dab). The long-term survey data from the RV *Prince Madog* fishing surveys will be examined to see whether these different fishing histories are reflected in changes in the population biology of the three species.

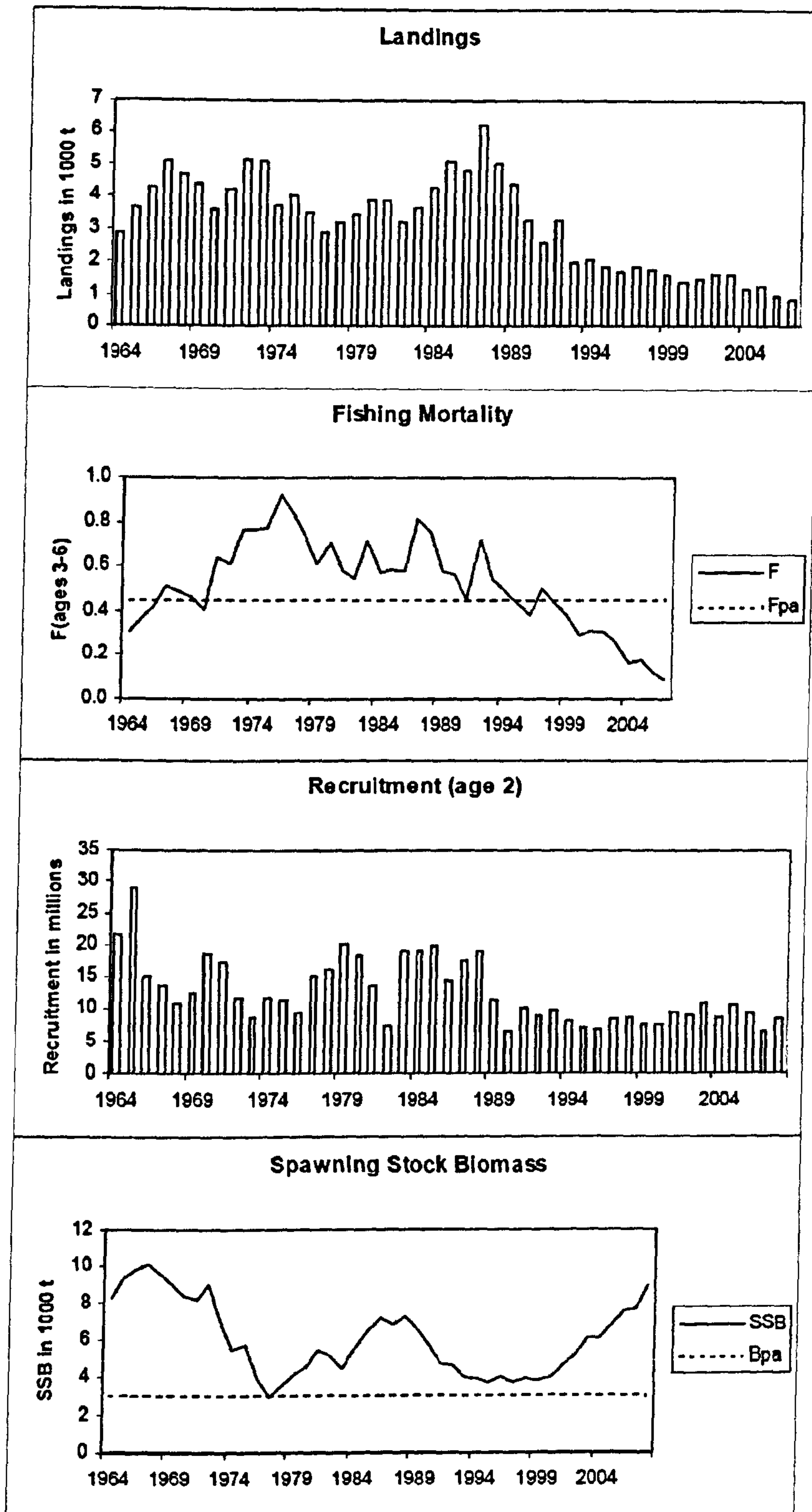


Figure 3.33: Landings (tonnes), fishing mortality (F , year⁻¹), recruitment (millions of fish) and spawning stock biomass (tonnes) for plaice *P. platessa* in the Irish Sea between 1964 and 2007 (copied from ICES, 2008a).

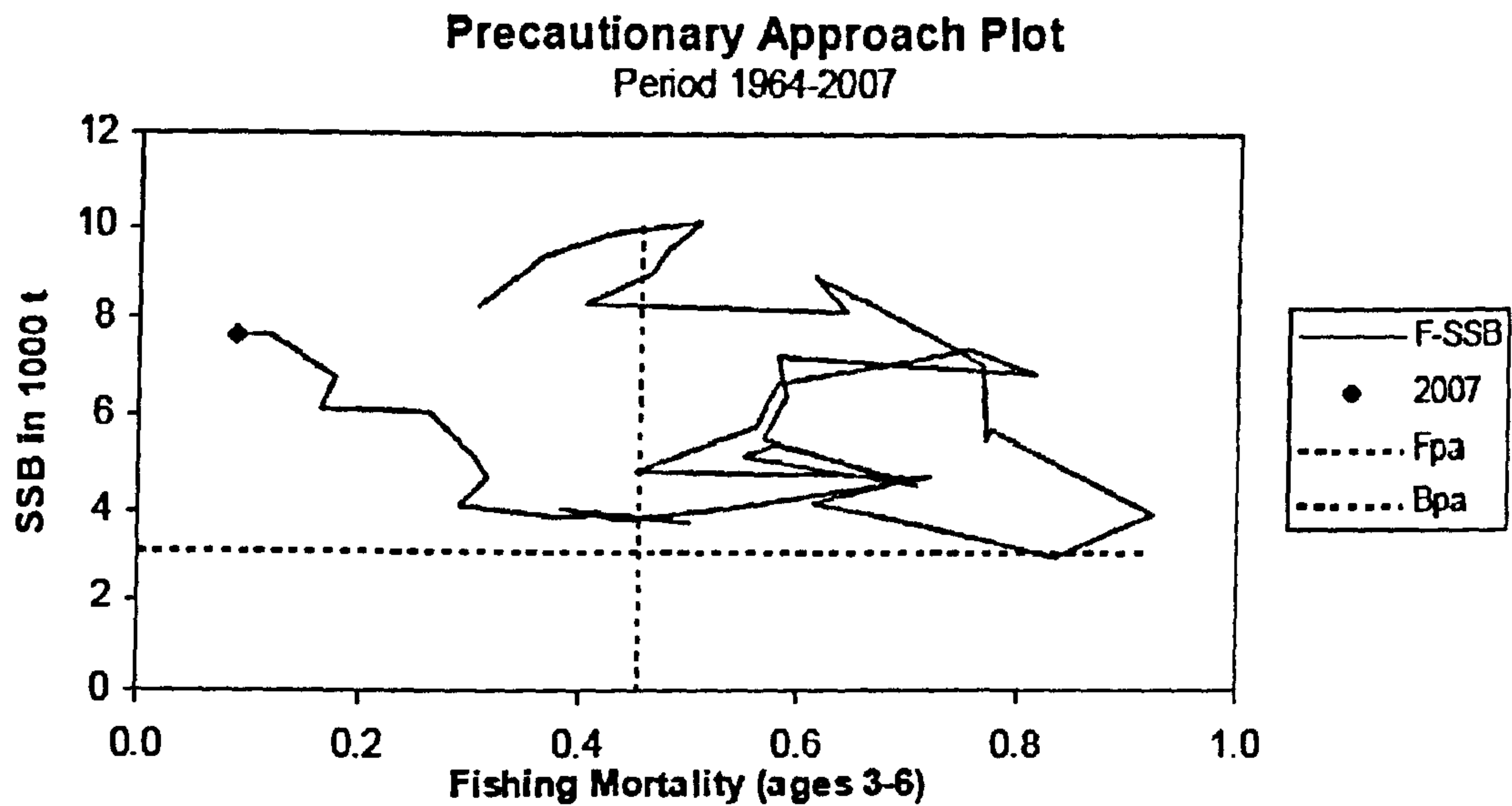


Figure 3.34: ICES precautionary approach plot for, plaice *P. platessa* in the Irish Sea between 1964 and 2007. F_{pa} (0.45 y^{-1}) and B_{pa} (3100 t) are overlain on the plot for comparison. (Copied from ICES, 2008a),

The percentage length frequency distributions for the three species are presented in Figures 3.35 (dab), 3.36 (whiting) and 3.37 (plaice). The data for dab for the time period 1966-2000 are taken from Seisay (2001) and the data for 2001-2007 are taken from recent MSc fisheries data (McCarthy, unpublished), spanning a 40 year time period in total (Figure 3.35). The length frequency data for whiting are taken from Preston (2007) and span a 30 year time period, 1976-2006. In her data analysis, Preston grouped the data into 5 year intervals (Figure 3.36). The length frequency data for plaice span a 36 year time period 1970-2006 (Figure 3.37). Given that the raw size data are not available for dab and whiting, comparisons of the size frequency distributions over time for the three species are limited to being descriptive only rather than involving quantitative statistical analysis.

Figure 3.35 shows that dab ranged in size between 10 and 30 cm total length size with a modal total length of around 20 cm. Although dab discards in the Irish Sea fisheries appears to be high for all the fishing gears used (*i.e.* beam trawl, otter trawl and other gears) (Enever *et al.*, 2007), there is no evidence from the RV *Prince Madog* fisheries surveys that dab size has changed over time. This may be due to much lower levels of fishing pressure on dab in NW Wales coastal waters compared

to other areas of the Eastern Irish Sea, *e.g.* Liverpool Bay and off the Cumbrian coast, where fishing pressure is higher (Dunn and Pawson, 2002). The degree of genetic differentiation and connectivity between dab found in different areas of the Irish Sea is not known and is the focus of current research activity at Bangor University (Tysklind *et al.*, 2009a and b). The adult dab found in the inshore waters along the NW Wales coastline are thought to be derived from fish spawned on the same offshore spawning grounds off the Great Orme as plaice (Macer, 1972) and to utilise nursery areas such as Red Wharf Bay (Macer, 1967; Carter *et al.*, 1991). The adults move offshore into deeper water but are thought to remain in the same coastal waters as the juveniles (Seisay, 2001). Therefore, given the lack of commercial fishing activity for demersal fishes along the NW Wales coastline, it is not surprising that the size frequency distributions of adult dab over the last 5 decades have been similar (Figure 3.35). The size data for 2001-2007 (Figure 3.35b) extend the data set collated by Seisay (2001) for 1966-2000 (Figure 3.35a) but the same size-frequency patterns are evident. Seisay (2001) noted that in some years there appeared to be stronger recruitment indicated by the appearance of a strong mode at 10-15 cm total length, *e.g.* 1994 and 2000 (Figure 3.35a). This is also supported by the size frequency distribution observed in 2001 (Figure 3.35b).

In contrast to dab, the size frequency distributions for whiting over the last 30 years has shown a shift towards a smaller modal size from 30 cm in 1975-1979 to 25 cm in 2006-2007 (Figure 3.36). As discussed earlier, whiting have been subject to heavy directed and indirect fishing activities in the Irish Sea and the average total length for male and female whiting caught in the RV *Prince Madog* fisheries surveys has declined from *ca.* 29 and 31 to 20 cm and 24 cm respectively (Preston, 2007). Although larval and small juvenile whiting can be found in inshore coastal waters during the spring and summer spawning period (Parker-Humphreys 2004a), many juveniles are carried offshore into deeper water by the Irish Sea gyre (Conway *et al.*, 1997) and can be found in large numbers in the central western Irish Sea in June (Dickey-Collas *et al.*, 1997). In addition, adult whiting are known to undertake seasonal migrations from inshore coastal waters in the spring into deeper offshore water in the summer before returning inshore in the late autumn (McCarthy pers. obs.). Thus, at two critical stages of the lifecycle, whiting which may have spawned in the inshore coastal waters of NW Wales (the exact spawning

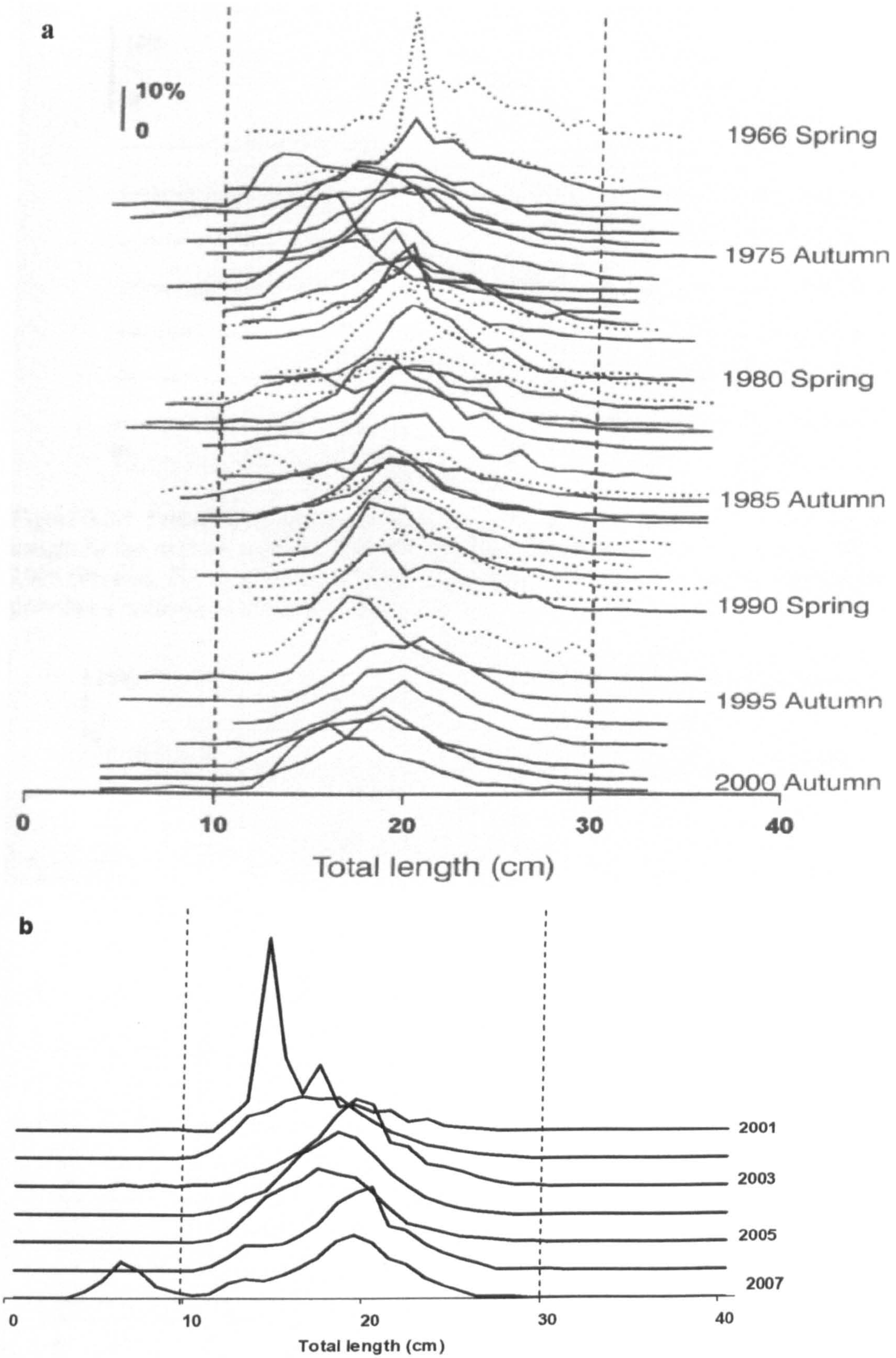


Figure 3.35: Percentage total length frequency distributions for dab *L. limanda* caught in the inshore waters of NW Wales and E Anglesey for the time period 1966-2007. (a) Data for 1966-2000 (copied from Seisay, 2001) and (b) Data for 2001-2007 (McCarthy, unpubl.). The vertical bar provides a scale for abundance (10%).

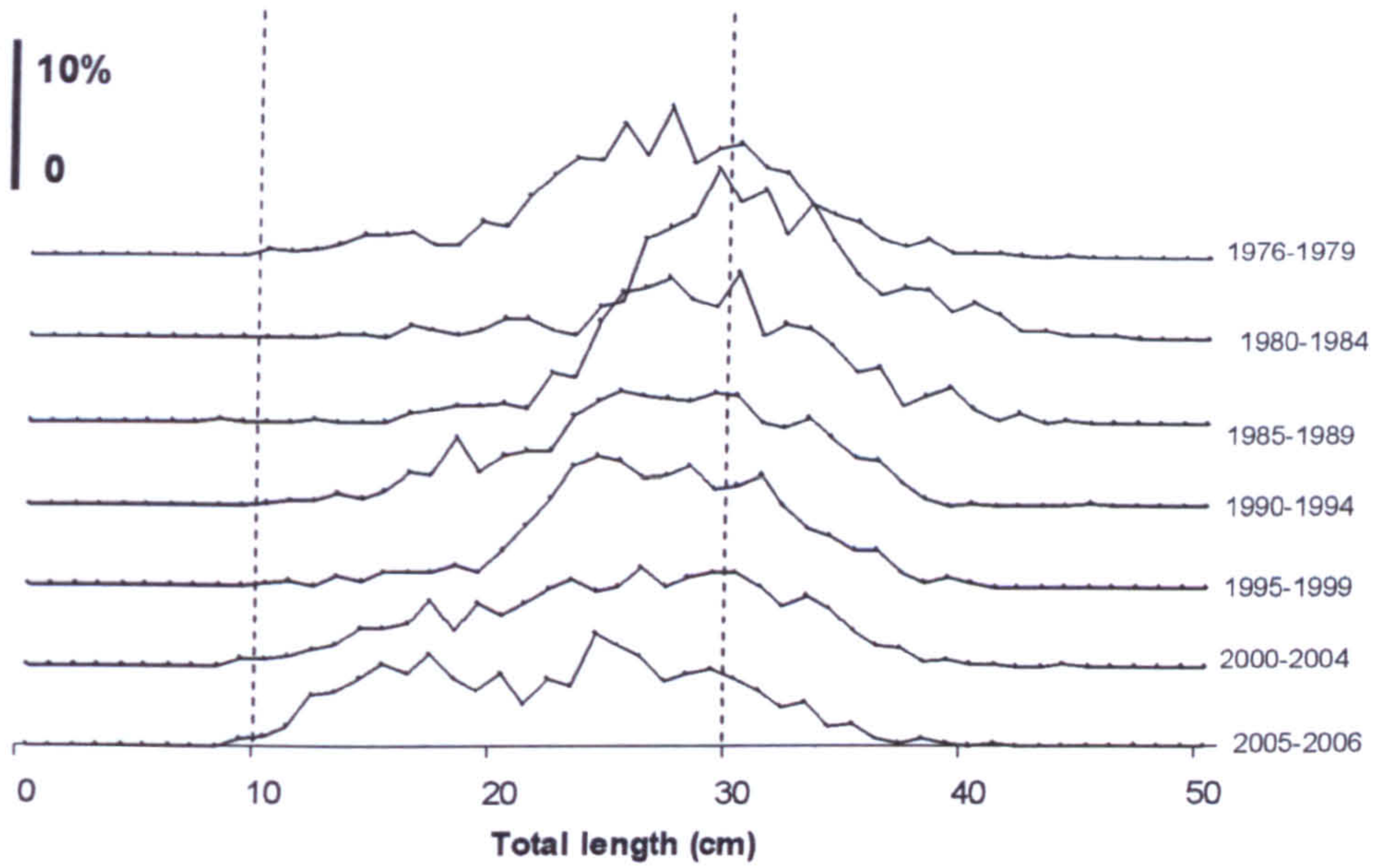


Figure 3.36: Percentage total length frequency distributions for whiting *M. merlangus* caught in the inshore waters of NW Wales and E Anglesey for the time period 1975-2006 (Preston, 2007). Data are grouped into 5 year time intervals and the vertical bar provides a scale for abundance (10%).

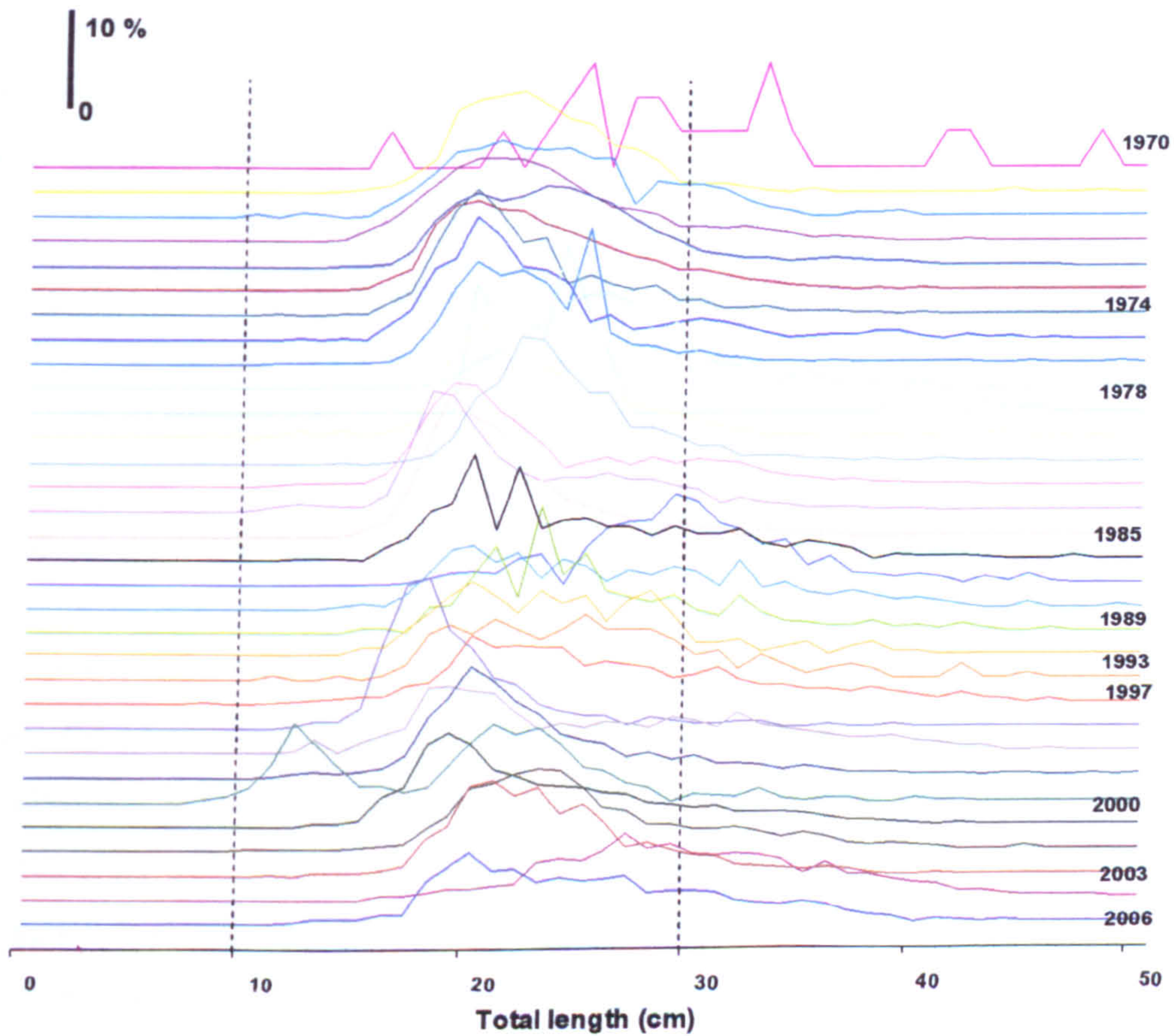


Figure 3.37: Percentage total length frequency distributions for plaice *P. platessa* caught in the inshore waters of NW Wales and E Anglesey for the time period 1970-2006. The vertical bar provides a scale for abundance (10%).

locations for whiting in the Irish Sea are unknown apart from one area off the coast of SE Ireland; Dickey-Collas *et al.*, 1997) would be subjected to fishing activity; as juvenile bycatch in the *Nephrops* fishery which is centred in the western Irish Sea (ICES, 2008a) and as adults in the targeted demersal fisheries in the Eastern Irish Sea (which includes Liverpool Bay) (ICES, 2008a). The 30 year set for whiting shows that the modal size of whiting caught in the autumnal RV *Prince Madog* fisheries surveys has declined over time (Figure 3.36), with the faster rate of decline in modal total length occurring in the 1980s and 1990s at the time when the stock was being overfished (Figure 3.32). As well as exhibiting a decrease in modal size between 1975 and 2006, the abundance of whiting caught in the fisheries survey has also decreased. Preston (2007), analysing the available catch data, showed that the autumn catch of whiting in the inshore coastal waters of NW Wales and E Anglesey decreased from 93 to 33 fish nm^{-1} between 1992 and 2007. This decline in abundance mirrors results reported by other authors for the Irish Sea (Parker-Humphreys, 2004a), off the west coast of Scotland (ICES, 2008a) and the North Sea (Hislop, 1996).

Although, as discussed earlier, the plaice stocks have gone through periods of heavy and light fishing pressure in the last 40 years, the size frequency distributions of plaice caught in the autumnal RV *Prince Madog* fisheries surveys have shown little change over time (Figure 3.37). The modal total length of plaice aggregating in local inshore waters during the autumn has tended to be between 20-24 cm over the last 4 decades of surveying the fish, with average modal total length of 22.4 cm.

An alternative way to present changes in the size distribution of fish over time is to examine the percentage of fish present in different size classes over time. Therefore, the catch data for dab, whiting and plaice were divided up into 5 TL size classes: < 15 cm, 15-20 cm, 20-25 cm, 25-30 cm and > 30 cm TL (Figure 3.38). The data for dab were redrawn from Seisay (2001) whilst raw data were used to draw the figures for whiting and plaice. For dab, so few fish > 30 cm TL were caught that this size class was not used for this species and the largest size class was >25 cm, the > 30 cm size class was used for the other two species. The data for dab shows that the population is dominated by fish in the 15-20 and 20-25 cm TL size classes (Figure 3.38a). There is evidence in recent years that a greater percentage of the catch is now comprised of smaller dab (*i.e.* >20 cm) with fewer larger fish (> 25 cm TL) present in the catches. It is not known whether this is a result of a change in the seasonal movement patterns of adult fish or whether the increased incidental capture of dab as

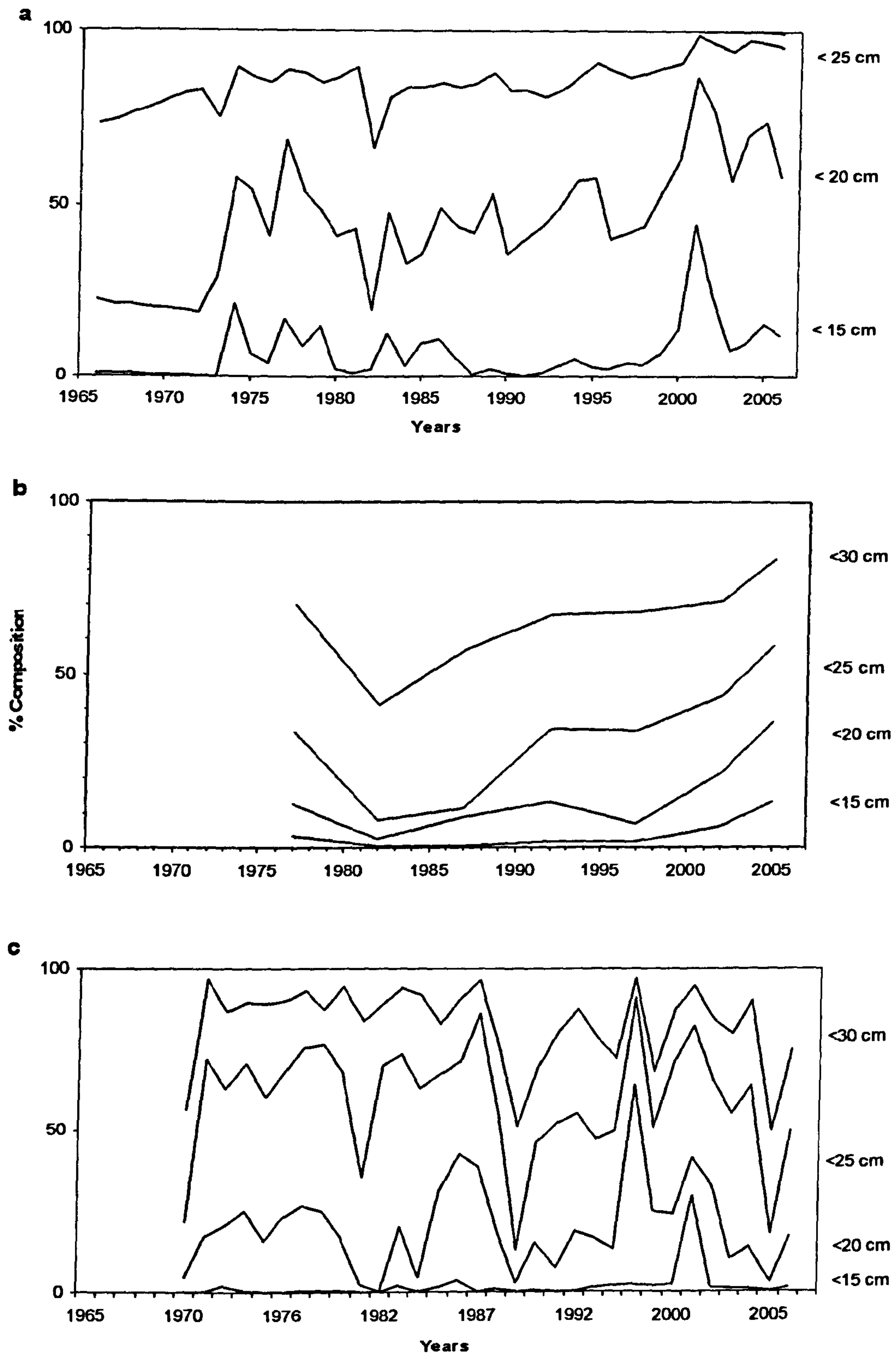


Figure 3.38: Changes in the percentage of fish in each of 4 total length size classes (< 15, 15-20, 20-25 and > 30 cm) over time for fish caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey. Data are presented for a) dab (1966-2005), b) whiting (1977-2005) and c) plaice (1970-2005).

discard in the eastern Irish Sea fisheries (Enever *et al.*, 2007) is beginning to exert an effect. For whiting there has been a clear decline in the percentage of larger fish (25-30 and > 30 cm TL) present in the catch over time and a corresponding increase in smaller fish (Figure, 3.38b). In the latest fisheries surveys, 40% of the whiting catch now comprises of fish < 20 cm TL whereas fish of this size averaged around 10% of the catch in the 1980s and 1990s (Figure, 3.38b). The data for plaice exhibits much more variability compared to the other two species (Figure, 3.38c) although it is possible to discern a trend in the data. Since 1990 there is a tendency for a larger percentage of the fish caught to be in the larger size classes (i.e. 25-30 and > 30 cm TL).

Data on the growth patterns of the three species were examined by comparing the von Bertalanffy growth constants L_{∞} and k to see whether there have been any changes over time and whether these changes could be related to fishing pressure. The L_{∞} data for the three species are shown in Figure 3.39. The data for dab are limited to those provided by Bakhsh (1982), Seisay (2001) and from recent MSc fisheries data (McCarthy, unpublished) and provide discontinuous data for the time period 1978-2006 (Figure 3.39a). The data for whiting and plaice are more extensive and cover time periods of 1975-2007 for whiting (Figure 3.39b) and 1970-2006 for plaice (Figure 3.39c) respectively. Changes in L_{∞} over time were examined using Spearman's Rank correlation test on the raw data and also on the smoothed L_{∞} values calculated as a three year running average (data not shown). The correlation analyses are presented in Table 3.25. All three species revealed significant correlations between L_{∞} and time for both male and female fish for both the raw and smoothed L_{∞} data. For dab (both sexes) and female plaice, maximum size values were positively correlated with time (Table 3.25) with L_{∞} values for male and female dab increasing from *ca.* 23 cm (male) and *ca.* 29 cm (female) in the late 1970s to *ca.* 28 cm (male) and *ca.* 32 cm (female) post-2000 respectively (Figure 3.39a) and L_{∞} values for female plaice increasing from *ca.* 45 cm in the early 1970s to *ca.* 47 cm post-2000 (Figure 3.39c). In contrast, maximum size values were negatively correlated with time for male plaice and for whiting (both sexes) (Table 3.25) with L_{∞} values for male plaice decreasing from *ca.* 34 cm in the early 1970s to *ca.* 44 cm post-2000 (Figure 3.39c) and L_{∞} values for male and female dab increasing from *ca.* 22 cm (male) and *ca.* 29 cm (female) in the late 1970s to *ca.* 29 cm (male) and *ca.* 34 cm (female) in post 2000 respectively (Figure 3.39a).

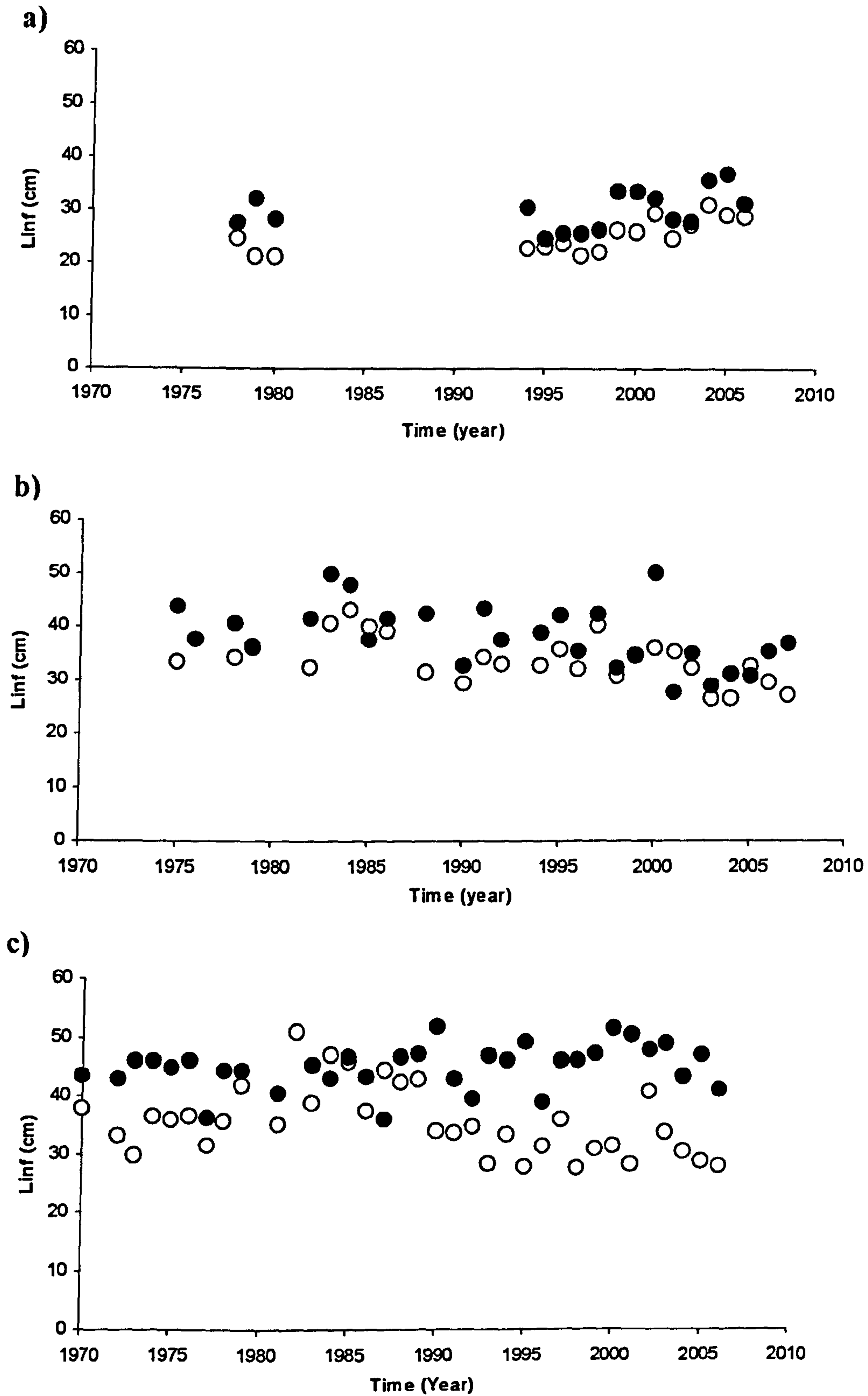


Figure 3.39: The maximum length L_{∞} (cm) of female (solid circles) and male (open circles) a) dab (1979-2006), b) whiting (1975-2007) and c) plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey.

Table 3.25: Spearman Rank correlation coefficients (r_s) relating maximum total length (L_∞ , cm) and von Bertalanffy growth constants (K , year⁻¹) to time for male (♂) and female (♀) dab (1979-2006), whiting (1975-2007) and plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey. Correlation analyses have been conducted using the raw data and smoothed data, calculated as a three year running average. Significant correlations are highlighted in bold and trends ($0.05 < P < 0.10$) underlined.

Species	L_∞ (cm)	L_∞ (cm)	K (y ⁻¹)	K (y ⁻¹)
		(Smoothed data)		(Smoothed data)
Dab : ♂	$r_s = 0.792$ P < 0.001	$r_s = 0.903$ P < 0.001	$r_s = -0.155$ P = 0.57	$r_s = -0.106$ P = 0.70
Dab : ♀	$r_s = 0.487$ P = <u>0.056</u>	$r_s = 0.685$ P = 0.003	$r_s = -0.088$ P = 0.75	$r_s = -0.035$ P = 0.90
Whiting : ♂	$r_s = -0.522$ P = 0.005	$r_s = -0.559$ P = 0.001	$r_s = -0.054$ P = 0.74	$r_s = -0.057$ P = 0.75
Whiting : ♀	$r_s = -0.555$ P = 0.003	$r_s = -0.682$ P < 0.001	$r_s = 0.093$ P = 0.64	$r_s = 0.079$ P = 0.66
Plaice : ♂	$r_s = -0.480$ P = 0.003	$r_s = -0.523$ P = 0.001	$r_s = 0.531$ P < 0.001	$r_s = 0.692$ P < 0.001
Plaice : ♀	$r_s = 0.372$ P = 0.03	$r_s = 0.465$ P = 0.004	$r_s = -0.126$ P = 0.48	$r_s = -0.136$ P = 0.42

Samples sizes: dab = 16 (♂ & ♀), whiting = 27(♂ & ♀), plaice = 35 (♂) & 35 (♀)

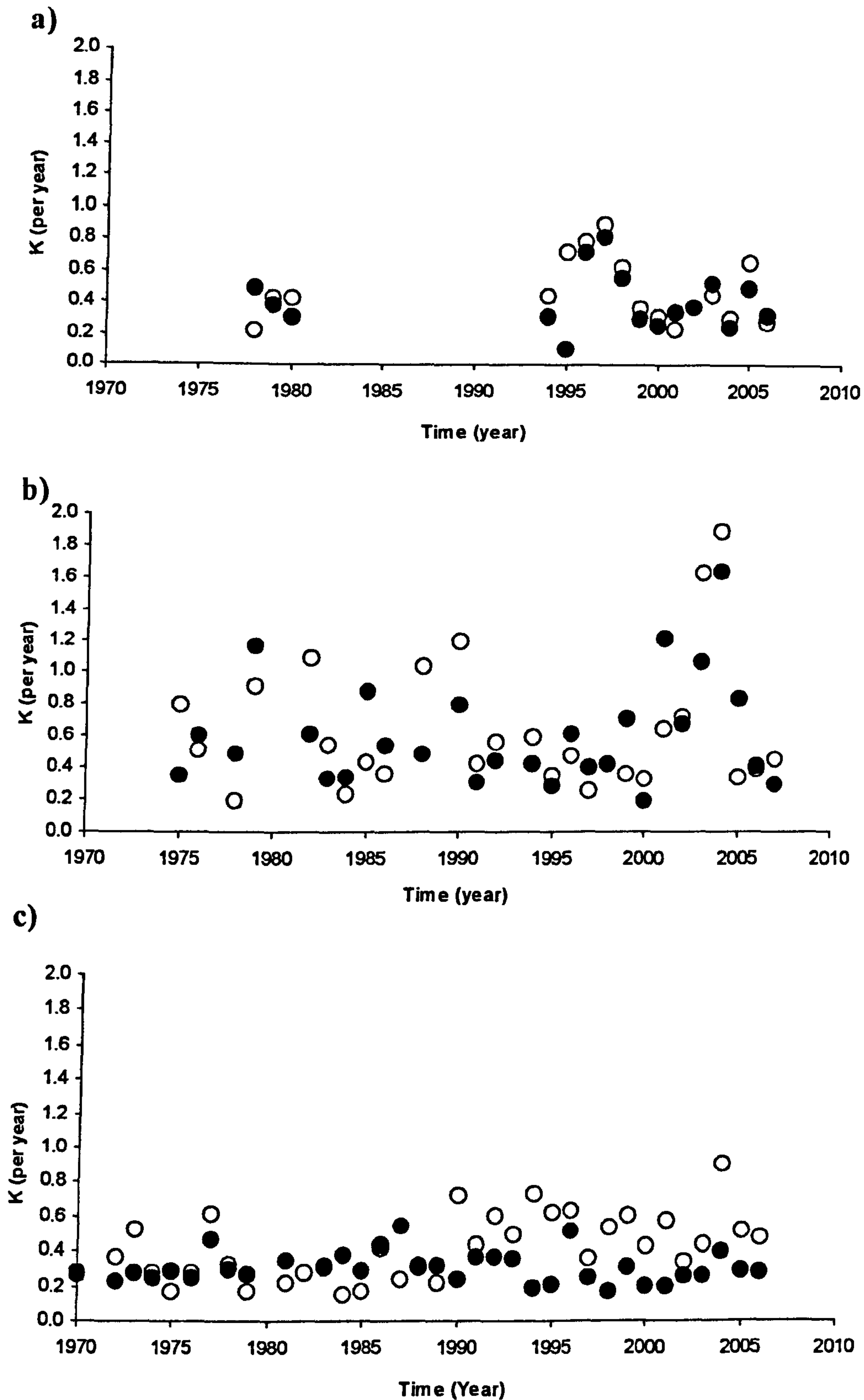


Figure 3.40: The von Bertalanffy growth coefficient values (k , year^{-1}) of female (solid circles) and male (open circles) a) dab (1979-2006), b) whiting (1975-2007) and c) plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey.

For each species, the von Bertalanffy growth coefficient data (L_{∞} and K) were grouped by decade and analysed to see if there were any significant differences over time for the three species with differing histories of exploitation. Statistical analyses were conducted using the raw data and smoothed data, calculated as three year moving averages (see Chapter 2 for explanation). Although the data for dab are limited to the 1970s, 1990s and 2000s, data for all 4 decades were available for whiting and plaice. The statistical analyses are summarised in Tables 3.26 to 3.31.

When the L_{∞} data for the unexploited dab population were grouped by decade, the L_{∞} values for both sexes were normally distributed (σ , $Z = 0.13$, $n = 16$, $P = 0.20$; ϕ , $Z = 0.19$, $n = 16$, $P = 0.15$) with both data sets having equal variances between time periods (σ , $W_{2,13} = 0.60$, $P = 0.57$; ϕ , $W_{2,13} = 0.37$, $P = 0.70$). There was a tendency for decadal average L_{∞} values of female dab to increase over time but this was not significant at the 5% level (ANOVA, $F_{(2,13)} = 3.19$, $P = 0.074$), however, in contrast, decadal average L_{∞} values for male dab increased significantly over time (ANOVA, $F_{(2,13)} = 12.93$, $P = 0.001$) (Table 3.26). When the L_{∞} data were “smoothed” (*i.e.* calculated as three year running averages), both data sets exhibited equal variance between time periods (σ , $W_{2,13} = 1.73$, $P = 0.22$; ϕ , $W_{2,13} = 2.24$, $P = 0.15$). The female smoothed L_{∞} data were normally distributed ($Z = 0.11$, $n = 16$, $P = 0.20$) but the male data were not ($Z = 0.24$, $n = 16$, $P = 0.02$). However, since both datasets exhibited equal variance, statistical comparisons between time periods could be conducted using ANOVA. This analysis showed a significant difference between smoothed L_{∞} values over time for both males (ANOVA, $F_{(2,13)} = 52.76$, $P < 0.0001$) and females (ANOVA, $F_{(2,13)} = 11.03$, $P = 0.002$). For male dab, smoothed L_{∞} values increased in the 2000s, in contrast smoothed L_{∞} values for female dab were significantly larger in the 1990s (Table 3.27). When the L_{∞} data for the overexploited whiting were grouped by decade, the L_{∞} values for both sexes were normally distributed (σ , $Z = 0.09$, $n = 27$, $P = 0.20$; ϕ , $Z = 0.10$, $n = 27$, $P = 0.20$) with both data sets having equal variances between time periods (σ , $W_{3,23} = 1.81$, $P = 0.17$; ϕ , $W_{3,23} = 0.49$, $P = 0.69$). Both male and female whiting exhibited a significant difference between decadal average L_{∞} values (σ , ANOVA, $F_{(3,23)} = 4.31$, $P = 0.015$; ϕ , ANOVA, $F_{(3,23)} = 3.41$, $P = 0.035$) with average L_{∞} values for both sexes being significantly larger in the 1980s compared to the 2000s (Table 3.28) when using the raw data. However, when the data are “smoothed”, greater differences over time can be observed (Table 3.29). When the L_{∞} data were “smoothed” (*i.e.* calculated as

Table 3.26: (a) Average theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) for male and female dab caught in the autumn surveys conducted by the RV *Prince Madog* in 1978-1980, 1994-1999 and 2000-2006. Data are presented as mean values \pm SD except for female K values which are median values \pm interquartile range. Significance values for the *post-hoc* comparisons between time periods using Scheffe's multiple comparison test for (b) average L_{∞} values and (c) average K values. (significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{∞}	Female L_{∞}	Male K	Female K
1970s (n=3)	22.2 \pm 2.0	29.0 \pm 2.4	0.35 \pm 0.12	0.38*
1990s (n=6)	23.1 \pm 1.7	27.5 \pm 3.4	0.63 \pm 0.21	0.43 \pm 0.49
2000s (n=7)	25.0 \pm 3.2	32.1 \pm 3.4	0.37 \pm 0.15	0.34 \pm 0.24

* note no interquartile range due to sample size

b)

	Male L_{∞}			Female L_{∞}		
	1970s	1990s	2000s	1970s	1990s	2000s
1970s						
1990s	0.81			0.81		
2000s	0.004	0.003		0.43	<u>0.08</u>	

c)

	Male K		
	1970s	1990s	2000s
1970s			
1990s	<u>0.098</u>		
2000s	0.994	0.041	

Table 3.27: (a) Average smoothed theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) for male and female **dab** caught in the autumn surveys conducted by the RV *Prince Madog* in 1978-1980, 1994-1999 and 2000-2006. Smoothed values are calculated as a three year running average. Data are presented as mean values \pm SD. Significance values for the *post-hoc* comparisons between time periods using Scheffe's multiple comparison test for (b) average L_{∞} values and (c) average K values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{∞}	Female L_{∞}	Male K	Female K
1970s (n=3)	22.0 \pm 0.9	29.5 \pm 0.4	0.36 \pm 0.05	0.39 \pm 0.05
1990s (n=6)	23.1 \pm 0.8	27.4 \pm 2.1	0.64 \pm 0.13	0.45 \pm 0.17
2000s (n=7)	27.8 \pm 1.2	32.2 \pm 1.9	0.38 \pm 0.07	0.37 \pm 0.10

b)

	Male L_{∞}			Female L_{∞}		
	1970s	1990s	2000s	1970s	1990s	2000s
1970s						
1990s	0.34			0.30		
2000s	< 0.001	< 0.001		0.15	0.002	

c)

	Male K		
	1970s	1990s	2000s
1970s			
1990s	<u>0.066</u>		
2000s	0.98	0.001	

Table 3.28: (a) Average theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) grouped by decade for male and female whiting caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1975-2006. Data are presented as mean values \pm SD for L_{∞} values and median values \pm interquartile range for K values. (b) Significance values for the *post-hoc* comparisons between average L_{∞} values for the 4 time periods using Scheffe's multiple comparison test. (Significant differences at the 5% level are highlighted in bold).

a)

	Male L_{∞}	Female L_{∞}	Male K	Female K
1970s (n=4)	35.2 \pm 1.9	39.4 \pm 3.4	0.65 \pm 0.60	0.54 \pm 0.64
1980s (n=6)	37.7 \pm 4.7	43.4 \pm 4.5	0.49 \pm 0.72	0.51 \pm 0.35
1990s (n=9)	33.6 \pm 3.2	37.7 \pm 4.3	0.42 \pm 0.23	0.43 \pm 0.31
2000s (n=8)	30.8 \pm 3.9	34.5 \pm 7.1	0.55 \pm 1.05	0.76 \pm 0.85

b)

	Male L_{∞}				Female L_{∞}			
	1970s	1980s	1990s	2000s	1970s	1980s	1990s	2000s
1970s								
1980s	0.77				0.71			
1990s	0.91	0.24			0.96	0.26		
2000s	0.30	0.018	0.48		0.51	0.038	0.68	

three year running averages), both data sets were normally distributed (σ , $Z = 0.12$, $n = 27$, $P = 0.20$; ϕ , $Z = 0.11$, $n = 27$, $P = 0.20$) but exhibited variances that tended to be unequal between time periods (σ , $W_{3,23} = 2.85$, $P = 0.06$; ϕ , $W_{3,23} = 2.35$, $P = 0.099$). Therefore, statistical comparisons were made using the non-parametric Kruskal Wallis test which showed significant differences between smoothed decadal L_{∞} values for both male (Kruskal Wallis, $\chi^2 = 12.15$, 3df. $P = 0.007$) and female whiting (Kruskal Wallis, $\chi^2 = 19.48$, 3df. $P = 0.002$). Pairwise comparisons of the decadal L_{∞} values for both male and female whiting for each time interval using Wilcoxon's signed rank test showed that L_{∞} values were highest in the 1980s and lowest in the 2000s (Table 3.29). Although the time series data for plaice have already been

Table 3.29: (a) Average smoothed theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) grouped by decade for male and female whiting caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1975-2006. Smoothed values are calculated as a three year running average. Data are presented as median values \pm interquartile range. Significance values for the *post-hoc* comparisons using Wilcoxon's Signed Rank test between time periods for (b) smoothed L_{∞} values for both sexes and (c) smoothed k vales for female whiting. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{∞}^*	Female L_{∞}	Male K	Female K
1970s (n=4)	35.1 \pm 2.1	39.4 \pm 4.6	0.55 \pm 0.27	0.54 \pm 0.41
1980s (n=6)	39.1 \pm 5.5	43.7 \pm 4.3	0.81 \pm 0.49	0.52 \pm 0.44
1990s (n=9)	33.9 \pm 2.2	38.7 \pm 2.9	0.58 \pm 0.29	0.43 \pm 0.17
2000s (n=8)	29.7 \pm 5.3	33.4 \pm 6.2	1.00 \pm 0.85	0.99 \pm 0.46

b)

	Male L_{∞}				Female L_{∞}			
	1970s	1980s	1990s	2000s	1970s	1980s	1990s	2000s
1970s								
1980s	<u>0.068</u>				<u>0.068</u>			
1990s	<u>0.068</u>	0.046			0.47	0.028		
2000s	0.27	0.028	<u>0.069</u>		<u>0.068</u>	0.028	0.012	

c)

	Female K			
	1970s	1980s	1990s	2000s
1970s				
1980s	0.89			
1990s	0.35	0.013		
2000s	0.043	0.263	0.025	

Table 3.30: (a) Average theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) grouped by decade for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the *post-hoc* comparisons between L_{∞} values and K values for male plaice for the 4 time periods using Scheffe's multiple comparison test. (significant differences at the 5% level are highlighted in bold and trends are underlined).

a)

	Male L_{∞}	Female L_{∞}	Male K	Female K
1970s (n=9)	35.3 \pm 3.6	43.9 \pm 3.1	0.33 \pm 0.15	0.28 \pm 0.07
1980s (n=9)	42.7 \pm 5.0	43.5 \pm 3.8	0.25 \pm 0.08	0.36 \pm 0.08
1990s (n=10)	31.6 \pm 3.1	45.5 \pm 4.0	0.57 \pm 0.12	0.29 \pm 0.10
2000s (n=7)	31.4 \pm 4.7	47.1 \pm 3.8	0.52 \pm 0.18	0.26 \pm 0.07

b)

	Male L_{∞}				Male K			
	1970s	1980s	1990s	2000s	1970s	1980s	1990s	2000s
1970s								
1980s	0.007				0.70			
1990s	0.30	<0.001			0.005	<0.001		
2000s	0.33	<0.001	0.33		<u>0.066</u>	0.005	0.90	

analysed grouped into 5 year intervals in Section 3.4, the analysis is repeated here grouped into decade for comparability with the dab and whiting data. When the L_{∞} data for the underexploited plaice population were grouped by decade, the L_{∞} values for both sexes were normally distributed (σ , $Z = 0.14$, $n = 35$, $P = 0.08$; ϕ , $Z = 0.08$, $n = 34$, $P = 0.20$) with both data sets having equal variances between time periods (σ , $W_{3,31} = 0.60$, $P = 0.62$; ϕ , $W_{3,30} = 0.39$, $P = 0.76$). Analysis of variance showed a significant difference between decadal L_{∞} values over time for male plaice (ANOVA, $F_{(3,31)} = 14.63$, $P < 0.001$) but not for females (ANOVA, $F_{(3,30)} = 1.54$, $P = 0.23$). For male plaice, L_{∞} values were significantly higher in the 1980s compared to other time periods (Table 3.30). However, when the data are “smoothed”, greater differences over time can be observed for both sexes (Table 3.31). When the L_{∞} data were

Table 3.31: (a) Average smoothed theoretical maximum length values (L_{∞} , cm) and von Bertalanffy growth coefficients (K , year⁻¹) grouped by decade for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as mean values \pm SD. Significance values for the *post-hoc* comparisons between (b) L_{∞} values and (c) K values for male and female plaice for the 4 time periods using Scheffe's multiple comparison test. (significant differences at the 5% level are highlighted in bold and trends are underlined).

a)

	Male L_{∞}	Female L_{∞}	Male K	Female K
1970s (n=9)	35.1 \pm 2.3	43.9 \pm 1.5	0.34 \pm 0.07	0.29 \pm 0.04
1980s (n=9)	42.6 \pm 1.7	43.6 \pm 2.4	0.27 \pm 0.06	0.36 \pm 0.05
1990s (n=10)	31.9 \pm 2.1	45.5 \pm 1.7	0.55 \pm 0.06	0.29 \pm 0.04
2000s (n=7)	31.7 \pm 2.3	47.1 \pm 2.5	0.53 \pm 0.08	0.27 \pm 0.04

b)

	Male L_{∞}				Female L_{∞}			
	1970s	1980s	1990s	2000s	1970s	1980s	1990s	2000s
1970s								
1980s	< 0.001				0.99			
1990s	0.023	< 0.001			0.46	0.34		
2000s	0.03	< 0.001	1.00		0.039	0.026	0.46	

c)

	Male K				Female K			
	1970s	1980s	1990s	2000s	1970s	1980s	1990s	2000s
1970s								
1980s	0.30				0.010			
1990s	< 0.001	< 0.001			0.98	0.019		
2000s	< 0.001	< 0.001	0.93		0.91	0.003	0.74	

“smoothed” (*i.e.* calculated as three year running averages), the female plaice data were normally distributed ($Z = 0.13$, $n = 34$, $P = 0.15$) but the male data were not ($Z = 0.15$, $n = 35$, $P = 0.047$). However, both data sets exhibited equal variances ($\hat{\sigma}^2$, $W_{3,31} = 0.73$, $P = 0.54$; $\hat{\sigma}^2$, $W_{3,30} = 0.85$, $P = 0.48$) allowing the use of ANOVA. Analysis of variance showed significant differences between decadal smoothed L_{∞} values over time for both male plaice (ANOVA, $F_{(3,31)} = 52.06$, $P < 0.001$) and female plaice (ANOVA, $F_{(3,30)} = 4.63$, $P = 0.009$). Comparisons of the 4 decades data for male plaice using Scheffe’s multiple comparison test showed significant differences in smoothed L_{∞} between all pairwise comparisons except between the 1990s and 2000s with the general pattern being smoothed L_{∞} values decreasing significantly between the 1970s and the 2000s. In contrast, smoothed L_{∞} values for female plaice were significantly larger in the 2000s compared to the 1970s and 1980s (Table 3.31).

When the growth coefficient data, K , for the unexploited dab population were grouped by decade, the values for male dab showed equal variance between time periods but the female data did not ($\hat{\sigma}^2$, $W_{2,13} = 0.92$, $P = 0.42$; $\hat{\sigma}^2$, $W_{2,13} = 6.55$, $P = 0.011$). Similarly, one data set was normally distributed ($\hat{\sigma}^2$, $Z = 0.17$, $n = 16$, $P = 0.20$) whilst the other was not ($\hat{\sigma}^2$, $Z = 0.23$, $n = 16$, $P = 0.03$). Therefore, given the distribution of the data, the male K values were analysed using ANOVA but the female K values were analysed using a Kruskal Wallis test. For male dab, the decadal growth coefficient values were significantly different (ANOVA, $F_{(2,13)} = 4.90$, $P = 0.03$), with K values higher in the 1990s compared to the 1970s and 2000s (Table 3.26) but there was no pattern for increasing or decreasing growth coefficients over time. There were no differences between decadal growth coefficient values for female dab (Kruskal Wallis, $\chi^2 = 0.48$, 2df. $P = 0.79$) (Table 3.26). The same patterns in the data were observed when the dab K data are “smoothed” and expressed as a three year running average. Both dab data sets exhibited equal variance between time periods ($\hat{\sigma}^2$, $W_{2,13} = 1.34$, $P = 0.30$; $\hat{\sigma}^2$, $W_{2,13} = 1.32$, $P = 0.29$) and were normally distributed (both $Z = 0.21$, $n = 16$, $P = 0.06$). For male dab, the decadal growth coefficient values were significantly different (ANOVA, $F_{(2,13)} = 13.60$, $P = 0.001$), with K values higher in the 1990s compared to the 1970s and 2000s (Table 3.27) but there was no pattern for increasing or decreasing growth coefficients over time. There were no differences between decadal growth coefficient values for female dab (ANOVA, $F_{(2,13)} = 0.99$, $P = 0.40$) (Table 3.27). When the growth coefficient data for the overexploited whiting were grouped by decade, the K values for both sexes were not normally distributed ($\hat{\sigma}^2$,

$Z = 0.20$, $n = 27$, $P = 0.006$; ♀, $Z = 0.17$, $n = 27$, $P = 0.055$) with both data sets having unequal variances between time periods (♂, $W_{3,26} = 2.40$, $P = 0.093$; ♀, $W_{3,26} = 3.46$, $P = 0.033$). Therefore, given the significant, or near-significant results of the Kolmogorov-Smirnov and Levene's tests, the data were tested using the non-parametric Kruskal Wallis test. Both male and female whiting exhibited no significant differences between decadal average K values (♂, $\chi^2 = 0.68$, 3df. $P = 0.88$; ♀, $\chi^2 = 1.59$, 3df. $P = 0.66$) (Table 3.28). When the von Bertalanffy growth coefficient data were calculated as three year running averages, the "smoothed" K values for both sexes were not normally distributed (♂, $Z = 0.15$, $n = 27$, $P = 0.058$; ♀, $Z = 0.21$, $n = 27$, $P = 0.001$) with both data sets having unequal variances between time periods (♂, $W_{3,26} = 2.40$, $P = 0.093$; ♀, $W_{3,26} = 4.82$, $P = 0.008$). Therefore, the data were tested using the non-parametric Kruskal Wallis test. Male whiting exhibited no significant differences between decadal average smoothed K values ($\chi^2 = 4.82$, 3df. $P = 0.19$) but female whiting exhibited significant differences over time (♀, $\chi^2 = 9.68$, 3df. $P = 0.021$) with smoothed K values significantly higher in the 2000s (Table 3.29). When the von Bertalanffy growth coefficient data for the underexploited plaice population were grouped by decade, the K values for both sexes were normally distributed (♂, $Z = 0.10$, $n = 35$, $P = 0.20$; ♀, $Z = 0.16$, $n = 34$, $P = 0.066$) with both data sets having equal variances between time periods (♂, $W_{3,31} = 0.87$, $P = 0.47$; ♀, $W_{3,30} = 1.34$, $P = 0.28$). Analysis of variance showed significant differences in K values between decades for male plaice (ANOVA, $F_{(3,34)} = 11.50$, $P < 0.001$) but not for females (ANOVA, $F_{(3,33)} = 0.15$, $P = 0.13$). Comparisons of the 4 decades data for male plaice using Scheffe's multiple comparison test showed a significant differences between higher K values in the 1990s/2000s and lower K values in the 1970s/1980s (Table 3.30). When the plaice growth coefficient data are "smoothed" and expressed as a three year running average, both male and female plaice data were normally distributed (♂, $Z = 0.13$, $n = 35$, $P = 0.12$; ♀, $Z = 0.07$, $n = 34$, $P = 0.20$) and exhibited equal variance between time periods (♂, $W_{3,31} = 0.66$, $P = 0.58$; ♀, $W_{3,30} = 1.32$, $P = 0.94$). For both sexes, ANOVA revealed that the decadal smoothed growth coefficient values were significantly different between time periods (ANOVA: ♂, $F_{(3,34)} = 36.57$, $P < 0.001$; ♀, $F_{(3,33)} = 7.24$, $P = 0.001$). Comparisons of the decadal smoothed K data for male plaice using Scheffe's multiple comparison test showed significant differences between higher K values in the 1990s/2000s and lower K values in the 1970s/1980s (Table 3.31). Comparisons of the decadal smoothed K data for female

plaice using Scheffe's multiple comparison test showed significantly higher K values in the 1980s compared to other decades but shift in growth rate over the 4 decades (Table 3.31).

Therefore, to summarise the comparisons between the patterns of growth for the three species, as assessed using the von Bertalanffy growth coefficients, the following patterns were observed in the data. For the unexploited dab population, there has been no significant change in the size range or modal size of dab caught in the autumnal fisheries surveys, although there is evidence (based on limited data) of a change in the pattern of growth with an increase in L_{∞} . For the underexploited plaice population, there has been no significant change in the modal size of plaice caught in the autumnal fisheries surveys, however larger fish (> 30 cm TL) make up a greater proportion of catch than they did 20-30 years ago. Over the last 4 decades there have been changes in the patterns of growth for both sexes with male plaice showing a decrease in L_{∞} and an increase in K and female plaice showing an increase in L_{∞} over time. Finally for the overexploited whiting caught in the autumnal fisheries surveys, there has been a significant decrease in the modal size over time and a tendency for smaller whiting (< 25 cm TL) to make up a greater proportion of the catch. There has been a decrease in L_{∞} over time for both sexes and also an increase in K values for female whiting. These changes in the size and growth patterns for the three species are discussed in detail in relation to fishing pressure and fisheries induced evolution in the next section.

The available data on size (L_{50} , cm) and age (A_{50} , year⁻¹) at first maturity for the three species are presented in Figures 3.41 and 3.42. The maturity ogive data for dab and plaice cover the time periods 1975 to 2006 and 1970 to 2006 respectively. Preston (2007) reported that whiting showed decrease in L_{50} and A_{50} over the period studied 1975-2007, although the data available for study period were only 6 years between 2002 and 2007. Also, since there were no differences in L_{50} and A_{50} between male and female whiting, Preston (2007) presented data for both sexes combined in her thesis. Therefore, detailed statistical comparisons can only be made between the maturity ogives for plaice and dab from the RV *Prince Madog* autumnal fishing surveys.

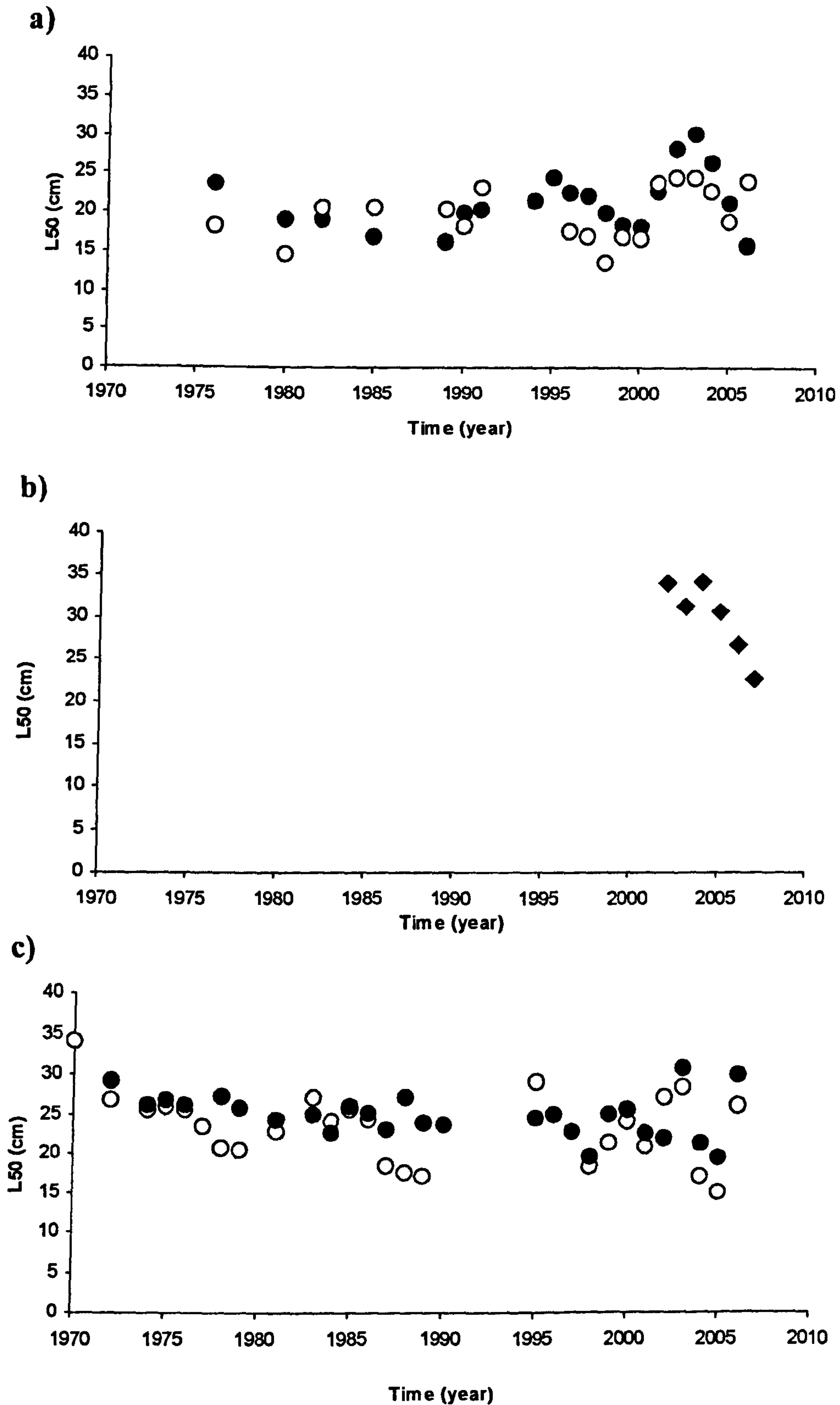


Figure 3.41: Total length at 50% maturity (L_{50} , cm) of female (solid circles), male (open circles) or both sexes combined (diamonds) for a) dab (1975-2006), b) whiting (2002-2007) and c) plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey.

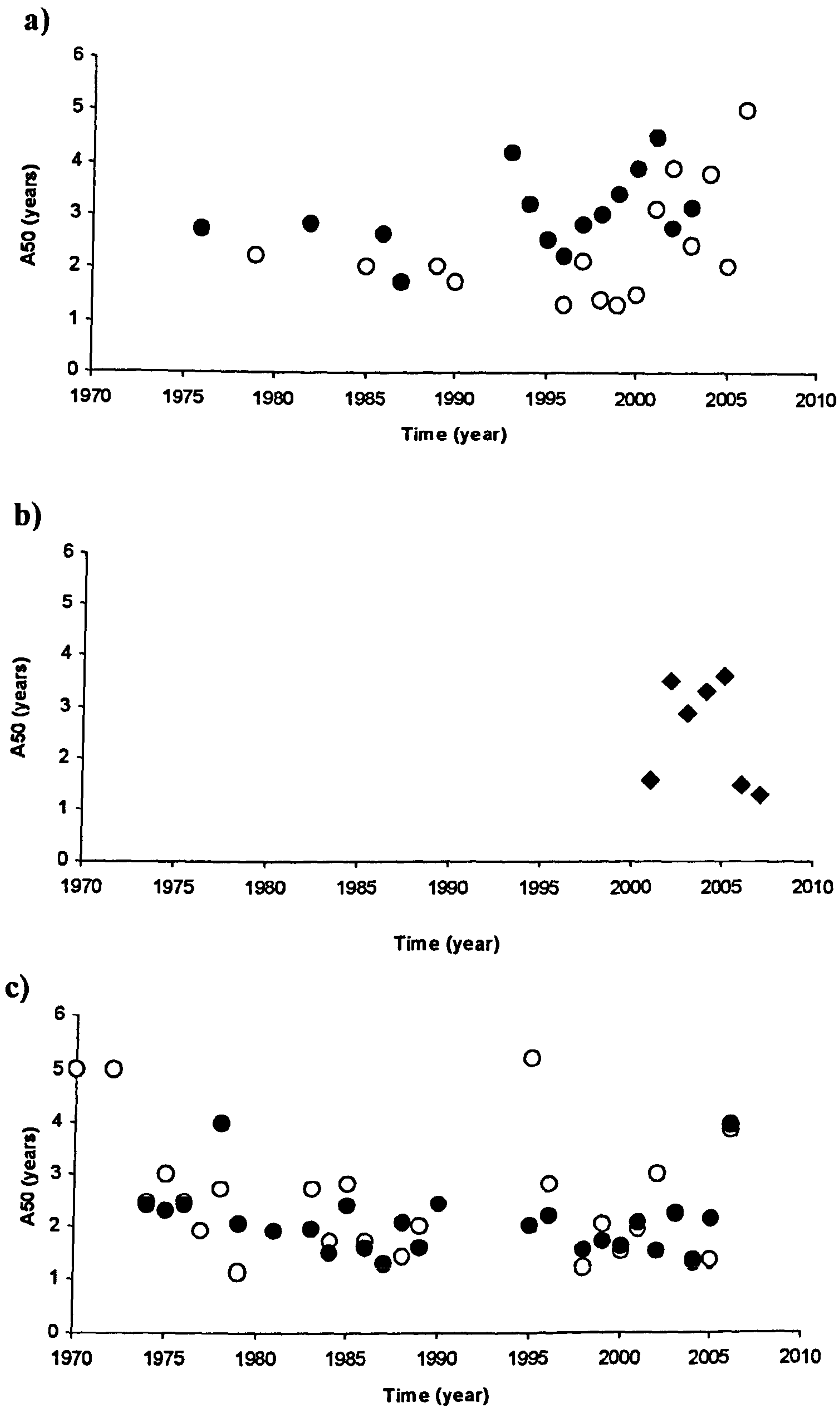


Figure 3.42: Age at 50% maturity (A_{50} , cm) of female (solid circles), male (open circles) or both sexes combined (diamonds) for a) dab (1975-2006), b) whiting (2002-2007) and c) plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey.

Changes in L_{50} over time for dab and plaice were examined using Spearman's Rank correlation test on the raw data and also on the smoothed L_{50} values calculated as a three year running average (data not shown). The correlation analyses for the raw data, presented in Table 3.32, showed no significant correlation between L_{50} and time for male and female dab and male plaice but a significant negative correlation between L_{50} and time for female plaice. However, when the L_{50} data are "smoothed" by calculating a three year running averages to remove some of the noise in the data so the long term pattern can become more evident, both dab and plaice showed significant, but differing, relationships between L_{50} and time (Figure 3.41, Table 3.32). For dab, the smoothed L_{50} data showed a significant positive correlation over time whilst for plaice, the smoothed L_{50} values showed a significant negative correlation over time. Although the average L_{50} values for dab between 1975 and 2006 were 21.2 and 19.6 cm for female and male dab, L_{50} values increased from averages of 18.1 and 16.2 cm for female and male dab in the early 1980s to averages of 23.2 and 22.0 cm for female and male dab in the 2000s, an increase of *ca.* 0.2-0.25 cm year⁻¹. In contrast, although the average L_{50} values for plaice between 1970 and 2006 were 24.8 and 23.3 cm for female and male plaice, L_{50} values decreased from averages of 27.3 and 26.1 cm for female and male dab in the early 1980s to averages of 25.6 and 23.8 cm for female and male plaice in the 2000s, an increase of *ca.* 0.06 cm year⁻¹. The available data for whiting shows a significant negative correlation with time (raw data, $r_s = -0.829$, $P = 0.042$; smoothed data, $r_s = -0.943$, $P = 0.005$). However, the data set is limited to a 6 year time interval in the 2000s and so no conclusions can be drawn about the long term patterns in L_{50} for this species over time.

For dab and plaice, the length at first maturity data were grouped by decade and analysed to see there were any significant differences over time for either species with differing histories of exploitation. Statistical analyses were conducted using the raw data and smoothed data, calculated as three year moving averages (see Chapter 2 for explanation). Since there was only a single data point for dab in the 1970s, statistical analyses were limited to the 1980s, 1990s and 2000s whilst 4 decades of data were available for plaice. The statistical analyses are summarised in Tables 3.33 to 3.36.

Table 3.32: Spearman Rank correlation coefficients (r_s) relating size at first maturity (L_{50} , cm) and age at first maturity (A_{50} , year⁻¹) to time for male (♂) and female (♀) dab (1979-2006) and plaice (1970-2006) caught in the autumnal (October/November) RV *Prince Madog* fisheries surveys in the inshore waters of NW Wales and E Anglesey. Correlation analyses have been conducted using the raw data and smoothed data, calculated as a three year running average. Significant correlations are highlighted in bold and trends ($0.05 < P < 0.10$) are underlined.

Species	L_{50} (cm)	L_{50} (cm)	A_{50} (y ⁻¹)	A_{50} (y ⁻¹)
		(Smoothed data)		(Smoothed data)
Dab : ♂	$r_s = 0.409$ P = <u>0.092</u>	$r_s = 0.580$ P = 0.012	$r_s = 0.519$ P = 0.048	$r_s = 0.628$ P = 0.012
Dab : ♀	$r_s = 0.0421$ P = 0.305	$r_s = 0.413$ P = <u>0.070</u>	$r_s = 0.441$ P = <u>0.099</u>	$r_s = 0.615$ P = 0.015
Plaice : ♂	$r_s = -0.276$ P = 0.163	$r_s = -0.461$ P = 0.015	$r_s = -0.271$ P = 0.180	$r_s = -0.387$ P = 0.046
Plaice : ♀	$r_s = -0.410$ P = 0.034	$r_s = -0.606$ P = 0.001	$r_s = -0.218$ P = 0.295	$r_s = -0.243$ P = 0.242

Samples sizes (♂ & ♀): dab, $L_{50} = 18$ & 20 , $A_{50} = 15$ & 15 ; plaice, L_{50} and $A_{50} = 27$ & 27 .

For dab, when L_{50} data are grouped by decade, both sexes were normally distributed (♂, $Z = 0.14$, $n = 18$, $P = 0.20$; ♀, $Z = 0.14$, $n = 20$, $P = 0.20$) with male dab having equal variance (♂, $W_{2,14} = 0.13$, $P = 0.88$) and female dab having unequal variance (♀, $W_{2,14} = 6.64$, $P = 0.008$). Therefore, the male data were analysed using ANOVA whilst the female data were analysed using a Kruskal Wallis test. For both male and female dab there was a trend for L_{50} values to be different between decades although this was not significant at the 5% level (♂, ANOVA, $F_{(2,16)} = 3.55$, $P = 0.057$;

Table 3.33: Average size at first maturity (L_{50} , cm) for male and female dab caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1980-2006. Data are presented as mean values \pm SD for males and median values \pm interquartile range for females.

	Male L_{50}	Female L_{50}
1980s (n=4)	18.9 \pm 3.0	17.8 \pm 2.5
1990s (n=8)	17.5 \pm 3.2	20.8 \pm 2.6
2000s (n=7)	22.0 \pm 3.2	22.6 \pm 10.2

♀, Kruskal Wallis, $\chi^2 = 5.03$, 2df. $P = 0.081$) (Table 3.33). For male dab, L_{50} values tended to be lower in the 1990s compared to the 2000s (Scheffe's multiple comparison test, $P=0.063$). For female dab, L_{50} values tended to be lower in the 1980s compared to the 1990s (Wilcoxon signed rank test, $P=0.068$). When the L_{50} data are smoothed (calculated a 3 year running average), both datasets were normally distributed (♂, $Z = 0.206$, $n = 18$, $P = 0.055$; ♀, $Z = 0.17$ $n = 20$, $P = 0.163$), however, male dab exhibited equal variance ($W_{2,14} = 1.16$, $P = 0.34$) whilst female dab showed unequal variance (♀, $W_{2,16} = 7.56$, $P = 0.005$). Therefore, the male data were analysed using ANOVA whilst the female data were analysed using a Kruskal Wallis test. For both male and female dab there were significant differences between L_{50} values in the 1980s, 1990s and 2000s (♂, ANOVA, $F_{(2,16)} = 6.62$, $P = 0.009$; ♀, Kruskal Wallis, $\chi^2 = 6.75$, 2df. $P = 0.034$) (Table 3.34). Pairwise comparisons of the L_{50} values between decades for both males and females showed a trend for L_{50} to increase over time (Table 3.34).

Although the time series L_{50} data for plaice have already been analysed grouped into 5 year intervals in Chapter 3, the analysis is repeated here grouped by decade for comparability with the dab data. The plaice L_{50} data for both sexes were normally distributed (♂, $Z = 0.12$, $n = 27$, $P = 0.20$; ♀, $Z = 0.082$, $n = 27$, $P = 0.20$) with males having equal variance (♂, $W_{3,23} = 0.531$, $P = 0.67$) and females having unequal variance (♀, $W_{3,23} = 6.18$, $P = 0.003$). Analysis of the raw L_{50} data by decade revealed no differences for male plaice (ANOVA, $F_{(3,26)} = 0.83$, $P = 0.49$) but significant differences for female plaice (Kruskal Wallis, $\chi^2 = 7.91$, 3df. $P = 0.043$). Pairwise comparisons of the L_{50} values for each decade showed a tendency to decrease over time (Table 3.35). When the L_{50} data for male and female plaice were smoothed by calculating three year moving averages to reduce the noisiness, both data sets confirmed equal variances (♂, $W_{3,26} = 0.46$, $P = 0.71$; ♀, $W_{3,23} = 1.42$, $P = 0.26$). The male smoothed L_{50} data were normally distributed (♂, $Z = 0.11$, $n = 28$, $P = 0.20$) whereas female plaice data were not normal (♀, $Z = 0.18$, $n = 27$, $P = 0.03$). As both datasets exhibited equal variance between time periods, ANOVA was used to compare the smoothed L_{50} values grouped by decade. This analysis revealed a highly significant difference between smoothed L_{50} values for female plaice over time (ANOVA, $F_{(3,26)} = 22.94$, $P < 0.0001$), but not for male (ANOVA, $F_{(3,26)} = 1.58$, $P = 0.22$). For female plaice, smoothed L_{50} values showed a tendency to decrease over time (Table 3.36).

Table 3.34: (a) Smoothed average size at first maturity (L_{50} , cm) for male and female dab caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1980-2006. Data are presented as mean values \pm SD for males and median values \pm interquartile range for females. (b) Significance values for the comparisons between time periods using Scheffe's multiple comparison test for males and Wilcoxon's signed rank test for female L_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{50}	Female L_{50}
1980s (n=4)	18.7 \pm 2.9	18.4 \pm 1.7*
1990s (n=8)	17.5 \pm 2.4	20.7 \pm 3.7*
2000s (n=7)	21.9 \pm 1.7	22.6 \pm 7.4*

* note: median \pm interquartile range

b)

	Male L_{50}			Female L_{50}		
	1980s	1990s	2000s	1980s	1990s	2000s
1980s						
1990s	0.73			0.14		
2000s	0.106	0.012		<u>0.068</u>	<u>0.091</u>	

Table 3.35: (a) Average length at first maturity (L_{50} , cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as mean values \pm SD. (b) Significance values for the comparisons between time periods using Scheffe's multiple comparison test for female L_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{50}	Female L_{50}
1970s (n=8)	21.3 \pm 4.1	26.9 \pm 1.1
1980s (n=8)	22.0 \pm 3.4	24.5 \pm 0.4
1990s (n=4)	23.3 \pm 3.4	23.4 \pm 0.9
2000s (n=7)	22.3 \pm 2.3	24.2 \pm 0.7

b)

Decadal Years	Female L_{50}			
	1970s	1980s	1990s	2000s
1970s				
1980s	< 0.001			
1990s	< 0.001	<u>0.099</u>		
2000s	< 0.001	0.842	0.413	

Table 3.36: (a) Smoothed average size at first maturity (L_{50} , cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as mean values \pm SD for males and median values \pm interquartile range for females. (b) Significance values for the comparisons between time periods using Scheffe's multiple comparison test for males and Wilcoxon's signed rank test for female L_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male L_{50}	Female L_{50}
1970s (n=8)	25.3 \pm 4.2	26.5 \pm 1.6*
1980s (n=8)	22.0 \pm 3.9	24.5 \pm 2.6*
1990s (n=4)	23.4 \pm 4.6	24.1 \pm 2.9*
2000s (n=7)	22.5 \pm 5.2	22.6 \pm 8.4*

* Note: median \pm interquartile range

b)

Decadal Years	Female L_{50}			
	1970s	1980s	1990s	2000s
1970s				
1980s	0.043			
1990s	<u>0.068</u>	0.023		
2000s	0.144	0.893	1.00	

A similar set of analyses were conducted for the A_{50} maturity ogive data: the data sets for dab and plaice covered the time period from the 1970s to the 2000s although the whiting data set was limited to the 2000s. Therefore, detailed statistical comparisons can only be made between the A_{50} data for plaice and dab from the RV *Prince Madog* autumnal fishing surveys.

Examination of the dab raw A_{50} data revealed that the female data were normally distributed (♀ , $Z = 0.15$, $n = 15$, $P = 0.20$) but the male data were not (♂ , $Z = 0.23$, $n = 15$, $P = 0.029$). Both data sets exhibited unequal variance between decades (♂ , $W_{2,12} = 5.43$, $P = 0.021$; ♀ , $W_{2,12} = 3.13$, $P = 0.08$) and therefore the non-parametric Kruskal Wallis test was used to test for differences between time periods. The Kruskal Wallis test showed no significant differences between female A_{50} values (Kruskal Wallis, $\chi^2 = 3.70$, 2df. $P = 0.16$) but a significant difference between male A_{50} values over time (Kruskal Wallis, $\chi^2 = 7.19$, 2df. $P = 0.027$) (Table 3.37). Pairwise comparisons of male dab A_{50} values showed a tendency for A_{50} to be higher in the 2000s (Table 3.37). When the age at first maturity data were smoothed by calculating a three year running average, the data for both sexes were normally distributed (♂ , $Z = 0.20$, $n = 15$, $P = 0.11$; ♀ , $Z = 0.13$, $n = 15$, $P = 0.20$) and both showed equal variance (♂ , $W_{2,12} = 1.51$, $P = 0.26$; ♀ , $W_{2,12} = 1.41$, $P = 0.28$). Therefore, for both sexes the smoothed A_{50} data for each decade were compared using ANOVA which showed a significant difference for male dab (ANOVA, $F_{(2,12)} = 9.29$, $P = 0.004$) and a non-significant trend for female dab (ANOVA, $F_{(2,12)} = 3.08$, $P = 0.083$) (Table 3.38). Pairwise comparisons of the smoothed A_{50} data for male dab indicated that A_{50} values in the 2000s tended to be higher than in the 1980s and 1990s (Table 3.38).

Although the time series A_{50} data for plaice have already been analysed grouped into 5 year intervals in Chapter 3, the analysis is repeated here grouped by decade for comparability with the dab data. Overall, plaice A_{50} values ranged between 1.1 and 5.2 years for male plaice with average 2.5 years and between 1.3 to 4.0 years and average of 2.1 years for female plaice (Figure 3.42; Table 3.39). The plaice A_{50} data for both sexes exhibited equal variance (♂ , $W_{3,22} = 1.55$, $P = 0.23$; ♀ , $W_{3,21} = 0.85$, $P = 0.48$) although they were not normally distributed (♂ , $Z = 0.17$, $n = 27$, $P = 0.051$; ♀ , $Z = 0.23$, $n = 25$, $P = 0.001$). However, since the data exhibited equal variances between time periods they could be compared using ANOVA. ANOVA indicated no significant difference has shown over time for both male and female plaice (ANOVA: ♂ , $F_{(2,22)} = 1.07$, $P = 0.38$; ♀ , $F_{(3,21)} = 1.86$, $P = 0.17$).

Table 3.37: (a) Average age at first maturity values (A_{50} , cm) for male and female dab caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1979-2006. Data are presented as median values \pm interquartile range. (b) Significance values for the comparisons between time periods using Wilcoxon's signed rank test for male average A_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male A_{50}	Female A_{50}
1980s (n=2)	2.0*	2.7*
1990s (n=5)	1.4 \pm 0.6	2.5 \pm 1.8
2000s (n=7)	3.1 \pm 1.9	3.1 \pm 1.1

b)

Decadal Years	Male A_{50}		
	1980s	1990s	2000s
1980s			
1990s	0.29		
2000s	0.29	<u>0.078</u>	

Table 3.38: a) Smoothed average age at first maturity values (A_{50} , cm) for male and female dab caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1979-2006. Data are presented as mean values \pm SD. (b) Significance values for the comparisons between time periods using Scheffe's multiple comparison test for male average smoothed A_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male A_{50}	Female A_{50}
1980s (n=3)	2.0 \pm 0.2	2.6 \pm 0.3
1990s (n=5)	1.6 \pm 0.1	2.9 \pm 0.7
2000s (n=7)	3.2 \pm 0.9	3.3 \pm 0.4

b)

Decadal Years	Male A_{50}		
	1980s	1990s	2000s
1980s			
1990s	0.70		
2000s	<u>0.068</u>	0.005	

Table 3.39: (a) Average age at first maturity values (A_{50} , cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as mean values \pm SD and as median values \pm interquartile range (indicated by *).

	Male A_{50}	Female A_{50}	Male A_{50}^*	Female A_{50}^*
1970s (n=8)	2.9 \pm 1.4	2.6 \pm 0.8	2.6 \pm 2.5	2.4 \pm 1.0
1980s (n=8)	2.0 \pm 0.5	1.8 \pm 0.4	1.9 \pm 1.0	1.7 \pm 0.5
1990s (n=5)	2.8 \pm 1.7	2.0 \pm 0.4	2.4 \pm 3.2	2.0 \pm 0.7
2000s (n=7)	2.2 \pm 1.0	2.1 \pm 0.9	1.9 \pm 1.6	2.1 \pm 0.7

When the A_{50} data for male and female plaice were smoothed (calculated as a 3 year running average) and tested for normality, neither sex exhibited normal distribution (σ , $Z = 0.23$, $n = 27$, $P = 0.001$; φ , $Z = 0.17$, $n = 25$, $P = 0.062$) or equal variance (σ , $W_{3,23} = 9.69$, $P < 0.0001$; φ , $W_{3,21} = 4.59$, $P = 0.013$). Therefore the decadal smoothed A_{50} data for both sexes were tested using the non-parametric Kruskal Wallis test. For male plaice, there were no differences in smoothed A_{50} values over time (Kruskal Wallis, $\chi^2 = 5.33$, 3df. $P = 0.15$), however, smoothed A_{50} values over time were significantly different for female plaice (Kruskal Wallis, $\chi^2 = 10.21$, 3df. $P = 0.017$) (Table 3.40). Pairwise comparisons of the female decadal smoothed A_{50} data using a Wilcoxon signed rank test showed that age at first maturity in 1970s was older compared to the 1980s and 1990s (Table 3.40).

To summarise the detailed analyses of L_{50} and A_{50} of dab and plaice, the preceding pages have shown that there is an indication that both L_{50} and A_{50} values have increased for male and female dab over time. In contrast, the data for plaice shows that length at first maturity for female plaice has declined over time. In addition, the limited whiting data presented here, plus the comments presented by Preston (2007) would suggest changes in the maturity ogives for this species also. These changes in maturity patterns for the three species are discussed in detail in relation to fishing pressure and fisheries induced evolution in the next section.

Table 3.40: (a) Smoothed average age at first maturity values (A_{50} , cm) for male and female plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Data are presented as median values \pm interquartile range. (b) Significance values for the comparisons between time periods using Wilcoxon's signed rank test for female average smoothed A_{50} values. (Significant differences at the 5% level are highlighted in bold, trends are underlined).

a)

	Male smoothed A_{50}	Female smoothed A_{50}
1970s (n=4)	2.5 \pm 2.4	2.3 \pm 0.7
1980s (n=8)	2.0 \pm 0.5	1.8 \pm 0.3
1990s (n=4)	2.8 \pm 2.4	2.0 \pm 0.5
2000s (n=7)	2.2 \pm 0.6	1.9 \pm 0.8

b)

Decadal Years	Female smoothed A_{50}			
	1970s	1980s	1990s	2000s
1970s				
1980s	0.043			
1990s	<u>0.068</u>	1.00		
2000s	1.00	0.69	0.29	

3.4.2 Evidence for Fisheries Induced Evolution in our local fish stocks?

It is well established that rates of natural mortality are very high in the early life history stages of fishes, for example natural mortality rates can be as high as 50-70% day⁻¹ for eggs and larvae of some marine fish species due to high predation rates (Jennings *et al.*, 2001; Houde, 2002), however, natural mortality rates decline with increasing size (Peterson and Wroblewski, 1984; Sogard, 1997). For any given species, a range of life-history phenotypes (such as fast growing and slow growing individuals, differences in the age and size at maturity and in reproductive investment) can be expressed which are adaptive responses to allow the species to cope with environmental variability and the differential mortality that this produces (Heino and Dieckmann, 2008). In commercially exploited fish stocks, fishing will be the major source of mortality in the post-larval phase of the lifecycle, often exceeding the rate of natural mortality by several hundred percent, and will affect the phenotypic adaptive responses observed (Policansky, 1993; Conover, 2000; Law 2000; Ernande *et al.*, 2004). There has been considerable interest in modelling how increased mortality rates affect harvested populations, dependent on whether fishing is size-specific or indiscriminate, in order to predict how fish stocks may respond to over-exploitation (*e.g.* Ernande *et al.*, 2004; De Roos *et al.*, 2006). There is now a growing body of evidence to show that sustained fishing pressure can result in evolutionary changes in the population biology of fish stocks, a phenomenon that has been termed '*Fisheries-Induced Evolution*' (Kuparinen and Merila, 2007; Law, 2007; Hutchings and Fraser, 2008).

Fisheries can act as a selective force as the mortality rate of individuals above the size at first capture can potentially remove particular genotypes from the gene pool (Rijnsdorp *et al.*, 2005). Life history theory predicts that this shift in mortality rates amongst larger individuals may select for earlier maturation, increased reproductive investment and a change in growth rate (Roff, 1992; Law 2000) and there is evidence to support these predictions from laboratory experiments (Reznick *et al.*, 1990; Conover and Munch 2002) and for populations in the wild. Tables 3.41 and 3.42 summarise data for temperate northern latitude fresh water and marine fish species where changes in growth or reproductive traits have been observed in response to heavy commercial or recreational exploitation. These data are derived from long term studies spanning 20 to 111 years and are mostly for salmonids (*e.g.* *S.*

salar and *Oncorhynchus* spp.), pleuronectids (e.g. *P. platessa* and *H. platessoides*) and gadid species (e.g. *G. morhua* and *M. aeglefinus*). As predicted from the life history models, the most common response to sustained overexploitation is a change in the timing of first reproduction, although some differences between freshwater and marine teleosts are evident. In freshwater, the most common response, observed amongst the anadromous salmonids, is a reduction in the size at maturity (L_{50}) with a reduction in the age at first maturity (A_{50}) observed in lacustrine fishes (Table 3.41). However, this observation may be biased by the predominance of salmonid studies in the literature rather than being the typical freshwater response. Amongst marine teleosts, all three predicted responses to heavy fishing pressure are observed – *i.e.* selection for earlier maturation, increased reproductive investment and changes in growth rate – but it is the selection for a reduction in the age and size at first maturity that is observed in the majority of the studies (Table 3.42). The changes in A_{50} and L_{50} observed vary from study to study and are dependent in part on the degree of exploitation in terms of how long the stock has been overexploited and the intensity of overfishing. For example, fisheries-induced evolutionary changes can occur very rapidly. Studies on orange roughy *Hoplostethus atlanticus* in Tasmanian coastal waters show evidence of fisheries-induced evolution, through changes in fecundity, within a 5 year time period (Koslow *et al.*, 1995). The rapidity and magnitude of selection in age and size at maturity can also exhibit variation between stocks within a species (Table 3.42). A good example here is the Atlantic cod *G. morhua*, which comprises of a number of important stocks in the Northern Atlantic in the coastal shelf seas of northern Europe and North America. These stocks have a long history of industrial fishing/overexploitation and there are long term data sets collected by fisheries scientists that can be examined to detect any responses in the population biology of the stock to sustained overexploitation. For example, the northeast Arctic cod stock (located off the coast of northern Norway) has seen a dramatic decline in A_{50} from 10-11 years in the 1930s to 7 years in the 2000s with a parallel decrease in L_{50} from *ca* 90 to *ca* 75 cm (Heino *et al.*, 2002a). However, in Canadian waters, decreases in A_{50} (6 to 4 years) and L_{50} (variable decline depending on stock and cohort) have been observed in the Grand Banks cod stocks and the Newfoundland/Labrador cod stock (Olsen *et al.*, 2004, 2005; Hutchings, 2005) whilst the Gulf of St Lawrence cod stock has shown changes in growth rate rather than changes in the timing of maturation (Sinclair *et al.*, 2002; Swain *et al.*, 2007). Spatial

variation in the responses to fishing pressure have also been observed for haddock *M. aeglefinus* stocks in the northern North Sea (Wright, 2005). The “inshore” haddock stock has shown a reduction in A_{50}/L_{50} and an increase in fecundity in the 1990s compared to 1970s whilst the decline in L_{50} has been less and there have been no changes in fecundity in the “offshore” haddock stock (Wright, 2005). Amongst commercially exploited flatfish species, there is evidence for fisheries induced evolution in North Sea plaice and sole *S. solea* stocks (Table 3.42) with changes in A_{50}/L_{50} observed in both species.

In this chapter, time series data on the population biology of the three main demersal teleost fish species – dab, plaice and whiting – found in the inshore waters of NW Wales and E. Anglesey have been examined to detect whether there have been any changes in the size structure, growth rate and maturity ogives in the last 25-40 years. These analyses have shown no changes in the unexploited dab population whilst significant changes in growth and size and age at maturity, suggestive of fisheries-induced evolution since they follow the same patterns seen in Table 3.42, have been observed in plaice and whiting. It is unfortunate that the surviving records of the maturity data for whiting are limited to the 2000s, but it is striking that a significant change in A_{50}/L_{50} is evident within that short time scale. Also, the magnitude of the decline in L_{50} (ca. 10 cm in 6 years) is comparable to the decline observed in some cod stocks over a 5 year period (Olsen *et al.*, 2005; Hutchings, 2005). When the maturity ogive data are taken together with the significant changes in growth patterns (observed over a 25 year time scale), and assuming that whiting will show the same responses to overfishing as the other demersal gadids (which all show the same fisheries-induced evolutionary responses to overfishing), this is all evidence to suggest fisheries-induced evolution has occurred for whiting in the Irish Sea. It is interesting to note that the currently underexploited plaice population, which has been caught in the inshore waters of NW Wales and E. Anglesey in the autumnal fisheries surveys but which forms part of the SE Irish Sea stock located within Liverpool Bay (Dunn and Pawson, 2002), has also shown significant changes in growth (male plaice) and in the age (male plaice) and size (male and female plaice) at first maturity over the last 36 years. These results would also be suggestive of fisheries-induced evolution even though fishing pressure has been relaxed in the last 15 years and the stock is currently underexploited. Studies on North Sea plaice by Rijnsdorp and co-workers (Rijnsdorp, 1993; Grift *et al.*, 2003; Rijnsdorp *et al.*, 2005) have shown that

fishing mortality rates of $F = 0.4-0.7 \text{ year}^{-1}$ (plus estimated discard rates equivalent to $F = 0.2-0.4 \text{ year}^{-1}$) between 1960 and 1990 have resulted in fisheries-induced evolution and a 4-6 cm decrease in L_{50} . Although stock size and landings are much lower for plaice in the Irish Sea compared to the North Sea (ICES, 2008a and b), comparable rates of fishing mortality ($F = 0.4-0.9 \text{ y}^{-1}$, excluding any estimate of discards) were observed during the period of peak fishing in the 1970s and 1980s. Over the same time period, L_{50} estimates for plaice, based on the autumnal fisheries survey and on Basimi and Grove (1985c) have decreased by 5 cm and A_{50} estimates by *ca.* 1 year. Thus, the same patterns of decline have been observed in this study as seen for the North Sea plaice stock.

It must be highlighted that in order to prove that changes in age and size at maturity are a result of fisheries-induced evolution, it is important to disentangle any genetic evolutionary response from a phenotypic response to changes in environmental conditions (Rijnsdorp *et al.*, 2005). For example, in an exploited population it is possible that fish may mature earlier since competition for resources with con-specifics is reduced, growth is faster and individuals may attain the size required for maturation more quickly (Wright, 2005); also, increased seawater temperatures in recent decades (*ca.* 0.5-1.0°C in the Irish Sea) will promote increased growth opportunity. This is known as the ‘compensatory response’ hypothesis and here, earlier maturation is a phenotypically plastic response where individuals adapt to changing environmental conditions (Law 2000, Heino *et al.*, 2002b; Engelhard and Heino, 2004). The second, ‘evolutionary response’ hypothesis predicts that earlier maturation is due to a genetic change in maturation characteristics, arising from the effects of size selective harvesting (Wright, 2005). For example, with high adult mortality rates, the proportion of late-maturing individuals surviving through to spawning and successfully passing on their genes to subsequent generations is reduced and selection should favour early-maturing phenotypes and increased reproductive effort at all ages (Law 2000, Heino *et al.*, 2002b; Wright, 2005). The majority of marine teleost studies to date, presented in Table 3.42, support the ‘evolutionary response’ hypothesis through the use of reaction norm analysis (of age and size at maturity although some studies suggest a compensatory response (*e.g.* Atlantic herring; Engelhard and Heino, 2004) which may be due to the more selective fishing practices for herring compared to demersal fish species. In recent years, changes in selective traits such as growth rates, age/size at first maturity and fecundity

have been examined using reaction norm analysis (reviewed in Kuparinen and Merila, 2007; Heini and Dieckmann, 2008). Probabilistic maturation reaction norm (PMRN) analysis involves the calculation of the age- and size-dependent probability that an immature individual will mature during a given time interval (Heini *et al.*, 2002b; Heini and Dieckmann, 2008). This approach differs from the classic maturity ogive approach (as used in this study) where no distinction is made between individuals that are already mature and have spawned at least once (Stage 3 in this study, see chapter 2) and those that are maturing for the first time (Stage 2). The PMRN technique is able to control for environmental variables such as growth rate, density and temperature and to look for trends in the residual (*i.e.* unexplained) variance in the data set. Trends in the residual variance are evidence of genetic changes (Heini *et al.*, 2002b; Kuparinen and Merila, 2007; Heini and Dieckmann, 2008). PMRN analysis has been developed within the last decade and has been used to re-analyse the time series data for species such as cod (*e.g.* Heino *et al.*, 2002a; Olsen *et al.*, 2004, 2005; Hutchings 2005) and plaice (*e.g.* Grift *et al.*, 2003; Rijnsdorp *et al.*, 2005). These analyses have confirmed the results obtained using classic maturity ogives published for these species 10 years earlier (plaice, Rijnsdorp, 1993; cod, Hutchings and Myers, 1994; Myers *et al.*, 1996). It was not possible within the time scale of this thesis to apply the PMRN technique to the maturation data available for plaice caught in the inshore waters of NW Wales and E. Anglesey in the autumnal fisheries surveys but it would be recommended that such an analysis is undertaken. Thus, although the results presented in this thesis cannot conclusively show that fisheries-induced evolution has occurred, the similarities observed in this study to the patterns observed in other demersal fish stocks would be suggestive that such a change has taken place.

It is critical for management purposes to identify the relative importance of phenotypically plastic and evolutionary changes in age and size at maturation since phenotypic changes are readily reversible by, for example, relaxing the exploitation rate, while genetic changes are not readily reversible (Law 2000; Grift *et al.*, 2003; Mollet *et al.*, 2007). Recovery from a genetic change could be slow as natural selection pressure toward the original genotype could be lower in the absence of fishing pressure than any directional selection caused by intensive fishing (Law, 2000). If directional selection as a result of fishing is too strong then the original genotype could be lost and the surviving genotypes may have reduced fitness. Thus,

Table 3.41: A summary of studies where a selection response in one or more traits (Fisheries induced evolution) has been observed for commercially or recreationally exploited temperate freshwater fish species. . (↑ = increased response, ↓ = decreased response)

<i>Species</i>	<i>Location</i>	<i>Time scale</i>	<i>Response</i>	<i>Reference</i>
Northern pike (<i>Esox lucius</i>)	Lake Windermere, UK	1944 - 1975	↑ fecundity	Law (1979)
Smallmouth bass (<i>Micropterus dolomieu</i>).	Opeongo Lake, Ontario	1936 - 2002	↓ A ₅₀	Dunlop <i>et al.</i> (2005).
Lake Whitefish (<i>Coregonus clupeaformis</i>)	Lesser Slave Lake, Alberta	1940 - 1975	↓ body size ↓ growth	Handford <i>et al.</i> (1977)
European grayling (<i>Thymallus thymallus</i>)	5 lakes in central Norway	1880 - 1991	↓ A ₅₀	Haugen (2000)
Pink salmon (<i>Oncorhynchus keta</i>)	Various rivers, British Columbia	1951 - 1975	↓ L ₅₀	Ricker (1981)
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Various rivers, British Columbia	1951 - 1975	↓ L ₅₀	Ricker (1981)
Sockeye salmon (<i>Oncorhynchus nerka</i>)	Various rivers, Bristol Bay, Alaska	1969 - 2003	Earlier spawning run	Quinn <i>et al.</i> (2007)
Atlantic salmon (<i>Salmo salar</i>)	Godbout River, Quebec	1859 - 1983	↓ L ₅₀	Bielak and Power (1986)
	4 rivers in N. Spain	1949 - 2000	↓ L ₅₀	Consegra <i>et al.</i> (2005)
	3 rivers in W. and S. Ireland	1926 - 1999	↓ L ₅₀	Quinn <i>et al.</i> (2006)
	River Asón, N. Spain	1948 - 2003	↓ A ₅₀ ↓ L ₅₀	Kuparinen <i>et al.</i> (2009)

Table 3.42: A summary of studies where a selection response in one or more traits (Fisheries induced evolution) has been observed for commercially exploited fish species in the Northern Atlantic. (↑ = increased response, ↓ = decreased response)

<i>Species</i>	<i>Location</i>	<i>Time scale</i>	<i>Response</i>	<i>Reference</i>
Atlantic cod (<i>Gadus morhua</i>)	NE Arctic	1932 - 1998	↓ A ₅₀	Heino <i>et al.</i> (2002)
	Georges Bank	1968 - 2000	↓ A ₅₀	Barot <i>et al.</i> (2004)
	N. Grand Bank	1981 - 2003	↓A ₅₀ ↓ L ₅₀	Olsen <i>et al.</i> (2004)
	Newfoundland/Labrador	1968 - 2001	↓A ₅₀ ↓ L ₅₀	Hutchings (2005)
	Gulf of St Lawrence	1971 - 1998	↓ growth	Sinclair <i>et al.</i> (2002)
	Gulf of St Lawrence	1977 - 1997	↓ growth	Swain <i>et al.</i> (2007)
Atlantic herring (<i>Clupea harengus</i>)	N. Sea	1930 - 2000	↓ A ₅₀ ↑ growth	Engelhard and Heino (2004)
	N. Sea	1990 - 2006	↓A ₅₀ ↓ L ₅₀	Enberg and Heino (2004)
American Plaice (<i>Hippoglossoides platessoides</i>)	NE Atlantic*	1969 - 2000	↓ A ₅₀	Barot <i>et al.</i> (2005)
Sole (<i>Solea solea</i>)	Southern N. Sea	1960 - 2002	↓A ₅₀ ↓ L ₅₀	Mollet <i>et al.</i> (2007)
European plaice (<i>Pleuronectes platessa</i>)	N. Sea	1900 - 1989	↓A ₅₀ ↓ L ₅₀	Rijnsdorp (1993)
	N. Sea	1955 - 2001	↓ A ₅₀	Grift <i>et al.</i> (2003, 2005)
Haddock (<i>Melanogrammus aeglefinus</i>)	N. Sea	1960 - 2002	↑ reproductive investment	Rijnsdorp <i>et al.</i> (2005)
	SE Irish Sea	1970 - 2006	↓A ₅₀ ↓ L ₅₀	This study
Whiting (<i>Merlangius merlangus</i>)	N. Sea	1977 - 1996	↓A ₅₀ ↓ L ₅₀ ↑ fecundity	Wright (2005)
	SE Irish Sea	1975 - 2006	↓A ₅₀ ↓ L ₅₀	Preston (2007)

* 4 separate stocks in the NE Atlantic studied (NE Labrador, Newfoundland, Grand Banks, St Pierre Bank)

identifying the onset of fisheries-induced evolution and remediating its effects early is critical (Mollet *et al.*, 2007). Recent modelling has shown that fisheries-induced evolutionary changes in ages and size at maturation can be reversible (De Roos *et al.*, 2006). De Roos *et al.* (2006) conclude that stepwise changes in maturation age can be used as an early warning of upcoming evolutionary changes which can be used to highlight the need for changes in management and the introduction of restrictions in the fishery.

3.4.3 Can the effects of climate change be detected in the long term population dynamics of plaice in the coastal waters of NW Wales and E Anglesey?

The climate on Earth is changing and the planet warming at an accelerated rate (IPCC, 2007) with knock-on effects for both terrestrial and aquatic ecosystems. It is well known that weather and climate affect the performance of individuals and as a result influence the abundance and distribution of species (Stenseth *et al.*, 2003). Historically ecologists have examined how weather patterns (*i.e.* short term daily and seasonal changes in atmospheric conditions) have influenced abundance and distribution of species on a local scale. However, more recently particular attention has focused on understanding the links between climate (*i.e.* the prevailing weather over the longer term) and ecology in order to predict how future predicted climate change may influence the biosphere and the effect that this may have on the structure and function of terrestrial and aquatic ecosystems (Ottersen *et al.*, 2001; Stenseth *et al.*, 2003; Forchhammer and Post, 2004). Long-term data sets are proving to be a valuable resource in understanding the cyclical nature in the distribution and abundance of marine organisms and analysis of these data sets in relation to climate various environmental/climatic variables is highlighting the effects of climate change on the distribution and abundance of marine organisms (*e.g.* Attrill & Power, 2002; Chavez *et al.*, 2003; Genner *et al.*, 2004; Hawkins *et al.*, 2008; Teal *et al.*, 2008; Polaczanska *et al.*, 2008; Frid *et al.*, 2009). In this section, the data from the RV *Prince Madog* fisheries survey will be used to examine whether changes in the population dynamics of plaice correlate with climatic variables such as sea surface temperature (SST) and climatic indices such as the North Atlantic Oscillation.

A number of dominant global climate patterns have been identified which are known to exert dominant effects on regional weather patterns and therefore regional

ecologies. Stenseth *et al.* (2003) report that there are 17 major large scale climate patterns which are divided by regions into those influencing climate in the North Pacific, the South Pacific and the North Atlantic. The North Atlantic climate patterns include the North Atlantic Oscillation (NAO), the East Atlantic pattern, the East Atlantic/Western Russia pattern and the Scandinavian Pattern (Stenseth *et al.*, 2003). In mid-latitudes in the North Atlantic, the NAO has a climatic influence that rivals that of the El Niño-Southern Oscillation (ENSO) in the Pacific exerting a dominant influence on temperatures, rainfall, storms, fisheries and ecosystems in the North Atlantic region (Marshall *et al.*, 2001). Climate indices such as the NAO and ENSO have been shown to be of great value to ecologists in understanding how climatic fluctuations explain various ecological patterns and processes (Stenseth *et al.*, 2002, 2003). The North Atlantic Oscillation refers to the interaction between two atmospheric masses: a low pressure zone located over Iceland and a high pressure zone located over the Azores (Figure 3.43). The strength of these two pressure systems can vary and this is known to influence weather patterns in Europe through changes in wind speed and direction between 40° N and 60°N affecting heat and moisture transport and the frequency, intensity and direction of storms across North Africa and Europe (Hurrell and van Loon, 1997; Stenseth *et al.*, 2003). Two distinct phases in the NAO have been recognised, a positive phase occurs when the two pressure systems are well developed resulting in stronger than average westerly winds at mid-latitudes which is associated with cold/wet conditions in Northwest Europe and warm/dry conditions in Southern Europe (Figure 3.43a) (Wanner *et al.*, 2001). When the two pressure systems are weaker and the NAO is in negative phase, moist air is directed over Southern Europe and it is relatively drier in Northwest Europe (Figure 3.43a) (Wanner *et al.*, 2001). This pattern of climate anomaly is most pronounced during the winter and the difference between the two pressure systems is used to calculate the North Atlantic Oscillation Index (NAOI). Figure 3.43b shows a plot of the NAOI from 1950 to 2006 which indicates that the general trend was for the NAOI to be in a negative phase in the 1960s and 1970s before entering a positive phase in the 1980s and 1990s. The current trajectory of the plot indicates that the NAO will be entering another negative phase in the 2010s.

One consequence of global climate change and atmospheric warming is a concomitant warming of the world's oceans (Gille, 2002; Gouretski and Koltermann 2007; IPCC, 2007) and some of the most rapid rates of warming are occurring in the

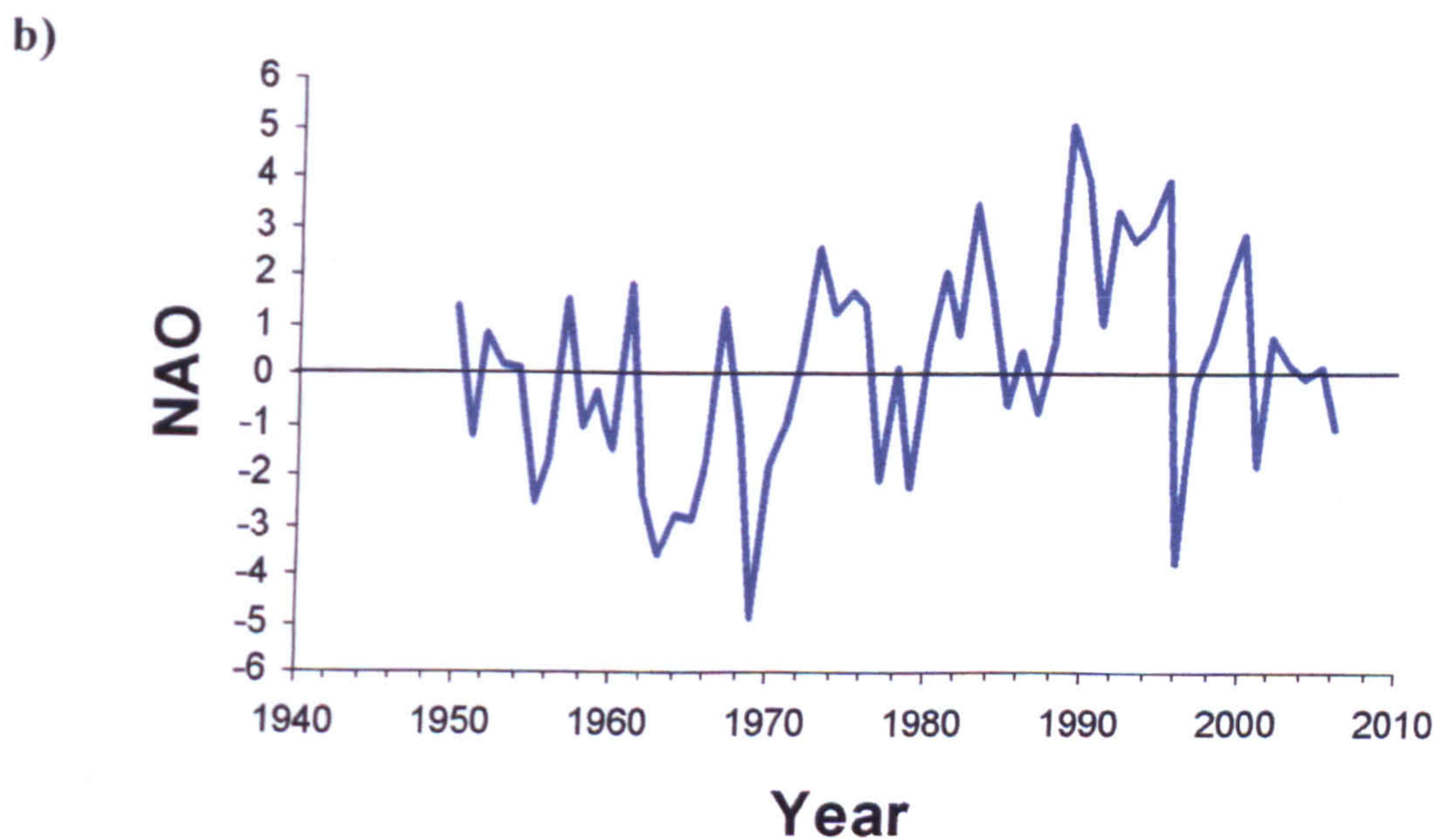
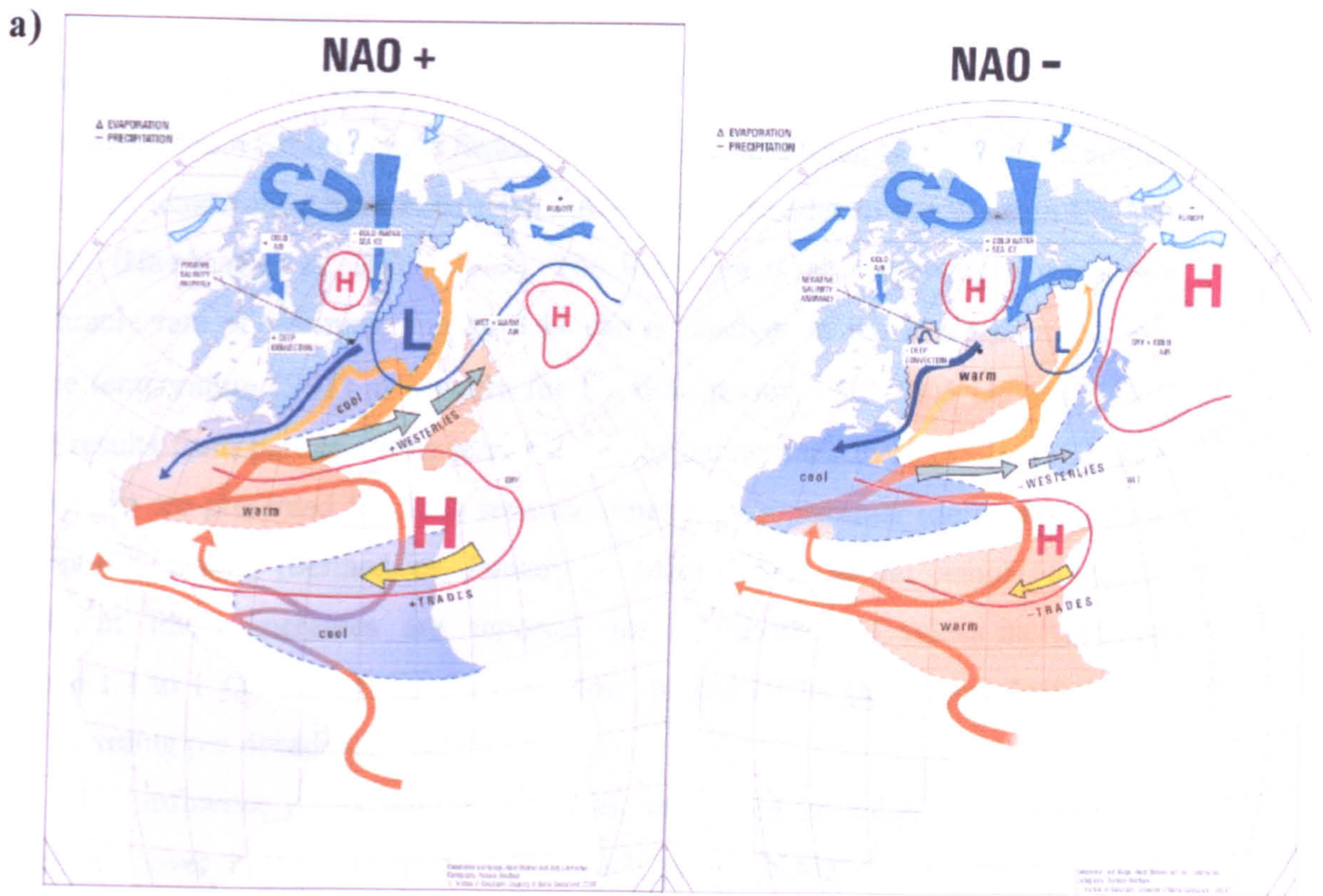


Figure 3.43: (a) Schematic representation of the positive and negative phases of the North Atlantic Oscillation (NAO). Note: L = low pressure, H = high pressure, red and blue represent warm and cold air masses respectively-(Images taken from URL 6). (b) A plot of the winter North Atlantic Oscillation Index 1950-2006.

Northeast Atlantic (IPCC, 2007). Around the UK, it is the western marine water bodies which are warming up the fastest, for example, increases of up to 1°C in annual sea surface temperature have been recorded in recent decades in the Western English Channel (Hawkins *et al.* 2003, 2008). The Irish Sea is also showing a rapid and comparable rate of warming, Figure 3.44 shows changes in the average annual sea surface temperature (SST) at Moelfre for the time period 1970-2006 (Joyce, 2006). These results form part of a long term data series dating back to 1966. The SST data for Moelfre are presented for three separate time periods: summer (defined as July – September), winter (defined as January – March) and as an annual average. Significant linear increases are reported for all three SST values increases of between 1.1 to 1.3°C during the 30 year time period 1970-2000 (equivalent to *ca.* 0.4°C warming per decade) (Figure 3.44).

The influence of temperature changes, expressed as either a °C change in temperature over time or using an index such as the NAO, on the structure and function of intertidal and shelf sea ecosystems has been the focus of much research over the last 10 years (*e.g.* Tunberg and Nelson, 1998; Ottersen *et al.*, 2002; Weijerman *et al.*, 2005; Broitman *et al.*, 2008; Hawkins *et al.*, 2008; Frid *et al.*, 2009). To briefly summarise this large body of research. Climate change has been shown to influence productivity and species composition of phytoplankton (*e.g.* Beaugrand and Reid, 2003; Hays *et al.*, 2005; Miller and Harding, 2007; Heath and Beare, 2008; Sommer *et al.*, 2008) and zooplankton (Tunberg and Nelson, 1998; Beaugrand and Reid, 2003; Hays *et al.*, 2005; Molinero *et al.*, 2008) in shelf sea ecosystems. This variability in production at the base of the food chain has knock-on effects for animals feeding at the secondary consumer level or higher in the food web. Research has shown that changes in SST and NAO correlate with factors such as abundance, adult survival, breeding success, juvenile recruitment and migration behaviour in fishes (*e.g.* Guisande *et al.*, 2001; Arnott and Ruxton, 2002; Salen-Picard *et al.*, 2002; Genner *et al.*, 2004; Hjermann *et al.*, 2004; MacKenzie and Koster, 2004; Sims *et al.*, 2004; Boylan and Adams, 2006; Stige *et al.*, 2006; Henriques *et al.*, 2007; Teixeira and Cabral, 2009) and seabirds (*e.g.* Forchhammer *et al.*, 2002; Durant *et al.*, 2004; Grosbois and Thompson, 2005; Sanvik *et al.*, 2008).

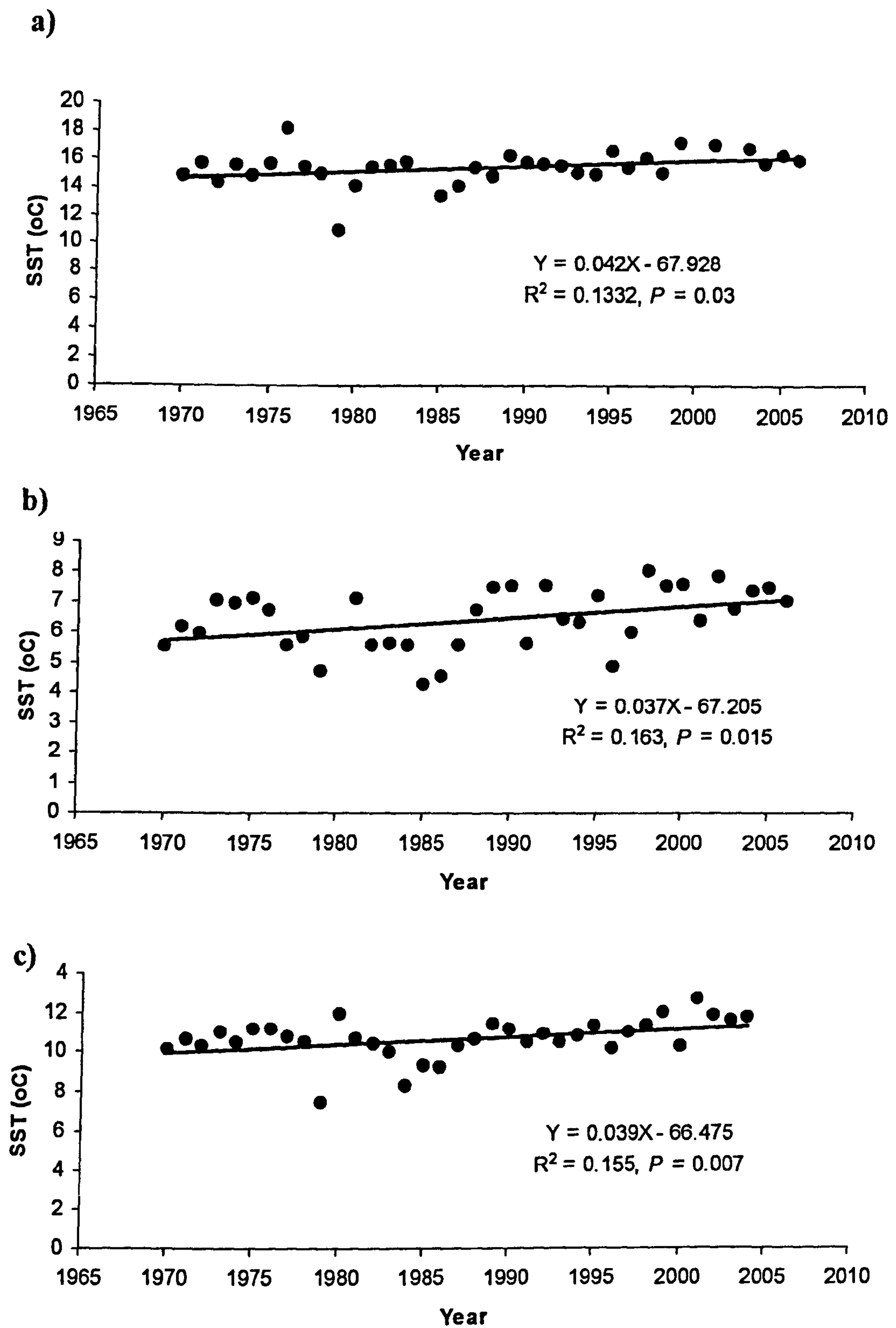


Figure 3.44: Surface seawater temperatures (SST, °C) for Moelfe (Eastern Anglesey) in the Irish Sea for the time period 1970-2006. Data are presented for the average SST in each year for the following time periods: (a) summer (July-September), (b) winter (January-March) and (c) annual. (Data source: Joyce, 2006).

In this section, changes in the population dynamics of plaice between 1970 and 2006 will be examined in relation to SST and the winter NAOI (wNAOI). The winter NAOI will be used as it is at this time of year that the effects of the NAO are strongest (Hurrell and van Loon, 1997; Stenseth *et al.*, 2003) and influences on fishes may be the strongest (*e.g.* Boylan and Adams, 2004). Three SST variables will be examined: summer (defined as July – September), winter (defined as January – March) and the annual average SST (Figure 3.44). The population biology parameters for male and female plaice in any given year that will be examined include abundance (number of fish caught hour⁻¹) modal and average total length, the von Bertalanffy growth coefficients (L_{∞} and K), total mortality rates (Z) and the maturity ogives, L_{50} and A_{50} . These parameters have been selected to examine whether SST or wNAOI have any influence on abundance, growth or reproductive patterns in any given year. Figure 3.45 presents a hypothetical model of how temperature might affect growth patterns. If the temperature conditions (in this case SST or wNAOI) are warmer in any given year then this will result in increased primary and secondary production in coastal shelf seas, which together with slightly warmer water temperatures will provide increased opportunity for growth. Production could be increased either through an earlier start to the phytoplankton bloom in the spring, through increased production over the summer or through a combination of the two. The hypothesis is that increased growth opportunity in inshore waters will result in a larger size-at-age in each cohort and therefore the length frequency distribution would shift to the right in Figure 3.45. This increased growth opportunity would also change the shape of the von Bertalanffy growth curve with plaice as the larger size at age would increase the rate at which the asymptotic maximum size (L_{∞}) is reached and therefore the value for the growth coefficient, K , would be higher in warmer years (Figure 3.45). This increase in the slope on the left hand of the growth curve is predicted to result in a small decrease in L_{∞} (Figure 3.45). In contrast in colder years, when the start of the spring phytoplankton bloom is delayed and lower temperatures affect the magnitude of primary/secondary production during the year, it is predicted that size-at age would be smaller than the long term average during these “cold” years resulting in a shift to the left in the length frequency distribution in Figure 3.45. This would result in a shallower growth curve, reducing the value for the growth coefficient, K , and increasing L_{∞} (Figure 3.45).

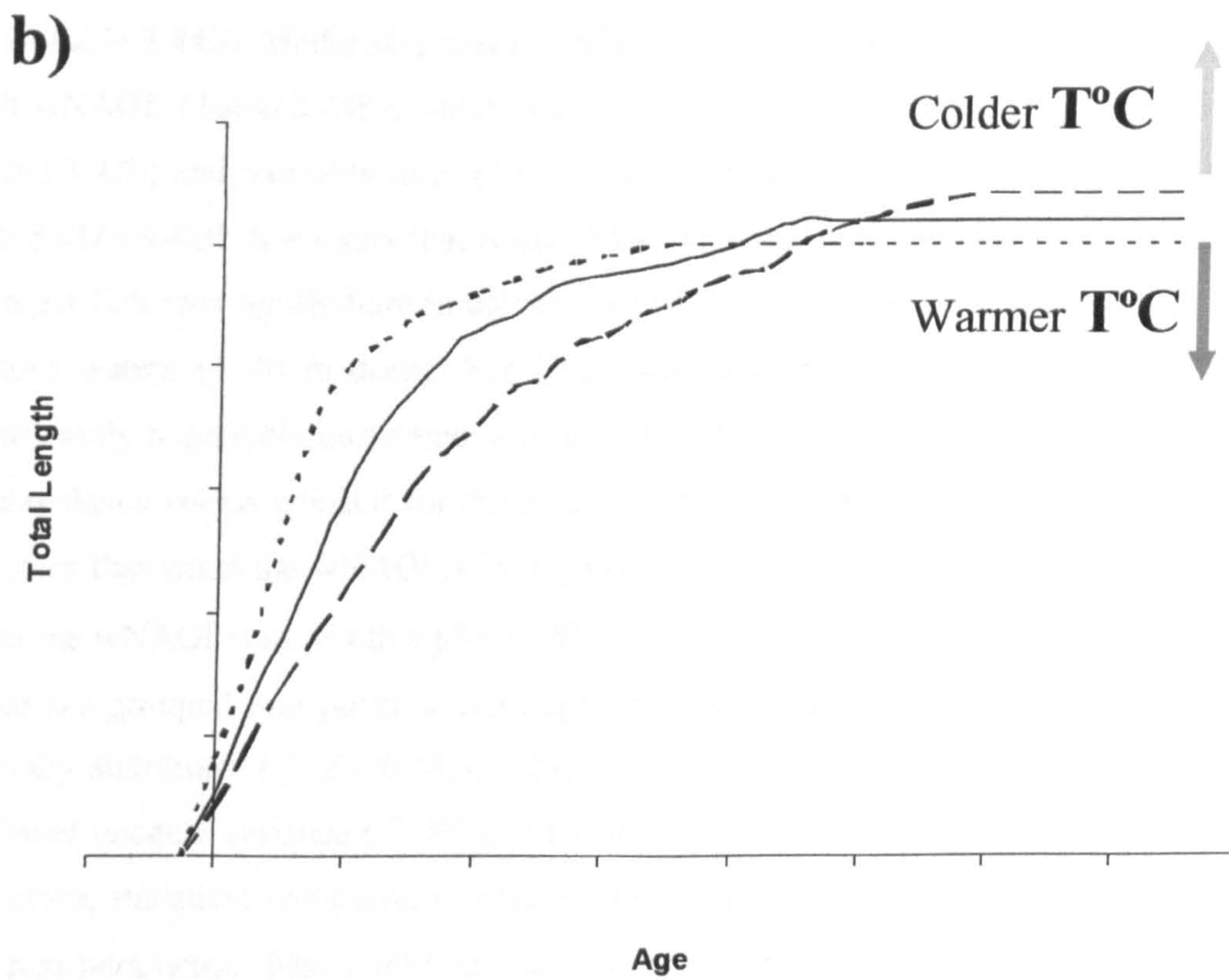
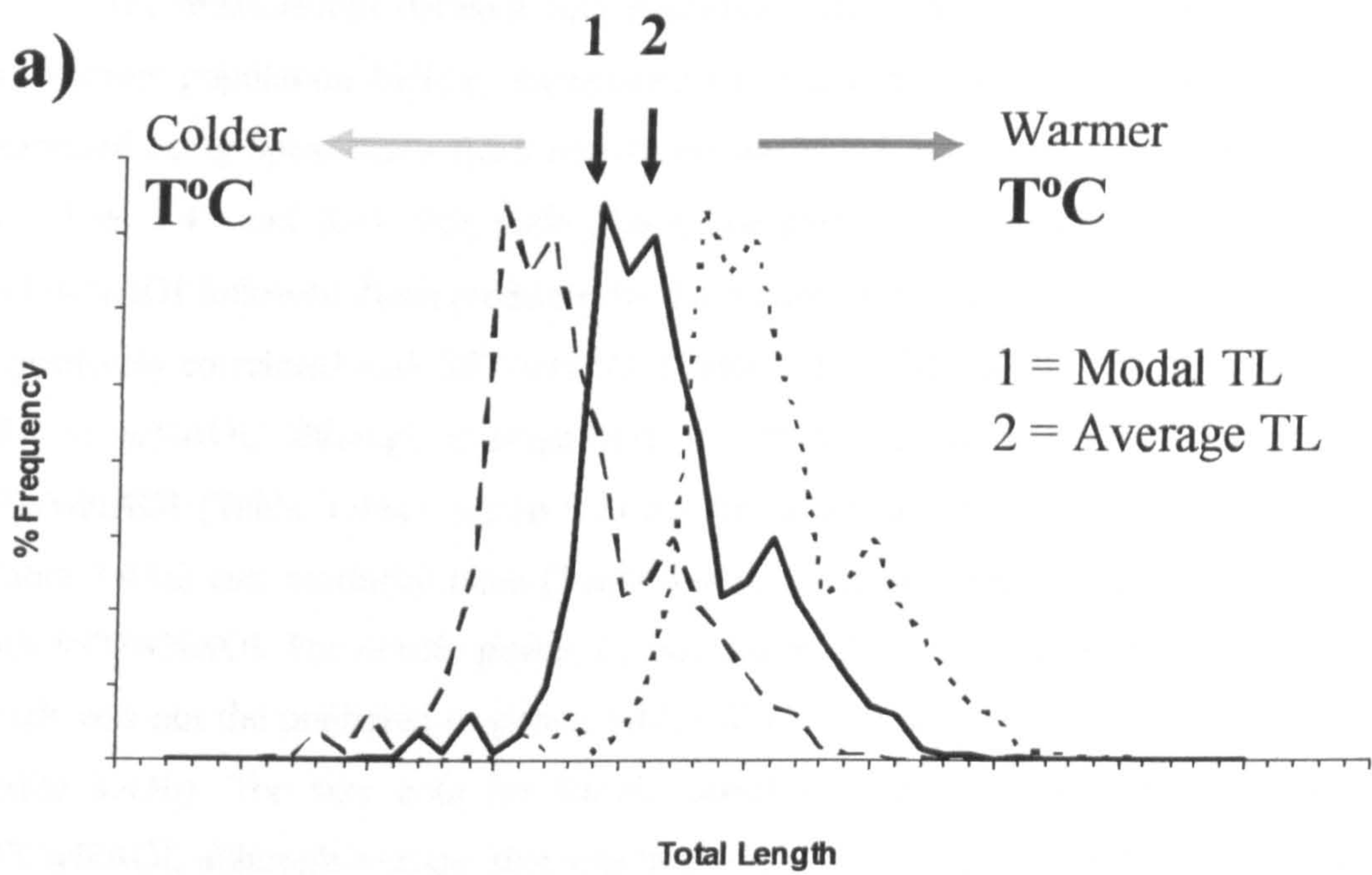


Figure 3.45: Models showing the hypothetical relationships between temperature and (a) length frequency distribution and (b) Von Bertalanffy growth curves for plaice. The dotted line/dark grey arrow and dashed line/light grey arrow represent how warmer or colder temperatures may affect the length frequency distribution and growth pattern of plaice.

The relationships between SST (summer, winter and annual) and wNAOI and the various population biology parameters for plaice between 1970 and 2006 were examined using Spearman's Rank correlation analysis and the results are summarised in Tables 3.43 and 3.44. For male plaice, the correlations between L_{∞} and K and SST/wNAOI followed those predicted by the model with L_{∞} negatively correlated and K positively correlated with SST/wNAOI (Table 3.43a). Modal size was not related to SST or wNAOI, although average size tended to be negatively correlated with SST/wNAOI (Table 3.44a), which was not the predicted response. Maturity ogives (Table 3.43a) and mortality rates (Table 3.44a) for male plaice were not correlated with SST/wNAOI. For female plaice, L_{∞} was positively correlated with SST/wNAOI, which was not the predicted response, whilst K was not correlated with SST/wNAOI (Table 3.43b). The size data for female plaice tended to not be correlated with SST/wNAOI, although average size was negatively correlated with winter and annual SST (Table 3.44b). Modal size was not related to SST in female plaice but correlated with wNAOI, (Table 3.44b), which was not the predicted response. Maturity ogives (Table 3.43b) and mortality rates (Table 3.44b) for female plaice were not correlated with SST/wNAOI. It is likely that some of the correlations observed may be the result of larger fish moving offshore in the winter to avoid colder water temperatures in the inshore waters (< 40 m deep). For both male and female plaice, abundance was significantly negatively correlated with wNAOI (Table 3.44b; Figure 3.46). The plot of abundance versus wNAOI for the time period 1970-2006 presented in Figure 3.46 indicates that when the wNAOI is in negative phase, plaice abundance is higher than when the wNAOI is in positive phase. When the abundance data for male and female plaice are grouped into positive and negative phase values, both data sets were not normally distributed (σ , $Z = 0.18$, $n = 29$, $P = 0.02$; ϕ , $Z = 0.17$, $n = 30$, $P = 0.04$) and exhibited unequal variance (σ , $W_{1,27} = 13.34$, $P = 0.001$; ϕ , $W_{1,28} = 9.29$, $P = 0.005$). Therefore, statistical comparisons were made between the two wNAOI phases using the non-parametric Mann-Whitney test which showed a significant difference between the abundance of female plaice in the two phases ($U = 54.0$, $n = 30$, $P = 0.04$) and a trend for male plaice ($U = 59.0$, $n = 29$, $P = 0.099$). Median (\pm IQ range) in the positive and negative wNAOI phases were 42.4 (\pm 45.8) and 98.4 (\pm 112.2) for female plaice and 58.4 (\pm 75.0) and 104.1 (\pm 214.8) for male plaice respectively.

Table 3.43: Spearman Rank Correlation coefficients (r) and P values for the relationships between climatic variables and population biology variables for plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Climatic variables are summer, winter and annual sea surface temperatures and the North Atlantic Oscillation index (NAOI). Population biology variables are the Von Bertalanffy growth coefficients (L_{∞} and K) and length (L_{50}) and age (A_{50}) at first maturity. Data are presented for (a) male plaice and (b) female plaice.

a)

	Summer SST	Winter SST	Annual SST	NAOI
L_{∞}	r = -0.35 (P = 0.04)	r = -0.46 (P = 0.006)	R = -0.58 (P < 0.001)	r = -0.02 (P = 0.92)
K	r = 0.30 (P = <u>0.08</u>)	r = 0.35 (P = 0.04)	R = 0.30 (P = <u>0.08</u>)	r = 0.06 (P = 0.75)
L_{50}	r = 0.07 (P = 0.75)	r = -0.17 (P = 0.39)	R = -0.26 (P = 0.19)	r = 0.12 (P = 0.54)
A_{50}	r = 0.10 (P = 0.65)	r = -0.14 (P = 0.50)	R = -0.06 (P = 0.76)	r = 0.07 (P = 0.74)

n = 35 for L_{∞}/K , n = 27 for L_{50} , n = 26 for A_{50}

b)

	Summer SST	Winter SST	Annual SST	NAOI
L_{∞}	r = 0.48 (P = 0.004)	r = 0.47 (P = 0.005)	R = 0.32 (P = <u>0.06</u>)	r = 0.38 (P = 0.03)
K	r = -0.25 (P = 0.16)	r = -0.37 (P = 0.03)	R = -0.25 (P = 0.16)	r = -0.17 (P = 0.35)
L_{50}	r = -0.20 (P = 0.33)	r = -0.32 (P = 0.11)	R = -0.12 (P = 0.54)	r = -0.05 (P = 0.82)
A_{50}	r = -0.03 (P = 0.90)	r = -0.23 (P = 0.26)	R = 0.16 (P = 0.46)	r = -0.15 (P = 0.47)

n = 34 for L_{∞}/K , n = 27 for L_{50} , n = 25 for A_{50}

Table 3.44: Spearman Rank Correlation coefficients (r) and P values for the relationships between climatic variables and population biology variables for plaice caught in the autumn surveys conducted by the RV *Prince Madog* for the period 1970-2006. Climatic variables are summer, winter and annual sea surface temperatures and the North Atlantic Oscillation index (NAOI). Population biology variables are modal size (TL_{mod}) and average size (TL_{ave}), abundance (N, number of fish hour⁻¹), instantaneous coefficient of total mortality (Z, year⁻¹). Data are presented for (a) male plaice and (b) female plaice.

a)

	Summer SST	Winter SST	Annual SST	NAOI
TL _{mod}	r = -0.05 (P = 0.79)	r = -0.13 (P = 0.50)	r = 0.07 (P = 0.73)	r = -0.07 (P = 0.71)
TL _{ave}	r = -0.35 (P = 0.047)	r = -0.23 (P = 0.19)	r = -0.38 (P = 0.03)	r = -0.38 (P = 0.03)
N	r = -0.32 (P = <u>0.09</u>)	r = -0.45 (P = 0.39)	r = -0.26 (P = 0.19)	r = -0.52 (P = 0.004)
Z	r = -0.03 (P = 0.87)	r = -0.21 (P = 0.25)	r = -0.23 (P = 0.21)	r = 0.19 (P = 0.33)

n = 33 for TL_{mod}/TL_{ave}, n = 29 for N, n = 30 for Z

b)

	Summer SST	Winter SST	Annual SST	NAOI
TL _{mod}	r = 0.19 (P = 0.33)	r = 0.22 (P = 0.25)	r = 0.18 (P = 0.35)	r = 0.41 (P = 0.03)
TL _{ave}	r = -0.18 (P = 0.32)	r = -0.35 (P = 0.045)	r = -0.46 (P = 0.007)	r = -0.03 (P = 0.89)
N	r = -0.11 (P = 0.57)	r = -0.38 (P = 0.04)	r = -0.37 (P = 0.04)	r = -0.58 (P = 0.001)
Z	r = -0.06 (P = 0.74)	r = -0.44 (P = 0.02)	r = -0.33 (P = <u>0.08</u>)	r = -0.01 (P = 0.94)

n = 33 for TL_{mod}/TL_{ave}, n = 30 for N, n = 29 for Z

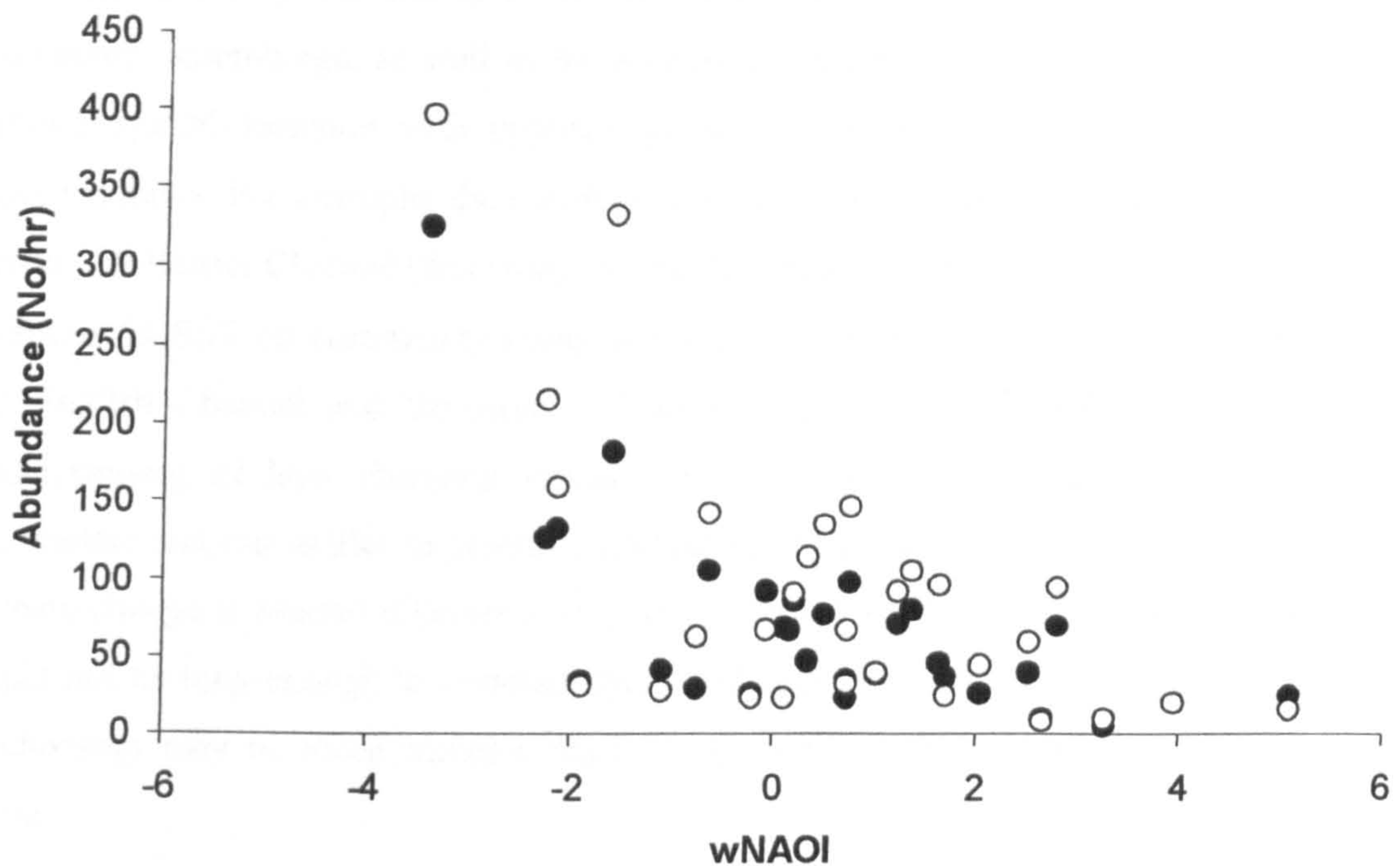


Figure 3.46: Relations between the winter North Atlantic Oscillation Index and abundance of male (open circles) and female (solid circles) plaice *P. platessa* caught in the RV *Prince Madog* fishing surveys conducted in October-December in the inshore waters of NW Wales and E Anglesey (1970-2006).

Previous studies have also shown a correlation between wNAOI and fish abundance. Boylan and Adams (2006) examined the catches of Atlantic salmon caught in the estuary/catchment of the River Foyle in Northern Ireland between 1875 and 2001 and found that the wNAOI was significantly negatively correlated with catches of migrant Atlantic salmon ($r = 0.66$, $P < 0.001$). A more detailed analysis, using breakpoint linear regression revealed that a significant linear relationship existed between salmon catches and wNAOI below index values of 0.151, above this value the relationship between wNAOI and salmon catches was uncoupled (Adams and Boylan, 2006). The results of Boylan and Adams (2006) analyses of a 126 year data set show clearly the influence of wNAOI on salmon abundance but indicate that the value of the NAOI as a predictive tool for forecasting salmon abundance may be limited, since the ability to predict abundance breaks down when the wNAOI is in positive phase. Henderson and Seaby (2005) have also shown that both SST and wNAOI are correlated with the abundance of sole *S. solea* in the Bristol Channel in Southwest England. However, in their study, abundance, growth and recruitment were all positively correlated with SST and wNAOI which is in contrast to the results of other studies (this study; Boylan

and Adams, 2006). As discussed earlier, it is clear that the factors influencing community assemblage, as well as the abundance and growth of individual species, exhibits spatial variation with opposite patterns being observed in geographically close locations. For example, the correlation between abundance and wNAOI in Irish Sea vs. the Bristol Channel (this study vs. Henderson and Seaby, 2005) or the effect of increases in SST on community composition and abundance of fish assemblages in the English Channel and the Bristol Channel (Genner *et al.*, 2004). Clearly our understanding of how changing climate processes impact on marine ecology is incomplete and our ability to predict a community-level or species-level response to climate change is limited (Genner *et al.*, 2004). Therefore, the time period examined might not be long enough to correlate these biological variables with NAOI and the relationship may be more complex than can be solely correlated with temperature alone.

3.4.4 Summary

- This chapter has presented a detailed analysis of the population biology of plaice *P. platessa* L. in the coastal waters of Northwest Wales and Eastern Anglesey based on the fish caught in the RV *Prince Madog* autumnal fisheries surveys between 1970 and 2006.
- The fisheries survey has sampled the same inshore (Red Wharf Bay, Conwy bay, Colwyn Bay) and offshore (Offshore Point Lynas, Offshore Colwyn Bay) locations each year using the same fishing gear (Rockhopper otter trawl; cod-end stretched mesh size, 76 mm) using a standardised sampling technique. Fishing effort consisted of 13.2 ± 6.8 trawls per year with an average trawl tow time of 59 ± 14 minutes.
- When the data were grouped into 5 year time intervals (1970-1974, 1975-1979 etc), fishing effort in terms of number of trawls was similar between 5 year time periods but trawls times were significantly lower in 1985-1989 and 1990-1994, therefore catches were expressed per unit time.
- Although there were no differences in the number of plaice caught hour⁻¹ between 5 year time periods, a cyclical trend in abundance was apparent in the

data which was correlated with the winter index for the North Atlantic Oscillation.

- Analysis of the size data between 1970 and 2006 indicated that there were no changes in the minimum or maximum size caught or in the size range of fish caught for male and female plaice. There was no change in the modal size class for female plaice between 1970 and 2006, however the modal size of male plaice decreased from *ca.* 23 cm to *ca.* 20 cm Total Length. When the size data for male and female plaice between 1970 and 2006 is taken in its entirety, the results indicate that the size composition of the plaice caught in the fisheries surveys has not changed over the last 4 decades.
- Analysis of the age structure of the catches between 1970 and 2006 indicated that there were no significant changes in the percentage composition of the main age classes (0-4 years old). However, maximum ages of male and female plaice, and therefore average ages of plaice, decreased over time.
- Analysis of the sex-ratio data between 1970 and 2006 indicated a decrease in the number of male plaice caught in the fisheries surveys over the last 4 decades.
- The size at age data from the fisheries surveys were used to derive von Bertalanffy growth curves for male and female plaice. Analysis of the theoretical maximum total length (L_{∞}) for male and female plaice indicated that the two sexes showed contrasting patterns. For female plaice, L_{∞} tended to increase over time, although this was not significant at the 5% level. For male plaice, L_{∞} increased between the 1970s and 1980s before returning to L_{∞} values in the 1990s and 2000s that were similar to the 1970s values. The von Bertalanffy growth coefficient (K , year⁻¹) values for male and female plaice between 1970 and 2006 were examined. This analysis indicated that there had been little significant, long-lasting change in K values over time for female plaice, however, K values for male plaice indicated a significant increase post-1990 compared to K values in the 1970s and 1980s.
- The size at age data were grouped in 5 year time intervals to examine whether the pattern of growth, as assessed by the shape of the von Bertalanffy growth curve, had changed over time for male or female plaice. This analysis revealed that, although there were differences for both sexes in the shape of the growth

curve between time periods, when each time period was compared to the long-term 36 year average growth curve, the only 5 year time period that exhibited a significant difference in shape for both male and female plaice was 2000-2006.

- Data for maturity ogives, *i.e.* length and age at 50% maturity (L_{50} and A_{50}) between 1970 and 2006 were the most limited data set. Analysis of the available data indicated a decrease in L_{50} and A_{50} values for male and female plaice over time.
- The population biology data for plaice, a stock which is currently under-exploited but historically was overexploited in the 1970s and 1980s, were compared with the population biology data for dab *L. limanda* (an unexploited species) and whiting *M. merlangus* (an overexploited species) obtained from the same fisheries surveys.
- Analysis of the time series data revealed changes in the size and growth patterns for the three species (*i.e.* no changes for dab vs. changes for plaice and whiting) that were consistent with their levels of fisheries exploitation. A similar analysis for maturity ogives for the three species was more limited but evidence of decreases in L_{50} and A_{50} values were evident for plaice and whiting compared to dab. These results are suggestive of fisheries-induced evolution in plaice and whiting in the Southeast Irish Sea.
- The population biology of plaice in the coastal waters of Northwest Wales and Eastern Anglesey were examined in relation to summer, winter and annual sea surface temperatures (SST) and the winter North Atlantic Oscillation index (wNAOI) to examine whether any changes in population biology were related to recent climate change. This analysis indicated a correlation between the abundance of male and female plaice and the wNAOI with higher abundances recorded when the wNAOI was in negative phase. A simple model outlining the effects of increased/decreased SST on size and growth was proposed. For male plaice, the correlations between L_{∞}/K and SST/wNAOI followed those predicted by the model, but the predicted response was not observed for female plaice.
- Although the results of this chapter have shown clear, significant correlations between the population biology of plaice and both fishing pressure and recent

climate change, it is obvious that the relationships are complex. It is recommended that a more detailed, multivariate analysis of the data is conducted in order to further investigate the data and to identify the relative importance of these two factors on the population biology of plaice in the coastal waters of Northwest Wales and Eastern Anglesey.

Chapter 4:

Growth of juvenile plaice *Pleuronectes platessa* L. in Red Wharf Bay and Conwy Bay (2004-2006).

4.1 Introduction

Although plaice *P. platessa* L. in the Irish Sea (ICES region VIIa) are managed by ICES as a single management unit (ICES, 2008a), 4 sub-stocks have been recognised by Dunn and Pawson (2002) in the North East Irish Sea, South East Irish Sea, Cardigan Bay and Western Irish Sea. Tagging studies conducted over the last 30 years have shown that each of these substocks has their own spawning ground and nursery grounds within the geographic area of the Irish Sea in which they are located (Dunn and Pawson, 2002; Figure 4.1). It is thought that each of these 4 substocks are relatively self-contained with little movement/exchange of fish between the different regions (Dunn and Pawson, 2002), although recent modelling work has suggested that, due to the prevailing winds and currents in the Irish Sea, spawning in the western Irish Sea could supply juveniles into nursery grounds in the Eastern Irish Sea along the Scottish, English and Welsh coasts (Fox *et al.*, 2009).

In the South east Irish Sea, plaice are known to spawn in an area of Liverpool Bay that is about 10 miles north of the Great Orme (Simpson, 1959; Macer, 1967; Basimi and Grove, 1985c; Armstrong *et al.*, 2001; Dunn and Pawson, 2002). Fertilised eggs and the subsequent larval stages are transported away from this spawning ground and, under the predominant influence of wind-driven currents, drift passively into coastal areas where suitable nursery grounds are located (Fox *et al.*, 2006, 2007) and where the plaice undergo metamorphosis and settle (Gibson, 1999; Fox *et al.*, 2007). The timing and length of the spawning season can vary, but spawning usually takes place between January and May with peak spawning usually between mid-February and mid-March (Al-Hossaini *et al.*, 1989; Fox *et al.*, 2007). Plaice are batch spawners and during the spawning season individual mature females will come into ovulation at different times within the 3 to 5 month spawning season and release batches of eggs at 2 to 5 day intervals over a 4 to 6 week period (Rijnsdorp, 1989; Nash *et al.*, 2000). This results in the immigration of newly settled juveniles into the coastal nursery grounds in 'pulses' (Rijnsdorp *et al.*, 1985; van der Veer, 1986; Al-Hossaini *et al.*, 1989; Hovenkamp, 1991; Fox *et al.*, 2007). The timing of when the newly settled juveniles first appear on the nursery grounds and the timing and magnitude of each settlement 'pulse' also varies from year to year (Lockwood, 1974; Zijlstra *et al.*, 1982; Al-Hossaini *et al.*, 1989; Nash and Geffen, 2000; van der Veer *et al.*, 2000; Wennhage and Pihl, 2001).

Once the juvenile plaice have settled out and recruited onto the nursery ground they will remain there for at least one year until they move offshore and recruit into their parent spawning stock (Lockwood and Lucassen, 1984) although some studies have shown that fish can remain on the nursery ground for up to 24 months before migrating offshore to recruit (Nash *et al.*, 1992). Research has shown that they settle out in about 5m water depth (Lockwood, 1974) and then move inshore to concentrate in waters < 1m deep to feed whilst 30-50 mm in size (Gibson *et al.*, 2002). 0-group plaice are known to exhibit diurnal movement patterns in the shallow waters (Burrows *et al.*, 1994; Gibson *et al.*, 1998) and within their first year of growth they undertake a seasonal migration into deeper water (Lockwood, 1974; Gibson *et al.*, 2002).

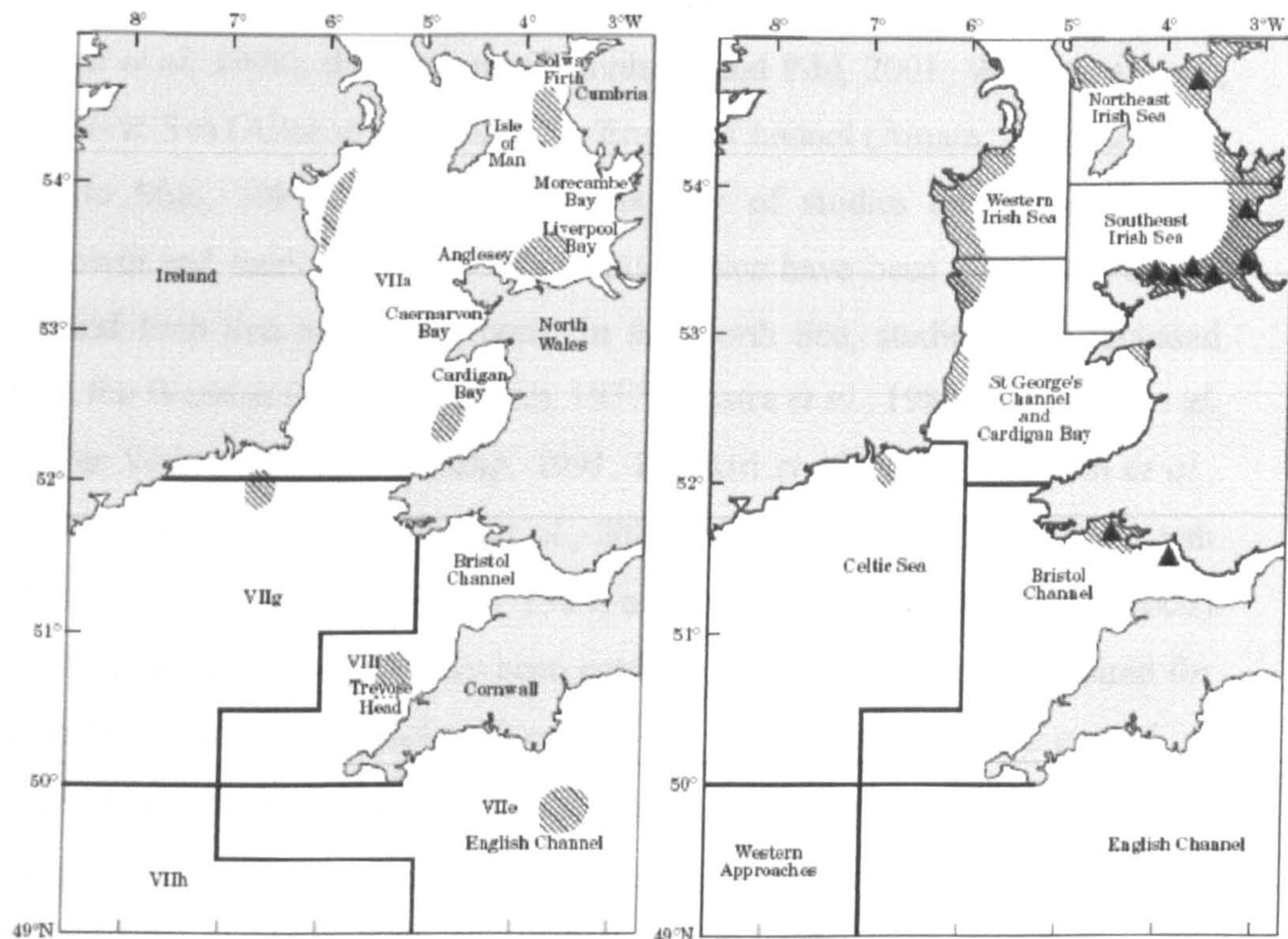


Figure 4.1: Maps of the West coast of England and Wales showing the ICES divisions and approximate locations of the main spawning grounds (hatched areas in the left panel) and the approximate locations of the main nursery grounds (hatched areas in the right panel). Nursery grounds have been defined from CEFAS beam trawl surveys (1986-2000) where the mean abundance of plaice < 16 cm Total Length was > 50 fish hour⁻¹. (Figure taken from Dunn and Pawson, 2002).

As juvenile plaice attain *ca.* 50 mm in size, they move offshore and a positive relationship exists between size and depth such that fish between 60-80 mm are found between 1.5-3.0m water depth and 100 mm plaice are found at depths in excess of 4m (Gibson *et al.*, 2002). Alongshore dispersal and site fidelity were examined by Burrows *et al.* (2004) using a tagging/transplantation experiment to show that 0-group plaice exhibit limited movement (< 500 m movement in 40 days) and a high degree of long-shore site fidelity despite undertaking depth-related migrations within a relatively homogenous sandy habitat.

Studies into the post-settlement survival, growth and feeding ecology of juvenile plaice on their nursery grounds have been conducted throughout the geographical range for the species in the North Atlantic, for example Iceland (Hjörleifsson and Pálsson, 2001), the West coast of Scotland (Edwards and Steele, 1968; Gibson *et al.*, 1998), the Kattegat (Wennhage and Pihl, 2001; Wennhage *et al.*, 2007), the Celtic Sea (Allen *et al.*, 2008), the English Channel (Amara, 2004) and Bay of Biscay (le Mao, 1986). However, the majority of studies on post-settlement survival, growth and feeding ecology of juvenile plaice have been conducted on the North Sea and Irish Sea nursery grounds. In the North Sea, studies have focussed primarily on the Wadden Sea (*e.g.* Kuipers, 1977; Zijlstra *et al.*, 1982; Rijnsdorp *et al.*, 1985; van der Veer, 1986; Hovenkamp, 1991; Karakiri *et al.*, 1991; Bergahn *et al.*, 1995; van der Veer *et al.*, 2000; Teal *et al.*, 2008) but have also included the North East coast of England (Lockwood, 1974, 1984) and the Southern Bight (Amara, 2003). In the Irish Sea, studies have primarily been conducted on a small nursery ground for the North east Irish Sea plaice stock in Port Erin Bay on the Isle of Man (*e.g.* Nash *et al.*, 1992, 1994; Hyder and Nash, 1998; Nash and Geffen, 1999, 2000; Nash *et al.*, 2007). The post-settlement survival, growth and feeding ecology of juvenile plaice in the South East Irish Sea have been less studied. At the time of the inception of the study presented in this chapter (2004), research had been limited to two studies on trophic ecology (Macer, 1967; Carter *et al.*, 1991) and one study on growth and mortality (Al-Hossaini *et al.*, 1989). However, in recent years, a series of studies by Fox and co-workers have been published which have examined the dispersal patterns of eggs and larvae away from the spawning ground in Liverpool Bay (Fox *et al.*, 2006; von der Molen *et al.*, 2007; Fox *et al.*, 2009) and the settlement dates and size/age structure on the nursery grounds in the South East Irish Sea (Fox *et al.*, 2007).

It is clear from the references cited above that the post-settlement survival, growth and feeding ecology of juvenile plaice have been well studied. However, as Nash and Geffen (2000) highlight, it is important to study these processes on nursery grounds throughout the range for the species since the factors influencing survival, growth and recruitment (such as temperature, food availability and predation pressure) could vary with location. The data on the size structure and growth rates of juvenile plaice on the nursery grounds along the coast of North West Wales and Eastern Anglesey are still extremely limited (*e.g.* Al-Hossaini *et al.*, 1989).

The aims of this chapter:

- 1) To examine changes in the size frequency distributions for juvenile 0-group plaice on two nursery grounds (Red Wharf Bay and Conwy Bay) along the coast of North West Wales and Eastern Anglesey during their first year of residence on the nursery ground.
- 2) To examine the growth rates of juvenile 0-group plaice on two nursery grounds (Red Wharf Bay and Conwy Bay) along the coast of North West Wales and Eastern Anglesey during their first year of residence on the nursery ground.
- 3) To examine the length-weight relationship, and using these data to calculate and examine changes in condition factor for juvenile 0-group plaice on two nursery grounds (Red Wharf Bay and Conwy Bay) along the coast of North West Wales and Eastern Anglesey during their first year of residence on the nursery ground.
- 4) To compare the growth rates and condition of juvenile 0-group plaice on two nursery grounds (Red Wharf Bay and Conwy Bay) along the coast of North West Wales and Eastern Anglesey with the available data for other nursery grounds throughout the geographical range for the species.

4.2 Materials and methods

4.2.1 Field and lab work

Juvenile plaice *P. platessa* were collected from two nursery grounds in the coastal inshore waters of North West Wales and Eastern Anglesey: Llanfairfechan in Conwy Bay (52°16' N, 3°58' W; NGR SH67955) and Llanddona in Red Wharf Bay (52°18' N, 4°9' W; NGR SH566807) (Figure 4.2). Fish were collected from April 2004 until March 2007 to follow three successive cohorts of 0-group juvenile plaice (2004, 2005 and 2006) through their first year on the two nursery grounds. The initial settlement of juvenile plaice is known to take place around March/April (Al-Hossini et al., 1989; Basimi and Grove, 1985c) so push-net sampling was initiated in March to ensure that settlement-sized plaice were sampled. Initially samples were collected every two weeks for the first three months after settlement and thereafter samples were collected monthly. However, it was not possible to collect samples by boat for some months due to adverse weather conditions during the winter. Samples were therefore not collected from Llanfairfechan during the following months: December 2004; January – February and October 2005; February, May and November 2006; February 2007. Samples were also not collected from Llanddona during the following months: October and December 2004; January, March, April and October 2005; February, July and November 2006; February 2007.

Sampling on the two nursery grounds was limited to a restricted area (Figure 4.2). After settlement in April/May (depending on year), Juvenile plaice (predominately post-settlement 0-group fish) were caught at low tide using the push net (5 mm code end) for the first 4-5 months. Fish usually caught in the outflow from small streams draining into each sampling area, in shallow water at the low tide mark, or in lagoons left behind on the beach by the retreating tide. As the year progressed from summer to autumn, the juvenile fish began to offshore into deeper water than could be sampled by pushnetting and therefore sampling was conducted by both pushnetting (to catch the late settlement 0-group plaice) and by beam trawl (to catch the largest, early-settled 0-group plaice). From the late autumn onwards and over the winter, sampling was conducted by beam trawling only. Beam trawling was conducted using a 1.9 m beam trawl gear with a 4 m long net comprising of 2 m of net with a mesh size of 15 mm and a 2 m long cod end with a stretched mesh size of 10

mm. The beam trawl was deployed from a 5 meter small boat equipped with a 60 hp engine. Tows were conducted for 10 minutes at an average speed of 1.6 knots depending on the tide and wind direction. Trawls were initially conducted in the autumn at the depth of *ca.* 3 m at the beginning of autumn increasing to 7 m over the winter. The sea bed of both sampling locations in Red Wharf Bay and Conwy Bay are sandy with no rocks or obstructions (Rees, 2004; Berwyn Roberts per. Obs.). A target sample size of 100-200 fish each month was aimed for, although in some months, particularly during the winter, it was not possible to collect this number of plaice within the time available in the field. In addition, because of time constraints and logistics, beam trawling was restricted to 8 trawls of ten minutes tow per site. Sampling bycatch varied depending on the method used with pushnetting bycatch comprising principally of dab *L. limanda*, and brown shrimp *C. crangon*, whilst a wider range of bycatch were collected by beam trawl. The beam trawl bycatch comprised of dab, lesser weever fish *Echiichthys vipera*, sand smelt *Atherina presbyter*, pipefish *Sygnathus* sp., whiting *M. merlangos*, cuttlefish *Sepiola atlantica*, shore crab *Carsinus meanas*, common starfish *Asterias rubens*, sea cucumber *Holothuria forskali*, brown shrimp and brittle stars *Ophiura* spp.

All juvenile plaice caught were kept alive in a small bucket filled with sea water and aerated using a small battery-powered air pump until return to the laboratory. In the laboratory, the fish were killed in accordance with home office regulations using a Schedule 1 method by overdose in seawater a solution containing 2-phenoxyethanol (Sigma, UK). Care was taken with anaesthetic overdose to ensure that the very small 0-group plaice were killed rapidly but did not bend as this made morphometric measurement more difficult to obtain. After anaesthetisation and death, the total length (TL) and standard length (SL) of each fish were measured to the nearest 0.5 millimetre using vernier callipers for small 0-group fish and to the nearest millimetre using a measuring board for the larger juvenile plaice. In addition, the fish were carefully blotted dry and their wet weight measured to the nearest milligramme. For the monthly samples where > 200 fish were caught, a random sample of 100-150 fish were measured by resuspending in the water by stirring and dipping a small net in to collect fish. All fish sampled were placed on foil, identified by a unique code (to identify location, date and fish number) and frozen in case they were needed for any subsequent work. All field work and laboratory was conducted in accordance with the

School of Ocean Sciences (SOS) health and safety risk and assessment COCHH protocols.

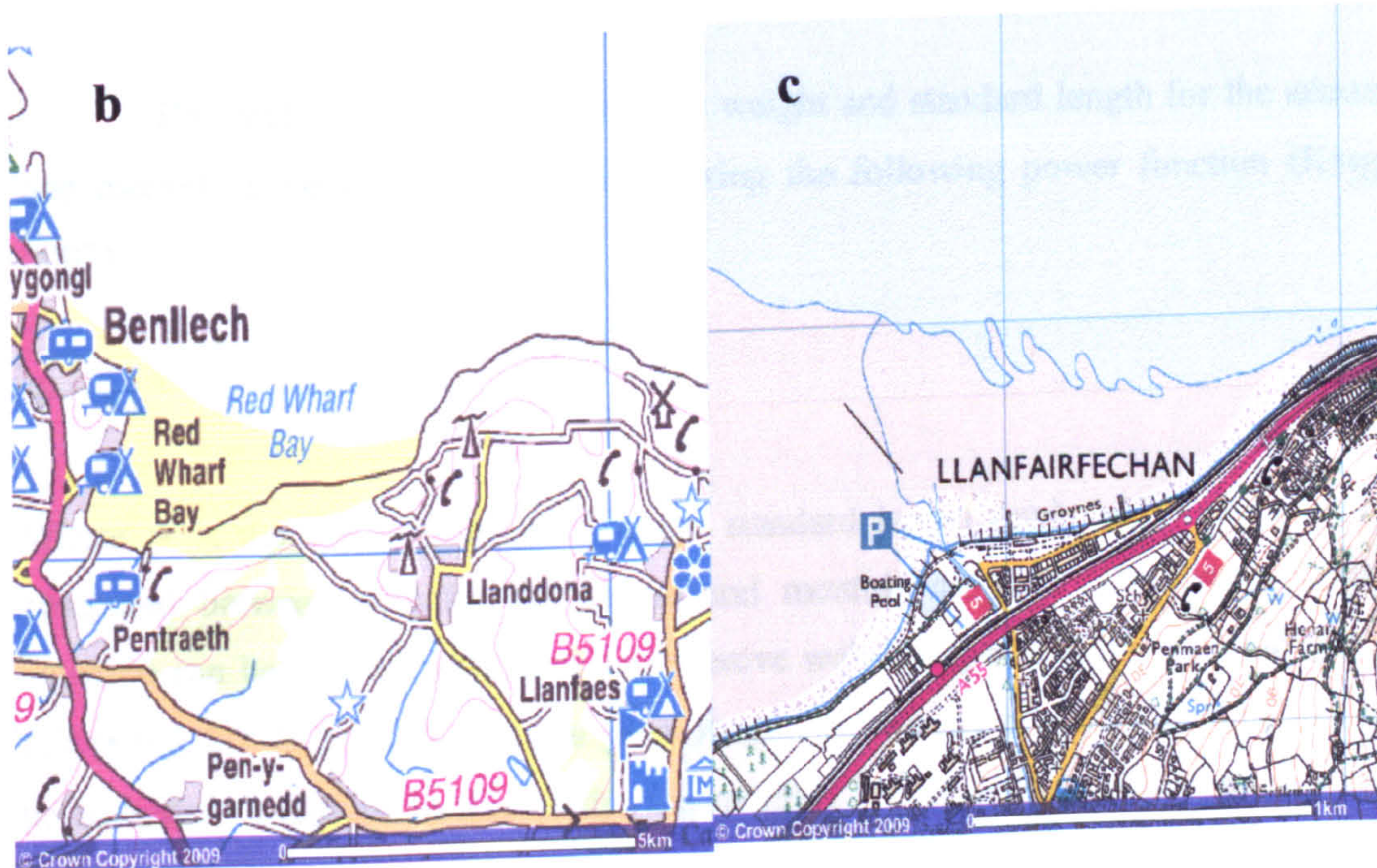
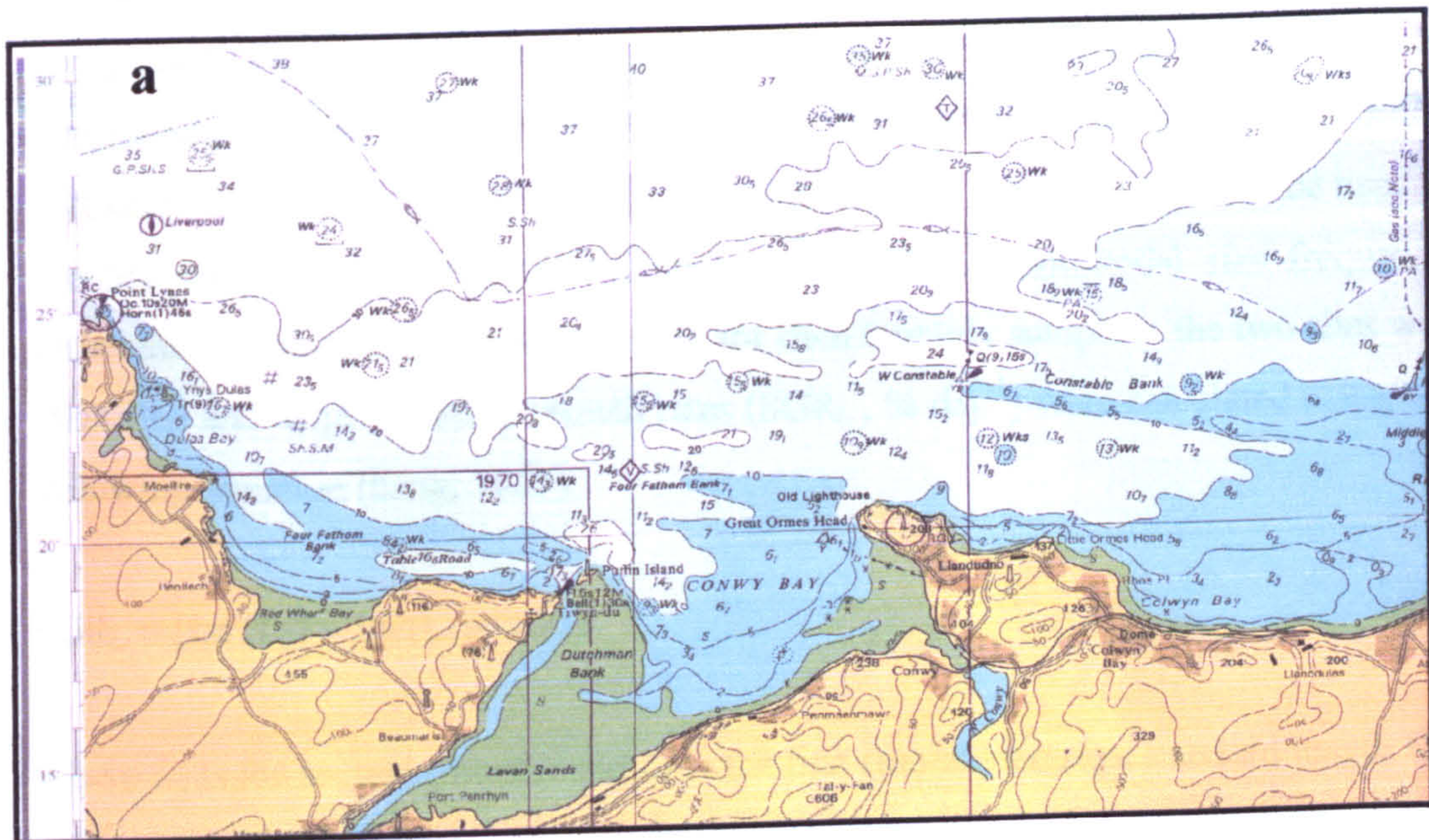


Figure 4.2: a) A wide view of Red Wharf Bay and Conwy Bay, b) Red Wharf Bay, c) Conwy Bay.

4.2.2 Data analysis

In order to standardise for differences in sample size, annual and monthly percentage length-frequency distributions are presented. In order to identify the 0-group and 1-group cohorts of juvenile plaice in the 2004-2007 data, modal progression analysis (Bhattacharya's method) was performed using the FAO FiSat software (Gayanilo and Pauly, 1995 and 1997). This is a method which can be used to identify cohorts of normally distributed data within a multimodal size frequency distribution. The average standard length for each monthly sample at the two sites was identified and length-specific growth rates (SGR_L , % day⁻¹) were calculated using the following equation (King, 2007):

$$SGR_L = [\ln(L_2) - \ln(L_1)] * 100/t$$

Where L_2 is the second (month) and L_1 is the first (month) average standard length for two months samples and t is the time interval by days between the two samples.

The relationship between the body weight and standard length for the annual and monthly samples were determined using the following power function (King, 2007):

$$W = a L^b$$

Where W is the wet weight (g), L is the standard length (cm), and a and b were compared between sites for the annual and monthly samples. The length-weight equation can be used to determine the "relative well-being or condition factor" for a fish (King, 2007). For two fish of a given length, the heavier of the two can be said to be in better condition. In this study, the monthly length-weight relationships were used to calculate the average condition factor (CF) using the following equation (King, 2007):

$$CF = W_m/W_p$$

Where W_m is the average wet weight for that monthly sample and W_p is the predicted wet weight for a fish of the average standard length for that monthly sample, determined from the length-weight relationship for that month (King, 2007).

4.3 Results

4.3.1 Monthly size frequency distributions

The total number and size range of fish sampled from the Llanfairfechan area of Conwy Bay and the Llanddona area of Red Wharf Bay between April 2004 and March 2007 are shown in Table 4.1. The length frequency distributions of all juvenile plaice caught at Llanfairfechan and Llanddona in 2004, 2005 and 2006 are shown in Figure 4.3. The maximum size of juvenile plaice caught were *ca.* 15 cm SL and 50-60 g wet weight (Table 4.1). In most years, more juvenile fish were collected from Llanfairfechan compared to Llanddona. Data on the monthly sampling at the two sites are shown in Table 4.2 (Llanfairfechan) and Table 4.3 (Llanddona).

Table 4.1: Summary stats for annual catches for juvenile plaice *P. platessa* L. caught in (a) Llanfairfechan (Conwy Bay) and (b) Llanddona (Red Wharf Bay).

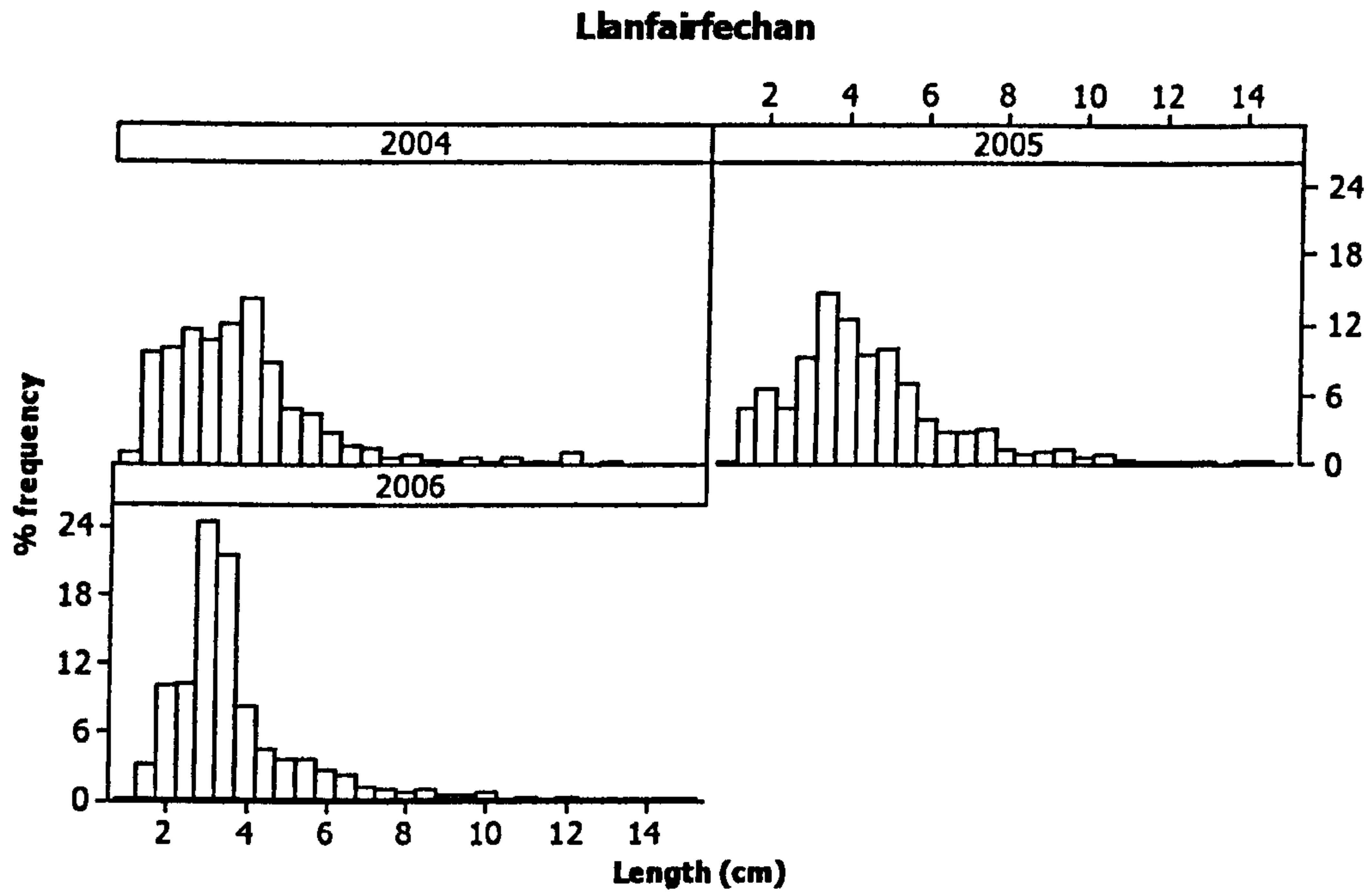
a)

	Year	N	Average	Median	Minimum	Maximum
Length (cm)	2004-05	970	3.837	3.543	1.160	14.800
	2005-06	812	4.537	4.108	1.115	14.600
	2006-07	1066	3.702	3.300	1.300	15.030
Weight (g)	2004-05	970	1.988	0.676	0.016	50.773
	2005-06	812	2.248	1.049	0.018	50.576
	2006-07	1066	1.439	0.554	0.025	55.914

b)

	Year	N	Average	Median	Minimum	Maximum
Length (cm)	2004-05	990	3.855	3.500	1.160	14.800
	2005-06	610	3.611	2.953	1.115	14.600
	2006-07	818	3.290	3.400	1.300	15.030
Weight (g)	2004-05	990	1.900	0.680	0.022	33.817
	2005-06	610	1.986	0.404	0.011	64.645
	2006-07	818	1.613	0.877	0.016	60.329

a)



b)

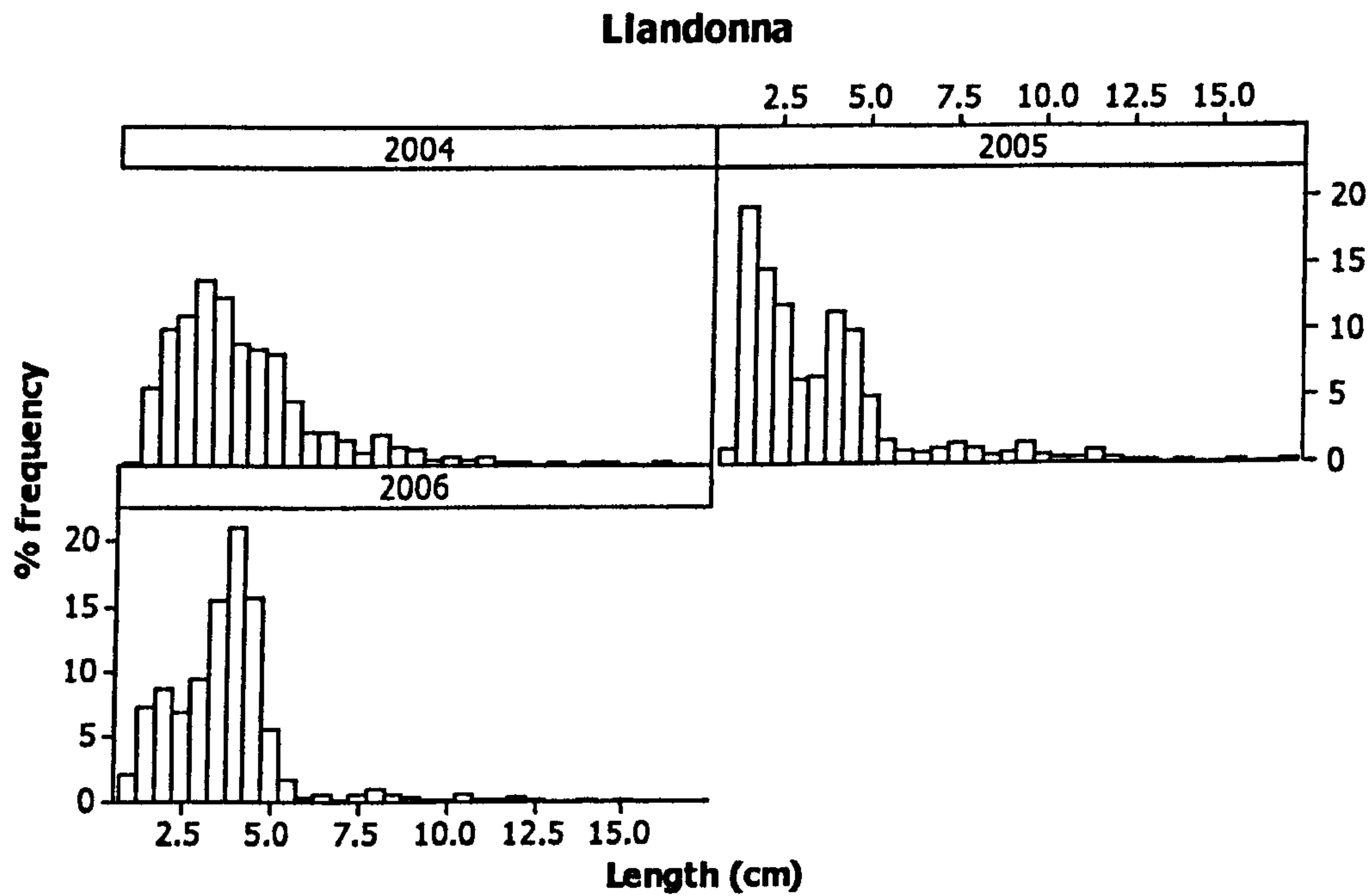


Figure 4.3: Annual percentage length-frequency distributions of juvenile plaice *P. platessa* L. caught in (a) Llanfairfechan (Conwy Bay) and (b) Llandonna (Red Wharf Bay) in 2004, 2005 and 2006.

Table 4.2: Summary statistics for the standard length data (cm) for the monthly catches for juvenile plaice *Pleuronectes platessa* L. caught in Llanfairfechan (Conwy Bay) between April 2004 and March 2007.

Month	n	Average	Median	Minimum	Maximum
Apr-04	75	1.478	1.390	1.200	2.500
May-04	149	2.054	2.100	1.160	3.745
Jun-04	150	2.654	2.598	1.620	4.735
Jul-04	75	4.084	3.485	1.980	11.865
Aug-04	100	3.526	3.403	2.625	5.680
Sep-04	100	4.474	4.185	3.040	11.975
Oct-04	100	4.742	4.228	3.240	11.775
Nov-04	172	6.436	5.710	3.115	14.800
Mar-05	49	4.471	4.310	3.420	5.780
Apr-05	62	6.313	6.105	4.220	9.485
May-05	100	1.875	1.813	1.115	3.280
Jun-05	100	3.147	3.030	1.770	5.440
Jul-05	100	3.520	3.510	2.360	5.435
Aug-05	100	3.982	3.778	3.005	7.475
Sep-05	100	4.258	4.000	2.900	8.130
Nov-05	41	8.951	8.900	3.800	14.600
Dec-05	43	6.053	5.100	4.110	14.000
Jan-06	17	6.749	5.850	4.000	12.025
Mar-06	149	5.853	5.400	3.650	12.400
Apr-06	111	2.125	1.940	1.400	7.300
Jun-06	152	2.590	2.525	1.550	4.640
Jul-06	214	3.393	3.140	2.060	8.550
Aug-06	152	3.946	3.325	1.300	8.500
Sep-06	105	3.804	3.310	2.500	8.430
Oct-06	151	4.287	3.550	3.020	12.000
Dec-06	111	5.075	4.500	3.050	11.400
Jan-07	47	5.370	5.000	3.330	15.030
Mar-07	23	5.571	4.800	3.540	12.100

In most months the target sample size of >100 fish was collected, although over the winter months when sample collection was switched from push netting to beam trawling, monthly sample sizes were smaller at between 9 to 43 fish (Tables 4.2 and 4.3). Juvenile plaice were harder to collect from Llanddona during the winter compared to Llanfairfechan. Due to bad weather, it was not possible to collect fish in some winter months: this presented more of a problem in Red Wharf Bay than Conwy Bay.

Table 4.3: Summary statistics for the standard length data (cm) for the monthly catches for juvenile plaice *Pleuronectes platessa* L. caught in Llanddona (Red Wharf Bay) between April 2004 and March 2007.

Month	n	Mean	Median	Minimum	Maximum
Apr-04	75	2.185	2.270	1.250	3.220
May-04	75	1.876	1.820	1.110	3.245
Jun-04	150	2.858	2.795	1.635	5.075
Jul-04	174	3.463	3.088	1.615	9.990
Aug-04	100	4.002	3.668	2.130	8.945
Sep-04	200	4.644	4.105	2.810	10.545
Nov-04	192	5.875	5.400	1.360	12.765
Feb-05	24	10.025	9.150	6.200	15.900
May-05	100	1.588	1.538	0.980	2.910
Jun-05	100	1.915	1.765	1.290	4.500
Jul-05	100	2.554	2.435	1.720	6.000
Aug-05	98	3.419	3.395	2.080	5.400
Sep-05	100	4.451	4.295	3.630	8.075
Nov-05	26	10.596	9.765	7.255	16.900
Dec-05	14	7.352	7.315	5.020	10.110
Jan-06	9	5.354	4.735	4.415	7.000
Mar-06	63	6.200	5.020	3.930	12.670
Apr-06	77	1.635	1.480	1.020	2.720
May-06	151	2.938	3.000	1.355	5.510
Jun-06	152	2.892	2.840	1.650	5.060
Aug-06	142	4.207	4.000	3.000	8.400
Sep-06	102	4.103	3.935	3.170	8.800
Oct-06	150	5.075	4.435	3.200	12.000
Dec-06	18	5.399	4.605	3.950	12.540
Jan-07	15	8.837	7.810	5.400	15.070
Mar-07	11	4.698	4.700	3.900	5.640

Push netting surveys at both sites captured juvenile plaice from initial settlement size of *ca.* 1.1-1.3 cm SL and *ca.* 11-25 mg wet weight (Table 4.1). The timing of first settlement appeared to be later in 2005 (May) compared to 2004 (April) and 2006 (April). As monthly sampling progressed through the year, the size range of fish in the catch increased (Tables 4.2-4.3; Figures 4.4-4.6). Settlement-sized juvenile plaice (*ca.* 1.1-1.3 cm SL) continued to be caught by push net over the summer until August/July at both sites. In each year of sampling, small juvenile plaice of *ca.* 3-4 cm SL were caught at both sites during the autumn and winter. As expected, the maximum size of juvenile plaice caught on both nursery grounds increased as the 0-group cohort grew over the summer with maximum sizes caught in the beam trawl surveys over the winter (*i.e.* November – March) at both Llanfairfechan (Table 4.2; Figures 4.4 & 4.6) and Llanddona (Table 4.3; Figure 4.5 & 4.6). The maximum size of juvenile plaice increased from *ca.* 3 cm SL in the spring (*i.e.* April-May) to *ca.* 12-15 cm SL in the winter samples. It is likely that some of the largest juveniles (*ca.* 15-16 cm SL) caught by beam trawl during the winter sampling are 1-group juveniles from the previous year's cohort with the size of that year's cohort attaining sizes of *ca.* 10 cm SL over the winter. Figures 4.7 and 4.8 present the length frequency distributions of all the juvenile plaice caught in the sampling at Llanfairfechan and Llanddona. From these plots, it is possible to trace the size structure of the 2004, 2005 and 2006 year classes during their first year of growth on the nursery ground. Modal Progression Analysis using Bhattacharya's method identified the three cohorts of juvenile plaice on both nursery grounds (Figures 4.7 and 4.8). From these plots it is also possible to discern the presence of 1-group fish in the catches. For example, the presence of fish > 7.5 cm SL in July 2004, fish > 10.0 cm SL in November 2004 and November 2005 in the Llanfairfechan samples (Figure 4.7). At Llanddona, it is likely that juvenile plaice *ca.* 15.0 cm SL in February 2005, November 2005 and January 2007 are 1-group individuals rather than 0-group. Due to the scatter of sizes in this age class, Modal Progression Analysis using Bhattacharya's method tended to mis-identify two modal groups instead of one. The progression of the length-frequency histograms over time would suggest that as well as delayed settlement in 2005, growth rates were slower in that year on both nursery grounds. This can be seen from the incremental increase in both modal size and in skew to the right in the monthly length-frequency plots (Figures 4.7 and 4.8).

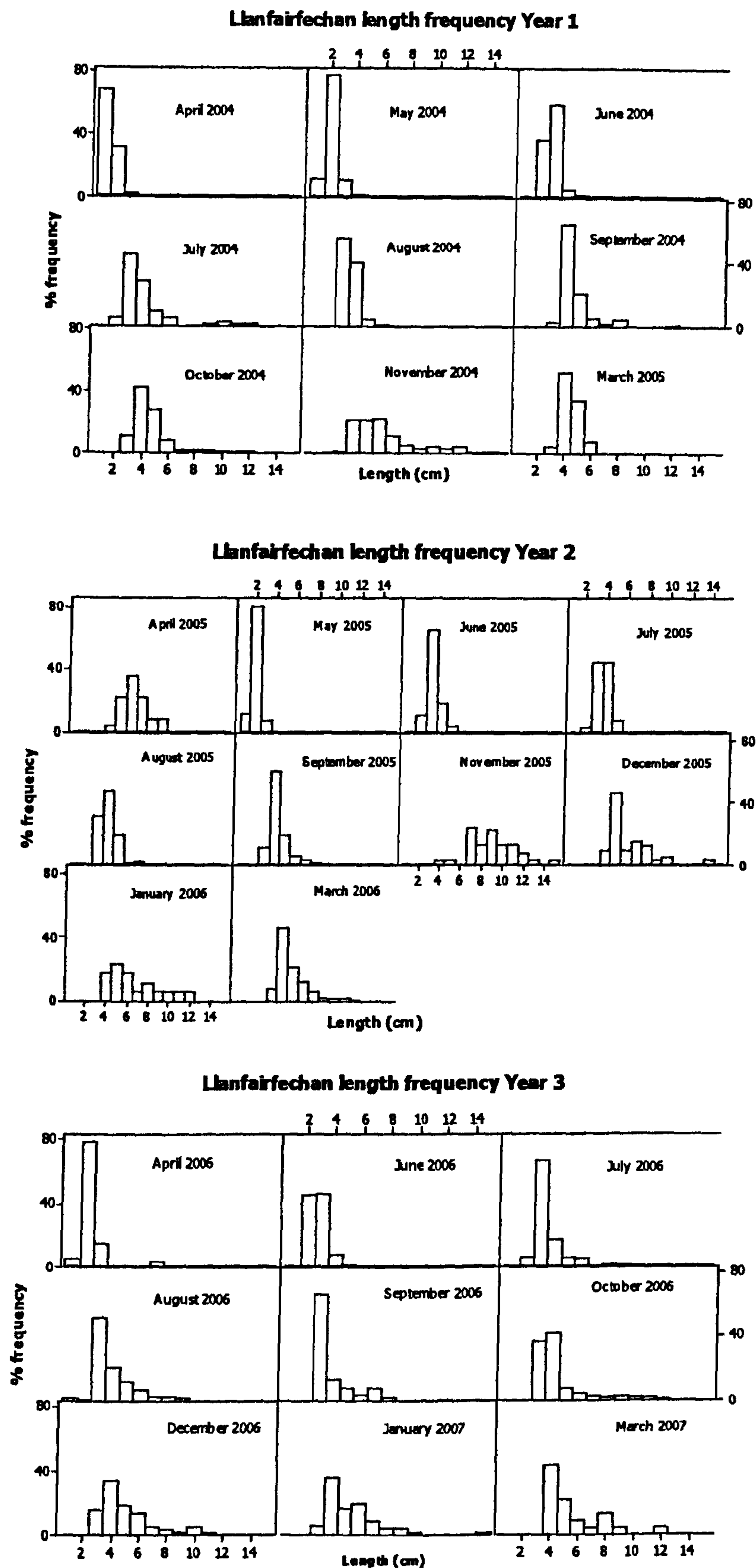


Figure 4.4: Monthly percentage length-frequency distributions of juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) between April 2004 and March 2007.

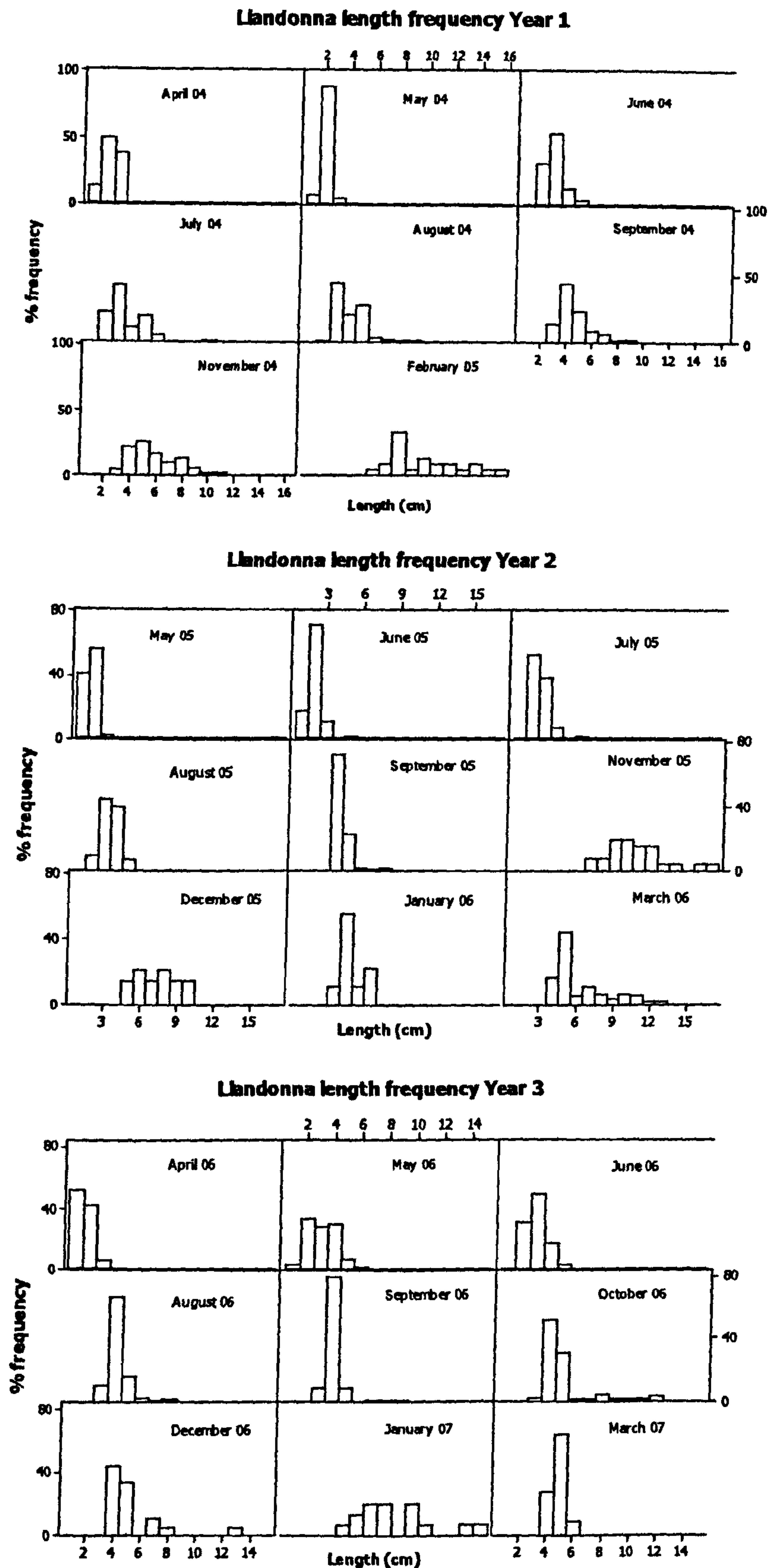
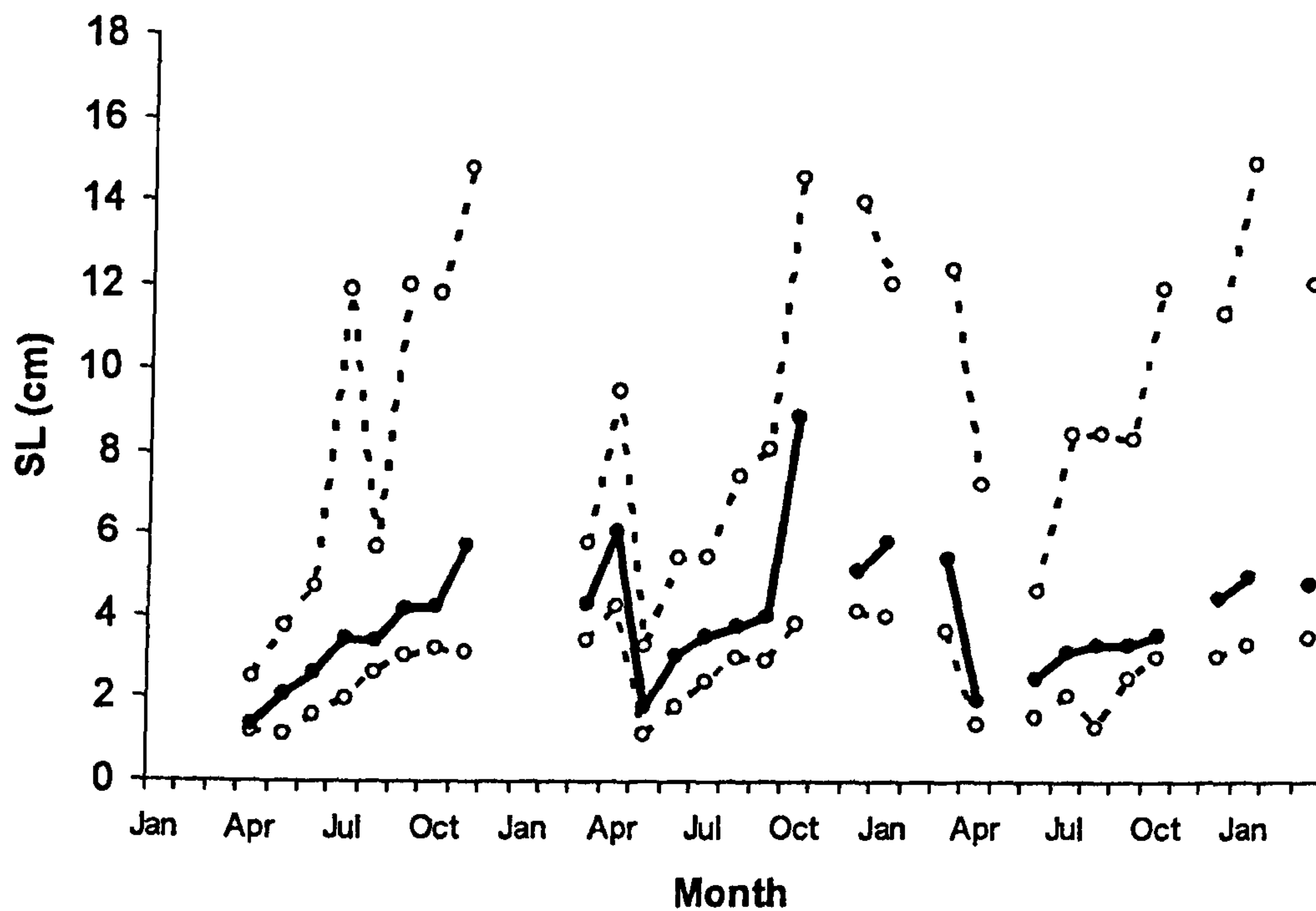


Figure 4.5: Monthly percentage length-frequency distributions of juvenile plaice *P. platessa* L. caught in Llandonna (Red Wharf Bay) between April 2004 and March 2007.

a)



b)

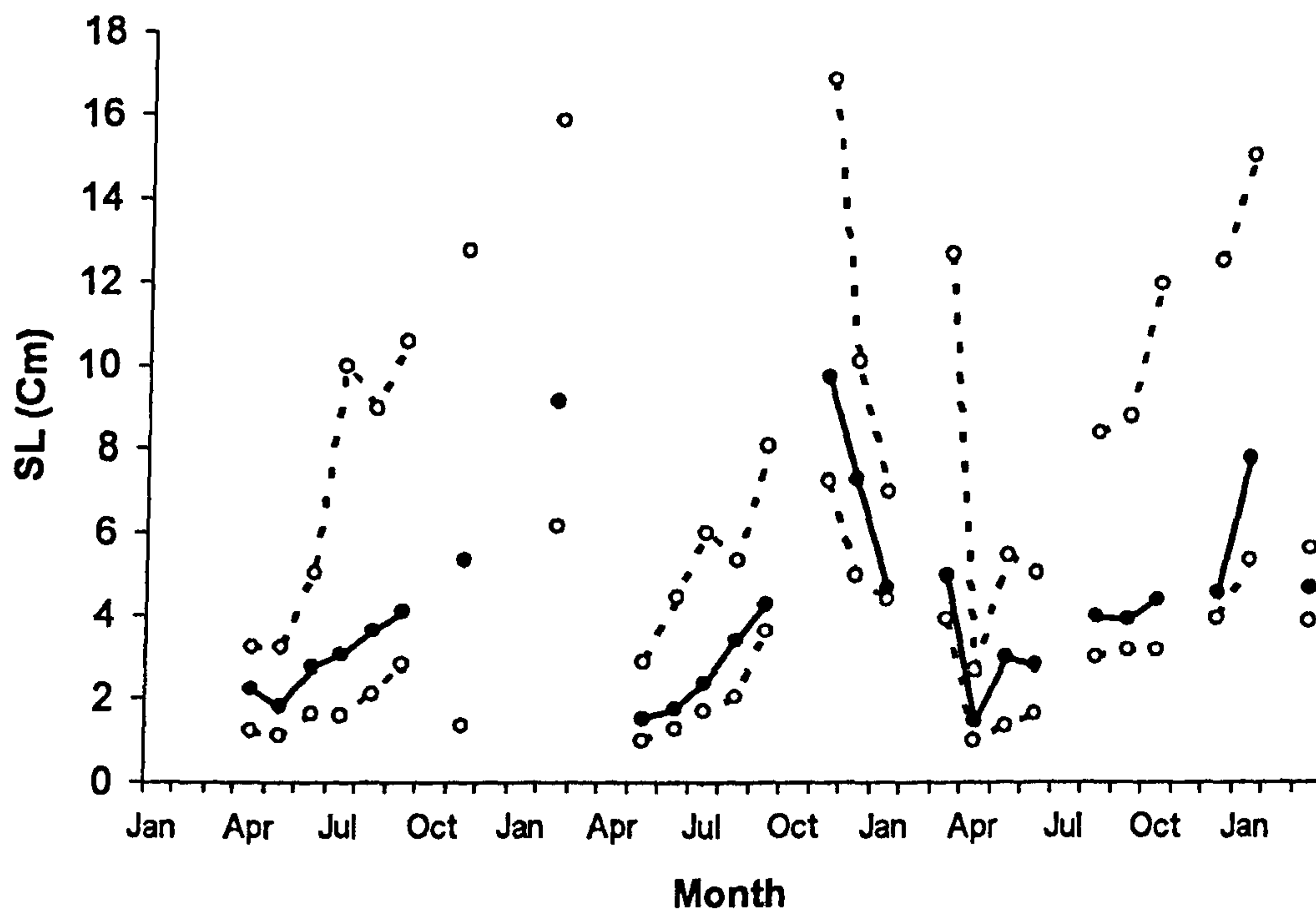


Figure 4.6: The size range of juvenile plaice *P. platessa* L. caught in (a) Llanfairfechan (Conwy Bay) and (b) Llanddona (Red Wharf Bay) between April 2004 and March 2007. Data are presented for the median (solid circles/line) and minimum/maximum (open circles/dotted lines) standard length for each monthly sample.

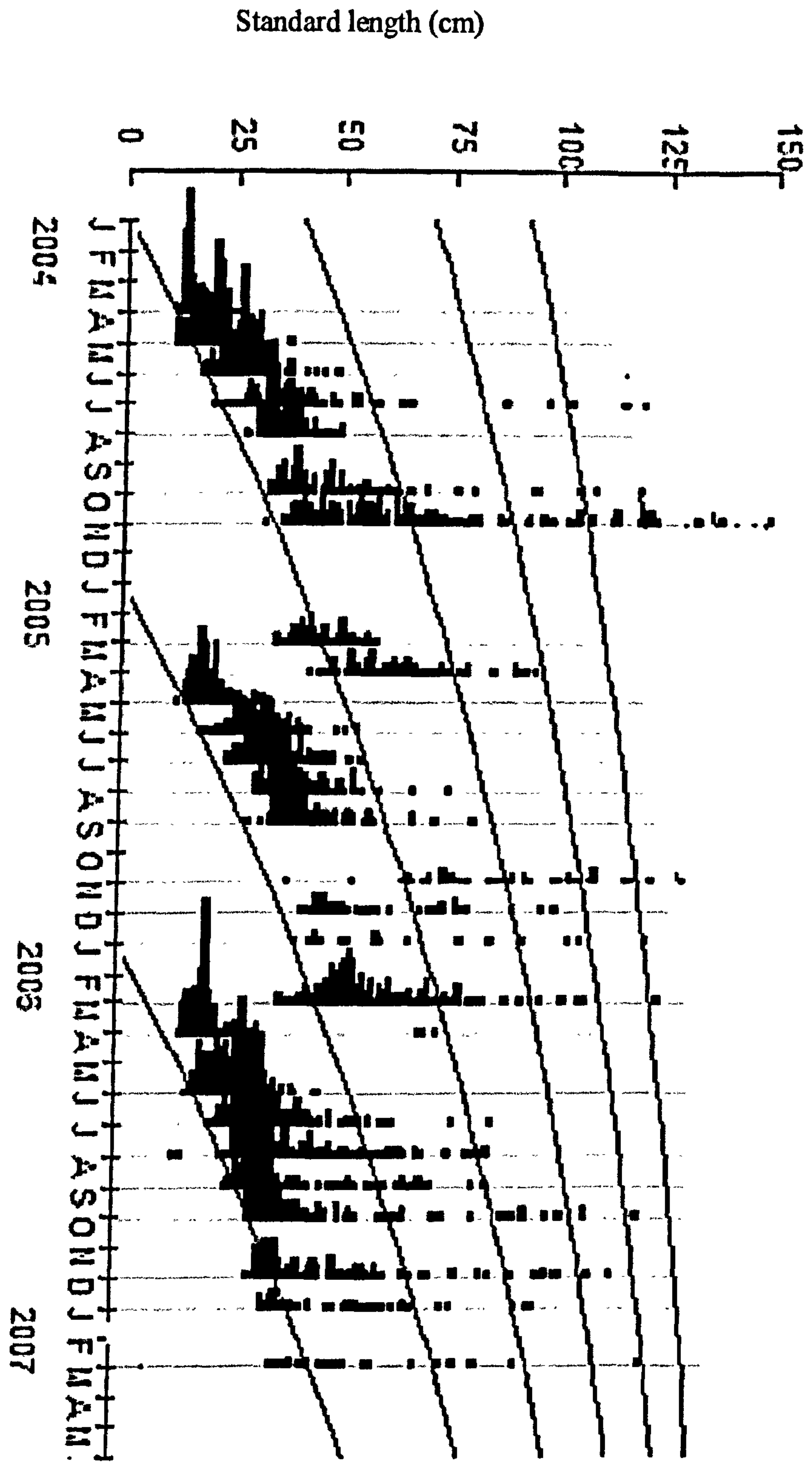


Figure 4.7: Modal progression analysis (using Bhattacharya's method), based on monthly length-frequency distributions of juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) between April 2004 and March 2007.

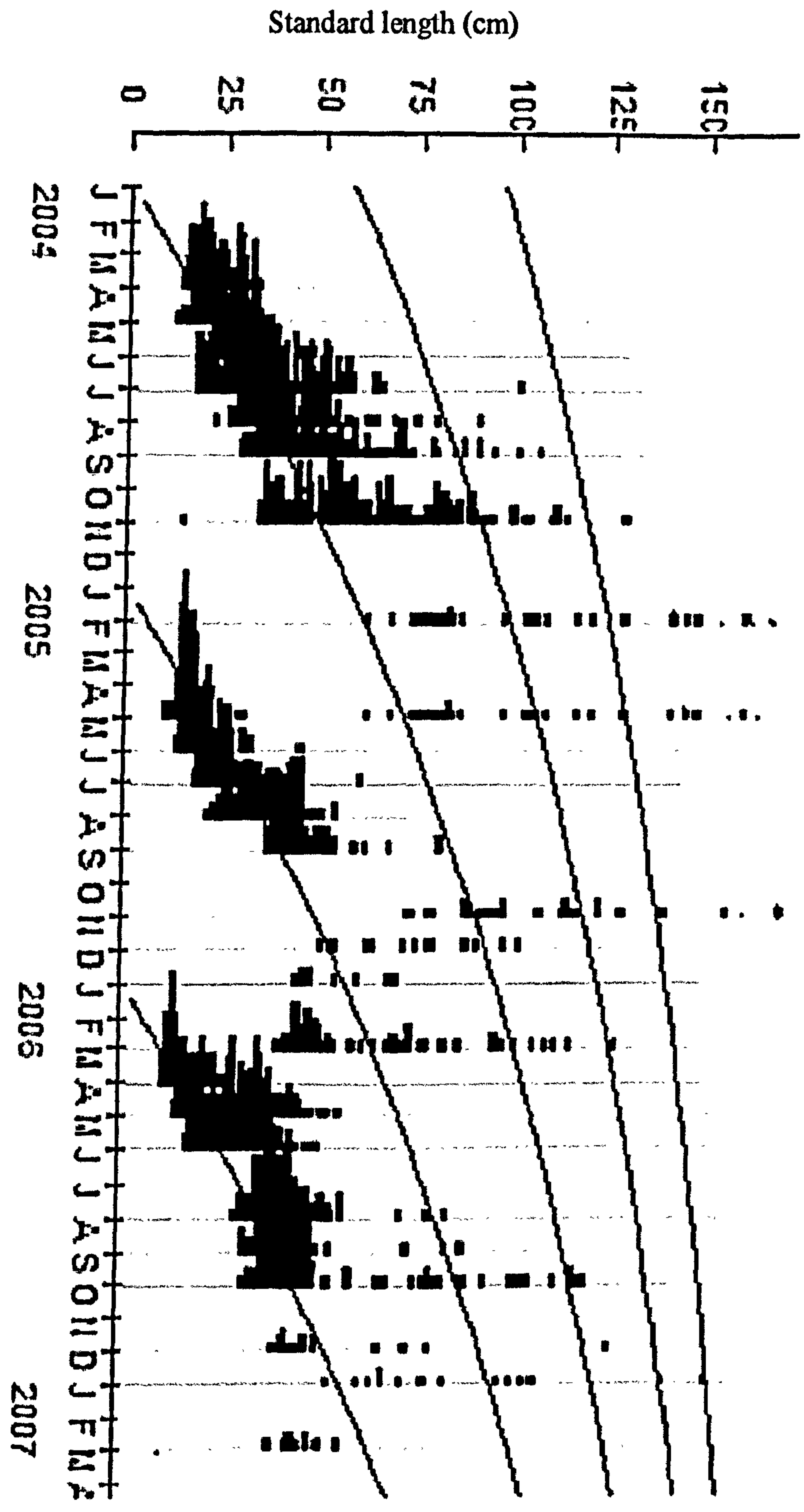
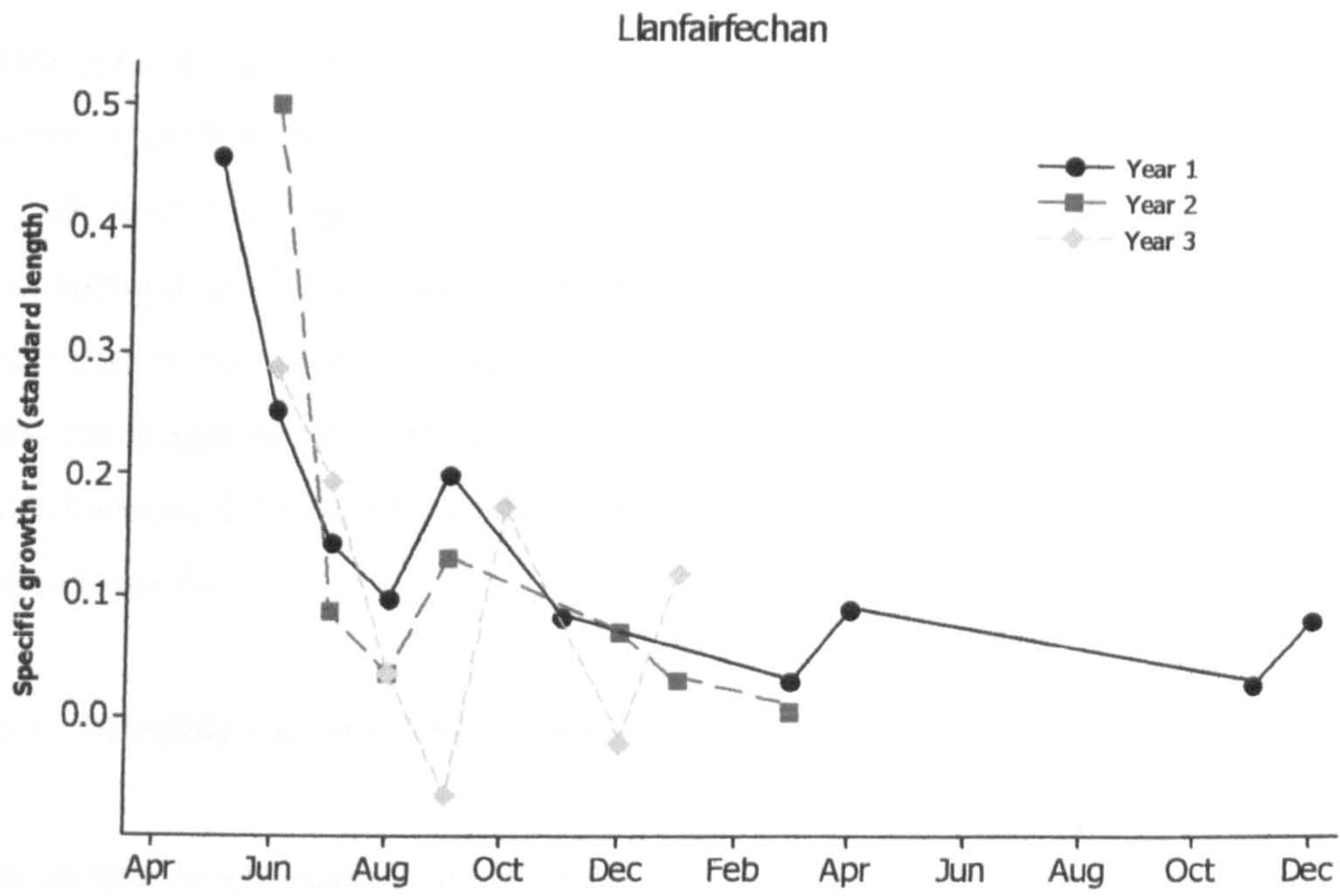


Figure 4.8: Modal progression analysis (using Bhattacharya's method), based on monthly length-frequency distributions of juvenile plaice *P. platessa* L. caught in Llanddona (Red Wharf Bay) between April 2004 and March 2007.

a)



b)

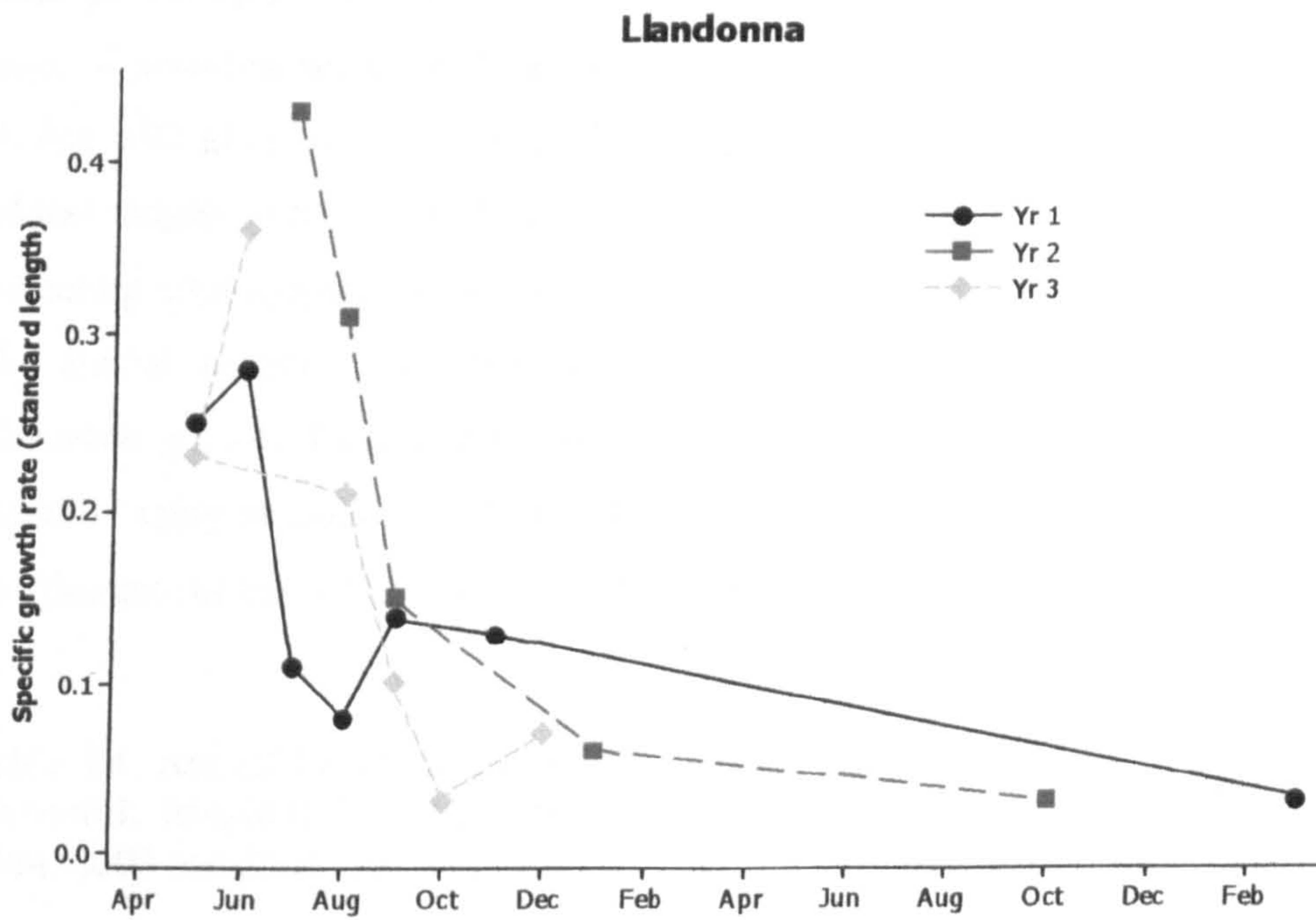


Figure 4.9: Changes in specific growth rate (% Standard length day⁻¹) of juvenile plaice *P. platessa* L. caught in (a) Llanfairfechan (Conwy Bay) and (b) Llanddona (Red Wharf Bay) for the 2004 cohort (Yr 1; April 2004–March 2005; circles), 2005 cohort (Yr 1; April 2005–March 2006; squares) and 2006 cohort (Yr 3; April 2006–March 2007; diamonds).

The monthly changes in the specific growth rate for length (% standard length day⁻¹) of the 2004, 2005 and 2006 cohorts of 0-group juvenile plaice at Llanfairfechan and Llanddona are shown in Figure 4.9. These plots do not indicate any differences in growth rates between the two sites. At both Llanfairfechan and Llanddona, specific growth rates for length in the summer (*ca.* June) are between 0.2 and 0.4 % day⁻¹, decreasing to *ca.* 0.15 % day⁻¹ in August/September and 0.1 % day⁻¹ at the end of the first year on the nursery ground. In addition, Figure 4.9 indicates that specific growth rates for length of the 2004 and 2005 cohorts at both Llanfairfechan and Llanddona were between 0.05 to 0.1 mm day⁻¹ as they entered their second year of growth as 1-group juveniles.

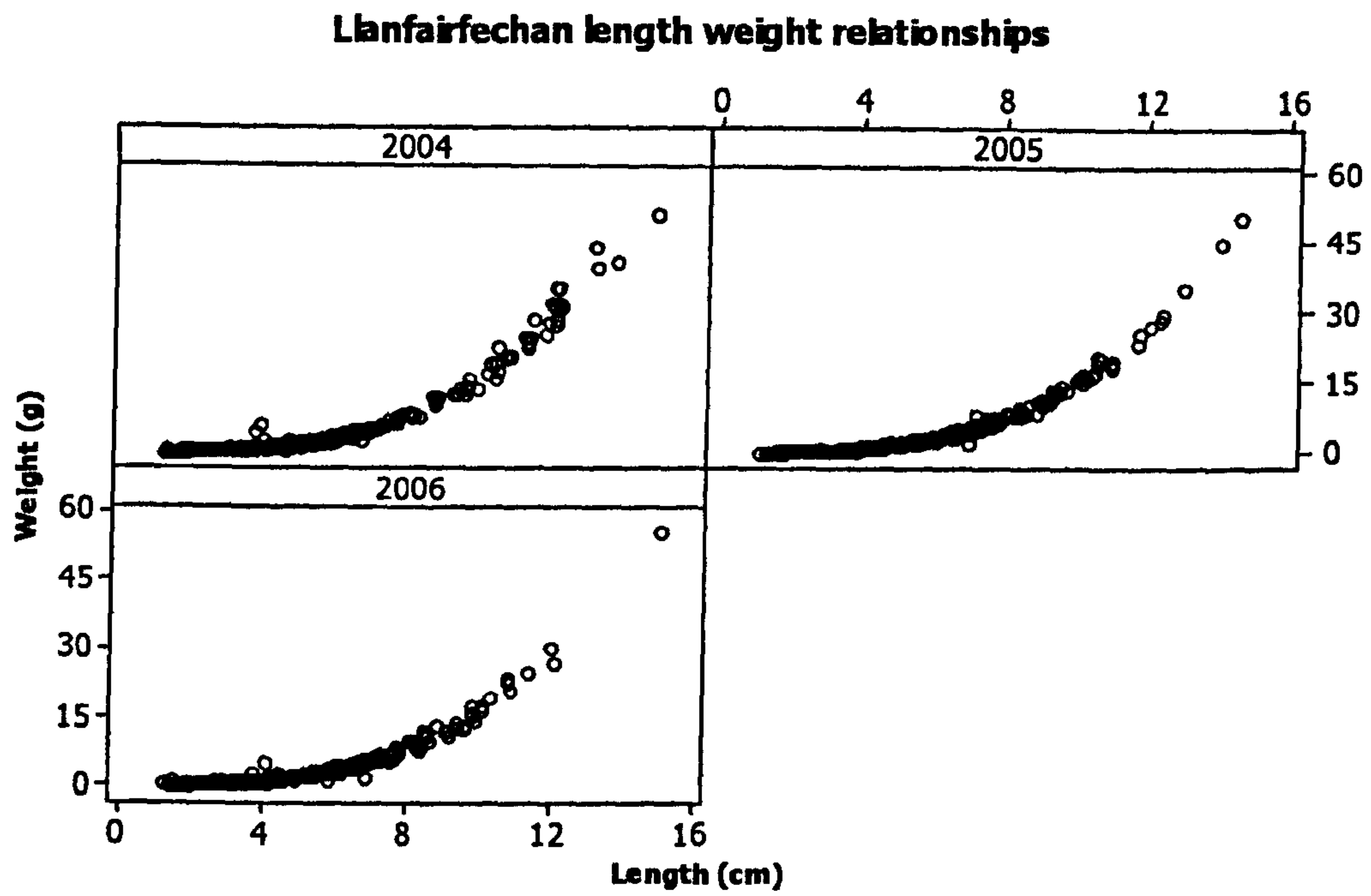
4.3.2 Monthly Length-weight relationships and condition factors

The length-weight relationships for 2004, 2005 and 2006 (*i.e.* all 12 monthly samples combined) are presented in Figure 4.10 with the regression coefficients for the non-linear power curve ($W = a \cdot L^b$) presented in Table 4.4. For both sites, a similar size range of juveniles were caught in each year ranging from settlement size (*ca.* 1.2 cm SL and 0.02 g) to *ca.* 16 cm SL and 60 g (Figure 4.10). The weight exponents (*i.e.* *b* values) ranged from 2.96 to 3.16 (Table 4.4) with 5 of the 6 data sets for the 3 years indicating approximate isometric growth for the juveniles on both nursery grounds. The annual length-weight relationship for Llanddona in 2005 exhibited positive allometric growth. Figures 4.11 and 4.12 present the length-weight relations for the monthly samples collected at Llanfairfechan and Llanddona with the regression coefficients for the non-linear power curve ($W = a \cdot L^b$) presented in Table 4.5.

Table 4.4: Annual length-weight relationships (Weight = $a \cdot L^b$) for juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) and Llanddona (Red Wharf Bay) in 2004, 2005 and 2006.

Year	Site	<i>n</i>	A	<i>b</i>	<i>r</i> ²
2004	Llandonna	991	0.0161	2.96	0.960
	Llanfairfechan	970	0.0154	2.99	0.986
2005	Llandonna	610	0.0114	3.16	0.991
	Llanfairfechan	812	0.0138	3.04	0.993
2006	Llandonna	818	0.0150	3.05	0.979
	Llanfairfechan	1066	0.0148	3.02	0.965

a)



b)

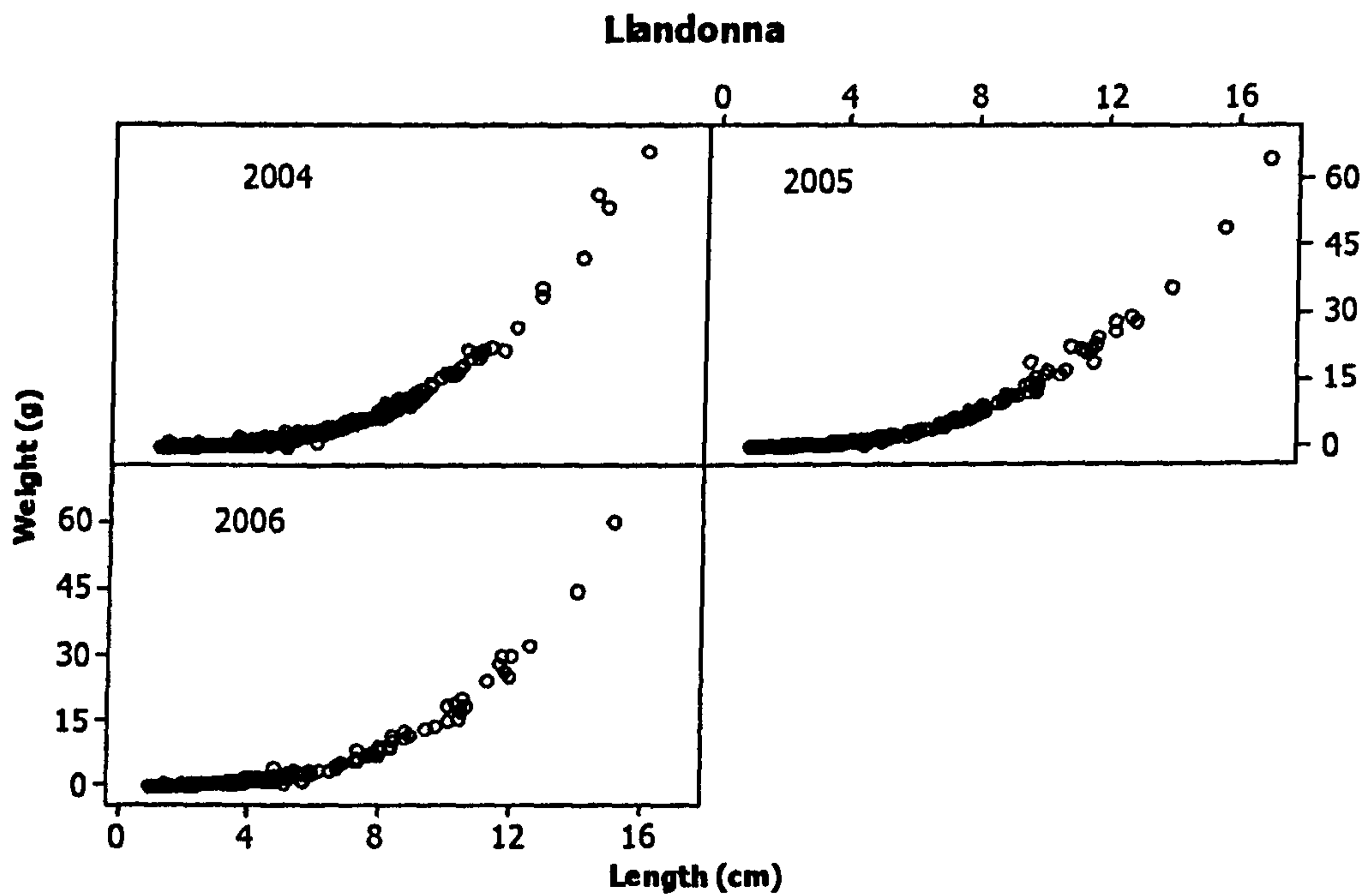
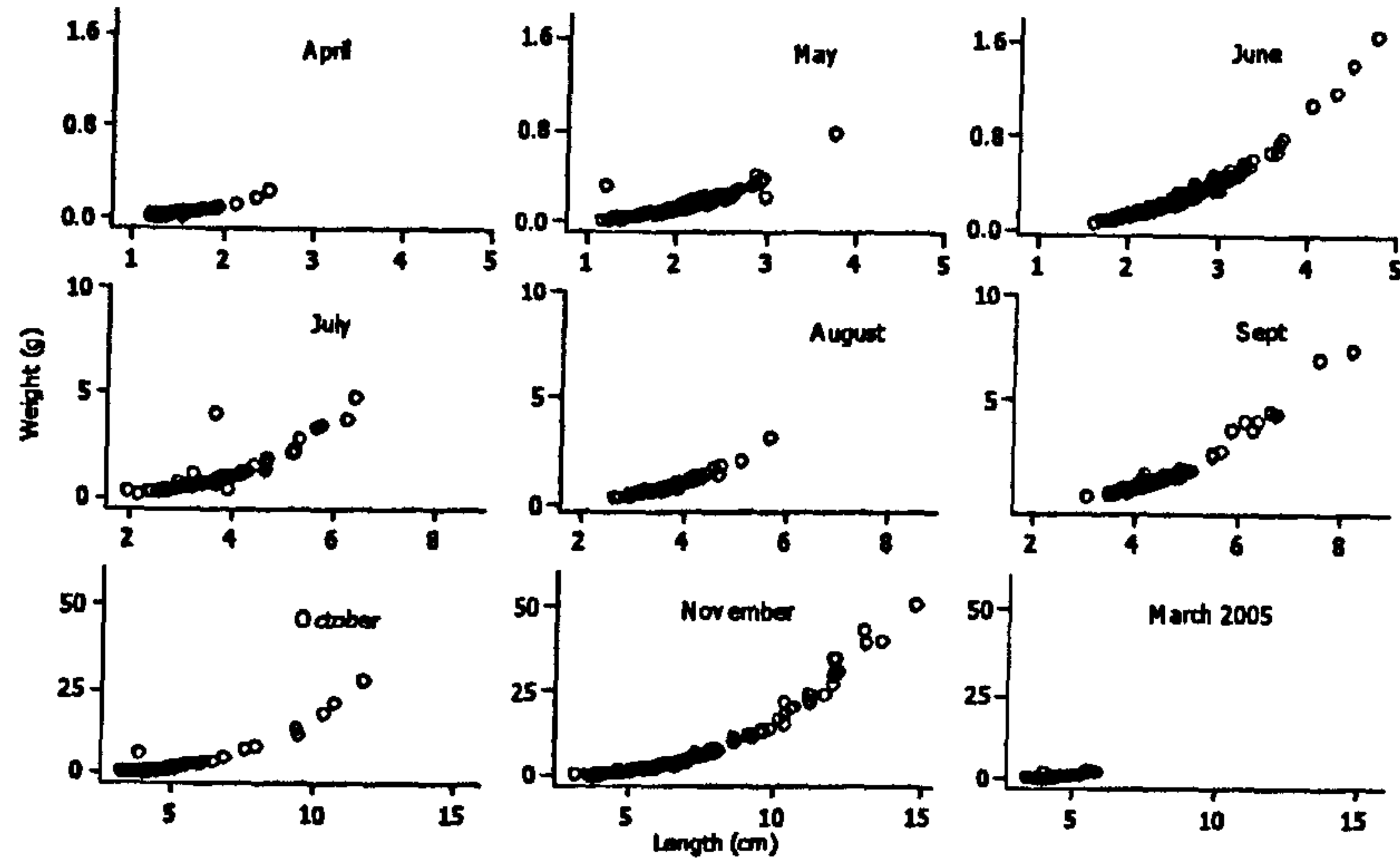


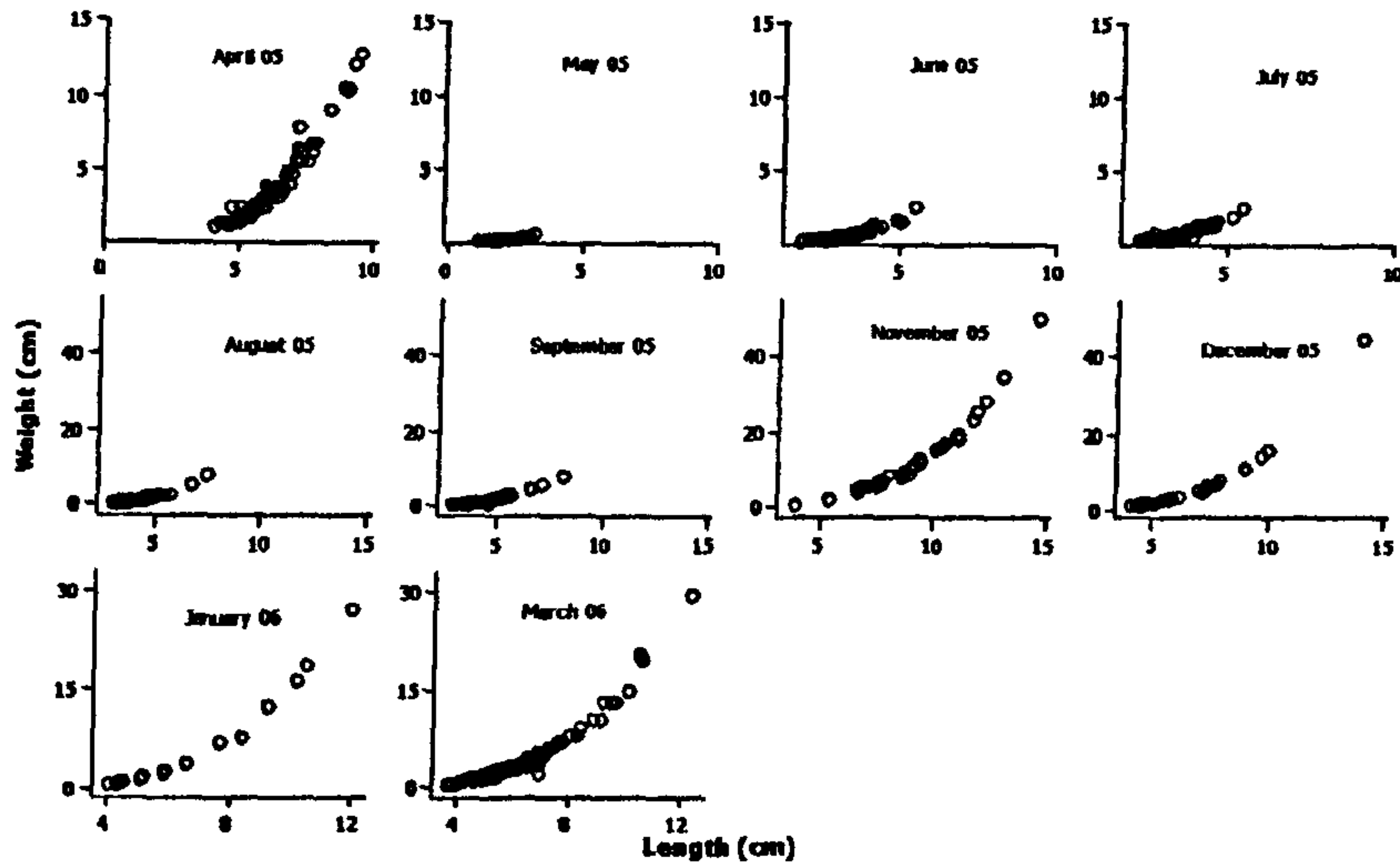
Figure 4.10: Annual length-weight relationships of juvenile plaice *P. platessa* L. caught in (a) Llanfairfechan (Conwy Bay) and (b) Llandonna (Red Wharf Bay) in 2004, 2005 and 2006.

The weight exponents (*i.e.* *b* values) for Llanfairfechan ranged from 2.60 to 3.34 (Figure 4.13; Table 4.4) and between 2.81 and 3.20 for Llanddona (excluding the March 2007 sample; Figure 4.13; Table 4.4). It is likely that the variability observed in the monthly *b*-values will be due, in part, to seasonal variations in condition but will also be influenced by the variable numbers and size range of fish caught each month. A two way ANOVA was used to test whether there was an effect of site (Llanfairfechan or Llanddona) or year on the monthly weight exponent values. This analysis showed a significant effect of year ($F_{3,44} = 671.5$, $P < 0.0001$) but no effect of site ($F_{1,44} = 0.65$, $P = 0.43$) and no significant site x year interaction ($F_{2,44} = 0.25$, $P = 0.98$). The monthly average condition factors values presented in Figure 4.14 with the data for both sampling sites in the same year on the same plot for comparison. This plot shows that condition was variable between months and two patterns can be identified. Firstly, the condition factors of fish in 2004 and 2006 year classes were higher than in the 2005 year classes, confirming that as well as faster growth in these 2 years, the fish were also in better overall condition, particularly during the summer months (Figure 4.14). In the 2004 and 2006 cohorts, the condition factor values are mainly 1.2 (except during the first few months after settlement) and as high as 1.6. In comparison, the condition factor values in the 2005 cohorts were *ca.* 1.2 year-round, with the exception of December 2005/January 2006 for Llanfairfechan (Figure 4.14). In these two months, condition factor values were higher, but this may be a sample size effect. The second pattern that can be observed in the data is the seasonal variation in condition factor in the 2004 and 2006 cohorts, with condition factors tending to be low in the spring (*i.e.* *ca.* 1.2 in April to June) and increasing during the rest of the year (*ca.* 1.4- 1.6) (Figure 4.14). A two way ANOVA was used to test whether the statistical significance of these observations by determining whether there was an effect of site (Llanfairfechan or Llanddona) or year on the monthly condition factor values. This analysis showed a significant effect of year ($F_{3,44} = 63.3$, $P < 0.0001$) but no effect of site ($F_{1,44} = 0.84$, $P = 0.36$) and no significant site x year interaction ($F_{2,44} = 1.29$, $P = 0.29$).

Length-weight relationships Llanfairfechan Year 1



Length-weight relationships Llanfairfechan Year 2



Llanfairfechan Year 3

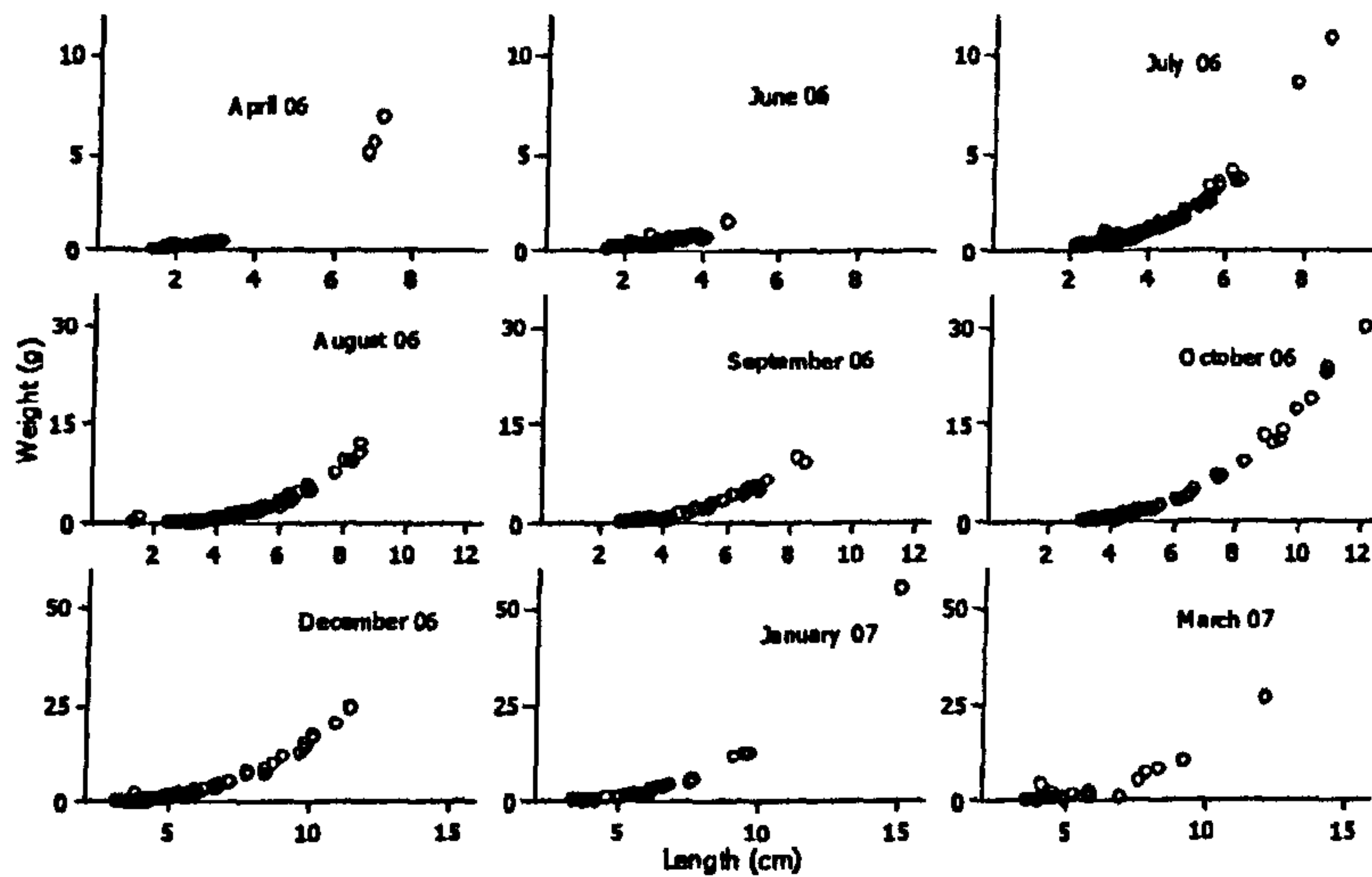


Figure 4.11: Monthly length-weight relationships of juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) between April 2004 and March 2007.

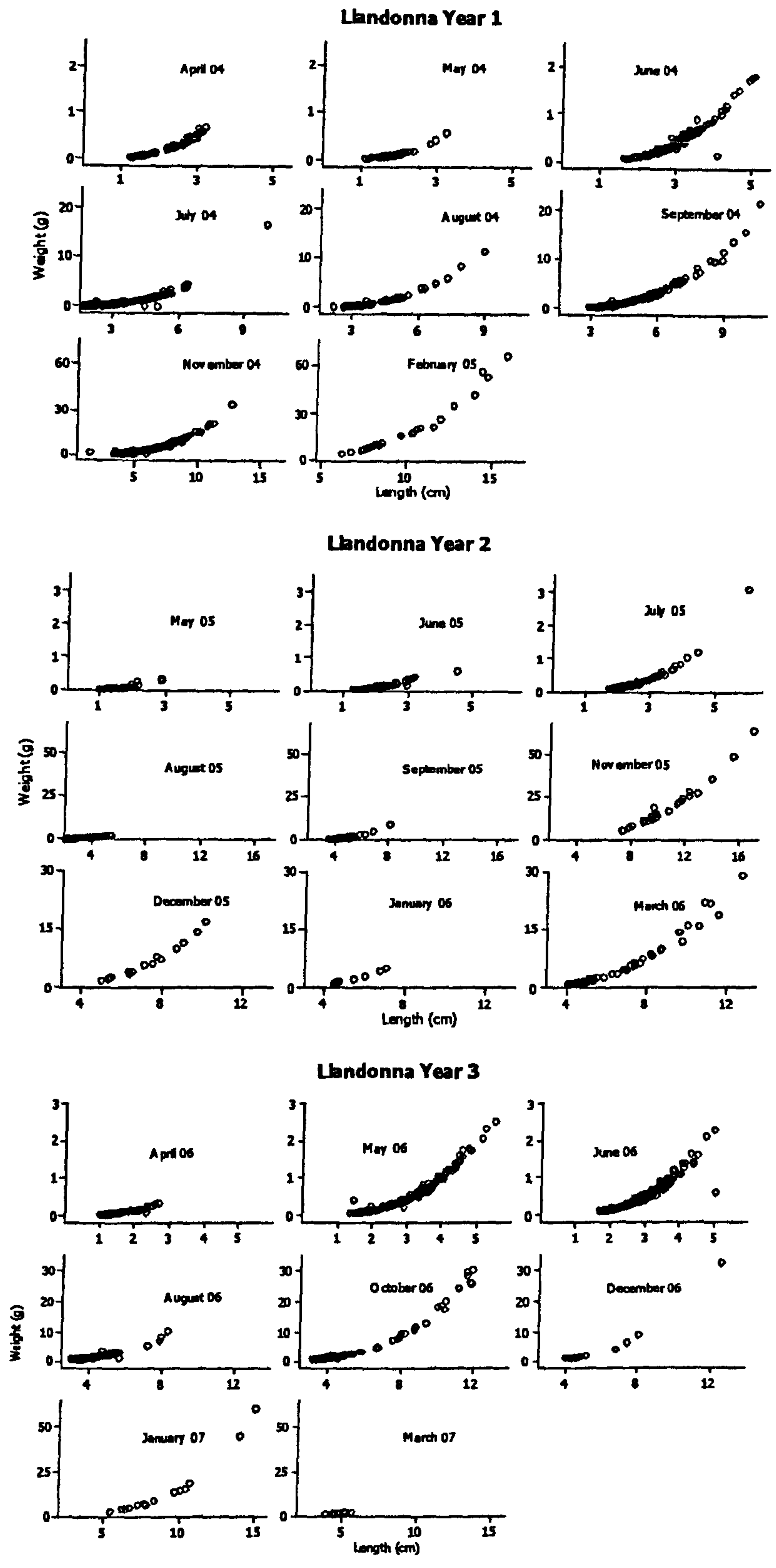


Figure 4.12: Monthly length-weight relationships of juvenile plaice *P. platessa* L. caught in Llandonna (Red Wharf Bay) between April 2004 and March 2007.

Table 4.5: Monthly length-weight relationships (Weight = $a \cdot L^b$) for juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) and Llandonna (Red Wharf Bay) in 2004, 2005 and 2006.

		Llanfairfechan				Llandonna							
Year	Month	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> ²	Year	Month	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> ²		
2004	April	75	0.0134	3.08	0.899	2004	April	75	0.0171	3.09	0.984		
	May	149	0.0201	2.67	0.887		May	75	0.0161	2.89	0.967		
	June	150	0.0161	2.97	0.979		June	150	0.0150	2.97	0.936		
	July	75	0.0178	2.98	0.946		July	174	0.0160	2.97	0.917		
	August	100	0.0177	2.93	0.963		August	100	0.0133	3.103	0.984		
	September	100	0.0166	2.95	0.979		September	200	0.0132	3.100	0.981		
	October	100	0.0130	3.07	0.928								
	November	172	0.0124	3.11	0.990		November	192	0.0180	2.88	0.899		
2005						2005	February	24	0.0118	3.13	0.993		
	March	49	0.0202	2.70	0.747								
	April	62	0.0107	3.34	0.951								
	May	100	0.0132	3.06	0.970		May	100	0.0101	3.16	0.897		
	June	100	0.0147	2.96	0.983		June	100	0.0128	2.89	0.948		
	July	100	0.0159	2.90	0.905		July	100	0.0135	3.01	0.987		
	August	100	0.0184	2.91	0.981		August	98	0.0204	2.87	0.966		
	September	100	0.0179	2.88	0.964		September	100	0.0114	3.15	0.946		
	November	41	0.0154	2.99	0.992		November	26	0.0230	2.81	0.978		
	December	43	0.0112	3.13	0.995		December	14	0.0107	3.17	0.995		
	2006	January	17	0.0099	3.12		0.996	2006	January	9	0.0142	2.99	0.976
		March	149	0.0161	2.97		0.977		March	63	0.0119	3.10	0.994
April		111	0.0106	3.26	0.968	April	77		0.0142	2.93	0.918		
June		152	0.0172	2.86	0.899	May	151		0.0156	2.99	0.963		
July		214	0.0161	2.98	0.965	June	152		0.0155	3.08	0.959		
August		152	0.0258	2.65	0.875	August	142		0.0191	2.87	0.921		
September		105	0.0236	2.80	0.976	September	102		0.0222	2.89	0.972		
October		151	0.0131	3.11	0.989	October	150		0.0145	3.06	0.991		
December		111	0.0133	3.05	0.980	December	18		0.0106	3.18	0.995		
2007		January	47	0.0105	3.14	0.995	2007		January	15	0.0097	3.20	0.996
	March	23	0.0275	2.60	0.736	March		11	0.0536	2.06	0.679		

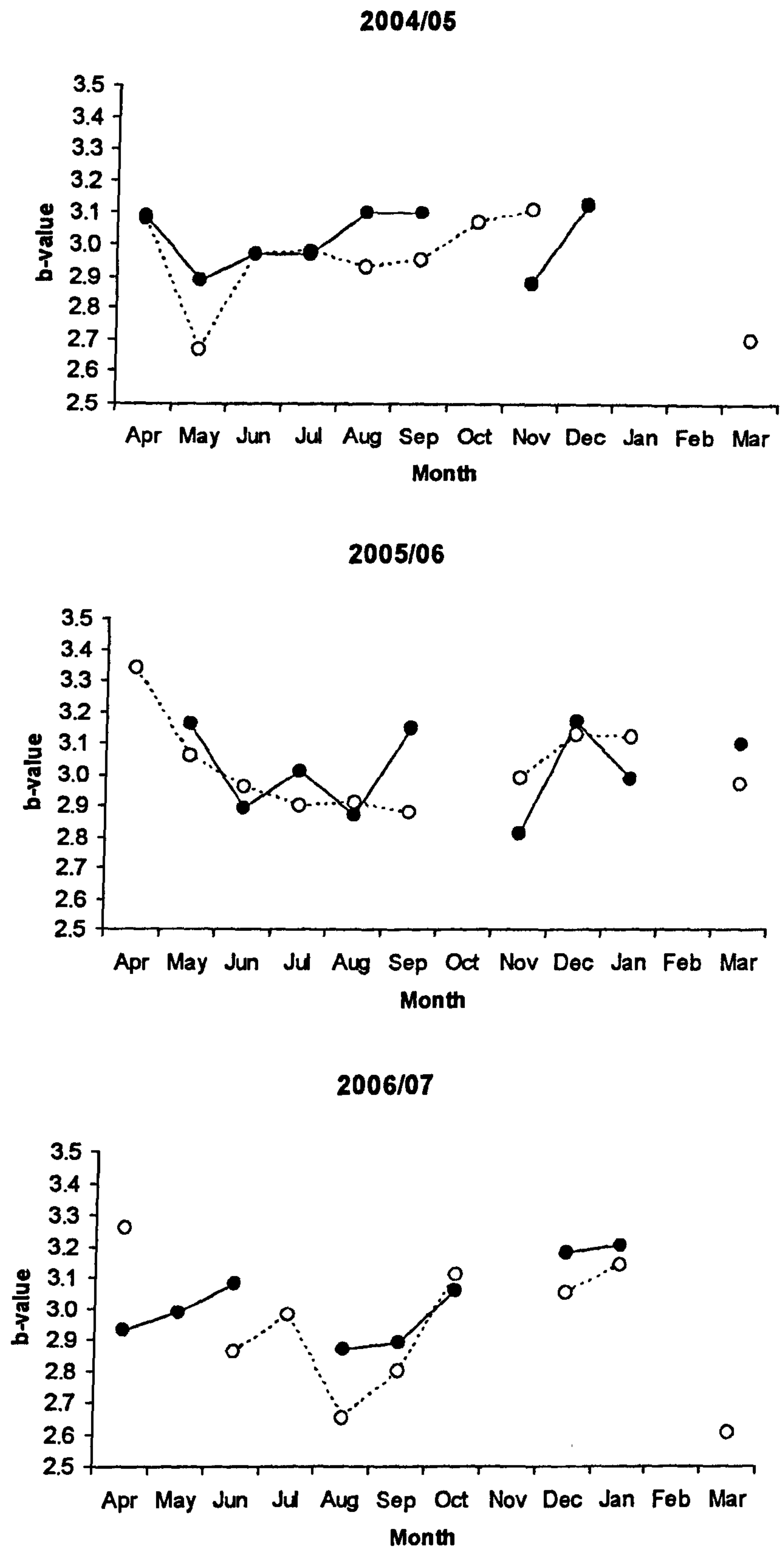


Figure 4.13: Monthly changes in weight exponent for juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay; open circles, dotted line) and Llanddona (Red Wharf Bay; solid circles, solid line) between April 2004 and March 2007.

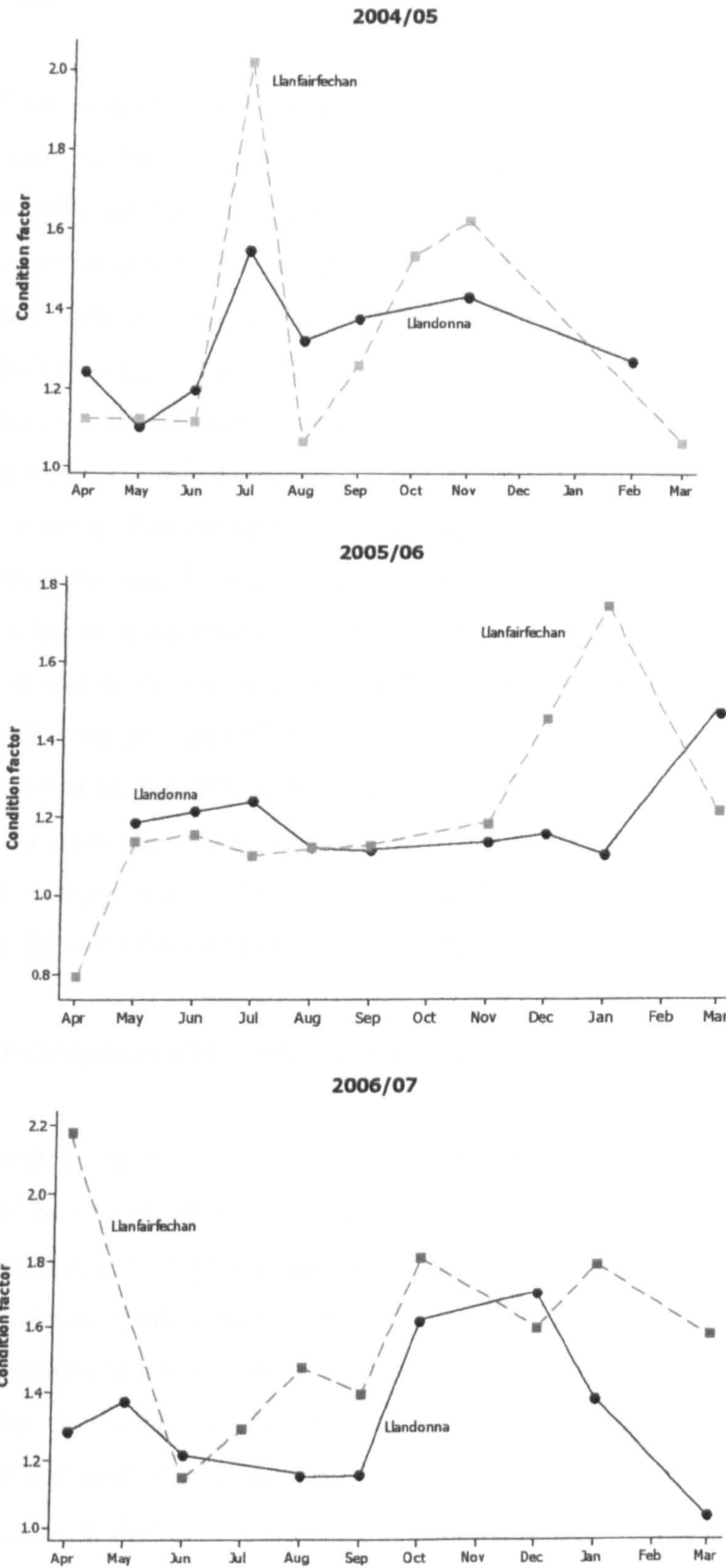


Figure 4.14: Monthly changes in condition factor for juvenile plaice *P. platessa* L. caught in Llanfairfechan (Conwy Bay) and Llanddona (Red Wharf Bay) between April 2004 and March 2007.

4.4 Discussion

The aim of this chapter was to study three cohorts of 0-group juvenile plaice during their first year on two nursery grounds in North West Wales (Llanfairfechan in Conwy bay and Llanddona in Red Wharf Bay) in order to assess seasonal and inter-annual changes in growth and condition. In order to do so, it is important to be confident that juvenile plaice are not exhibiting movement patterns between nursery grounds which may affect the results. Tagging experiments have shown that juvenile plaice exhibit very little movement on the nursery grounds, usually staying within 500 m of release (Macer, 1967; Riley, 1973; Burrows *et al.*, 2004) and moving offshore into deeper water as they increase in size (Lockwood, 1974; Gibson *et al.*, 2002). In addition, plaice can spend up to 24 months on the nursery grounds before moving offshore into deeper water (Nash *et al.*, 1992). Therefore, we can be confident that the fish caught in this study will be from fish that settled onto that nursery ground and have remained in the general vicinity of the survey area, *i.e.* Llanfairfechan in Conwy Bay or Llanddona in Red Wharf Bay, since settlement rather than individuals that have migrated onto that nursery ground from other coastal nursery areas in the vicinity. For example, it is unlikely that juvenile plaice will have migrated from one survey site to the other during the course of the study.

4.4.1 Length frequency distribution and abundance

In this study, cohorts of fish could be identified based on the length frequency distribution of fish caught on the nursery ground. The results show, as expected, that in each year sampled, the 0-group dominated the catch with some larger 1-group fish caught in the autumn and winter months (Figures 4.7 and 4.8). The use of length frequency distributions to examine growth patterns in cohorts of juvenile flatfish is well established for plaice (*e.g.* Edwards and Steele, 1968; Al-Hossaini *et al.*, 1989; Amara, 2004) and other flatfish species, for example dab, *L. limanda* (Edwards and Steele, 1968; Amara, 2004), Dover sole *S. solea* and Senegal sole *Solea senegalensis* (Cabral, 2003; Amara, 2004), English sole *Pleuronectes vetulus* (Shi *et al.*, 1997) and winter flounder *Pseudopleuronectes americanus* (Sogard *et al.*, 2001). In this study, modal progression analysis was used to identify the 0-group and 1-group cohorts and to determine the nodal length of that cohort in a given month to calculate growth rates.

Modal progression analysis is a widely used technique that has been used to identify cohorts within size-frequency distributions and to describe the growth patterns of these cohorts. For example, other larval and juvenile 0-group fish studies that have used modal progression analysis include work on European sardine *Sardina pilchardus* (Romanelli *et al.*, 2002), European hake *Merluccius merluccius* (Morales-Nin and Aldebert, 1997), English Sole (Shi *et al.*, 1997), Dover sole and Senegal sole (Cabral, 2003), and tilapias *Oreochromis niloticus baringoensis* and *O. leucostictus* (Britton and Harper, 2008). Although, this technique can also be used to determine growth curves in adult fishes, for example, mosquitofish *Gambusia holbrooki* (Scalici *et al.*, 2007) and grey snapper *Lutjanus griseus* (Faunce and Serafy, 2008), it is more common to use ageing techniques using hard part analysis, for example, otoliths, scales and bones (King, 2007), to derive growth curves in fishes. In contrast, the use of hard parts to age individuals is more difficult or even impossible in invertebrates and often modal progression analysis had been applied to length frequency distributions in order to identify cohorts to calculate growth rates and derive growth curves. This technique has been used in molluscs, for example, *Nassarius reticulatus*, (Chatzinikolaou and Richardson, 2008) and *Octopus mimus* (Cortez *et al.*, 1999) and has been commonly applied to crustaceans, for example brown shrimp *C. crangon* (Oh *et al.*, 1999; Al-Rashada, 2003), banana prawns *Penaeus merguensis* (Haywood and Staples, 1993), white shrimp *Litopenaeus vannamei* (Ramos-Cruz, 2000) and spanner crabs *Ranina ranina* (Kirkwood *et al.*, 2005).

In this study, although the depth distribution of juvenile plaice was not assessed, it was apparent that the fish moved offshore as they increased in size. Recently-settled juveniles, known locally as “slips”, were very easy to catch by push net in shallow water < 0.5 m deep in the late spring and early summer. In these initial samples, it was not uncommon for the required sample size of 0-group plaice to be caught in a single push. Over the summer, as the fish increased in size and became less abundant, greater push netting effort was needed in order to obtain the relevant sample size of 100-150 individuals. During the autumn, as the fish moved offshore into deeper water, and during the winter, juvenile plaice were caught using a 2 m beam trawl. During the second half of their first year of growth, the juvenile plaice became less abundant and harder to catch in the deeper water. The distribution of juvenile plaice on nursery grounds is known to be related to size and temperature and predation risk (Gibson *et al.*, 1998, 2002). It is thought that initial settlement of newly

metamorphosed juvenile plaice occurs in water > 5 m deep, however, in the weeks following settlement, they are concentrated in shallow water < 1 m deep (Gibson *et al.*, 2002). This may be due to the onshore movement of the newly settled juveniles into shallower water (Lockwood, 1974) or the high predation rates and rapid depletion of the newly settled juveniles in deeper water (Gibson *et al.*, 2002). Whatever the explanation, once settlement is complete, the majority of small juveniles are found in shallow water < 1 m deep (Gibson *et al.*, 2002). The results of this study agree with this conclusion, as large numbers of newly settled juveniles were easily collected by push net just below the tide line in water *ca.* 50 cm deep in the early summer. Previous work has shown that once a size refuge has been reached, there is a progressive movement into deeper water by juvenile 0-group plaice later in the year with positive relationship between length and depth (Gibson *et al.*, 2002). Inshore residence in shallower warmer water over the summer is thought to promote faster growth in the newly settled plaice and to avoid predation by brown shrimp *C. crangon* and other predators in deeper water until the size refuge has been reached (Burrows *et al.*, 2001; Gibson *et al.*, 2002). In addition, the use of shallow water avoids inter-specific competition for food with dab *L. limanda* which settle into deeper water over the summer (Gibson *et al.*, 2002; Beggs and Nash, 2007). As plaice increase in size and move offshore into deeper water and co-habit with dab, the two species exhibit trophic resource partitioning to avoid competition for food (Carter *et al.*, 1991).

In this study it was not possible to accurately assess abundance or catch per unit effort. Although records of trawling effort [*i.e.* trawl depth, trawl time and boat speed (which allow calculation of trawl distance and area swept)] were kept, it was not possible to accurately record the time spent push netting or the area of nursery ground covered during sampling. In addition, the time spent sampling on each field trip was not standardised and so catch per unit effort (time) could not be calculated. However, from the catches recorded during sampling, and the effort needed to catch them, it is clear that the abundance of juvenile 0-group plaice was highest during the initial post-settlement phase over the summer with a decrease in abundance over the rest of the year. This observation agrees with previous studies that have measured the temporal changes in abundance of 0-group plaice on nursery grounds. For example, Pihl and Rosenberg (1985) report that the abundance of 0-group plaice in two bays in Western Sweden peaked at 0.5 – 2.5 individuals per m² following settlement decreasing to < 0.1 per m² later in the year. In addition, Gibson *et al.* (2002) reported

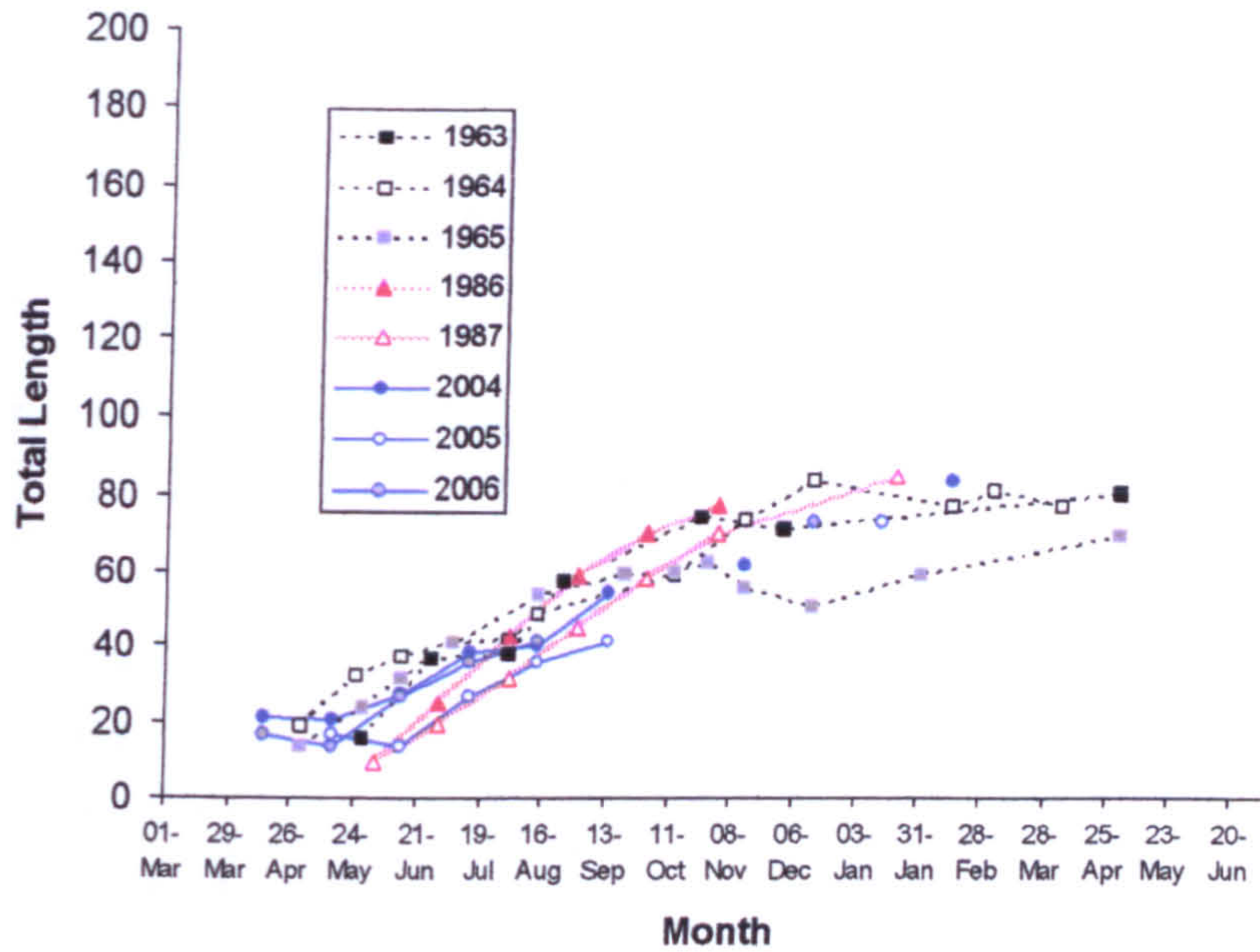
that the abundance of 0-group plaice in Tralee Bay (W. Scotland) decreased from *ca.* 30-50 plaice per 100 m² in spring/summer (April – September) to < 10 per 100 m² over the winter.

The size distribution of fish caught each month in this study changed from a discrete unimodal size frequency plot in the spring to a more dispersed pattern over time (Figures 4.7 and 4.8). A similar change in size frequency distribution was reported for 0-group plaice in Loch Ewe where the size range of individuals (minimum – maximum length) increased from 15-25 mm in April to 40-110 mm in January (Edwards and Steele, 1968). This increase in the size range of 0-group plaice recorded on the nursery grounds will be due to a combination of the settlement time of individuals (which will influence growth opportunity during the first summer/autumn growth season) and individual differences in feeding success and physiological efficiency influencing growth rate. Since plaice spawn over an extended spawning season, multiple settlements of newly-metamorphosed juveniles occur over the course of the summer (Ruack, 1974; Al-Hossaini *et al.*, 1989; Allen *et al.*, 2008). However, research has shown that the survival of these different subcohorts varies. For example, Al Hossaini *et al.* (1989) found that 3 subcohorts settled in Red Wharf Bay in both 1986 and 1987 but mortality was highest for the earliest settling cohort and lower for later settling cohorts. Also, growth rates were highest for the second cohort (Al-Hossaini *et al.*, 1989). By studying otolith substructure of fish caught in September to backcalculate settlement dates, Al-Hossaini and co-workers were able to show that most of the surviving fish had come from the second or third cohorts that had settled in Mid-may or June with very few fish surviving from the first subcohort that settled earlier. However, the presence of a combination of surviving early and late settling juveniles in the winter samples could, in part, explain the sizes range of fish recorded in the winter catches. In addition, individual fish are known to vary in feeding success and in the efficiency with which they convert ingested food to somatic growth (*e.g.* Carter *et al.*, 1993; McCarthy *et al.*, 1994), a factor which will also contribute to an increase in the size dispersion within the cohort over time.

4.4.2 Growth rates

From the monthly sampling strategy employed in this study, it was possible to calculate temporal changes in growth rate for each of the three 0-group cohorts during

a)



b)

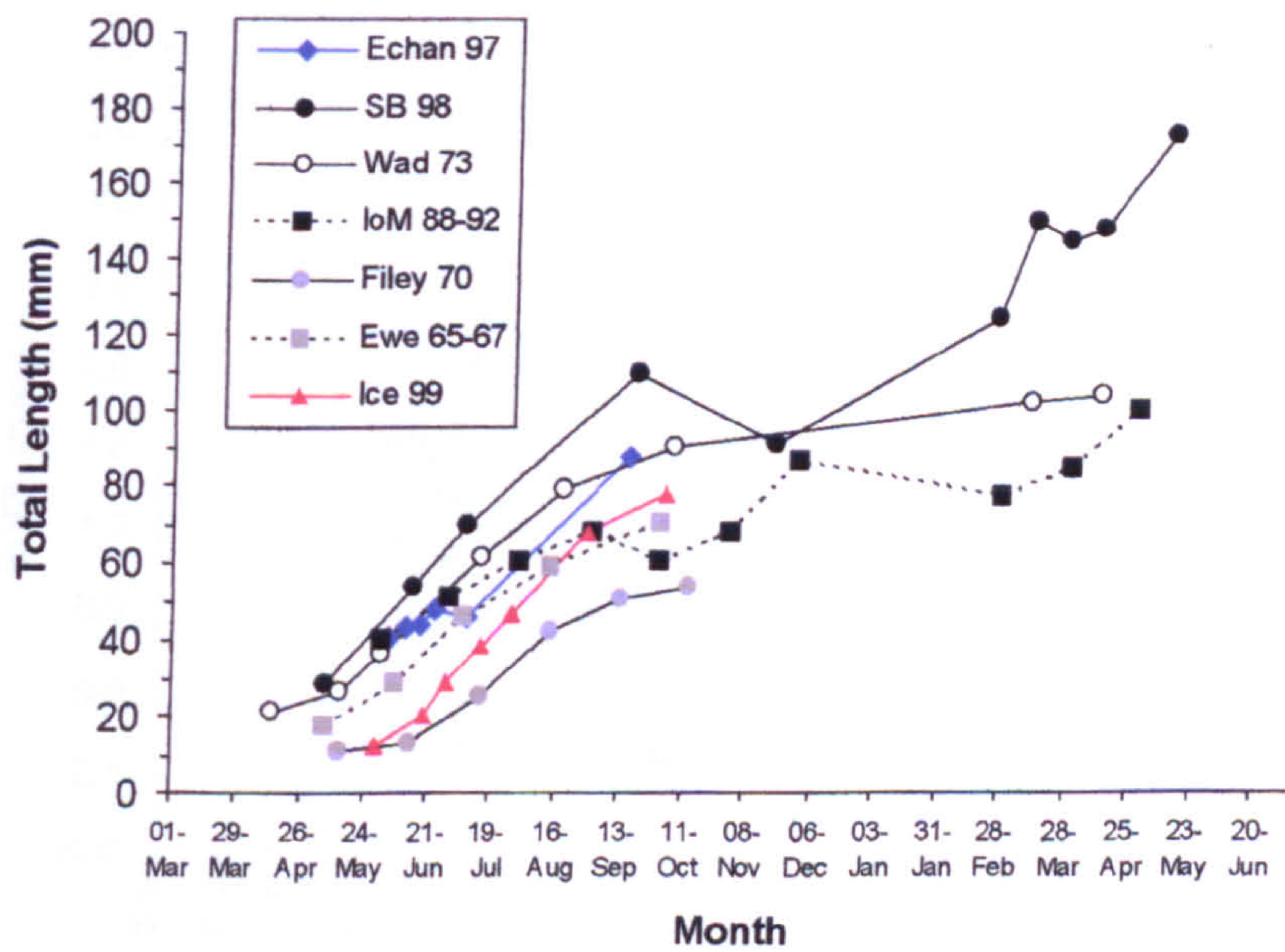
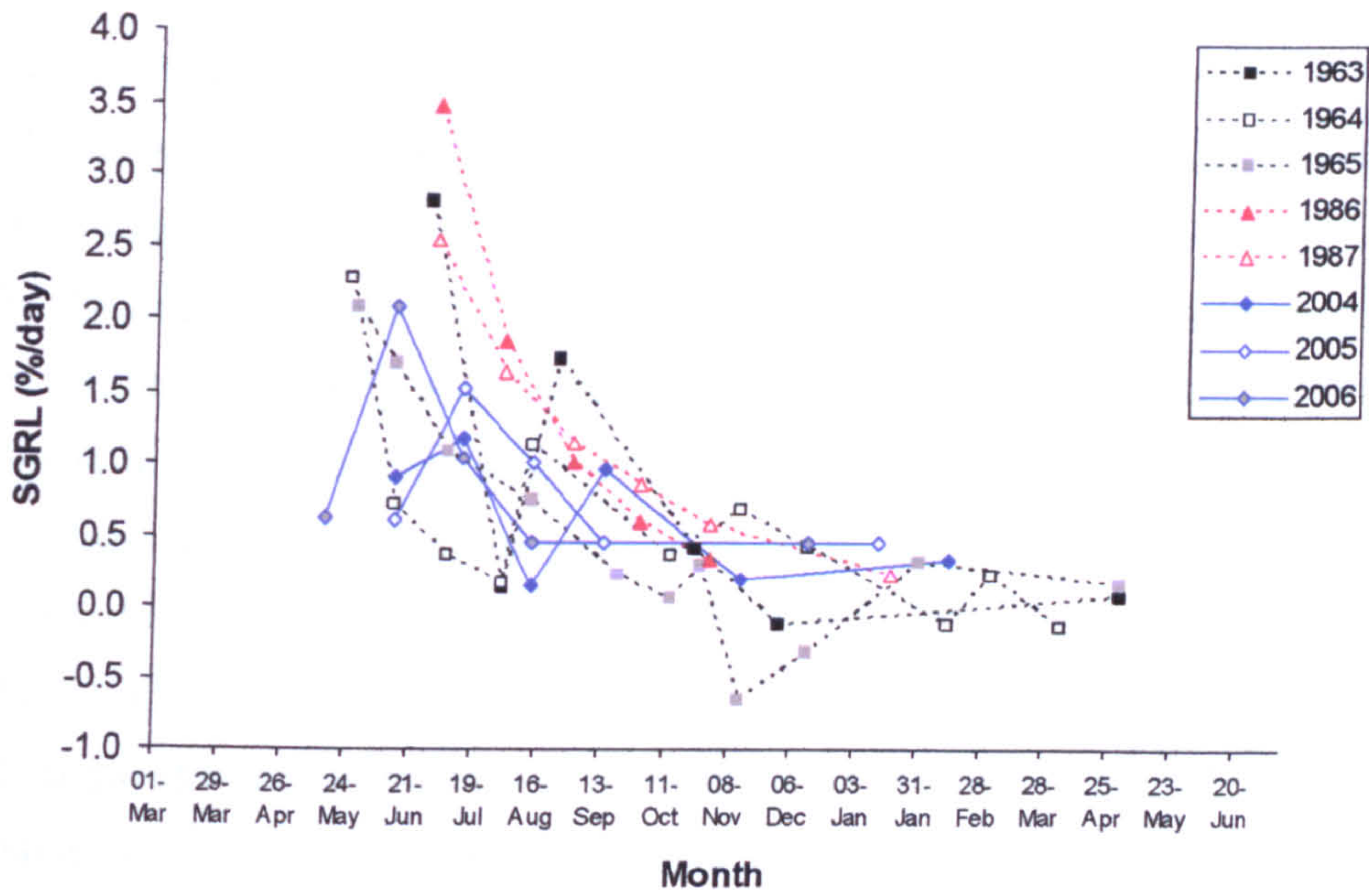


Figure 4.15: Mean total length (cm) for juvenile plaice *P. platessa* L. after settlement during their first year of residence on (a) Red Wharf Bay [1963 - 1965, Macer (1967); 1986 - 1987, Al-Hossaini *et al.* (1989); 2004 - 2006, this study] and (b) various nursery grounds in the North East Atlantic [English Channel (E Chan), Amara (2004); Southern Bight (SB), Amara (2003); Wadden Sea (Wad), Kuipers (1977); Isle of Man (IoM), Nash *et al.* (1994); North Sea (Filey), Lockwood (1972; cited in Kuipers, 1977); Loch Ewe, Edwards and Steele (1968); Iceland (Ice), Hjörleifsson and Pálsson (2001)].

a)



b)

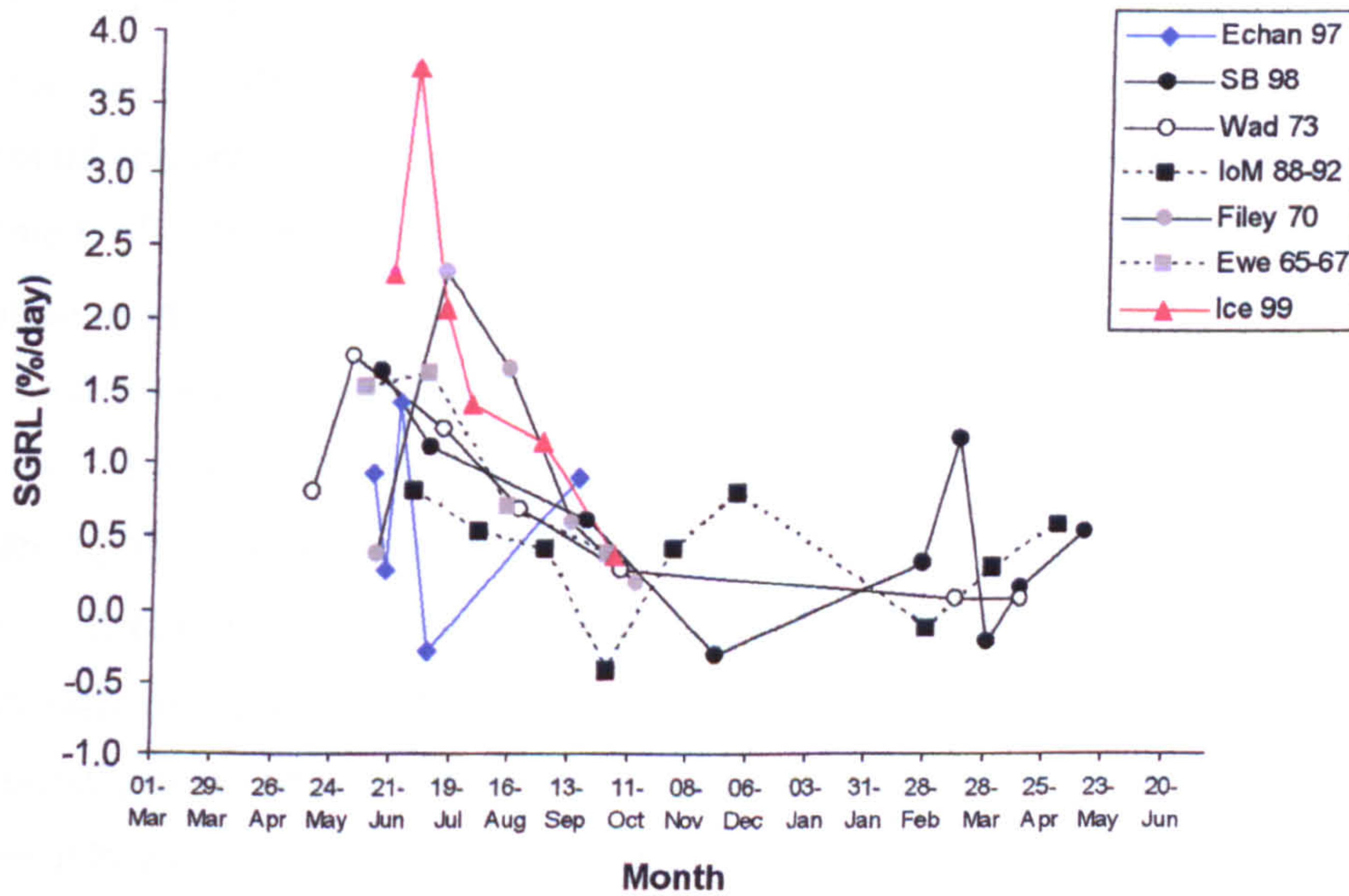


Figure 4.16: Length-specific growth rates (SGR_L , $\% \text{ day}^{-1}$) for juvenile plaice *P. platessa* L. after settlement during their first year of residence on (a) Red Wharf Bay [1963 - 1965, Macer (1967); 1986 - 1987, Al-Hossaini et al. (1989); 2004 - 2006, this study] and (b) various nursery grounds in the North East Atlantic [English Channel (E Chan), Amara (2004); Southern Bight (SB), Amara (2003); Wadden Sea (Wad), Kuipers (1977); Isle of Man (IoM), Nash *et al.* (1994); North Sea (Filey), Lockwood, 1972 (cited in Kuipers, 1977); Loch Ewe, Edwards and Steele (1968); Iceland (Ice), Hjörleifsson and Pálsson (2001)].

their first year on the nursery ground. Modal progression analysis was used to identify the nodal size of the 0-group cohort in each monthly sample (Figures 4.7 and 4.8) and these standard length values were used to calculate length-specific growth rates for each cohort on the two nursery grounds (Figure 4.9). The growth data showed that growth rates were highest over the summer at 2 – 4 % day⁻¹ decreasing to ca. 1 % day⁻¹ for the rest of the year (Figure 4.9). Figures 4.15 and 4.16 summarise the available data on the growth of juvenile plaice during their first year of residency on nursery grounds in the North East Atlantic. Figures 4.15a and 4.16a show the increase in length and length-specific growth rate for 0-group plaice on Red Wharf Bay covering the periods 1963-1965 (Macer, 1967), 1986-1987 (Al-Hossaini *et al.*, 1989) and 2004-2006 (this study) respectively. Figures 4.15b and 4.16b show the increase in length and length-specific growth rate for 0-group plaice on nursery grounds in the English Channel (Amara, 2004), North Sea [Lockwood, 1972 (cited in Kuipers, 1977); Kuipers, 1977; Amara, 2003], Irish Sea (Nash *et al.*, 1994), and Iceland (Hjörleifsson and Pálsson, 2001). The growth data for Red Wharf Bay, recorded over a 40 year period by the three studies (Macer, 1967; Al-Hossaini *et al.*, 1989; this study) show a consistency in the pattern of growth during the first year of residency on the nursery ground (Figures 4.15a and 4.16a). As expected, due to latitudinal differences in the timing of settlement, food availability and growth opportunity, there is greater variation in the pattern of growth during the first year of residency on the nursery ground observed for different areas of the North East Atlantic (Figures 4.15b and 4.16b). However, the same pattern is observed on each nursery ground with growth rates highest over the summer at ca. 1-4 % day⁻¹, decreasing to < 0.5 % day⁻¹ during the winter/spring. Overwinter growth rates measured for juvenile plaice in Port Erin Bay (Isle of Man) in 1989/1990 and 1990/1991 by Nash *et al.* (1992) also provide seasonal growth rates similar to those recorded in this study with relative growth rates over autumn/winter of 0.07-0.13 % day⁻¹.

4.4.3 Length/weight relationships and condition

This study has examined seasonal changes in the length/weight relationship and condition factor of 0-group juvenile plaice in Conwy Bay and Red Wharf Bay. There are a very large number of published papers reporting the length/weight relationships in fishes due to the inclusion of the length/weight power function ($W =$

aL^b) in many fisheries management models to convert length frequency data to biomass data (e.g. Al-Mamry, 2006). For example, the fisheries journal *Journal of Applied Ichthyology* regularly publishes short communications reporting the length/weight relationships for fish species and has recently published a paper presented a meta-analysis of the length/weight relationships for 1773 species of fishes (Froese, 2006). Length/weight relationships have been published for many flatfish species (e.g. Jones, 1974; Ortega-Salas, 1980; Brodziak and Mikus, 2000; Seisay, 2001; Froese, 2006; Bayhan *et al.*, 2008) including plaice (e.g. Bowers and Lee, 1971; Rauck, 1975; Basimi and Grove, 1985c; Chuenpagdee, 1990; Seyhan, 1990; Chapter 3). However, research on the length/weight relationships of juvenile flatfish, and the seasonal changes in this relationship have been more limited (Nash *et al.*, 1992; this study). To summarise the general patterns observed in these published flatfish studies: length/weight relationships have generally shown species to show positive allometric growth (*i.e.* $b > 3$) although where the data are sorted by sex, male fish sometimes show isometric growth (*i.e.* $b \approx 3$) whereas females exhibit positive allometric growth. In addition, where data have been collected by season or month, studies have shown a cyclical pattern in the b-values observed with b-values increasing and positive allometric growth seen desiring the summer growth season and leading into the start of the breeding season followed by a decline in b-value to values < 3 and a switch to negative allometric growth during the spawning seasonal and in the immediate aftermath of spawning. A similar seasonal cyclical pattern has been observed for juvenile plaice (Nash *et al.*, 1992; this study) and other flatfish (e.g. Rosenberg, 1982) which follows the seasonal cycle of food availability and growth opportunity, although it must be pointed out that some variation in b-values may also be due to the limited sample sizes collected during some monthly sampling (Nash *et al.*, 1992; Table 4.5).

In this study, condition factor was calculated for each month by comparing the actual weights with those predicted by the length-weight relationship (King, 2007) as opposed to the calculation of Fulton's Condition factor ($CF = W/L^3$) (Bolgor and Connolly, 1989). This analytical approach takes into account the actual b-value relating length to weight instead of assuming a value of 3, expresses condition as the proportional increase/decrease in observed weight compared to predicted weight ($CF = W_{obs}/W_{pred}$) and allows seasonal patterns in condition to be elucidated (King, 2007). The study of seasonal patterns of condition, and its relation to food abundance,

growth opportunity and stage of the reproductive cycle has been well studied for adult fishes in both freshwater (*e.g.* Wilson and Pitcher, 1983; Encina *et al.*, 1997; Yildirim *et al.*, 2006; Arslan and Yildirim, 2007; Yildirim *et al.*, 2008) and marine environments (*e.g.* Knust, 1996; Hansen and Courtenay, 1997; Mello and Rose 2005; Andreu-Soler *et al.*, 2006; Tzikas *et al.*, 2007; Wang *et al.*, 2008; Wuenschel *et al.*, 2009), including studies on adult plaice (White and Fletcher, 1984). The data for seasonal changes in condition of juvenile fishes is less extensive (*e.g.* Kuipers, 1977; Nash *et al.*, 1992; Pangle and Sutton, 2005; Gilliers *et al.*, 2004; this study).

Assessing the condition of juvenile fishes on nursery grounds is an area of considerable research interest both to assess the habitat quality of these nursery areas and to predict recruitment into the adult stock. Various markers have been used to assess condition ranging such as biochemical markers, for example nucleic acids (RNA and DNA) and protein/lipid content, and morphometric markers, for example condition indices relating weight to length (see reviews by Bolgor and Connolly, 1989; Buckley *et al.*, 1999; Fonseca and Cabral, 2007). The number of studies that have examined differences in the condition of 0-group juvenile flatfishes is limited but the available data relates condition to either seasonal variation within a nursery ground or between-nursery ground variation to assess differences in habitat quality and growth (*e.g.* Nash *et al.*, 1992; Gilliers *et al.*, 2004, 2006; Amara *et al.*, 2007; Vasconcelos *et al.*, 2009; this study). In this study, seasonal variation in condition was observed, as expected, with juveniles in better condition during the summer/autumn, when food availability is higher and growth opportunity is better, compared to the winter/spring (Figure 4.9). This result agrees with earlier studies on plaice by Costopoulos and Fonds (1989) and Nash *et al.* (1992). Costopoulos and Fonds (1989), calculating monthly condition factors using a b-value of 3, showed that condition factor ($CF = 100W/L^3$) of juvenile plaice (9-17 cm total length) on two nursery areas in the Dutch Wadden Sea increased from 0.7-0.8 in April to 0.9-0.95 in October. Seasonal variation in length/weight relations and condition was also observed for overwintering juvenile plaice caught in Port Erin Bay Isle of Man by Nash *et al.* (1992). Nash *et al.* (1992) showed a similar seasonal fluctuation in b-values over a similar range to that observed in this study. In addition to showing seasonal variations in condition, the results of this study have also shown interannual-variation in condition (Figure 4.9), which has also been observed in previous studies (Al-Hossaini *et al.*, 1989). Although there was little difference in length/weight relationships and

condition factors in the two sites surveyed in this study, presumably due to their close geographical proximity (and hence similar annual temperature regimes) and their similar benthic community structures (Rees, 2004), previous studies have shown differences in condition of juvenile flatfishes between geographically more separated nursery grounds (*e.g.* Kuipers, 1977; Gilliers *et al.*, 2004, 2006).

4.4.4 Summary

- This chapter has presented a detailed survey of the growth, length/weight relationship and condition of juvenile European plaice *P. platessa* L. on two nursery grounds in the inshore coastal waters of North West Wales (Llanfairfechan in Conwy Bay) and Eastern Anglesey (Llanddona in Red Wharf Bay).
- Surveys were conducted between April 2004 and March 2007 at monthly intervals (weather permitting) with juvenile plaice (predominately 0-group) collected by push netting in shallow water (< 1 m depth) during the summer/autumn and 2m beam trawl (3-7 m depth) in the winter/spring.
- Detailed analysis of the length frequency distributions collected over three year time period revealed that settlement occurred in April-May and continued over the summer until August at both sites. The average length of plaice caught increased over time from *ca.* 1.5-2.0 cm standard length in April/may to *ca.* 8-10 cm the following Feb/March. Modal progression analysis (using Bhattacharya's method) was used to identify the 0-group and 1-group plaice cohorts present on the nursery grounds each year and to determine monthly nodal lengths for each cohort in order to calculate growth rates.
- Length-specific growth rates were highest in the early summer, *ca.* 2.5- 4.0 % day⁻¹, and declined over the autumn to attain rates of *ca.* 0.5-1.0 % day⁻¹ over the winter. There were no apparent differences in growth rate between Llanfairfechan and Llanddona although some interannual variation was observed with growth rates higher in 2004 and 2006 compared to 2005. The growth rates observed on the plaice nursery grounds in North Wales are similar to those observed on nursery grounds throughout the North East

Atlantic by previous studies in the English Channel, North Sea, Irish Sea and in Iceland.

- Seasonal variation in the 'a' and 'b' values of the length/weight relationship ($W = aL^b$) and in condition factor were observed on both nursery grounds. Condition was lowest in the winter/spring and increased in the summer autumn as a result of increased food availability and growth opportunity.

Chapter 5:

General Discussion.

5. General discussion

The aim of this thesis has been to study the population dynamics of the inshore population of plaice *P. platessa* L. found in the coastal inshore waters of North West Wales and Eastern Anglesey. This has been achieved through autumnal surveys of the adult population in the inshore waters where the adults will congregate in October-December before the fish moving offshore onto the spawning grounds in January-February to breed (Basimi and Grove, 1985c; Dunn and Pawson, 2002). In addition, data from the annual RV *Prince Madog* autumnal fisheries surveys conducted since 1970 have been used to examine changes in the population dynamics of this inshore population of plaice over a 4 decade time span in relation to fishing pressure and recent climate change and to compare changes in the population dynamics of this species with other demersal fish species, also included in the fisheries survey, but which differ in their level of fisheries exploitation. The comparison made being between dab *L. limanda* (unexploited, 1970-2006; Seisay, 2001), plaice (heavily exploited 1970-1989, underexploited 1990-2006; ICES, 2008a) and whiting *M. merlangus* (heavily exploited 1970-2006; ICEAS, 2008a). Finally, seasonal changes in the growth and condition of three cohorts of 0-group juvenile plaice were studied on two of the main nursery areas in North West Wales and Eastern Anglesey, *i.e.* Conwy bay (Llanfairfechan) and Red Wharf Bay (Llanddona).

5.1 Population dynamics

The study of the ecology, biology and population dynamics of exploited fish species is a critical area of research that provides data for inputting into modern virtual population analysis fisheries models (Hillborn and Walters, 1992). These models require knowledge of the age and size structure of the exploited population, the length-weight coefficient (b), the VBG coefficients (k , L_{∞}), the instantaneous coefficient of natural mortality (M) and maturity ogives (L_{50}) (Jennings *et al.*, 2001; Hart and Reynolds, 2002; King 2007). Estimates of these values are derived by conducting detailed fisheries surveys (such as the one conducted in this present study) to obtain estimates for these population parameters. Since the values of these parameters can vary between stocks depending on their geographical location (see Chapter 2) and can vary over time in response to environmental and fisheries-related

changes (see Chapter 3), it is important that regular surveys are conducted in order to ensure that the management decisions taken are informed by accurate data in the modelling process. Thus, the value of regular surveys cannot be understated. Within the Northern Atlantic, such surveys are conducted by ICES for many of the commercially exploited species (e.g. plaice, cod *G. morhua* L., herring *C. harengus* L., mackerel *S. scombrus* L. etc; e.g. ICES, 2008a, 2008b) although, surprisingly, these data are not available, or are considered inaccurate, for the stocks of some commercial species e.g. whiting and *N. norvegicus* in the Irish Sea (ICES, 2008a). This lack of fundamental information becomes even more apparent when the fisheries in the developing world are considered where a lack of scientific infrastructure and funding preclude the collation of accurate data on landings, fishing effort and population dynamics of exploited species (FAO, 2009). However, in some areas of the world, this situation appears to be improving: for example, the Western Indian Ocean is recognised as one area of the World's oceans where abundant fish resources still remain and there is potential for further expansion and an increase in landings (FAO, 2009). In order to ensure that any expansion is based on an accurate scientific assessment of the fish stocks and the fishing industry, some nations in the Western Indian Ocean, for example the Sultanate of Oman, have been conducting detailed surveys of fish stocks (e.g. Al-Mamry, 2006; Ben Meriem *et al.*, 2006; Al-Mamry *et al.*, 2007, 2009) and have established a detailed system of reporting catches and fishing effort (Anon., 2006) in their coastal waters. There have also been a series of detailed studies on the population dynamics and stock assessment for exploited fish species in the southern Arabian Gulf (e.g. Grandcourt *et al.*, 2004a, 2004b, 2005a, 2005b, 2006a, 2006b, 2007). The importance of conducting stock-specific surveys can be seen in the comparison between different plaice stocks conducted in Chapter 2. This analysis has shown differences in the size structure, growth patterns and maturity ogives between different plaice stocks. For example, differences between plaice in the Irish Sea and North Sea are apparent even though they share a similar latitude. These differences are most likely the result of the different bathymetries (the North Sea is a much shallower and more productive sea than the Irish Sea) and due to genetic differences that have evolved over time. A second example of a striking difference in the population ecology of a fish species over a very short geographical scale can be seen in the king soldier bream *A. spinifer* which a commercially exploited sparid species that has a wide distribution from southern Africa eastward to northern

Australia including the western Indian Ocean and the Indo-west Pacific (Randall, 1995). Recent studies have been conducted on the population dynamics of this species in the southern Arabian Sea (Grandcourt *et al.*, 2004a) and the Arabian Gulf (Al-Mamry *et al.*, 2009). It has become evident that significant differences in the growth patterns (*e.g.* timing of the formation of the opaque and translucent zones in the otolith and in the von Bertalanffy growth parameters) and in the timing of the spawning season are seen between the two stocks for this species which are related to the monsoon season which occurs in Omani waters and the associated elevation in biological productivity (Al-Mamry *et al.*, 2009).

As well as focussing attention on adult plaice, this thesis has also conducted a detailed study of juvenile plaice on two nursery grounds – Conwy Bay and Red Wharf Bay. The study of the juvenile phase of the life cycle for a commercially exploited species is also very important. An understanding of the ecology of juveniles and the environmental factors which determine growth rate and survival (*e.g.* temperature, food availability and predation pressure) are very important from a fisheries management point of view since accurate information on juvenile recruitment, *i.e.* the number of juvenile fish joining the adult stock each year and becoming vulnerable to capture by fishing gear, is necessary in order to determine annual year class strength and to set catch quotas (King, 2007). The ecology and “population dynamics” (in the sense that juvenile plaice can be considered as a population separate from the adults on the juvenile nursery grounds) of juvenile plaice have been well studied (see review of this subject area in Chapter 4). There are however, a number of key areas from a fisheries management viewpoint which still remain a matter of guesswork. One main area of uncertainty is the relative importance of the different nursery areas in producing recruits into the adult stock. The South East Irish Sea plaice stock utilises nursery areas that are located from the Cumbrian coast in the North, along the coast of North West England and North Wales to Eastern Anglesey (Dunn and Pawson, 2002). However, although the feeding ecology, growth and survival rates of juvenile plaice on those nursery ground has been well studied (*e.g.* Macer, 1967; Carter *et al.*, 1991; Fox *et al.*, 2007; Chapter 4), it is still not known which nursery areas are the most important in terms of supplying recruits into the adult stock. If this was known then appropriate management strategies of these areas could be introduced to minimise anthropogenic disturbances and to ensure maximal juvenile production from these nursery areas. An area of recent research interest in fisheries science is the use of

internal chemical tags, such as the elemental or isotopic composition of otoliths to examine the movement patterns of marine fishes (*e.g.* Gillanders, 2005; Herzka, 2005). These techniques rely on there being measurable differences in water chemistry between geographically distinct water bodies (*e.g.* Gillanders, 2005; Herzka, 2005). There have been a number of recent studies which have shown that juvenile fish, reared on separate nursery grounds can have significant differences in the elemental composition of their otoliths which can be used to identify their point of natal origin (*e.g.* Brown, 2006; Vasconcelos *et al.*, 2007; Fodrie and Herzka, 2008; Ward, 2008). A recent study by Marriott (2008) has shown significant differences in the otolith elemental composition of juvenile plaice sampled from nursery grounds within the South East Irish Sea region. However, it is not currently known the degree to which these distinct chemical tags for each nursery ground are temporally stable – *i.e.* whether the spatial inter-nursery ground variability is greater than the temporal intra-nursery ground variability since the available data are all based on samples collected within a 1-2 year sampling period (Brown, 2006; Vasconcelos *et al.*, 2007; Fodrie and Herzka, 2008; Marriott, 2008; Ward, 2008). Confirming temporal stability is important since juvenile fish may remain in nursery areas for several years [*e.g.* plaice, Marriott (2008) and sea bass, Ward (2008)] before recruiting into the adult stock. If temporal stability can be confirmed, then this technique may be able to identify the relative proportions of adult fish derived from different nursery ground, or regional nursery areas.

5.2 Long-term fisheries surveys

As summarised in Chapter 3, there is clearly great value in the acquisition of long-term data sets, either through ongoing research surveys or from archived data material in order to examine temporal trends in the abundance and biology of animals in relation to environmental fluctuations (*e.g.* climate change) and anthropogenic disturbance such as fishing pressure and habitat destruction. Since 1970, the School of Ocean Sciences at Bangor University has conducted fishing surveys each year during October/November in the coastal inshore waters off eastern Anglesey and Northwest Wales. Although the primary aims of these trips are for teaching purposes, the data collected from these surveys has been archived and the results presented in Chapter 3 show that this is a valuable and ongoing research resource that can be used

to examine temporal changes in local demersal fish communities. For example, a detailed analysis of the data for dab, plaice and whiting indicated evidence of fisheries-induced evolution in the plaice and whiting stocks in the South East Irish Sea. Although it would be reasonable to surmise such a change for the whiting based on its history of overexploitation (ICES, 2008a) and the strong correlation between fishing intensity and changes in life-history characters such as growth rate and maturity ogives observed for other gadid species (*e.g.* haddock, *M. aegelfinus*, Wright, 2005; cod, Sinclair *et al.*, 2002; Barot *et al.*, 2004; Hutchings, 2005), such a response would not be expected for plaice in the Irish Sea. Although fisheries-induced evolution has been observed for plaice in the North Sea (*e.g.* Rijnsdorp, 1993b; Grift *et al.*, 2003, 2005; Rijnsdorp *et al.*, 2005), fishing pressure for plaice in the North Sea has been much more intense and more prolonged compared to the plaice fishery in the Irish Sea (ICES, 2008a, 2008b). Given the level of exploitation of plaice in the Irish Sea, where fishing pressure has not resulted in the adult spawning stock biomass falling below the B_{lim} value at any point during its history (ICES, 2008a), fisheries-induced evolution would not be expected. However, a careful analysis of the data from the RV *Prince Madog* fisheries survey does provide some indication of fisheries-induced evolution and it is important that the stock continues to be carefully monitored. Long-term data sets are also providing evidence for the effects of climate change on terrestrial and aquatic ecosystems (see Chapter 3) and the long-term plaice data set was also examined for evidence of climate change. The results of that analysis has provided some evidence of changes in abundance and growth in the local plaice stock since 1970. There was a correlation between plaice abundance and the winter North Atlantic Oscillation Index (wNAOI) with higher abundances (number plaice hour⁻¹) recorded in the survey when the wNAOI was in negative phase. A simple model outlining the effects of increased/decreased sea surface temperature (SST) on size and growth was proposed and for male plaice, the correlations between growth and SST/ wNAOI followed those predicted by the model, but the predicted response was not observed for female plaice. The climate change analysis conducted in Chapter 3 (*i.e.* correlations and ANOVAs) was relatively simple compared to some of the more complex time series analysis that can be conducted using data sets of this type (*e.g.* Teal *et al.*, 2008).

5.3 Areas for future research

The results of this thesis have provided valuable data on the population dynamics of the inshore population of plaice *P. platessa* L. found in the coastal inshore waters of North West Wales and Eastern Anglesey and have contributed to the body of knowledge for this commercially important fish species. Based on the results of this thesis a number of areas of future research are suggested:

- It is evident that there is much to be gained by regular surveying fish populations. It is fortunate that the annual RV *Prince Madog* fisheries surveys form part of the undergraduate teaching programme at Bangor University as it has allowed a 4 decade-long data set to be collected for demersal fish species such as plaice, dab and whiting. It is recommended that this survey be continued since its continuation will allow a continual monitoring of the plaice stock to confirm whether fisheries-induced evolution has occurred in the South East Irish Sea plaice stock and to provide a longer time series of data for correlating with environmental variables to detect the effects of climate change on this fish stock.
- In relation to determining the effects of climate change, it is recommended that a more detailed analysis of the plaice long-term data set be conducted using time series statistics.
- It is recommended that the otolith archive for juvenile plaice caught in Red Wharf Bay and Conwy Bay be used to determine whether elemental signatures of plaice otoliths exhibit temporal stability. If this proves to be the case, then this will provide a new and exciting area of research using the otolith archive derived from the long-term fisheries survey.

References:

- Al-Hamdani, Z.K., Reker, J., Leth, J.O., Reijonen, A., Kotilainen, A.T., Dinesen, G.E. (2007). Development of marine landscape maps for the Baltic Sea and the Kattegat using geophysical and hydrographical parameters. *Geological Survey of Denmark and Greenland Bulletin* **13**, 61-64.
- Al-Hossaini, M., Pitcher, T.J. (1988). The relation between daily rings, body growth and environmental-factors in plaice, *Pleuronectes platessa* L, juvenile otoliths. *Journal of Fish Biology* **33**, 408-418.
- Al-Hossaini, M., Liu, Q., Pitcher, T.J. (1989). Otolith microstructure indicating growth and mortality among plaice, *Pleuronectes platessa* L., post-larval sub-cohorts. *Journal of Fish Biology* **35** (Suppl. A), 81-90.
- Allen, B.M., Brophy, D., McGrath, D., King, P.A. (2008). Hatching times, larval duration, settlement and larval growth of plaice (*Pleuronectes platessa* (L.) in Galway Bay determined using otolith microstructure. *Biology and Environment-Proceedings of the Royal Irish Academy* **108B**, 127-134.
- Al-Mamry, J.M.A. (2006). Biology and fisheries management of King soldier bream, *Argyrops spinifer* and Spangled emperor, *Lethrinus nebulosus* in the Arabian sea, Oman. PhD, Bangor University, 351 pp.
- Al-Mamry, J.M., El Ganainy, A.A., McCarthy, I., Richardson, C., Ben Mariem, S. (2007). Age, growth and reproductive biology of Spangled Emperor, *Lethrinus nebulosus* (Forsskal, 1775), from the Arabian Sea, Oman. *Egyptian Journal of Aquatic Research* **33**, 395- 410.
- Al-Mamry, J.M., McCarthy, I.D., Richardson, C.A., Ben-Meriem, S. (2009). Biology of the king soldier bream, *Argyrops spinifer* (Forsskal 1775), from the Arabian Sea, Oman. *Journal of Applied Ichthyology* in press.
- Al-Rashada, Y.N. (2003). Population dynamic of the brown shrimp *Crangon crangon* (L.) in Traeth Melynog, Irish Sea. M.Sc., Bangor University, 59 pp.
- Amara, R. (2003). Seasonal ichthyodiversity and growth patterns of juvenile flatfish on a nursery ground in the Southern Bight of the North Sea (France). *Environmental Biology of Fishes* **67**, 191-201.
- Amara, R. (2004). 0-group flatfish growth conditions on a nursery ground (Bay of Canche, Eastern English Channel). *Hydrobiologia* **518**, 23-32.
- Amara, R., Laffargue, P., Dewarumez, J.M., Maryniak, C., Lagardere, F., Luczac, C. (2001). Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *Journal of Fish Biology* **58**, 788-803.
- Amara, R., Meziane, T., Gilliers, C., Hermell, G., Laffargue, P. (2007). Growth and condition indices in juvenile sole *Solea solea* measured to assess the quality of essential fish habitat. *Marine Ecology Progress Series* **351**, 201-208.
- Amezcu, F. Nash, R.D.M. (2001). Distribution of the order Pleuronectiformes in relation to the sediment type in the North Irish Sea. *Journal of Sea Research* **45**, 293-301.

- Amezcuca, F. Nash, R.D.M., Veale, L. (2003). Feeding habits of the Order Pleuronectiformes and its relation to the sediment type in the north Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* **83**, 593-601.
- Andreu-Soler, A., Oliva-Paterna, F.J., Torralva, M. (2006). Seasonal variations in somatic condition, hepatic and gonad activity of sand smelt *Atherina boyeri* (Teleostei, Atherinidae) in the Mar Menor coastal lagoon (SE Iberian Peninsula). *Folia Zoologica* **55**, 151-161.
- Anon., 2006: Fisheries statistics of Oman for 2006. Directorate General of Planning and Investment Promotion, Muscat, Sultanate of Oman. Statistics and Information Department Report 120/2008, 239 p.
- Armstrong, M.J., Connolly, P., Nash, R.D.M., Pawson, M.G., Alesworth, A., Coulahan, P.R., Dickey-Collas, M., Milligan, M., O'Neill, M.F., Witthames, P.R., Woolner, L. (2001). An application of the annual egg method to estimate the spawning biomass of cod (*Gadus morhua* L.), plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) in the Irish Sea. *ICES Journal of Marine Science* **58**, 183-203.
- Arneri, E., Colella, S., Giannetti, G. (2001). Age determination and growth of turbot and brill in the Adriatic Sea: reversal of the seasonal pattern of otolith zone formation. *Journal of Applied Ichthyology* **17**, 256-261.
- Arnott, S.A., Ruxton, G.D. (2002). Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. *Marine Ecology Progress Series* **238**, 199-210.
- Arslan, M., Yildirim, A. (2007). Seasonal changes in condition and gonadal maturation of brown trout (*Salmo trutta*) in a Turkish stream. *Journal of Freshwater Ecology* **22**, 529-531.
- Attrill, M.J., Power, M. (2002). Climatic influence on a marine fish assemblage. *Nature* **417**, 275-278.
- Bagenal, T.B. (1957). The breeding and fecundity of the long rough dab *Hippoglossoides platessoides* (Fabr.) and the associated cycle in condition. *Journal of Marine Biological Association of UK* **36**, 339-375.
- Bagenal, T.B. (1966). The ecological and geographical aspects of the fecundity of plaice. *Journal of the Marine Biological Association of the United Kingdom* **46**, 161-186.
- Bakhsh, A.A. (1982). Population studies of the flatfish *Limanda limanda* (L.) in Anglesey waters. Unpublished PhD thesis, Bangor University, 136 pp.
- Barot, S., Heino, M., O'Brien, L., Dieckmann, U. (2004). Long-term trend in the maturation reaction norm of two cod stocks. *Ecological Applications* **14**, 1257-1271.
- Barot, S., Heino, M., Morgan, M.J., Dieckmann, U. (2005). Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? *ICES Journal of Marine Science* **62**, 56-64.
- Barry, J.P., Baxter, C.M., Sagarin, R.D., Gilman, S.E. (1995). Climate-related, long-term faunal changes in a Californian rocky intertidal community. *Science* **267**, 672-675.
- Basimi, R. A. (1978). Feeding and growth in an inshore population of plaice *Pleuronectes platessa* L. Unpublished PhD, Bangor University, 145 pp.

- Basimi, R. A., Grove, D.J. (1985a). Gastric emptying rate in *Pleuronectes platessa* L. *Journal of Fish Biology* 26, 545-552.
- Basimi, R. A., Grove, D.J. (1985b). Estimates of daily food intake by an inshore population of *Pleuronectes platessa* L. off eastern Anglesey, North Wales. *Journal of Fish Biology* 27, 505-520.
- Basimi, R. A., Grove, D.J. (1985c). Studies on feeding, growth and production of recruited inshore population off East Anglesey, North Wales. *Journal of Fish Biology* 27, 765-783.
- Baumgartner, T.R., Soutar, A., Ferreira-Bartolina, V. (1992). Reconstruction of the history of Pacific sardine and northern anchovy populations over the past 2 millennia from sediments of the Santa Barbara basin, California. *California Cooperative Oceanic Fisheries Investigations Reports* 33, 24-40.
- Bayhan, B., Sever, T.M., Taşkavak, E. (2008). Length-weight relationships of seven flatfishes (Pisces: Pleuronectiformes) from Aegean Sea. *Turkish Journal of Fisheries and Aquatic Sciences* 8, 377-379.
- Beaman, R.J., Harris, P.T. (2005). Bioregionalization of the George V Shelf, East Antarctica. *Continental Shelf Research* 25, 1657-1691.
- Beaugrand, G., Reid, P.C. (2003). Long term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* 9, 801-817.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661-664.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibanez, F. (2008). Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters* 11, 1157-1168.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M. (2002). Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692-1694.
- Beddington, J.R., Agnew, D.J., Clark, C.W. (2007). Current problems in the management of marine fisheries. *Science* 316, 1713-1716.
- Beggs, S.E., Nash, R.D.M. (2007). Variability in settlement and recruitment of 0-group dab *Limanda limanda* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research* 58, 90-99.
- Ben Meriem, S., Al-Marzouqi, A., Al-Mamry, J. (2006). Fisheries exploitation pattern of narrow-barred Spanish mackerel, *Scomberomorus commerson*, in Oman and potential management options. *Journal of Applied Ichthyology* 22, 218-224.
- Bergahn, R., Ludemann, K., Ruth, M. (1995). Differences in individual growth of newly settled 0-group plaice (*Pleuronectes platessa* L) in the intertidal of neighbouring Wadden Sea areas. *Netherlands Journal of Sea Research* 34, 131-138.
- Beverton, R.J.H., Holt, S.J. (1957). *On the dynamics of exploited fish populations*. Fishery Investigations Series 2 Volume 19, Ministry of Agriculture, Fisheries and Food.
- Beverton, R.J.H., Holt, S.J. (1959). A review of the lifespan and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquium on Ageing* 5, 142-180.

- Beverton, R.J.H. (1963). Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. *Rapports et Proces-Verbaux des Reunions (Conseil Permanent International pour l'Exploration de la Mer)* 154, 44–67.
- Bielak, A.T., Power, G. (1986). Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec, 1859–1983. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 281–287.
- Bolgor, T., Connolly, P.L. (1989). The selection of suitable indexes for the measurement and analysis of fish condition. *Journal of Fish Biology* 34, 171–182.
- Bolle, L.J., Rijnsdorp, A.D., van Neer, W., Millner, R.S., van Leeuwen, P.I., Ervynck, A., Ayers, R., Ongena, E. (2004). Growth changes in plaice, cod, haddock and saithe in the North Sea: a comparison of (post-) medieval and present-day growth rates based on otolith measurements. *Journal of Sea Research* 51, 313–328.
- Bone, Q., Moore, R.H. (2008). *Biology of Fishes*, 3rd edition, Taylor and Francis, London, 478 pp.
- Booker, D.J., Wells, N.C., Smith, I.P. (2008). Modelling the trajectories of migrating Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 65, 352–361.
- Bowers, A.B. (1963). Growth of young plaice in Port Erin Bay. *Annual Report of the Biological Station, Port Erin* 75, 28–32.
- Bowers, A.B., Lee, J.W. (1971). The Growth of Plaice in Laxey Bay (Isle of Man). *Journal du Conseil* 34, 43–50.
- Boylan, P., Adams, C.E. (2006). The influence of broad scale climatic phenomena on long term trends in Atlantic salmon population size: an example from the River Foyle, Ireland. *Journal of Fish Biology* 68, 276–283.
- Braber, L., de Groot, S.J. (1973). The food of five flatfish species (Pleuronectiformes) in southern North Sea. *Netherlands Journal of Sea Research* 6, 103–172.
- Brander, K.M., Dickson, R.R. (1984). An investigation of the low level of fish production in the Irish Sea. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* 183, 234–242.
- Brander, K.M., Dickson, R.R., Edwards, M. (2003). Use of Continuous Plankton Recorder information in support of marine management: Applications in fisheries, environmental protection and in the study of ecosystem response to environmental change. *Progress in Oceanography* 58, 175–191.
- Brander, K.M., Mohn, R. (2004). Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 61, 1558–1564.
- Britton, J.R., Harper, D.M. (2008). Juvenile growth of two tilapia species in lakes Naivasha and Baringo, Kenya. *Ecology of Freshwater Fish* 17, 481–488.
- Brodziak, J., Mikus, R. (2000). Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon and northern California. *Fishery Bulletin* 98, 661–673.
- Broitman, B.R., Mieszkowska, N., Helmuth, B., Blanchette, C.A. (2008). Climate and recruitment of rocky shore intertidal invertebrates in the eastern North Atlantic. *Ecology* 89, S81–S90.

- Bromley, P.J. (2000). Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa* L.), and the generation of maturity ogives from commercial catch data. *Journal of Sea Research* 44, 27-43.
- Brown, J.A. (2006). Classification of juvenile flatfishes to estuarine and coastal habitats based on elemental composition of otoliths. *Estuarine Coastal and Shelf Science*. 66, 594-611.
- Brunel, T., Boucher, J. (2007). Long-term trends in fish recruitment in the north-east Atlantic related to climate change. *Fisheries Oceanography* 16, 336-349.
- Buckley, L., Caldarone, E., Ong, T.L. (1999). RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. *Hydrobiologia* 401, 265-277.
- Burrows, M.T., Gibson, R.N., Robb, L., Comely, C.A. (1994). Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *Journal of Experimental Marine Biology and Ecology* 177, 251-268.
- Burrows, M.T., Gibson, R.N., Robb, L., Maclean, A. (2004). Alongshore dispersal and site fidelity of juvenile plaice from tagging and transplants. *Journal of Fish Biology* 65, 620-634.
- Burrows, M.T., Gontarek, S.J., Nash, R.D.M., Gibson, R.N. (2001). Shrimp predation on 0-group plaice: contrasts between field data and predictions of an individual-based model. *Journal of Sea Research* 45, 243-254.
- Cabral, H.N. (2000). Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. *Journal of Fish Biology* 57, 1550-1562.
- Cabral, H.N. (2003). Differences in growth rates of juvenile *Solea solea* and *Solea senegalensis* in the Tagus estuary, Portugal. *Journal of the Marine Biological Association of the UK* 83, 861-868.
- Campana, S.E., (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* 47, 2219-2227.
- Carter, C.G., Grove D.J., Carter, D.M. (1991). Trophic resource partitioning between 2 coexisting flatfish species off the north coast of Anglesey, North Wales. *Netherlands Journal of Sea Research* 27, 325-335.
- Carter, C.G., Houlihan D.F., Brechin, J., McCarthy, I.D. (1993). The relationships between protein-intake and protein accretion, synthesis, and retention efficiency for individual grass carp, *Ctenopharyngodon idella* (Valenciennes), *Canadian Journal of Zoology* 71, 392-400.
- Casini, M., Cardinale, M., Hjelm, J., Vitale, F. (2005). Trends in cpue and related changes in spatial distribution of demersal fish species in the Kattegat and Skagerrak, eastern North Sea, between 1981 and 2003. *ICES Journal of Marine Science* 62, 671-682.
- Cefas (2001). SAMFISH Fisheries information – cod, whiting, plaice and sole in the Irish Sea. Unpublished report 16 pp (http://www.cefas.co.uk/publications/files/fishinfo_cspw.pdf) accessed 30/5/09.
- Cefas (2004). Final report, Programme 7: North Sea plaice and lemon sole. Fisheries science Partnership: 2004/2005, Cefas, Lowestoft, 42 pp.
- Cefas (2008). Plaice in the North Sea, (ICES sub-area IV) – 2008. Cefas, Lowestoft, 2 pp.
- Chatzinikolaou, E., Richardson, C.A. (2008). Population dynamics and growth of *Nassarius reticulatus* (Gastropoda : Nassariidae) in Rhosneigr (Anglesey, UK). *Marine Biology* 153, 605-619.

- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niguen, M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* **299**, 217-221.
- Chen, D.G., Liu, C.G., Dou, S.Z. (1992). The biology of flatfish (Pleuronectinae) in the coastal waters of China. *Netherlands Journal of Sea Research* **29**, 25-33.
- Chuenpagdee, R. (1990). Population study of female plaice, MSc thesis, Bangor University, 71 pp.
- Cloern, J.E., Nicholls, F.H. (1978). Von-Bertalanffy growth model with a seasonally varying coefficient. *Journal of the Fisheries Research Board of Canada* **35**, 1479-1482.
- Colebrook, J.M. (1978). Continuous plankton records - zooplankton and environment, northeast Atlantic and North Sea, 1948-1975. *Oceanologica Acta* **1**, 9-23.
- Collie, J.S., Wood, A.D., Jeffries, H.P. (2008). Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1352-1365.
- Conover, D.O. (2000). Darwinian fisheries science. *Marine Ecology Progress Series* **208**, 303-307.
- Conover, D.O., Munch, S.B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94-96.
- Conrath, C.L., Gelsleichter, J., Musick, J.A. (2002). Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. *Fisheries Bulletin* **100**, 674-682.
- Consuegra, S., De Leaniz, C.G., Serdio, A., Verspoor, E. (2005). Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. *Journal of Fish Biology* **67** (Suppl. 1), 129-145.
- Conway, D.V.P., Coombs, H., Smith, C. (1997). Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea. *ICES Journal of Marine Science* **54**, 136-147.
- Cortez, T., Gonzalez, A.F., Guerra, A. (1999). Growth of *Octopus mimus* (Cephalopoda, Octopodidae) in wild populations. *Fisheries Research* **42**, 31-39.
- Costopoulos, C.G., Fonds, M. (1989). Proximate body-composition and energy content of plaice (*Pleuronectes platessa*) in relation to the condition factor. *Netherlands Journal of Sea Research* **24**, 45-55.
- Coull, K.A., Jermyn, A.S., New A.W., Henderson, G.I., Hall, W.B. (1989). Length/weight relationships of 88 species of fish encountered in the North East Atlantic. Scottish Fisheries report No. 43, 82 pp.
- Cunningham, J.T. (1895). North Sea investigations. *Journal of the Marine Biological Association of the United Kingdom* **4**, 10-47.
- Cushing, D.H. (1975). The natural mortality of the plaice. *Journal du Conseil: Conseil International pour l'Exploration de la Mer* **36**, 150-157.
- Daan, N. (1997). TAC management in North Sea flatfish fisheries. *Journal of Sea Research* **37**, 321-341.
- Daan, N., Gislason, H., Pope, J.G., Rice, J.C. (2005). Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science* **62**, 177-188.
- Damberg, N. (1964). Extractives of fish muscle. 4. Seasonal variations of fat, water solubles, protein and water in cod (*Gadus morhua* L.) fillets. *Journal of the Fisheries Research Board of Canada* **21**, 703-709.

- Dawson, A.S., Grimm, A.S. (1980). Quantitative seasonal changes in the protein, lipid and energy content of the carcass, ovaries and liver of adult female plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 16, 493-504.
- Deevey, E. S. Jr. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology* 22, 283-314.
- De Roos, A.M., Boukal, D.S., Persson, L. (2006). Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society of London B* 273, 1873-1880.
- Dickey-Collas, M., Fox, C.J., Nash, R.D.M., O'Brien, C.M. (2003). Plaice egg mortality: can we determine survivorship? *Journal of Sea Research* 80, 211-225.
- Doggett, M.J. (2006). Polychlorinated biphenyls and their effects on the early life stages of the European plaice, *Pleuronectes platessa* L. Unpublished PhD thesis, Bangor University, 276 pp.
- Dulčić, J., Kokan, B., Vrgoč, N., Glamuzina, B., Conides, A.J., Skaramuca, B. (2008). Age, growth and mortality of red bandfish, *Cepola macrophthalmus* (L.), in the eastern Adriatic Sea (Croatian coast). *Journal of Applied Ichthyology* 24, 351-353.
- Dunlop ES, Shuter BJ, Ridgway MS (2005). Isolating the influence of growth rate on maturation patterns in the smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 844–853.
- Dunn, M.R., Pawson, M.G. (2002). The stock structure and migrations of plaice populations on the west coast of England and Wales. *Journal of Fish Biology* 61, 360-393.
- Durant, J.M., Anker-Nilssen, T., Hjermann, D.O., Stenseth, N.C. (2004). Regime shifts in the breeding of an Atlantic puffin population. *Ecology Letters* 7, 388-394.
- Dwyer, K.S., Veitch, M.F., Walsh, S.J. (2001). Age and Growth of Yellowtail Flounder in NAFO Divisions 3LNO: An Update. Northwest Atlantic Fisheries Organization, Scientific Council Meeting Research Document 01/52. 8 pp.
- Easey, M.W., Millner, R.S. (2008). Improved methods for the preparation and staining of thin sections of fish otoliths for age determination. *Science Series Technical Reports, Cefas Lowestoft*, 143, 12pp.
- Edwards, R., Steele, J.H. (1968). The ecology of 0-group plaice and common dabs at Loch Ewe I. Population and food. *Journal of Experimental Marine Biology and Ecology* 2, 215-238.
- Ellis, J.R., Rogers, S.I., and Freeman, S.M. (2000). Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel. *Estuarine, Coastal and Shelf Science* 51, 299–315.
- Enberg, K., Heino, M. (2007). Fisheries-induced life history changes in herring (*Clupea harengus*). ICES CM 2007/E: 23, 12pp, ICES, Copenhagen.
- Encina, L., Granado Lorencio, C. (1997). Seasonal changes in condition, nutrition, gonad maturation and energy content in barbel, *Barbus sclateri*, inhabiting a fluctuating river. *Environmental Biology of Fishes* 50, 75-84.
- Enever, R., Revill, A., Grant, A. (2007). Discarding in the English Channel, Western approaches Celtic and Irish seas (ICES subarea VII). *Fisheries Research* 86, 143-152.

- Engelhard, G.H., Heino, M. (2004). Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Marine Ecology Progress Series* 272, 245-256.
- Ernande, B., Dieckmann, U., Heino, M. (2004). Adaptive changes in harvested populations and evolution of age and size at maturation. *Proceedings of the Royal Society of London B* 271, 415-423.
- Erzini, K., Salgado, M., Castro, M., (2006). Dynamic of black spot sea bream (*Pagellus bogaraveo*) mean length: evaluating the influence of life history parameters, recruitment, size selectivity and exploitation rate. *Journal of Applied Ichthyology* 22, 183-188.
- FAO (2009). *The State of World Fisheries and Aquaculture 2008*. Food and Agriculture Organisation of the United Nations, Rome, 196 pp.
- Faunce, C.H., Serafy, J.E. (2008). Growth and secondary production of an eventual reef fish during mangrove residency. *Estuarine Coastal and Shelf Science* 79, 93-100.
- Filer, K.R., Sedberry, G.R. (2008). Age, growth and reproduction of the barrelfish *Hyperoglyphe perciformis* (Mitchill) in the western North Atlantic. *Journal of Fish Biology* 72, 861-882.
- Finney, B.P., Gregory-Eaves, I., Douglas, M.S.V., Smol, J.P. (2002). Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* 416, 729-733.
- Fodrie, F.J., Herzka, S.Z. (2008). Tracking juvenile fish movement and nursery contribution within arid coastal embayment via otolith microchemistry. *Marine Ecology Progress Series*. 361, 253-265.
- Fonseca, V.F., Cabral, H.N. (2007). Are fish early growth and condition patterns related to life-history strategies? *Reviews in Fish Biology and Fisheries* 17, 545-564.
- Forchhammer, M.C., Post, E., Stenseth, N.C. (2002). North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology* 71, 1002-1014.
- Forchhammer, M.C., Post, E. (2004). Using large-scale climate indices in climate change ecology studies. *Population Ecology* 66, 1-12.
- Fossen, I., Albert, O.T., Nilssen, E.M. (1999). Back-calculated individual growth of long rough dab (*Hippoglossoides platessoides*) in the Barents Sea. *ICES Journal of Marine Science* 56, 689-696.
- Fox, C.J., Geffen, A.J., Blyth, R., Nash, R.D.M. (2003). Temperature-dependent development rates of plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. *Journal of Plankton Research* 25, 1319-1329.
- Fox, C.J., Geffen, A.J., Taylor, N., Davison, P., Rossetti, H., Nash, R.D.M. (2007). Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles). *Marine Ecology Progress Series* 345, 255-269.
- Fox, C.J., McCloaghrie, P., Nash, R.D.M. (2009). Potential transport of plaice eggs and larvae between two apparently self-contained populations in the Irish Sea. *Estuarine and Coastal Shelf Science* 81, 381-389.
- Fox, C.J., McCloaghrie, P., Young, E.F., Nash, R.D.M. (2006). The importance of individual behavior for successful settlement of juvenile plaice (*Pleuronectes platessa* L.): a modelling and field study in the eastern Irish Sea. *Fisheries Oceanography* 15, 301-313.

- Francis, R.I.C.C. (1990). Back calculation of fish length: a critical review. *Journal of Fish Biology* **36**, 883-902.
- Frid, C.L.J., Garwood, P.R., Robinson, L.A. (2009). The North Sea benthic system: a 36 year time-series. *Journal of the Marine Biological Association of the United Kingdom* **89**, 1-10.
- Friedland, K.D., Walker, R.V., Davis, N.D., Myers, K.W., Boehlert, G.W., Urawa, S., Ueno, Y. (2001). Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Marine Ecology Progress Series* **216**, 235-252.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**, 241-253.
- Frøysa, K.G., Bogstad, B., Skagen, D.W. (2002). Fleksibest - an age-length structured fish stock assessment model. *Fisheries Research* **55**, 87-101.
- Gayanilo, F.C., Pauly, D. (1995). FAO-ICLARM stock assessment tools (FiSAT) User's Guide. FAO Computerized Information Series (Fisheries). No. 8. Rome, FAO, 126 pp.
- Gayanilo, F.C., Pauly, D. (1997). FAO-ICLARM stock assessment tools (FiSAT) Reference Manual. FAO Computerized Information Series (Fisheries). No. 8. Rome, FAO, 262 pp.
- Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A., Hawkins, S.J. (2004). Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**, 655-661.
- Gerritsen, H.D., McGrath, D. (2006). Variability in the assignment of maturity stages of plaice (*Pleuronectes platessa* L.) and whiting (*Merlangius merlangus* L.) using macroscopic maturity criteria. *Fisheries Research* **77**, 72-77.
- Gerritsen, H.D., McGrath, D. (2007). Precision estimates and suggested sample sizes for length-frequency data. *Fishery Bulletin* **106**, 116-120.
- Gibson, R.N. (1973). The intertidal movements and distribution of young fish on a sandy beach, with special reference to the plaice (*Pleuronectes platessa* L.). *Journal of Experimental Marine Biology and Ecology* **12**, 79-102.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A. (1998). Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* **165**, 145-159.
- Gibson, R.N. (1999). The ecology of the early life history stages of the plaice *Pleuronectes platessa* L: a review. *Bulletin of the Tohoku National Fisheries Research Institute* **62**, 17-50.
- Gibson, R.N., Robb, L., Wennhage, H., Burrows, M.T. (2002). Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Marine Ecology Progress Series* **345**, 233-244.
- Gibson, R.N. (2005). *Flatfish Biology and Exploitation*. Oxford: Blackwell, Science, 391pp.
- Gillanders, B.M. (2005). Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. *Estuarine Coastal and Shelf Science* **64**, 47-57.
- Gille, S.T. (2002). Warming of the Southern Ocean since the 1950s. *Science* **295**, 1275-1277.

- Gillers, C., Amara, R., Bergeron, J.P., Le Pape, O. (2004). Comparison of growth and condition indices of juvenile flatfish in different coastal nursery grounds. *Environmental Biology of Fishes* **71**, 189-198.
- Gillers, C., Le Pape, O., Desaunay, Y., Bergeron, J.P., Schreiber, N., Guerault, D., Amara, R. (2006). Growth and condition of juvenile sole (*Solea solea* L.) as indicators of habitat quality in coastal and estuarine nurseries in the Bay of Biscay with a focus on sites exposed to the Erika oil spill. *Scientia Marina* **70**, 183-192.
- Gouretski, V., Koltermann, K.P. (2007). How much is the ocean really warming? *Geophysical Research Letters* **34**, 1-5.
- Gowen, R.J., Bloomfield, S.P. (1996). Chlorophyll standing crop and phytoplankton production in the western Irish Sea during 1992 and 1993. *Journal of Plankton Research* **18**, 1735-1751.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A.T. (2004a). Biology and stock assessment of the Sparids, *Acanthopagrus bifasciatus* and *Argyrops spinifer* (Forsskal, 1775), in the Southern Arabian Gulf. *Fisheries Research* **69**, 7-20.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A. (2004b). Population biology and assessment of representatives of the family Carangidae - *Carangoides bajad* and *Gnathanodon speciosus* (Forsskal, 1775), in the Southern Arabian Gulf. *Fisheries Research* **69**, 331-341.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A. (2005a). Population biology and assessment of the orange-spotted grouper, *Epinephelus coioides* (Hamilton, 1822), in the southern Arabian Gulf. *Fisheries Research* **74**, 55-68.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A. (2005b). Preliminary assessment of the biology and fishery for the narrow-barred Spanish mackerel, *Scomberomorus commerson* (Lacepede, 1800), in the southern Arabian Gulf. *Fisheries Research* **76**, 277-290.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Al-Shamsi, A., Francis, F. (2006a). Biology and assessment of the painted sweetlips (*Diagramma pictum* (Thunberg, 1792)) and the spangled emperor (*Lethrinus nebulosus* (Forsskal, 1775)) in the southern Arabian Gulf. *Fishery Bulletin* **104**, 75-88.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A. (2006b). Fisheries biology of a short-lived tropical species: *Gerres longirostris* (Lacepede, 1801) in the Arabian Gulf. *ICES Journal of Marine Science* **63**, 452-459.
- Grandcourt, E.M., Al-Abdessalaam, T.Z., Francis, F., Al-Shamsi, A. (2007). Population biology and assessment of the white-spotted spinefoot, *Siganus canaliculatus* (Park, 1797), in the southern Arabian Gulf. *Journal of Applied Ichthyology* **23**, 53-59.
- Greenwood, M.F.D., Hill, A.S., McLusky, D.S. (2002). Trends in abundance of benthic and demersal fish populations of the lower Forth Estuary, East Scotland, from 1982-2001. *Journal of Fish Biology* **61A**, 90-104.
- Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M., Dieckmann, U. (2005). Three-dimensional maturation reaction norms for North Sea plaice. *Marine Ecology Progress Series* **334**, 213-224.
- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series* **257**, 247-257.

- Groenewold, S., Fonds, M. (2000). Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Science* **57**, 1395-1406.
- Grosbois, V., Thompson, P.M. (2005). North Atlantic climate variation influences survival in adult fulmars. *Oikos* **109**, 273-290.
- Grygiel, W., Wyszynski, M. (2003). Temporal (1980-2001) and geographic variation in the sexual maturity at age and length of herring and sprat inhabiting the southern Baltic. *Bulletin of the Sea Fisheries Institute* **2**, 1-159.
- Guillaud, A., Benzinou, A., Troadec, H., Rodin, V., Le Bihan, J. (2002). Autonomous agents for edge detection and continuity perception on otolith images. *Image and Vision Computing* **20**, 955-968.
- Guisande, C., Cabanas, J.M., Vergara, A.R., Riveiro, I. (2001). Effect of climate on recruitment success of Atlantic Iberian sardine *Sardina pilchardus*. *Marine Ecology Progress Series* **223**, 243-250.
- Gulland, J.A. (1977). *Fish Population Dynamics*. London, Wiley, 373 pp.
- Gunderson, D.R., Dygert, P.H. (1988). Reproductive effort as a predictor of natural mortality rate. *Journal du Conseil: Conseil International pour l'Exploration de la Mer* **44**, 200-209.
- Handford, P., Bell, G., Reimchen, T. (1977). A gillnet fishery considered as an experiment in artificial selection. *Journal of the Fisheries Research Board of Canada*, **34**, 954-961.
- Hannesson, R. (2007). Geographical distribution of fish catches and temperature variations in the northeast Atlantic since 1945. *Marine Policy* **31**, 32-39.
- Hanson, J.M., Courtenay, S.C. (1997). Seasonal distribution, maturity, condition, and feeding of smooth flounder (*Pleuronectes putnami*) in the Miramichi estuary, southern Gulf of St Lawrence. *Canadian Journal of Zoology* **75**, 1226-1240.
- Harden-Jones, F.R. (1968). *Fish Migration*. Edward Arnold, 325 pp.
- Harding, D., Nichols, J.H., Tungate, D.S. (1978). The spawning of plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. *Rapports et Proces-Verbaux des Reunions (Conseil Permanent International pour l'Exploration de la Mer)* **172**, 102-113.
- Harris, P.T., Heap, A.D., Whiteway, T., Post, A. (2008). Application of biophysical information to support Australia's representative marine protected area program. *Ocean and Coastal Management* **51**, 701-711.
- Hart, P.J.B., Reynolds, J.D. (2002). *Handbook of Fish Biology and Fisheries Volume 2 Fisheries*. Oxford: Blackwell Science, 410 pp.
- Haugen, T.O. (2000). Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. *Oikos*, **90**, 107-118.
- Hawkins, S.J., Moore, P.J., Burrows, M.T., Poloczanska, E., Mieszkowska, N., Herbert, R.J.H., Jenkins, S.R., Thompson, R.C., Genner, M.J., Southward, A.J. (2008). Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Research* **37**, 123-133.

- Hawkins, S.J., Southward, A.J., Genner, M.J. (2003). Detection of environmental change in a marine ecosystem - evidence from the western English Channel. *Science of the Total Environment* 310, 245-256.
- Hays, G.C., Richardson, A.J., Robinson, C. (2005) Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 337-344.
- Haywood, M.D.E., Staples, D.J. (1993). Field estimates of growth and mortality of juvenile banana prawns (*Penaeus merguensis*). *Marine Biology* 116, 407-416.
- Heath, M.R., Beare, D.J. (2008). New primary production in northwest European shelf seas, 1960-2003. *Marine Ecology Progress Series* 363, 183-203.
- Heino, M., Dieckmann, U. Godø, O.R. (2002a). Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM 2002/Y:14, 14pp, ICES, Copenhagen.
- Heino M., Dieckmann, U. Godø, O.R. (2002b). Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56, 669-678.
- Heino, M., Dieckmann, U. (2008). Detecting fisheries-induced life-history evolution: an overview of the reaction-norm approach. *Bulletin of Marine Science* 83, 69-93.
- Helfmann, G.S., Collette, B.B., Facey, D.E. (2004). *The Diversity of Fishes*. Blackwell Science, Oxford, 528pp.
- Henriques, M., Goncalves, E.J., Almada, V.C. (2007). Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions. *Marine Ecology Progress Series* 340, 259-270.
- Herzka, S.Z. (2005). Assessing connectivity of estuarine fishes based on stable isotope ratio analysis. *Estuarine Coastal and Shelf Science* 64, 58-69.
- Hiddink, J.G., Ter Hofstede, R. (2008). Climate induced increases in species richness of marine fishes. *Global Change Biology* 14, 453-460.
- Hilborn, R., Walters C.J. (1992). *Quantitative Fisheries Stock Assessment Choice, Dynamics and Uncertainty*. New York: Chapman and Hall, 570pp.
- Hill, H.W. (1971). Seasonal movements of young plaice in the Northeast Irish Sea. MAFF Fisheries Investigations Series II 26, 7, 24 pp.
- Hinz, H., Kroncke, I., Ehrich, S. (2005). The feeding strategy of dab *Limanda limanda* in the southern North Sea: linking stomach contents to prey availability in the environment. *Journal of Fish Biology* 67, 125-145.
- Hinz, H., Prieto, V., Kaiser, M.J. (2009). Trawl disturbance on benthic communities: chronic effects and experimental predictions. *Ecological Applications* 19, 761-773.
- Hiscock, K., Southward, A.J., Tittley, I., Hawkins, S.J. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 333-362.
- Hislop, J.R.G. (1996). Changes in North Sea Gadoid stocks. *ICES Journal of Marine Science* 53, 1146-1156.
- Hjermann, D.O., Stenseth, N.C., Ottersen, G. (2004). Indirect climatic forcing of the Barents Sea capelin: a cohort effect. *Marine Ecology Progress Series* 273, 229-238.

- Hjörleifsson, E., Pálsson, J. (2001). Settlement, growth and mortality of 0-group plaice (*Pleuronectes platessa*) in Icelandic waters. *Journal of Sea Research* 45, 321–324.
- Hoarau, G., Piquet, A.M.T., van der Veer, H.W., Rijnsdorp, A.D., Stam, W., Olsen, J.L. (2004). Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: a comparison of resolving power between microsatellites and mitochondrial DNA data. *Journal of Sea Research* 51, 183-190.
- Hoarau, G., Rijnsdorp, A.D., Van der Veer, H.W., Stam, W.T., Olsen, J.L. (2002). Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large-scale spatial and temporal homogeneity. *Molecular Ecology* 11, 1165-1176.
- Hoening, J.M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* 81, 898-903.
- Hoff, G.R. (2000). Biology and ecology of threaded sculpin, sculpin *Gymnocanthus pistilliger* in the eastern Bering Sea. *Fishery Bulletin* 98, 711-722.
- Horwood, J.W. (1990). Fecundity and maturity of plaice (*Pleuronectes platessa*) from Cardigan Bay. *Journal of the Marine Biological Association of the United Kingdom* 72, 199-212.
- Horwood, J.W. (1993). Fecundity and biomass of plaice (*Pleuronectes platessa*) in the northern Celtic Sea. *ICES Journal of Marine Science* 50, 315-323.
- Horwood, J.W., Bannister, R.C.A., Howlett, G.J. (1986). Comparative fecundity of North Sea plaice (*Pleuronectes platessa* L.). *Proceedings of the Royal Society of London Series B-Biological Sciences* 228, 401-431.
- Horwood, J.W., Walker, M.G., Witthames, P. (1989). The effect of feeding levels on the fecundity of plaice (*Pleuronectes platessa*). *Journal of the Marine Biological Association of the United Kingdom* 69, 81-92.
- Houde, E.D. (2002). Mortality. In *Fishery science : the unique contributions of early life stages*, L.A. Fuiman & R.G. Werner (eds.), Blackwell Science, Oxford, pp 64-87.
- Houghton, R.G., Harding, D. (1976). The plaice of the English Channel: spawning and migration. *Journal du Conseil* 36, 229-239.
- Hovenkamp, F. (1991). Immigration of plaice (*Pleuronectes platessa*) into the western Wadden Sea: a question of timing. *Netherlands Journal of Sea Research* 27, 287-296.
- Hunter, E., Metcalfe, J.D., Reynolds, J.D. (2003). Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270, 2097-2103.
- Hurrell, J.W., van Loon, H. (1997). Decadal variations in climate associated with the Northern Atlantic Oscillation. *Climate Change* 36, 301-326.
- Hutchings, J.A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 824–832.
- Hutchings, J.A., Fraser, D.J. (2008). The nature of fisheries- and farming-induced evolution. *Molecular Ecology* 17, 293-313.

- Hutchings, J.A., Myers, R.A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2126–2146.
- Hyder, K., Nash, R.D.M. (1998). Variations in settlement pattern of Irish Sea plaice (*Pleuronectes platessa* L.) as determined from a simulation model. *Journal of Sea Research* **40**, 59-71.
- Henderson, B.A., Triveri, T., Collins, N. (2000). Annual cycle of energy allocation to growth and reproduction of yellow perch. *Journal of Fish Biology* **57**, 122-133.
- Henderson, P.A., Seaby, R.M. (2005). The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* **85**, 197-204.
- ICES (2008a). Report of the ICES Advisory Committee 2008. ICES Advice (2008). Book 5: The Celtic Sea and the West of Scotland, 267 pp.
- ICES. (2008b). Report of the ICES Advisory Committee 2008. ICES Advice (2008). Book 6: The North Sea, 326 pp.
- ICES. (2008c). Report of the ICES Advisory Committee 2008. ICES Advice (2008). Book 8: The Baltic Sea, 133 pp.
- Iles, T.C., Beverton R.J.H. (1991). Mortality-rates of 0-group plaice (*Pleuronectes platessa* L), dab (*Limanda limanda* L) and turbot (*Scophthalmus maximus* L) in European waters .1. Statistical-analysis of the data and estimation of parameters. *Netherlands Journal of Sea Research* **27**, 217-235.
- IPCC (Intergovernmental Panel on Climate Change) (2007). Climate change 2007: the physical science basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge.
- Jenkins, J.T. (1936). *The Fishes of the British Isles*, 2nd ed, London: Warne and Co. Ltd, 408pp.
- Jennings, S., Kaiser, M.J. (1998). The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34**, 201-351.
- Jennings, S., Kaiser, M.J., Reynolds, J.D. (2001). *Marine Fisheries Ecology*. London: Blackwell Publishing, 417 pp.
- Jensen, A.L. (1984). Non-linear catch curves resulting from variation in mortality among subpopulations. *Journal, du Conseil* **41**, 121-124.
- Jobling, M. (2002). Environmental factors and rates of development and growth. In P. Hart and J. Reynolds (eds.) *Handbook of Fish Biology and Fisheries* Vol. 1, pp 97-102. Blackwell Science, Oxford.
- Johnstone, J.A.S., Birtwistle, W. Smith, W.C. (1922). The plaice fisheries of the Irish Sea. *Report for 1921 on the Lancashire Sea-fisheries Laboratory, University of Liverpool* **30**, 37–179.
- Jonas, T.D., Walne, A., Beaugrand, G., Gregory, L., Hays, G.C. (2004). The volume of water filtered by a Continuous Plankton Recorder sample: the effect of ship speed. *Journal of Plankton Research* **26**, 1499-1506.
- Jones, A. (1974). Sexual maturity, fecundity and growth of the turbot, *Scophthalmus maximus* L. *Journal of the Marine Biological Association of the UK* **54**, 109-125.

- Jones, R. (1984). Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). FAO Fisheries Technical Paper Number 256, Rome: FAO, 118 pp.
- Jonsson, J. (1994) Fisheries off Iceland, 1600-1900. *ICES Marine Science Symposium* 198, 3-16.
- Joyce, A.E. (2006). The coastal temperature network and ferry route programme: long-term temperature and salinity observations. *Science Series Data Report*, Cefas Lowestoft, 43: 129pp.
- Kaiser, M.J., Bergmann, M., Hinz, H., Galanidi, M., Shucksmith, R., Rees, E.I.S., Darbyshire, T., Ramsay, K. (2004). Demersal fish and epifauna associated with sandbank habitats. *Estuarine, Coastal and Shelf Science* 60, 445-456.
- Kaiser, M.J., Hiddink, J.H. (2007). Food subsidies from fisheries to continental shelf benthic scavengers. *Marine Ecology Progress Series* 350, 267-276.
- Kaiser, M.J., Spencer, B.E. (1996). Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series* 112, 41-49.
- Karakiri, M., Berghahn, R., Van der Veer, H.W. (1991). Variations in settlement and growth of 0-group plaice (*Pleuronectes platessa* L) in the Dutch Wadden Sea as determined by otolith microstructure analysis. *Netherlands Journal of Sea Research* 27, 345-351.
- Kell, L.T., O'Brien, C.M., Smith, M.T., Stokes, T.K., Rackham, B.D. (1999). An evaluation of management procedures for implementing a precautionary approach in the ICES context for North Sea plaice (*Pleuronectes platessa* L.). *ICES Journal of Marine Science* 56, 834-845.
- Kell, L.T., Pastoors, M.A., Scott, R.D., Smith, M.T., Van Beek, F.A., O'Brien, C.M., Pilling, G.M. (2005). Evaluation of management objectives for Northeast Atlantic flatfish stocks: sustainability vs. stability of yield. *ICES Journal of Marine Science* 62, 1104-1117.
- Kendall, M.A., Burrows, M.T., Southward, A.J., Hawkins, S.J. (2004). Predicting the effects of marine climate change on the invertebrate prey of the birds of rocky shores. *Ibis* 146 Suppl 1, 40-47.
- Kennedy, J., Witthames, P.R., Nash, R.D.M., Fox, C.J. (2008). Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? *Journal of Fish Biology* 72, 78-92.
- Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77, 765-776.
- King, M.J. (2007). *Fisheries biology, assessment and management*. Fishing News Books. 2nd edition, 382 pp.
- Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M., Reid, P.C. (2007). Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series* 330, 31-38.
- Kirkwood, J.M., Brown, I.W., Gaddes, S.W., Hoyle, S. (2005). Juvenile length-at-age data reveal that spanner crabs (*Ranina ranina*) grow slowly. *Marine Biology* 147, 331-339.
- Klyashtorin, L.B. (2001). Climate change and long-term fluctuations of commercial catches: The possibility of forecasting. FAO Fisheries Technical Paper 410, 86 pp

- Knust, R. (1996). Food ecology of North Sea dab (*Limanda limanda*). Seasonal changes in food uptake and condition in the German Bight and on Dogger Bank. *Archive of Fishery and Marine Research* 44, 1-12.
- Koslow, J.A., Bell, J., Virtue, P., Smith, D.C. (1995). Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. *Journal of Fish Biology* 47, 1063-1080.
- Kuipers, B.R. (1973). On the tidal migration of young plaice (*Pleuronectes platessa*) in the Wadden Sea. *Netherlands Journal of Sea Research* 6, 376-388.
- Kuipers, B.R. (1977). On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research* 11, 56-91.
- Kuparinen, A., Merila, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution* 22, 652-659.
- Kuparinen, A., Garcia de Leaniz, C., Consuegra, S., Merilä, J. (2009). Growth-history perspective on the decreasing age and size at maturation of exploited Atlantic salmon. *Marine Ecology Progress Series* 376, 245-252.
- Kuznetsova, E.N., Bondarenko, M.V., Poluektova, O.G. (2004). Long-term variability of the growth rate of Barents Sea plaice. *Journal of Sea Research* 51, 329-332.
- Law, R. (1979). Optimal life histories under age-specific predation. *American Naturalist*, 114, 399-417.
- Law, R. (2000). Fishing, selection and phenotypic evolution. *ICES Journal of Marine Science* 57, 659-668.
- Law, R. (2007). Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series* 335, 271-277.
- Le Cren, E.D. (1947). The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. *Journal of Animal Ecology* 16, 199-204.
- Le Mao, P. (1986). Feeding relationships between the benthic infauna and the dominant benthic fish of the Rance estuary France. *Journal of the Marine Biological Association of the UK* 66, 391-402.
- Lester, N.P., Shuter, B.J., Abrams, P.A. (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London B* 271, 1625-1631.
- Licandeo, R.R., Lamilla, J.G., Rubilar, P.G., Vega, R.M. (2006). Age, growth, and sexual maturity of the yellownose skate *Dipturus chelinsis* in the south-eastern Pacific. *Journal of Fish Biology* 68, 488-506.
- Lockwood, S.J. (1974). The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L.) in Iley Bay, Yorkshire. *Journal of Fish Biology* 6, 465-477.
- Lockwood, S.J. (1984). The daily food-intake of 0-group plaice (*Pleuronectes-platessa* L.) under natural conditions - changes with size and season. *Journal du Conseil* 41, 181-193.
- Lockwood, S.J., Lucassen, W. (1984). The recruitment of juvenile plaice (*Pleuronectes platessa* L.) to their parent spawning stock. *Journal du Conseil* 41, 268-275.

- Lorenzo, J.M., Pajuelo, J.G., Mendez-Villamil, M., Coca, J., Ramos, A.G. (2002). Age, growth, reproduction and mortality of the striped sea bream, *Lithognathus mormyrus* (Pisces, Sparidae), off the Canary Islands (Central-east Atlantic). *Journal of Applied Ichthyology* 18, 204-209.
- Love, R.M., (1960). Water content of cod (*Gadus morhua* L.) muscle. *Nature* 185, 692.
- Macer, C.T. (1967). The food web in Red Wharf bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*). *Helgolander Wissenschaftliche Meeresuntersuchungen* 15, 560-573.
- Macer, C.T. (1972). The movements of tagged adult plaice in the Irish Sea. MAFF Fisheries Investigations Series II 27, 6, 41 pp.
- MacKenzie, B.R., Koster, F.W. (2004). Fish production and climate: sprat in the Baltic Sea. *Ecology* 85, 784-794.
- MacKinnon, J.C. (1972). Summer storage of energy and its use for winter metabolism and gonad maturation in the American plaice (*Hippoglossoides platessoides*). *Journal of Fisheries Research Board of Canada* 29, 1749-1759.
- Maggs, C.A., Castilho, R., Foltz, D., Henzler, C., Jolly, M.T., Kelly, J., Olsen, J., Perez, K.E., Stam, W., Vainola, R., Viard, F., Wares, J. (2008). Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology* 89, S108-S122.
- Marriott, A.L. (2008). Otolith micro-chemistry as a delineator of juvenile plaice (*Pleuronectes platessa*) nursery grounds in the south eastern Irish Sea. Unpublished MSc thesis, Bangor University, 91 pp.
- Marshall J., Kushnir, Y., Battist, D., Chang, P., Czaja, A., Dickson, R., Hurrell, J., McCartney, M., Saravanan, R., Visbeck, . (2001). North Atlantic climate variability: phenomena, impacts and mechanisms. *International Journal of Climatology* 21, 1863-1898.
- Maschner, H.D.G., Betts, M.W., Reedy-Maschner, K.L., Trites, A.W. (2008). A 4500-year times series of Pacific cod (*Gadus macrocephalus*) size and abundance: archaeology, oceanic regime shifts, and sustainable fisheries. *Fishery Bulletin* 106, 386-394.
- McBreen, F., Wilson, J.G., Mackie, A.S.Y., Aonghusa, C.N. (2008). Seabed mapping in the southern Irish Sea: predicting benthic biological communities based on sediment characteristics. *Hydrobiologia* 606, 93-103.
- McCarthy, I.D., Houlihan, D.F., Carter, C.G. (1994). Individual variation in protein-turnover and growth efficiency in rainbow-trout, *Oncorhynchus mykiss* (Walbaum). *Proceedings of the Royal Society of London Series B-Biological Sciences* 257, 141-147.
- McCarthy, I.D., Waldron, S. (2000). Identifying migratory *Salmo trutta* using carbon and nitrogen stable isotope ratios. *Rapid Communications in Mass Spectrometry* 15, 1325-1331.
- McFarlane, G.A., King, J.R. (2001). The validity of the fin-ray method of age determination for lingcod (*Ophiodon elongatus*). *Fishery Bulletin* 99, 459-464.
- Mello, L.G.S., Rose, G.A. (2005). Seasonal cycles in weight and condition in Atlantic cod (*Gadus morhua* L.) in relation to fisheries. *ICES Journal of Marine Science* 62, 1006-1015.
- Metcalf, J.D., Hunter, E., Buckley, A.A. (2006). The migratory behaviour of North Sea plaice: Currents, clocks and clues. *Marine and Freshwater Behaviour and Physiology* 39, 25-36.

- Mieszowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J., Southward, A.J. (2006). Changes in the range of some common rocky shore species in Britain - a response to climate change? *Hydrobiologia* 555, 241-251.
- Miller, W.D., Harding, L.W. (2007). Climate forcing of the spring bloom in Chesapeake Bay. *Marine Ecology Progress Series* 340, 259-270.
- Millner, R.S., Whiting, C.L. (1996). Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES Journal of Marine Sciences* 53, 1185-1195.
- Molinero, A., Flos, R. (1992). Influence of season on the feeding-habits of the common sole *Solea solea*. *Marine Biology* 113, 499-507.
- Miller, W.D., Harding, L.W. (2007). Climate forcing of the spring bloom in Chesapeake Bay. *Marine Ecology Progress Series* 340, 259-270.
- Molinero, J.C., Ibanez, F., Souissi, S., Buecher, E., Dallot, S., Nival, P. (2008). Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. *Global Change Biology* 14, 11-26.
- Mollet, F.M., Kraak, S.B.M., Rijnsdorp, A.D. (2007). Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Marine Ecology Progress Series* 351, 189-199.
- Moore, S.E., Hesp, S.A., Hall, N.G., Potter, I.C. (2007). Age and size compositions, growth and reproductive biology of the breaksea cod *Epinephelides armatus*, a gonochoristic serranid. *Journal of Fish Biology* 71, 1407-1429.
- Morales-Nin, B. (1992). Determination of Growth in bony fishes from otolith microstructure. FAO Fisheries Technical Paper 322. 51 p.
- Morales-Nin, B., Aldebert, Y. (1997). Growth of juvenile *Merluccius merluccius* in the Gulf of Lions (NW Mediterranean) based on otolith microstructure and length-frequency analysis. *Fisheries Research* 30, 77-85.
- Myers, R.A., Hutchings, J.A., Barrowman, N.J. (1996). Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, 138, 293-308.
- Nash, R.D.M. (1998). Exploring the population dynamics of Irish Sea plaice, *Pleuronectes platessa* L., through the use of Paulik diagrams. *Journal of Sea Research* 40, 1-18.
- Nash, R.D.M., Geffen, A.J. (1999). Variability in Stage I egg production and settlement of plaice *Pleuronectes platessa* on the west side of the Isle of Man, Irish Sea. *Marine Ecology Progress Series* 189, 241-250.
- Nash, R.D.M., Geffen, A.J. (2000). The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research* 44, 101-110.
- Nash, R.D.M., Geffen, A.J., Hughes, G. (1992). Winter growth of juvenile plaice on the Port Erin Bay (Isle of Man) nursery ground. *Journal of Fish Biology* 41, 209-215.
- Nash, R.D.M., Geffen, A.J., Burrows, M.T., Gibson, R.N. (2007). Dynamics of shallow-water juvenile flatfish nursery grounds: application of the self-thinning rule. *Marine Ecology Progress Series* 344, 231-244.

- Nash, R.D.M., Geffen, A.J., Hughes, G. (1994). Individual growth of juvenile plaice (*Pleuronectes platessa* L.) on a small Irish Sea nursery ground (Port Erin Bay, Isle of Man, UK). *Netherlands Journal of Sea Research* 32, 369-378.
- Nash, R.D.M., Witthames, P.R., Pawson, M., Alesworth, E. (2000). Regional variability in the dynamics of reproduction and growth of Irish Sea plaice, *Pleuronectes platessa* L. *Journal of Sea Research* 44, 55-64.
- Nelson, J.S. (2006). *Fishes of the World*. John Wiley & Sons Inc, 4th edition, 601 pp.
- Nevarez-Martinez, M.O., Chavez E.A., Cisneros-Mata, M.A., Lluch-Belda, D. (1999). Modelling of the Pacific sardine *Sardinops caeruleus* fishery of the Gulf of California, Mexico. *Fisheries Research* 41, 273-283.
- Nielsen, E., Støttrup, J.G., Heilmann, J., MacKenzie, B.R. (2004). The spawning of plaice *Pleuronectes platessa* in the Kattegat. *Journal of Sea Research* 51, 219-218.
- Nitibhon, M. (1991). Population study of flounder (*Platichthys flesus* L.) in Anglesey: stock structure, growth, sexual maturity and mortality. Unpublished MSc thesis, Bangor University, 31 pp.
- Oddone, M.C., Paesch L., Norbis, W. (2005). Size at first sexual maturity of two species of rajoid skates, genera *Atlantoraja* and *Dipturus* (Pisces, Elasmobranchii, Rajidae), from the south-western Atlantic Ocean. *Journal of Applied Ichthyology* 21, 70-72.
- O'Connell, J.M., Turmcliffe, V. (2001). The use of sedimentary fish remains for interpretation of long-term fish population fluctuations. *Marine Geology* 174, 175-195.
- Oh, C.W., Hartnoll, R.G., Nash, R.D.M. (1999). Population dynamics of the common shrimp, *Crangon crangon* (L.), in Port Erin Bay, Isle of Man, Irish Sea. *ICES Journal of Marine Sciences* 56, 718-733.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Bratley, J., Ernande, B., Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428, 932-935.
- Olsen, E., Lilly, G.R., Heino, M., Morgan, M.J., Bratley, J., Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal Of Fisheries And Aquatic Sciences* 62, 811-823.
- Ortega-Salas, A.A. (1980). Seasonal changes in the common dab, *Limanda limanda* L., in the Isle of Man waters. *Journal of Fish Biology* 16, 75-82.
- OSPAR Commission 2000. Quality Status Report 2000, Region III – Celtic Seas. OSPAR Commission, London. 116 - xiii pp.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., Stenseth, N.C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia* 128, 1-14.
- Pajuelo, J.G., Lorenzo, J.M. (2004). Basic characteristics of the population dynamic and state of exploitation of Moroccan white seabream *Diplodus sargus cadenati* (Sparidae) in the Canarian archipelago. *Journal of Applied Ichthyology* 20, 15-21.
- Pajuelo, J.G., Lorenzo, J.M., Bilbao, A., Ayza, O. Ramos, A.G. (2006). Reproductive characteristics of the benthic coastal fish *Diplodus vulgaris* (Teleostei: Sparidae) in the Canarian archipelago, northwest Africa. *Journal of Applied Ichthyology* 22, 141-418.

- Panfili, J., de Pontual, H., Troadec, H. (2002). *Manual of Fish Sclerochronology*. IFREMER, Plouzané, France, 454 pp.
- Pangle, K.L., Sutton, T.M. (2005). Temporal changes in the relationship between condition indices and proximate composition of juvenile *Coregonus artedii*. *Journal of Fish Biology* 66, 1060-1072.
- Parker-Humphreys, M. (2004a). Distribution and relative abundance of demersal fishes from beam trawl surveys in the Irish Sea (ICES division VIIa) 1993-2001. Science Series Technical Reports, CEFAS Lowestoft, 120: 68pp.
- Parker-Humphreys, M. (2004b). Distribution and relative abundance of demersal fishes from beam trawl surveys in the Bristol Channel (ICES division VIIf) 1993-2001. Science Series Technical Reports, CEFAS Lowestoft, 123: 67pp.
- Parker-Humphreys, M. (2005). Distribution and relative abundance of demersal fishes from beam trawl surveys in the eastern English Channel (ICES division VIIId) and the southern North Sea (ICES division IVc) 1993-2001. Science Series Technical Reports, CEFAS Lowestoft, 124: 92pp.
- Pauly, D. (1980). On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stock. *Journal du Conseil: Conseil International pour l'Exploration de la Mer* 39, 195-212.
- Pawson, M.G., 1995. Biogeographical identification of English Channel fish and shellfish stocks. MAFF Fisheries Research Technical Report No. 99, 58pp.
- Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life-history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 503-518.
- Peterson, I., Wroblewski, J.S. (1984). Mortality rates of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 1117-1120
- Pihl, L., Rosenberg, R. (1985). Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, Western Sweden. *Journal of Experimental Marine Biology and Ecology* 57, 273-301.
- Policansky, D. (1983). Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist* 23, 57-63.
- Poloczanska, E.S., Hawkins, S.J., Southward, A.J., Burrows, M.T. (2008). Modeling the response of populations of competing species to climate change. *Ecology* 89, 3138-3149.
- Pope, J.G. (1972). An investigation of the accuracy of virtual population analysis using cohort analysis. *Research Bulletin of the International Commission of Northwest Atlantic Fisheries* 9, 65-74.
- Preston, K. (2007). Temporal changes in the population dynamics of the whiting *Merlangius merlangus* in the South Eastern Irish Sea between 1975 and 2007. Unpublished MSc thesis, Bangor University, 122pp.
- Quinn, T.P., Hodson, S., Flynn, L., Hilborn, R., Rogers, D.E. (2007). Directional selection by fisheries and the timing of sockeye salmon (*Oncorhynchus nerka*) migrations. *Ecological Applications*, 17, 731-739.
- Quinn, T.P., McGinnity, P., Cross, T.F. (2006). Long-term declines in body sizes and shifts in run-timing of Atlantic salmon in Ireland. *Journal of Fish Biology*, 68, 1713-1730.

- Ramos-Cruz, S. (2000). Size, age and growth distribution of *Litopenaeus vannamei* (Natantia: Penaeidae), in Mar Muerto lagoon, Oaxaca-Chiapas, Mexico. *Revista de Biología Tropical* 48, 873-882.
- Randall, J.E. (1995). *Coastal fishes of Oman*. University of Hawaii Press, Honolulu, 432p.
- Rauck, G. (1975). Seasonal changes of weight-length relationships of plaice in Eastern North Sea. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 24, 93-96.
- Raventos, N. (2007). Age, growth and reproduction parameters of the Mediterranean cardinal fish, *Apogon imberbis*. *Journal of Applied Ichthyology* 23, 675-678.
- Rees, E.L.S. (2004). Subtidal sediment biotopes in Red Wharf and Conwy Bays, North Wales: A review of their composition, distribution and ecology. Countryside Council for Wales Contract Science Report No 655, 48 pp.
- Reise, K., van Beusekom, J.E.E. (2008). Interactive effects of global and regional change on a coastal ecosystem. *Helgoland Marine Research* 62, 85-91.
- Reznick, D.N., Bryga, H., Endler, J.A. (1990). Experimentally induced life-history evolution in a natural population. *Nature* 346, 357-359.
- Richardson, C.A. (2001). Molluscs as archives of environmental change. *Oceanography and Marine Biology* 39, 103-164.
- Ricker, W.E. (1981). Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 1636-1656.
- Riley, J.D. (1973). Movements of 0-group plaice *Pleuronectes platessa* L. as shown by latex tagging. *Journal of Fish Biology* 5, 323-343.
- Rijnsdorp, A.D. (1989). Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *Journal du Conseil* 46, 35-51.
- Rijnsdorp, A.D. (1993a). Relationship between juvenile growth and the onset of sexual maturity of female north-sea plaice, *Pleuronectes platessa* L. *Canadian Journal of Fisheries and Aquatic Sciences* 50, 1617-1631.
- Rijnsdorp, A.D. (1993b). 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. *Netherlands Journal of Sea Research* 32, 207-223.
- Rijnsdorp, A.D., Berghahn, R., Miller, J.M., Van der Veer, H.W. (1985). Recruitment mechanisms in flatfish: What did we learn and where do we go? *Netherlands Journal of Sea Research* 34, 237-242.
- Rijnsdorp, A.D., Grift, R.E., Kraak, S.B.M. (2005). Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*). *Canadian Journal of Fisheries and Aquatic Sciences* 62, 833-843.
- Rijnsdorp, A.D., Ibelings, B. (1989). Sexual dimorphism in the energetics of production and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 35, 401-415.

- Rijnsdorp, A.D., van Beek, F.A. (1991). Changes in growth of plaice *Pleuronectes platessa* L and sole *Solea solea* (L) in the North Sea. *Netherlands Journal of Sea Research* 27, 441-457.
- Rijnsdorp, A.D., van Leeuwen, P.I. (1996). Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES Journal of Marine Science* 53, 1199-1213.
- Rijnsdorp, A.D., van Leeuwen, P.I., Visser, T.A.M. (1990). On the validity and precision of back-calculation of growth from otoliths of the plaice, *Pleuronectes platessa* L. *Fisheries Research* 9, 97-177.
- Rijnsdorp, A.D., Vethaak D., van Leeuwen, P.I. (1992). Population biology of dab *Limanda limanda* in the southeastern North Sea. *Marine Ecology Progress Series* 91, 19-35.
- Rijnsdorp, A.D., Vingerhoed, B. (2001). Feeding of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal of Sea Research* 45, 219-229.
- Roff, J.C., Taylor, M.E. (2000). National frameworks for marine conservation – a hierarchical geophysical approach. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10, 209-223.
- Rogers, S.I. (1993). The dispersion of sole, *Solea solea*, and plaice, *Pleuronectes platessa*, within and away from a nursery ground in the Irish Sea. *Journal of Fish Biology* 43(Suppl. A), 275-288.
- Romenelli, M., Colloca, F., Giovanardi, O. (2002). Growth and mortality of exploited *Sardina pilchardus* (Walbaum) larvae along the western coast of Italy. *Fisheries Research* 30, 77-85.
- Rooker, J.R., Secor, D.H., De Metrio, G., Schloesser, R., Block, B.A., Neilson, J.D. (2008). Natal homing and connectivity in Atlantic bluefin tuna populations. *Science* 322, 742-744.
- Rosenberg, A.A. (1982). Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. *Fishery Bulletin* 80, 245-252.
- Ruack, G. (1974). Arrival of different groups of young plaice in German Wadden Sea. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 23, 273-288.
- Ryland, J.S., Nichols, J.H., Sykes, A.M. (1975). Effect of temperature on embryonic-development of plaice, *Pleuronectes platessa* L (Teleostei). *Journal of Experimental Marine Biology and Ecology* 18, 121-137.
- Saborowski, R., Buchholz, F. (1996). Annual changes in the nutritive state of North Sea dab. *Journal of Fish Biology* 49, 173-194.
- Sagarin, R.D., Barry, J.P., Gilman, S.E., Baxter, C.H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* 69, 465-490.
- Salen-Picard, C., Darnaude, A.M., Arlhac, D., Harmelin-Vivien, M.L. (2002). Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. *Oecologia* 133, 380-388.
- Sandvik, H., Coulson, T., Saether, B.E. (2008). A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. *Global Change Biology* 14, 703-713.
- Scalici, M., Avetrani, P., Gibertini, G. (2007). Mosquitofish life history in a Mediterranean wetland. *Journal of Natural History* 41, 13-16.
- Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D.,

- Matsuura, Y., Nevarez-Martinez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N., Zuzunaga, J.Z. (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal Of Marine Science* 21, 289-347.
- Seisay, M.B.D. (2001). Population ecology of dab (*Limanda limanda* L.) in the Eastern Irish Sea, North Wales. Unpublished PhD thesis, Bangor University, 289 pp.
- Seyhan, K. (1990). A study on maturity, growth and mortality rates of Irish Sea male plaice (*Pleuronectes platessa* L.) in Anglesey waters, N. Wales. Unpublished MSc thesis, Bangor University, 67 pp.
- Seyhan, K. (1994). Gastric emptying, food consumption and ecological impact of whiting, *Merlangius merlangus* (L.) in the eastern Irish Sea marine ecosystem. Unpublished PhD thesis, Bangor University, 159 pp.
- Shelton, P.A., Healey, B.P. (1999). Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences* 56, 1521-1524.
- Shi, Y.B., Gunderson, D.R., Sullivan, P.J. (1997). Growth and survival of 0(+) English sole, *Pleuronectes vetulus*, in estuaries and adjacent nearshore waters off Washington. *Fishery Bulletin* 95, 161-173.
- Simpson, A.C. (1959). The spawning of plaice in the Irish Sea. MAFF Fisheries Investigations Series II 22, 7, 111pp.
- Sims, D.W., Wearmouth, V.J., Gemmer, M.J., Southward, A.J., Hawkins, S.J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* 73, 333-341.
- Sinclair, A.F., Swain, D.P., Hanson J.M. (2002). Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 361-371.
- Slotte, A. (1999). Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology* 54, 338-355.
- Slotte, A., Johannessen, A., Kjesbu, O.S. (2000). Effect of fish size on spawning time on Norwegian spring-spawning herring. *Journal of Fish Biology* 56, 295-310.
- Smith, B.B., Walker, K.F. (2004). Spawning dynamics of common carp in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. *Journal of Fish Biology* 64, 336-354.
- Sogard, S.M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60, 1129-1157.
- Sogard, S.M., Able, K.W., Hagan, S.M. (2001). Long-term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *Journal of Sea Research* 45, 189-204.
- Solmundsson, J., Karlsson, H., Palsson, J. (2003). Sexual differences in spawning behaviour and catchability of plaice (*Pleuronectes platessa*) west of Iceland. *Fisheries Research* 61, 57-71.

- Sommer, U., Lengfellner, K. (2008). Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom. *Global Change Biology* 14, 1199-1208.
- Southward, A.J. (1995). The importance of long time-series in understanding the variability of natural systems. *Helgolander Meeresuntersuchungen* 49, 329-333.
- Southward, A.J., Hawkins, S.J., Burrows, M.T. (1995). 70 years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English-channel in relation to rising sea temperature. *Journal of Thermal Biology* 20, 127-155.
- Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W., Hawkins, S.J. (2005) Long-term oceanographic and ecological research in the Western English Channel. *Advances in Marine Biology* 47, 1-105.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M. (2002). Ecological effects of climate fluctuations. *Science* 297, 1292-1296.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, N., Chan, K. S., Yoccoz N. G., Adlansvik, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. *Proceedings of the Royal Society B* 270, 2087-2096.
- Stergiou, K. (1999). Intraspecific variations in size- and age-at-maturity for red bandfish, *Cepola macrophthalma*. *Environmental Biology of Fishes* 54, 151-160.
- Stige, L.C., Ottersen, G., Brander, K., Chan, K.S., Stenseth, N.C. (2006). Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Marine Ecology Progress Series* 325, 227-241.
- Svedang, H. (2003). The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources *ICES Journal of Marine Science* 60, 23-31
- Swain, D.P., Sinclair, A.F., Hanson, J.M. (2007). Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society, Series B: Biological Sciences*, 274, 1015-1022.
- Teal, L.R., de Leeuw, J.J., van der Veer, H.W., Rijnsdorp, A.D. (2008). Effects of climate change on growth of 0-group sole and plaice. *Marine Ecology Progress Series* 358, 219-230.
- Teixeira, C.M., Cabral, H.C. (2009). Time series analysis of flatfish landings in the Portuguese coast. *Fisheries Research* 96, 252-258.
- Tilstone, G.H., Smyth, T.J., Gowen, R.J., Martinez-Vicente, V., Groom, A.B. (2005). Inherent optical properties of the Irish Sea and their effect on satellite primary production algorithms. *Journal of Plankton Research* 27, 1127-1148.
- Troadec, H., Benzinou, A., Rodin, V., Le Bihan, J. (2000). Use of deformable template for two-dimensional growth ring detection of otoliths by digital image processing: Application to plaice (*Pleuronectes platessa*) otoliths. *Fisheries Research* 46, 155-163.

- Tunberg, B.G., Nelson, W.G. (1998). Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? *Marine Ecology Progress Series* 170, 85-94.
- Tysklind, N, Taylor, M.I., Lyons, B.P., McCarthy, I.D., Carvalho, G.R. (2009a). Development of 30 microsatellite markers for dab (*Limanda limanda* L.): a key UK marine biomonitoring species. *Molecular Ecology Resources* 9, 951-955
- Tysklind, N, Taylor, M.I., Lyons, B.P., McCarthy, I.D., Carvalho, G.R. (2009b). Population Genetic Markers on Biomonitoring Flatfish Species. Unpublished report for DEFRA, 43 pp.
- Tzikas, Z., Ambrosiadis, I., Soultos, N., Georgakis, S. (2007). Seasonal size distribution, condition status and muscle yield of Mediterranean horse mackerel *Trachurus mediterraneus* from the North Aegean Sea, Greece. *Fisheries Science* 73, 453-462.
- Urban, H.J. (1991). Reproductive strategies of North Sea plaice, *Pleuronectes platessa*, and North Sea sole, *Solea solea* - batch spawning cycle and batch fecundity. *Meeresforschung - Reports on Marine Research* 33, 330-339.
- Valdes, J., Ortlieb, L., Gutierrez, D., Marinovic, L., Vargas, G., Sifeddine, A. (2008). 250 years of sardine and anchovy scale deposition record in Mejillones Bay, northern Chile. *Progress in Oceanography* 79Si, 198-207.
- van der Land, M.A. (1991). Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. *Netherlands Journal of Sea Research* 27, 277-286.
- van der Molen, J., Rogers, S.I., Ellis, J.R., Fox, C.J., McGloaghrie, P. (2007). Dispersal patterns of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. *Journal of Sea Research* 58, 313-330.
- van der Veer, H.W. (1986). Immigration, settlement, and density-dependent mortality of a larval and early post-larval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Marine Ecology Progress Series* 29, 223-236.
- van der Veer, H.W., Geffen, A.J., Witte, J.I.J. (2000). Exceptionally strong year classes in plaice *Pleuronectes platessa*: are they generated during the pelagic phase only, or also in the juvenile stage? *Marine Ecology Progress Series* 199, 255-262.
- van der Veer, H.W., Pihl, L., Bergman, M.I.N. (1990). Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*. *Marine Ecology Progress Series* 64, 1-12.
- Van Neer, W., Ervynck, A., Bolle, L.J., Millner, R.S., Rijnsdorp, A.D. (2002). Fish otoliths and their relevance to archeology: an analysis of medieval, post-medieval and recent material of plaice, cod and haddock from the North Sea. *Environmental Archeology* 7, 61-76.
- Vasconcelos, R.P., Reis-Santos, P., Fonseca, V., Ruano, M., Tanner, S., Costa, M.J., Cabral, H.N. (2009). Juvenile fish condition in estuarine nurseries along the Portuguese coast. *Estuarine Coastal and Shelf Science* 82, 128-138.
- Vasconcelos, R.P., Reis-Santos, P., Tanner, S., Fonseca, V., Latkoczy, C., Gunther, D., Costa, M.J., Cabral, H. 2007. Discriminating estuarine nurseries for five fish species through otolith elemental fingerprints. *Marine Ecology Progress Series*. 350, 117-126.
- Vetter, E.F. (1988). Estimation of natural mortality in fish stocks - a review. *Fishery Bulletin* 86, 25-43.

- Vinarge, C.; Fonseca, V.; Maia, A.; Amara, R.; Cabral, H. (2008). Habitat specific growth rates and condition indices for the sympatric soles *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup 1858, in the Tagus estuary, Portugal, based on otolith daily increments and RNA-DNA ratio. *Journal of Applied Ichthyology*, 24, 163-169.
- Vincent, M.A., Atkins, S.M., Lumb, C.M., Golding, N., Lieberknecht, L.M., Webster, M. (2004). *Marine nature conservation and sustainable development - the Irish Sea Pilot*. Report to Defra by the Joint Nature Conservation Committee, Peterborough. 176pp.
- Von Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology* 10, 181-213.
- Wallace, W. (1914). Report on age and growth and sexual maturity of the plaice in certain parts of the North Sea. *Fisheries Investigation Series*, 2, 1-79.
- Walmsley, S.A., Pawson, M.G. (2007). The coastal fisheries of England and Wales, Part V: A review of their status 2005-2006. Science Series Technical report, CEFAS Lowestoft, No. 140:83pp.
- Wang, S.-B., Chen, W.-K., Liu, K.-M. (2008). Reproductive biology and seasonal condition cycle of five spot flounder *Pseudorhombus pentophthalmus* in surrounding waters of Gui-Shan Island, northeastern Taiwan. *Journal of the Fisheries Society of Taiwan* 35, 45-59.
- Wanner, H., Bronnimann, S., Casty, C., Gyalistras, D., Luterbacher, J., Schmutz, C., Stephenson, D.B., Xoplaki, E. (2001). North Atlantic Oscillation - Concepts and studies. *Surveys in Geophysics* 22, 321-382.
- Ward, D. (2008). The biology and ecology of bass (*Dicentrarchus labrax*) in the Menai Strait, and an assessment of the applicability of otolith microchemistry and body-shape morphometric analysis as methods of discriminating between juvenile bass from disparate nursery areas around the coast of Wales. Unpublished MSc thesis, Bangor University, 94 pp.
- Watts, P.C., Nash, R.D.M., Kemp, S.J. (2004). Genetic structure of juvenile plaice *Pleuronectes platessa* on nursery grounds within the Irish Sea. *Journal of Sea Research* 51, 191-197.
- Weijerman, M., Lindeboom, H., Zuur, A.F. (2005). Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology Progress Series* 298, 21-39.
- Wennhage, H., Pihl, I. (2001). Settlement patterns of newly settled plaice (*Pleuronectes platessa*) in a non-tidal Swedish fjord in relation to larval supply and benthic predators. *Marine Biology* 139, 877-889.
- Wennhage, H., Pihl, L., Stål, J. (2007). Distribution and quality of (*Pleuronectes platessa*) nursery grounds on the Swedish west coast. *Journal of Sea Research* 57, 218-239.
- West, G. (1990). Methods of assessing ovarian development in fishes - a review. *Australian Journal of Marine and Freshwater Research* 41, 199-222.
- West, G.B., Brown, J.H., Enquist, B.J. (2001). A general model for ontogenetic growth. *Nature* 413, 628-631.
- White, A., Fletcher, T.C. (1983). Seasonal changes in serum glucose and condition of the plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 26, 755-764.
- Whittamore, J.M., McCarthy, I.D. (2005). The population biology of thornback ray, *Raja clavata* in Caernarfon Bay, North Wales. *Journal of Marine Biological Association of UK* 85, 1089-1094.

- Wilking, N.P. (1967). Starvation of the herring, (*Clupea harengus* L.) Survival and some gross biochemical changes. *Comparative Biochemistry and Physiology* **23**, 503-518.
- Wilson, J.P.F., Pitcher, T.J. (1983). The seasonal cycle of condition in the pollan, *Coregonus autumnalis* Thompson, of Lough Neagh, Northern Ireland. *Journal of Fish Biology* **23**, 365-370.
- Wimpenny, R.S. (1953). *The plaice*. Edward Arnold, 145 pp.
- Wright, P.J. (2005). Temporal and spatial variation in reproductive investment of haddock in the North Sea. ICES CM 2005/Q:07, 24pp, ICES, Copenhagen.
- Wuenschel, M.J., Able, K.W., Byrne, D. (2009). Seasonal patterns of winter flounder *Pseudopleuronectes americanus* abundance and reproductive condition on the New York Bight continental shelf. *Journal of Fish Biology* **74**, 1508-1524.
- Yildirim, A., Arslan, M., Bektas, S., Pegg, M. (2006). Spatial and seasonal variations in condition of *Barbus plebejus escherichi* in the upper Coruh River, Turkey. *Journal of Freshwater Ecology* **21**, 379-384.
- Yildirim, A., Arslan, M., Bektas, S. (2008). Length-weight relationship and seasonal condition in *Capoeta sieboldii* in the upper Coruh River, Turkey, *Journal of Applied Ichthyology* **24**, 711-712.
- Zar, J.H. (1984). *Biostatistical analysis*. Prentice-Hall international Editions, 718 pp.
- Ziljstra, J.J., Dapper, R., Witte, J.I. (1982). Settlement, growth and mortality of post-larval plaice in the Western Wadden Sea. *Netherlands Journal of Sea Research* **15**, 250-272.

Electronic sources:

- URL 1: Maps showing the ICES areas. <http://www.ices.dk/aboutus/icesareas.asp> (accessed 30/5/09)
- URL 2: Maps showing the distribution of plaice in the North East Atlantic <http://www.aquamaps.org> (accessed on 3/6/2009).
- URL 3: Species web page for *Gadus morhua*. <http://www.fishbase.org> (accessed 9/6/09).
- URL 4: Marine Institute Ireland, flatfish maturity key http://www.marine.ie/NR/rdonlyres/76C69EB2-4EBF-4A3B-9D15-FD122DF4B432/0/maturity_scales.pdf (accessed 4/06/2008).
- URL 5: FAO, 2007b. *Pleuronectes platessa*, *European plaice*. <http://fishbase.ifm-geomar.de/Summary/SpeciesSummary.php?id=1342> (accessed 13/02/2008).
- URL 6: http://www.geography.unibe.ch/lenya/giub/live/research/climatology_en.html (Climatology and Meteorology Research Group, Institute of Geography, University of Bern) (accessed 3/5/09).

Appendices.

Appendices

Appendix 1a:

The haul trawls data of the RV *Prince Magog*, for year 2004.

Date	Time	Shot	Haul	Ave Depth
17/10/04	10.30 to 11.39	53 18.890-04 22.125	53 18.937-03 54.756	17.9 m
18/10/04	11.30 to 12.18	53 28.678-03 49.690	53 28.976-03 34.473	40 m
19/10/04	11.11 to 12.11	53 28.403-03 12.415	53 28.946-04 05.767	42 m
20/10/04	10.22 to 11.23	53 20.263-04 10.610	53 22.005-04 13.289	17.7 m
22/10/04	10.45 to 11.43	53 21.205-03 49.627	53 21.234-03 45.394	18.1 m
23/10/04	11.45 to 12.36	53 21.289-04 12.589	53 20.116-04 09.637	9.5 m
24/10/04 Tow 1	11.45 to 12.40	53 19.767-04 08.280	53 20.402-04 04.532	15.5 m
24/10/04 Tow 2	12.54 to 13.50	53 20.785-04 04.446	53 21.718-04 09.213	18.8 m

Appendix 1b:**The haul trawls data of the RV *Prince Magog*, for year 2005.**

Date	Time	Shot	Haul	Ave Depth
16/10/05	10.26 to 11.23	53 18.938-04 00.368	53 18.476-03 55.900	14.4 m
Tow 1				
16/10/05	11.42 to 12.43	53 18.960-03 55.115	53 22.048-03 53.685	17.5 m
Tow 2				
17/10/05	10.58 to 12.00	53 26.463-04 08.861	53 28.647-04 14.476	43.3 m
Tow 1				
17/10/05	12.19 to 13.18	53 28.522-04 10.930	53 17.887-03 59.450	45 m
Tow 2				
18/10/05	10.28 to 11.28	53 17.887-03 59.450	53 28.976-03 34.473	13.4 m
Tow 1				
18/10/05	11.46 to 12.38	53 18.862-03 55.551	53 20.532-04 01.049	18.5 m
Tow 2				
19/10/05	10.48 to 11.30	53 21.127-03 49.364	53 21.321-03 43.896	20.8 m
Tow 1				
19/10/05	11.44 to 12.43	53 21.250-03 42.573	53 20.746-03 35.909	16.9 m
Tow 2				
19/10/05	13.47 to 14.37	53 27.420-03 43.146	53 28.497-03 48.741	37.8 m
Tow 3				
20/10/05	10.55 to 11.55	53 19.684-04 09.837	53 22.449-04 13.789	19.4 m
Tow 1				
21/10/05	10.52 to 11.53	53 18.924-04 00.122	53 18.202-03 55.457	16.9 m
Tow 1				
21/10/05	12.08 to 13.20	53 18.703-03 55.124	53 20.708-04 01.031	19.4 m
Tow 2				
22/10/05	11.28 to 12.32	53 28.022-04 05.991	53 28.353-04 10.586	43.2 m
Tow 1				
22/10/05	12.43 to 13.43	53 28.392-04 11.087	53 27.792-04 09.792	44.5 m
Tow 2				
23/10/05	10.10 to 11.10	53 19.426-04 03.999	53 19.653-04 09.441	14.2 m